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Foraging a new trail with northern fur seals (*Callorhinus ursinus*): Lactating seals from islands with contrasting population dynamics have different foraging strategies, and forage at scales previously unrecognized by GPS interpolated dive data

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Abstract

We reconstructed the foraging tracks of lactating northern fur seals (*Callorhinus ursinus*) from two eastern Bering Sea islands (St. Paul Island and Bogoslof Island) using linear interpolation between GPS locations recorded at a maximum of four times per hour and compared it to tri-axial accelerometer and magnetometer data collected at 16 Hz to reconstruct pseudotracks between the GPS fixes. The high-resolution data revealed distances swum per foraging trip were much greater than the distances calculated using linearly interpolated GPS tracks (1.5 times further for St. Paul fur seals and 1.9 times further for Bogoslof fur seals). First passage time metrics calculated from the high resolution data revealed that the optimal scale at which the seals searched for prey was 500 m (radius of circle searched) for fur seals from St. Paul Island that went off-shelf, and 50 m for fur seals from Bogoslof Island and surprisingly, 50 m for fur seals from St. Paul that foraged on-shelf. These area-restricted search scales were significantly smaller than those calculated from GPS data alone (12 km for St. Paul and 6 km for Bogoslof) indicating that higher resolution movement data can reveal novel information about foraging behaviors that have important ecological implications.

Key words: foraging ecology, biologging, northern fur seal, *Callorhinus ursinus*, marine mammal, Bering Sea, magnetometer, accelerometer, spatial analysis, area restricted search.

Scale is a simple but critical concept in ecological studies defining the limits of interpretation and ability to generalize results to larger contexts. However, the scales

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at which many earlier animal tracking studies have been conducted were more often than not set by the limitations of data resolution. Such limitations are being overcome with advances in technology that permit collecting substantially more data with increasing temporal and spatial resolution (decreasing scale). With each generation of electronic tags and improved statistical techniques has come a growing appreciation that areas of active foraging and movement occur on scales smaller than previously detected.

Existing technology can provide fine-scale data in theory, although in practice, location data depends upon weather, animal behavior, tag performance, satellite availability (Global Positioning System [GPS] or ARGOS) and other factors. Fastloc GPS technology in particular gives excellent location data, with errors of less than 400 m for locations using 5 or more satellites (Bryant 2007). Retrieved tags can provide full depth and temperature profiles (and other environmental information) usually collected on a per second basis. However, biologging tags carried by marine species are often not recovered in order to limit disturbance or handling or for logistic or financial reasons, thereby requiring high-resolution data to be summarized or subsampled for transmission *via* satellites with narrow bandwidth constraints. In marine ecology, heavily summarized pressure and temperature data combined with ARGOS or GPS satellite location estimates form the basis of many marine ecology studies (*e.g.*, Block *et al.* 2011). Ultimately, the amount (and consequently the scale) of data collected using these techniques is a compromise between technological barriers and the minimum data requirements necessary to answer the question of interest.

Accelerometers and magnetometers that sample at subsecond frequencies have been added to aquatic animal borne tags in the past decade (Johnson *et al.* 2000, Sato *et al.* 2002, Wilson *et al.* 2008) to address a number of different biological questions (*e.g.*, Goldbogen *et al.* 2006, Ropert-Coudert *et al.* 2006, Viviant *et al.* 2010, Iwata *et al.* 2012). Such high resolution tri-axial accelerometer and magnetometer data can be used to derive near continuous (sub Hz) location estimates by filling in the spatial gaps between the interval-based relocation positions, such as ARGOS doppler shift or GPS (Johnson and Tyack 2003, Wilson *et al.* 2007). However, analyzing tri-axial data to determine exact locations is complicated by the difficulty of determining the angle of the tag relative to the earth due to the confounding measurements of gravity and movement when measuring acceleration. Locations estimated *via* this method are therefore not exact and can only be corrected for drift/currents with GPS or alike, but are useful for certain analyses such as comparing relative positions to one another over time, or for differentiating between broad classes of behavior, such as when an animal is traveling in a relatively straight line to feeding grounds compared to when an animal is actively foraging.

The analysis of location data has seen considerable development in the last decade. A primary focus in the ecology of large marine vertebrates has been on determining foraging locations derived from the basic relocation data (location with associated time) that ARGOS and GPS data provide. Area restricted search (ARS) analysis, using the segment length or turning angle between successive relocations from tag data, is the predominant class of analyses used in marine foraging ecology. It depends on the assumption that animals forage in two modes, a traversing mode in which animals move in relatively straight lines to find patches of food, and a foraging mode where animals decrease speed and increase turning angles to forage within a patch more extensively. A number of theoretical distributions have been proposed and used to describe animal movement data (*e.g.*, random walk, correlated random walk, Brownian motion, Levy flights, *etc.*). A number of different area-restricted-search methods have also been developed to statistically distinguish between the two (or more) movement scales, including first passage time (Fauchald and Tveraa 2003, Freitas *et al.* 2008), tortuosity, fractal landscapes (Tremblay *et al.* 2007), residence time (Barraquand and Benhamou 2008), 2 (or more)-state Bayesian state space models (Jonsen *et al.* 2005), and many others (see Dragon *et al.* (2012) for a comparative analysis of some of these methods). Many of the methods have been implemented in commonly accessible programming languages, such as R, *e.g.*, Adehabitat (Calenge 2006), winBUGS (Jonsen *et al.* 2005) or MATLAB (Leising 2002). While many of these techniques have been developed with the relatively coarse ARGOS and GPS data in mind, the fundamental concepts remain the same for finer scale data.

The portion of the northern fur seal (*Callorhinus ursinus*) population that breeds in the eastern Bering sea use three islands as summer rookeries, St. Paul and St. George Islands as part of the Pribilof Islands complex, and Bogoslof Island. The Pribilof Islands have historically hosted the largest portion of the breeding population in the world, but pup production has declined by 80% since 1955 from a high of 461,000 (Lander 1980) to approximately 91,737 in 2014 (Towell *et al.* 2014) on St. Paul Island. In contrast, the Bogoslof Island population, just ~400 km south of the Pribilof Islands, produced 2 pups in 1980, but reached 22,905 in 2011 (Towell and Ream 2012). The St. Paul Island population of fur seals numbered ~500,000 in 2010 and has been declining since 1998 at an annual rate of 5.5% (Call *et al.* 2008, Towell *et al.* 2010) while the Bogoslof Island population numbered ~100,000 and has been increasing at an annual rate of 11.7% since 1997 (Towell and Ream 2012). The northern fur seal is perhaps the most intensely studied pinniped in the world (Scott *et al.* 2006) due to their historical significance in the fur trade. Despite this, the cause of the contrasting trends of the populations on the three breeding islands is uncertain. The most popular theory for the current continued decline on St. Paul contends that lactating females are unable to forage efficiently, pups do not reach optimal weights with sufficient fat reserves prior to weaning and thus have difficulty surviving the first year while developing their diving and foraging skills. Indeed Banks *et al.* (2006) found that pups on Bogoslof Island (15.8 kg) were significantly heavier that pups on St. Paul Island (11.9 kg) three months after birth, despite no significant difference in birth weights. Hence, understanding the foraging ecology of lactating female northern fur seals has been an ongoing priority for northern fur seal research.

A number of studies have found that juvenile walleye pollock (*Theragra chalcogramma*) and/or gonatid squid (Sinclair *et al.* 1994, Antonelis *et al.* 1997, Gudmundson *et al.* 2006, Zeppelin and Ream 2006, Zeppelin and Orr 2010, Sinclair *et al.* 2011) are the primary components of diets of lactating females breeding on the Pribilof Islands. While northern smoothtongue consistently appear in such studies, they were not major components. However, similar studies from animals breeding on Bogoslof Island indicate that northern smooth tongue are a major component of their diet while walleye pollock are considerably less so (Zeppelin and Orr 2010, Kuhn *et al.* 2014*b*). Northern smoothtongue (*Leuroglossus schmidti*) are generally thought to have a greater energy density than pollock and Vollenweider *et al.* (2011) found northern smoothtongue to be ~12% lipid while pollock had approximately one-quarter the lipid content at ~3%. Differences in diet such as these suggest Bogoslof animals may have a nutritional advantage over Pribilof Island animals, and diet differences may also manifest themselves in differences in foraging behavior.

Spatial studies comparing foraging tracks within and between islands have indicated that responses to prey density dynamics can be detected in northern fur seal foraging behavior. As animals have colonized Bogoslof Island and its population increased, foraging trips of lactating females have increased significantly in both time and distance traveled (Kuhn *et al.* 2014*b*). A number of studies have found animals at Bogoslof Island take shorter foraging trips both temporally and spatially relative to St. Paul Island animals (Banks *et al.* 2006, Nordstrom *et al.* 2013). In addition, animals from different islands, and even from different rookeries on the same island, are known to segregate spatially during foraging trips (Robson *et al.* 2004, Kuhn *et al.* 2014*a*). Further, it has also been shown that northern fur seals respond to oceanographic and environmental features such as eddies, fronts and thermoclines that are presumed to concentrate prey (Sterling 2009, Nordstrom *et al.* 2013, Pelland *et al.* 2014, Sterling *et al.* 2014).

Past studies indicate that animals from the different islands and rookeries have different diets and foraging patterns at certain scales, showing that they respond to habitat differences. If the differences in diet are causally linked to behavioral differences at the relatively course scale found with GPS and ARGOS based data loggers, there may also be differences in foraging strategies at a finer scale. Unfortunately, it is rare to have corresponding environmental data to relate to foraging behavior, particularly at very fine scales. However, metrics of foraging behavior can be compared at the fine scale to see if they are different from courser scale results and between populations at the fine scale.

We described the method of track reconstruction and compare the reconstructed foraging tracks of lactating northern fur seals (*Callorhinus ursinus*) from two breeding islands in the eastern Bering Sea, with one reconstruction using linear interpolations between GPS locations and the other using GPS data with tracks reconstructed using tri-axial accelerometer and magnetometer data. Using First Passage Time (FPT) analysis, we also compared the tri-axial movement data to the FPT results of Nordstrom *et al.* (2013) to determine differences in the scale of northern fur seal foraging patterns between islands and oceanic zones, and between the two types of reconstructed tracks. Finally, we used these results to make comparisons within and between two island populations of northern fur seals to gain new ecological insights into the foraging ecology of northern fur seals in the eastern Bering Sea.

METHODS

We captured and tagged lactating northern fur seals from 10 July to 19 September 2009 on two islands in the eastern Bering Sea: St. Paul Island in the Pribilof archipelago, and Bogoslof Island, a volcanic pinnacle south of the Pribilof Islands near the Aleutian Islands chain. Tags were mounted dorsally along the centerline of the animal between the shoulder blades. Further details of the capture and tagging methodologies can be found in Nordstrom *et al.* (2013).

We successfully retrieved data from 42 seals on Bogoslof Island (n = 117 foraging trips) and 41 seals on St. Paul Island (n = 51 foraging trips). We deployed two types of biologging tags on each fur seal: Wildlife Computers Mk-10F TDR scheduled to record GPS fixes every 15 min when at the surface, a first generation Wildlife Computers Daily Diary TDR containing tri-axial accelerometers and magnetometers as well as VHF transmitters. The Daily Diary tags recorded acceleration and the earth's magnetic field at 16 Hz in three spatial dimensions (anterior-posterior [surge], dorsal-ventral [heave], and lateral [sway]), as well as depth, internal tag temperature, and time while a conductivity sensor switch determined wet/dry periods.

The large amount of Daily Diary data (up to 3 GB text file for a 30 d deployment) were visualized graphically and transcribed into text files using the manufacturer's software (Instrument Helper and HextoText). Functions for the analysis of the data, once the data were downloaded from the tag to presenting the results in animated movies, are now available in the R package TrackReconstruction (Battaile 2014), which includes a manual detailing the functions and a vignette to step the user through the process. The vignette also includes PERL programs and DOS-Batch examples for those that might have data sets too large for R or their available computer to easily handle.

Fur seals typically feed at night, although St. Paul animals exhibit multiple foraging strategies including foraging in multiple hydrographic domains and day time foraging (Gentry *et al.* 1986, Loughlin *et al.* 1987, Goebel *et al.* 1991, Robson *et al.* 2004, Sterling and Ream 2004, Call *et al.* 2008, Nordstrom *et al.* 2013). We therefore categorized the data sets for St. Paul fur seals by feeding locations (*i.e.*, on-shelf or off-shelf) and time of day (day or night). Bogoslof animals are essentially off-shelf foragers while fur seals from St. Paul showed greater variability in their foraging behavior and location.

Track Reconstruction/Pseudotrack Estimation

For each foraging trip, return and departure to and from the rookery was determined from the wet-dry sensor on the Daily Diary tag. At-sea GPS locations between these time periods were stored in a separate file for each trip. Daily Diary data were divided into sections between each GPS point using the tag's time stamp. For example, a foraging trip with 100 successful GPS fixes at-sea and two on land (at the start and end of the trip) would result in 101 sections bookended at the rookery. Dividing the track into sections made the data files manageable for analysis and interpretation.

Some of the Daily Diary tags failed to record data for brief periods of the foraging trips. Data gaps occurred in nine trips from Bogoslof Island (all gaps <1 min long with one animal having four gaps, whereas all others had only one). For these animals, we simply ignored the gaps and processed the data normally as we believed such small gaps do not have a large effect on the reconstructed pseudotracks. Data gaps for the animals from St. Paul Island were more extensive with only three foraging trips having none at all. A total of 468 between-GPS sections had gaps for the St. Paul Island animals, but the gaps were rarely longer than a few minutes. We calculated the reconstructed pseudotracks for these sections, but did not include them in any analysis, resulting in 7,166 sections from St. Paul animals for further analyses.

The acceleration and magnetometer sensors were individually standardized between −1 and +1 using linear regression and oriented to the right hand rule prior to being fed into the track reconstruction algorithm. The right-hand-rule indicates the polarity of the magnetometers and accelerometers required for the pseudotrack reconstruction algorithm, so that when the front, top or left side of the tag is facing the earth, the accelerometers are at their minimal (−1) reading. A similar rule applies to the magnetic field except that the angle of inclination of the magnetic field is near 70° rather than perpendicular to the surface of the earth at most geographic locations in the Bering Sea and at this angle the tags will be at their maximal reading (+1, opposite to the accelerometers) given the right-hand-rule described above.

The algorithm for the georeferenced track reconstruction was written in R following Wilson *et al.* (2007) with the following clarifications. The earth's gravitational field, or "static" acceleration, in each dimension was estimated as a 2 s running mean of the three separate acceleration sensors. The running mean was then subtracted from its respective channel to estimate the "dynamic" acceleration due to animal movement. Speed was estimated as the running sum of the "dynamic" portion of the anterior-posterior acceleration channel and then normalized between 0 and 3.5 m/s (the approximate maximum speed of adult female northern fur seals). The exception to this was when behavioral analysis indicated animals were resting in which case the speed was set to 0. Resting behavior is clearly discernable in either the dorso-ventral or lateral axis of acceleration measuring consistent low variability readings indicating the animal is "laying" on one side or the other in the water (Battaile *et al.* 2015). The inclination and declination of the earth's magnetic field was calculated given the date, latitude, and longitude using the World Magnetic Model 2010 Calculator from the British Geological Survey (http://www.geomag.bgs.ac.uk/data_service/models_compass/wmm_calc.html). We used a single declination and inclination value for each island as our animals were not wide ranging relative to changes in the declination and inclination in this area. Finally, we georeferenced the raw dead reckoning tracks (Wilson *et al.* 2007), by forcing the tracks through known GPS relocations starting and ending on land and acquired at irregular intervals at sea throughout the animals foraging trip. Georeferencing adjusted the reconstructed pseudotracks for errors, such as ocean currents, that are not measurable by the tags as well as errors inherent to the technology and methodology. The georeferencing basically adjusts the speed and turning angles by a constant that results in a rotated raw dead reckoning track that is expanded or contracted like an accordion, hence the initial maximum speed limit of 3.5 m/s can be exceeded during the georeferencing. GPS units were programmed to record locations every 15 min but varied greatly between trips with time between relocations lasting more than 24 h in rare cases.

Pseudotrack Measures of Error

Statistically rigorous measures of error for pseudotracks are not yet available, though research is underway to fill this void (Liu *et al.* 2014). In lieu of this, we calculated five different comparisons of the unconstrained pseudotracks to the relatively accurate GPS locations used to geolocate our final tracks. These measures come in two different scales (complete foraging tracks and consecutive-points) and two different categories (unconstrained and anchored). The consecutive-point scale uses a subset of GPS points within a foraging track (usually just two or three adjacent GPS points in time). The unconstrained category indicates the track is not forced to go through subsequent GPS points, though it starts at a GPS point, while anchored tracks indicate the beginning and end of the pseudotrack start at a GPS point and is forced to end at a GPS point, but GPS points that lie temporally between are not used to geolocate the track.

Our first measure of pseudotrack error was the distance between the final GPS location (in this case at the rookery) and the end of an unconstrained complete track, which we plotted against the time of the trip. Track distance would have been a more natural parameter than trip time to use to "normalize" the measure. However, we had no consistent way to measure "true" trip length as it depends on the number of GPS points taken per time, which varied considerably between tracks. In addition, a distance measure becomes more troublesome as animal movements become more tortuous (such as when exhibiting Area Restricted Search) and animals begin to cross their own tracks.

Our second measure of error (complete and anchored) compared the interpolated distance of the GPS track to the georeferenced track using only the start and end GPS points (in this case at the rookery) to geolocate the track. In this case we interpolated distance for the geolocated track using points along the georeferenced track that matched in time to the GPS points. Again, this difference was plotted against the time of the foraging trip.

The third measure (unconstrained, consecutive point) simply calculated an unconstrained track between two GPS locations starting at the first GPS point, and calculated the difference between the second GPS point and the end of the pseudotrack. This was calculated for each successive pair of GPS points for each foraging trip. This difference was plotted against the time between the GPS points.

Our fourth measure of error (consecutive points, anchored) calculated the pseudotrack between three successive GPS points, but did not use the middle GPS point to geolocate the track. We then determined the difference between the middle GPS point and the corresponding point in time on the pseudotrack—and plotted this difference against the time between the nearest GPS point and the middle GPS point, presuming that the time to the nearest anchor point was most closely related to the amount of error. We calculated this measure of pseudotrack error along the entire track using a sliding window of three GPS points.

The final method was computationally much more time consuming than the other four methods, with each track requiring approximately 24 h of computational time. Hence, we calculated this for only our three example tracks. This method essentially repeats our fourth measure, but for every possible window size and GPS point within the window. For example, if a single track had 100 GPS points, we first calculated the constrained track using a 3-point window and calculated the difference between the middle GPS point and its corresponding point in time on the pseudotrack. We did this starting with the first and third GPS point, and sliding the 3-point window along until ending with the 98th and 100th GPS point. The distance to the nearest anchor GPS point was also calculated. This was again repeated for a GPS window size of 4 where the GPS-pseudotrack-differences were calculated for the two middle GPS locations 2 and 3, and the distance to the nearest anchor GPS point for the two middle points was also calculated. We repeated this until the window size equaled the number of GPS points in the track. Thus, for a 100-point track, there were 161,700 error distances with associated measures of time to the nearest anchoring GPS points.

Pseudotrack Summaries and Statistics

Total horizontal distances traveled were calculated from the pseudotracks using data at 1 Hz with a running sum of distances between relocations. Dive (vertical) distances traveled were calculated from the 1 Hz depth data as a running sum on the absolute value of the change in depth. Data were summarized by trip (Table 1) or by night/day and by hour (Table 2). The daily averages eliminated variability in horizontal distances swum due to foraging trip duration while per hour averages (stratified by night and day) eliminated variability in the swimming distances and diving distances due to the drastic differences in the amount of daylight and nighttime during the summer at higher latitudes. Data were further stratified by island and oceanographic foraging domain (on-shelf or off-shelf), and by day or night.

Table 1. Comparison of estimated distances swum by lactating northern fur seals while foraging from Bogoslof (n = 117) and St. Paul Islands (n = 51). Distances are in kilometers (± SE) and were calculated using GPS interpolations and Pseudotrack (PT) reconstructions. They include distances swum horizontally (PT or GPS), diving distance, and combined total (horizontal plus diving distances). Statistics are stratified by habitat (while on or off of the continental shelf) and forager type (day or night) for St. Paul.

		Distances swum (km)					
Island	Habitat	PT distance	GPS distance	Dive distance	PT total	GPS total	Ratio PT/GPS
St. Paul	All	972 ± 112	635 ± 86	111 ± 15	1,083 ± 124	746 ± 96	1.45 ± 0.07
	Off-shelf	1046 ± 94	690 ± 73	113 ± 14	1,159 ± 102	803 ± 81	1.44 ± 0.06
	On-shelf	905 ± 123	585 ± 93	110 ± 17	1,015 ± 137	695 ± 1.5	1.46 ± 0.07
Bogoslof	Off-shelf	427 ± 84	208 ± 39	44 ± 9.5	471 ± 93	252 ± 47	1.87 ± 0.02

Table 2. Mean distances traveled by lactating northern fur seals from St. Paul (n = 51) and Bogoslof Islands (n = 117) in kilometers (± SE) during day and night, and standardized per hour by the amount of daytime and nighttime. They include distances swum horizontally, while diving, and combined total (horizontal plus diving distances). Statistics are stratified by habitat (while on or off of the continental shelf) for St. Paul animals.

		Distance per day			Distance per hour		
Island	Habitat	Horizontal	Dive	Total	Horizontal	Dive	Total
St. Paul	Offshelf day	57.7 ± 1.46	1.8 ± 0.17	59.5 ± 1.51	4.2 ± 0.16	0.14 ± 0.01	4.4 ± 0.17
	Offshelf night	48.5 ± 0.7	12.4 ± 0.39	60.9 ± 0.9	5.3 ± 0.06	1.34 ± 0.04	6.7 ± 0.07
	Onshelf day	69.8 ± 1.3	6.6 ± 0.37	76.4 ± 1.54	4.97 ± 0.11	0.46 ± 0.03	5.4 ± 0.12
	Onshelf night	49.5 ± 0.97	7.2 ± 0.3	56.7 ± 1.02	5.5 ± 0.09	0.80 ± 0.03	6.3 ± 0.09
Bogoslof	Day	62.87 ± 0.90	2.23 ± 0.11	65.10 ± 0.94	4.32 ± 0.06	0.15 ± 0.01	4.47 ± 0.06
	Night	49.04 ± 0.4	9.35 ± 0.19	58.39 ± 0.49	5.33 ± 0.04	1.02 ± 0.02	6.35 ± 0.05

Linear mixed effects models with animal trip (some animals did multiple trips) as the random effect tested the influence of these parameters (island, oceanographic foraging domain, and day or night) on the hourly means of swimming distances (horizontal, dive, and total = horizontal + dive). Swimming distances averaged over night time or day time were ambiguous with respect to meeting standard modeling assumptions so we restricted our quantitative modeling to the hourly means, but interpreted these results in light of the differences caused by the relative amount of daylight and night each day. R (R Core Team 2013) and the nlme package was used to develop the model and test for standard statistical assumptions. We were guided by Zuur *et al.* (2009) and Pinheiro and Bates (2000) in the model building process. Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) were used to determine relative model strength.

The full model consisted of the three main effects, three two-way interactions, one three-way interaction and a three-way interaction of the explanatory variables to account for heterogeneity of variance. All nested models were compared from models derived from Maximum Likelihood (ML) estimation while coefficients for the final model were determined using Restricted Maximum Likelihood (REML).

Distributions of variables were examined to assess normality and presence of outliers. Five segments with respect to traveling speed were deemed outliers and removed from the data set. These five data points were above a natural break in the data at 9.05 km/h (~2.5 m/s) (Fig. S1). The hourly dive distance data was skewed and was square root transformed to normalize the data (Fig. S2). Heterogeneity in the variance in the residuals was found to vary with the explanatory variables for all three models (*e.g.*, The Pribilof Island data tended to be more dispersed than the Bogoslof Island data) and was modeled as a three way interaction of the explanatory variables (Pinheiro and Bates 2000, Zuur *et al.* 2009) (Figs. S3–S8). Student's *t*-tests were performed on GPS and Daily Diary derived track lengths for each island.

First Passage Time Analysis

A number of different measures of Area-Restricted Search (ARS) can be used to spatially analyze GPS and ARGOS positions and differentiate between foraging and nonforaging behaviors. One well developed methodology is First Passage Time (FPT), which has been applied to measure ARS (Fauchald and Tveraa 2003), by calculating the time it takes for an animal to move through a circle with a radius of a size (scale) that is statistically optimal to differentiate between behavioral states. The optimal sized radius is the one that produces the greatest variance in the transiting times through all of the sample circles, implying that the average ARS event occurs within a circle of that radius. We implemented first passage time analysis in R using functions from the adehabitat package (Calenge 2006) to determine the scale at which animals preformed area restricted search and to compare these scales between our stratifications of the data (*i.e.*, between the two islands, between animals that foraged on-shelf or off-shelf, and between night and day periods). We used contiguous sections of pseudotrack data that did not have missing data or periods of resting. Sections with resting were removed from the analysis because high FPT are used as an index of area restricted search, and resting behavior would have confounded our results by yielding the highest FPT.

RESULTS

Track Reconstruction/Pseudotrack Estimation

Pseudotrack reconstructions revealed considerably more fine-scaled detail movements of fur seals than did tracks created from linearly interpolated GPS points as shown by the increasingly zoomed images for a representative off-shelf track from St. Paul Island (Figs. 1, 2). Differences between the two types of tracks become more apparent as the scale decreases, but the magnitude of the difference depends upon where the seal was along the track and the type of activity in which it was engaged.

Basic Pseudotrack Summaries and Statistics

Distances traveled by the fur seals were significantly greater when calculated by the pseudotrack reconstruction compared to when tracks were calculated by interpolation solely between GPS points. Pseudotracks from St. Paul Island fur seals were

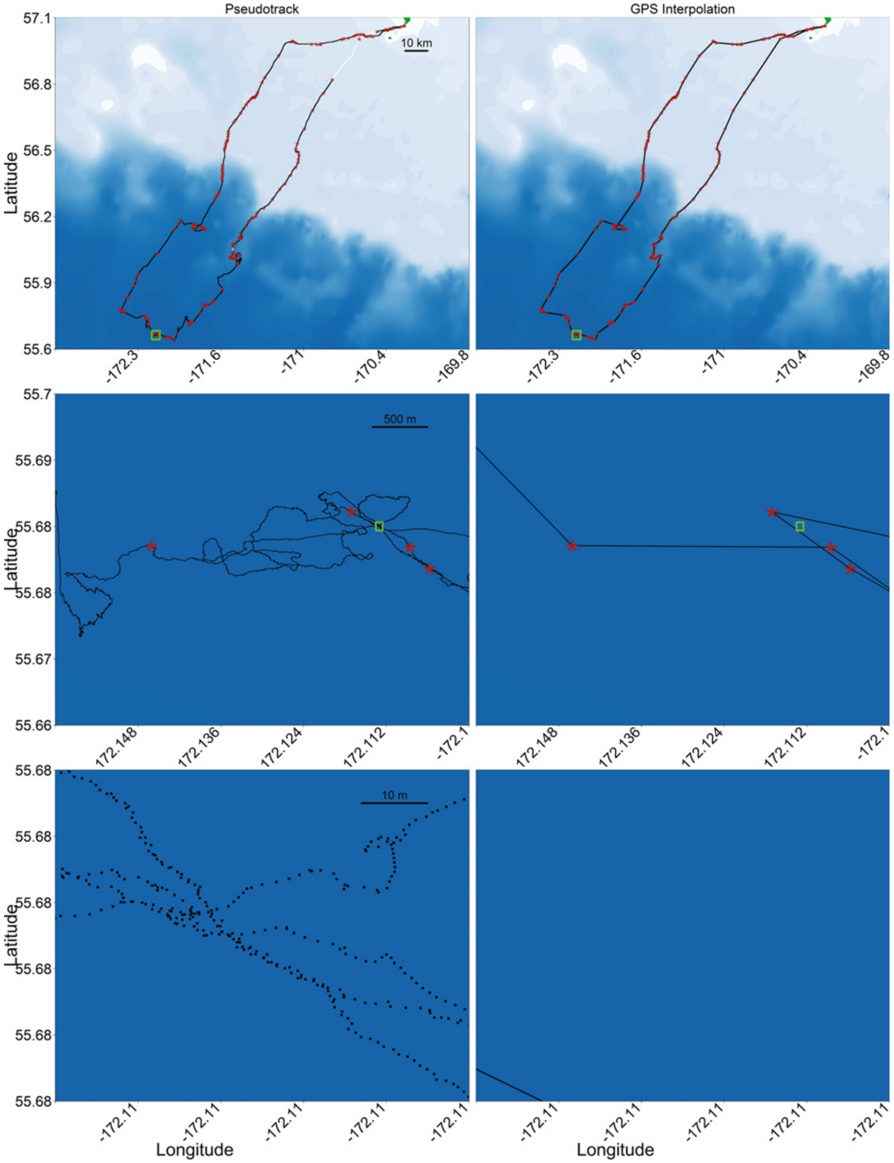

Figure 1. Increasing magnification (from top to bottom rows) of the two-dimensional tracks of a lactating northern fur seal from St. Paul Island (that went off-shelf) overlaid on color coded bathymetric maps (darker blue indicates increasing depth while green indicates land) with the left column being the pseudotrack calculated from Daily Diary data and the right column being the linear interpolation of GPS fixes (red *). The green boxes inserted into each panel reflect the portion of the track plotted in the row directly below it. White track-lines indicate sections between GPS points that had missing data.

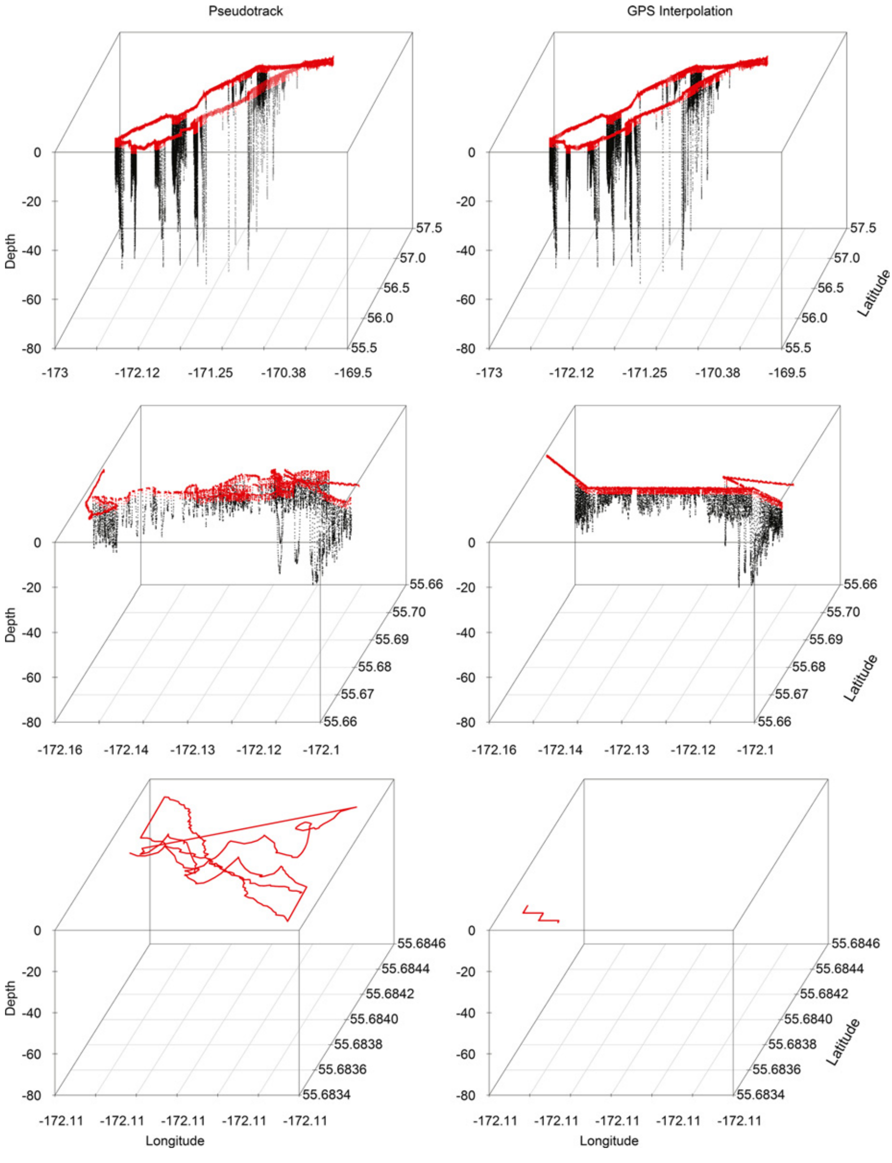

Figure 2. Increased magnification (from top to bottom rows) of the three dimensional tracks of a lactating northern fur seal from St. Paul Island with the left column being the pseudotrack calculated from the Daily Diary data and the right column being the linear interpolation of GPS fixes. Track sections are the same as in Figure 1. Red indicates surface activity (above 5 m) while black indicates subsurface (below 5 m) activity.

approximately 1.5 times longer than GPS only tracks ($t = 5.98$, df = 69, $P < 0.001$), while psesudotracks from Bogoslof Island animals were about 1.9 times longer ($t = 6.09$, df = 57, $P < 0.001$) (Table 1). This can be most explained by the fact that St. Paul animals averaged a greater number of GPS fixes per day (19.1, 1 per 75 min) and the ratio of pseudotrack:GPS trip lengths were subsequently more similar (ratio = 1.45:1) than Bogoslof seals (mean = 15.0 fixes per day , 1 per 96 min; trip length ratio = 1.87:1). Using the pseudotrack reconstructions, the average 3-dimensional distance a St. Paul animal traveled during a foraging trip was 972 km (range = 488–2,078 km), while Bogoslof Island animals traveled an average of 56% less per trip (429 km; range = 22–1,473 km) than St. Paul animals. In comparisons using animal as the sampling unit (multiple trips for a single animal were averaged), there was no significant difference in the distance traveled between seals that foraged on-shelf or off-shelf.

From the 42 animals that made 117 trips from Bogoslof Island, there were 314 night segments and 281 day segments, all of which were located off-shelf. From the 41 animals that made 51 trips from St. Paul Island, there were 129 day segments off-shelf, 141 night segments off-shelf, 188 day segments on-shelf and 220 night segments on-shelf. All segments totaled 1,273. Linear mixed effects models, using the hourly means of these segments as the sampling unit, indicated that the hourly means of swimming and dive distances differed by island of origin, oceanographic foraging domain (on-shelf or off-shelf), and time of day (night or day) (Table 3).

While we were unable to make quantitative comparisons in a linear modeling framework due to violations of assumptions with the distances swam summarized by nighttime and daytime, they did show different patterns from the hourly summaries because of the different number of day and night hours in a day. It is thus important to interpret the hourly summaries in light of a qualitative examination of the daily summaries. The hourly distances swum by the fur seals on their foraging trips were clearly affected by island of origin, day/night, and the oceanic domain with which the seals were associated (Tables 2–4). Fur seals were more active everywhere during the night than during the day with respect to both swimming distance in the horizontal plane and diving distances. However, the daily summaries indicated that because of the greater number of daylight hours, more swimming appears to have occurred during the day for all animals and nearly equal amounts of diving occurred during the day and night for the on-shelf animals. The end result is that the overall distance traveled (combined swimming and diving distances) of the off-shelf foragers appears

Table 3. Significant coefficients for linear mixed effects models testing the effects of Island of origin (Bogoslof or St. Paul), foraging domain (on or off shelf), and time of day (day or night) on distances traveled by lactating northern fur seals summarized on a per hour basis.

	Distance measure		
Coefficients	Horizontal	Dive	Total
Intercept	3.25	−0.32	2.51
Island	−0.77	−0.14	−1.09
Day/Night	0.99	0.65	1.84
On/Off	−1.54	0.81	−1.29[a]
Island:Day/Night	0.28	0.17	0.63
Island:On/Off	3.63	–	4.53
Day/Night:On/Off	0.56[a]	−0.57	0.34[a]
Island:Day/Night:On/Off	−1.26	–	−1.90

[a] Indicates a nonsignificant factor included in the most parsimonious model due to significance of higher order interactions.

the same during day and night periods, while on-shelf foragers appeared more active during the day. Not surprisingly, because Bogoslof Island is surrounded by deep water, the fur seals from Bogoslof behaved more like the St. Paul off-shelf animals than the St. Paul on-shelf animals.

First Passage Time Analysis

The optimal scale at which to calculate first passage times was generally similar for groups whether stratified by island, region, or night/day (Fig. 3). A notable exception was the group of animals from St. Paul that traveled off-shelf into the Bering Sea basin. While most other animals had an optimal scale near 50 m, whether they foraged during the day or night, the offshore animals from St. Paul that foraged at night had an optimal scale near 500 m with a dome shape at the peak (Fig. 3). The optimal scale for analysis of the reconstructed pseudotracks was 1–2 orders of magnitude smaller than that determined using GPS relocations by Nordstrom *et al.* (2013), which indicated an optimal scale of 6 km for seals from Bogoslof and an optimal scale of 12 km for seals from St. Paul Island. The smaller optimal scale for analyzing the pseudotracks naturally resulted in a greater number of FPT being calculated using the pseudotrack relocations relative to the GPS only relocations thus providing considerably more detail and variation in the first passage time calculations (Fig. 4).

Pseudotrack Measures of Error

The error in unconstrained complete tracks increases as tracks increase (Fig. 5), but there is no pattern in errors normalized by foraging trip length (Fig. 6). The full pseudotrack length constrained at the endpoints tended to be larger than the length of the track calculated using GPS points in shorter tracks, but not with longer tracks (Fig. 7). Plotting data in this way (Fig. 7) may be a useful approach to obtain an appropriate average speed that should be "optimal" when a least-squares fit line has a slope of 1. Figs. 8, 9 show examples of the unconstrained and anchored pseudotracks at the foraging trip scale. At the "consecutive point" scale Figs. 10, 11 indicate, with a smoother, that the unconstrained tracks have greater error with increasing time from an anchor point than the metric with anchor points at both ends. Finally,

Table 4. Model derived distances moved in km/h from St. Paul (n = 51) and Bogoslof Islands (n = 117) in kilometers (± SE) during day and night. They include distances swum horizontally, while diving, and combined total (horizontal plus diving distances). Statistics are stratified by habitat (while on or off of the continental shelf) for St. Paul animals.

		Distance measure (model derivations)		
Island	Habitat	Horizontal	Dive	Total
St. Paul	Offshelf day	3.75	0.12	3.90
	Offshelf night	5.01	1.38	6.38
	Onshelf day	5.13	0.35	5.58
	Onshelf night	5.69	0.71	6.50
Bogoslof	Day	4.24	0.11	4.35
	Night	5.23	0.94	6.19

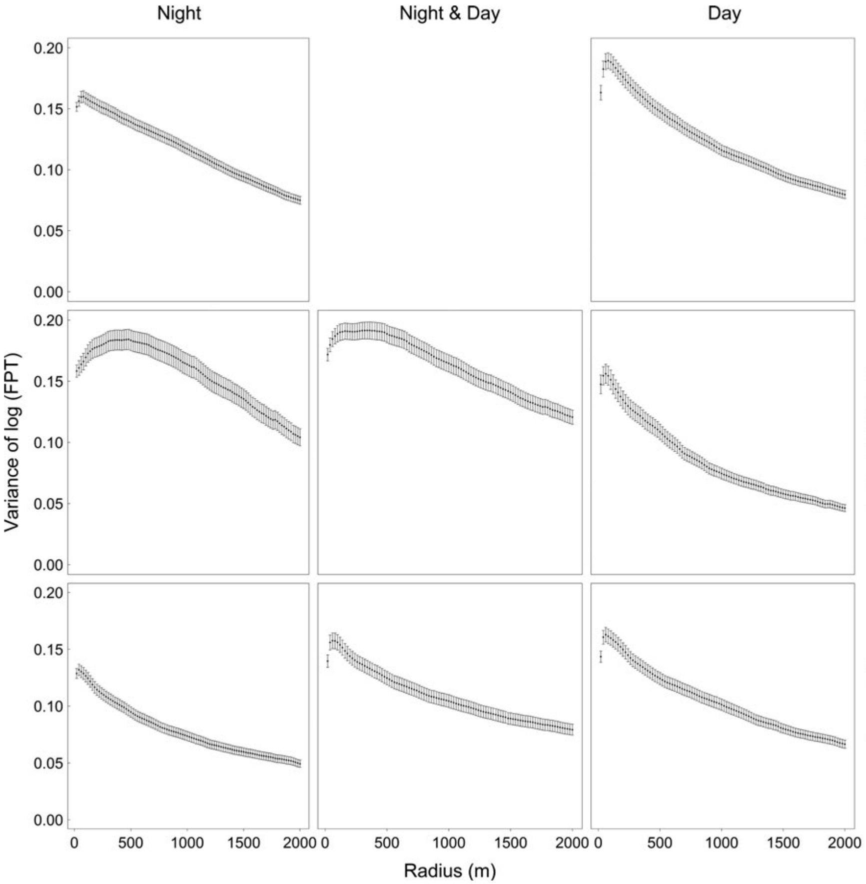

Figure 3. Variance of the log of first passage time of pseudotracks for lactating northern fur seals plotted against a range of radii using track data pooled by island. St. Paul Island data were stratified by oceanic domain (off-shelf and on-shelf shown in the small center panels); and then further stratified by night and day indicated by the larger panels. A peak in the log of the variance can be interpreted as the scale at which area restricted behaviors occurred.

Fig. 12 and Figs. S9, S10 show the "numerical" method of calculating anchored measures of error at all scales for a single track with a smoothed line.

DISCUSSION

The novel information obtained about distances travelled by lactating northern fur seals from the Daily Diary tags over GPS tags becomes more apparent as the spatial scale decreases to a resolution that matches the movements of animals engaged in feeding (Benoit-Bird *et al.* 2013). At the broad scale, where the entire tracks can be seen in a single image, there appears to be little difference between the two types of track reconstruction given reasonable GPS acquisition success. However, differences

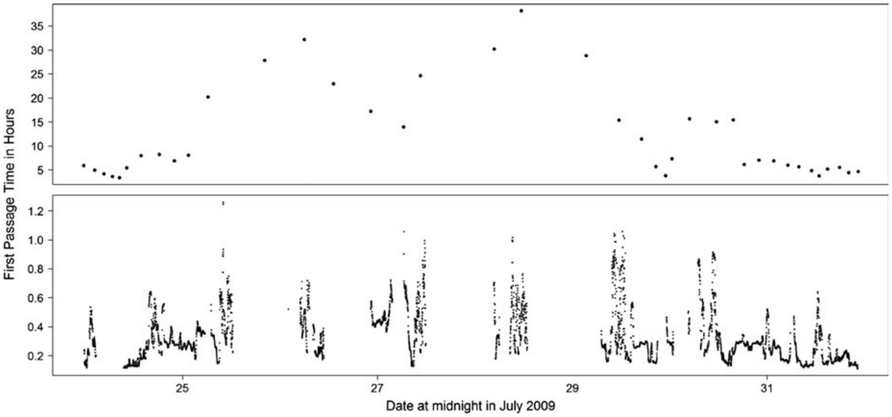

Figure 4. First Passage Times (FPTs) for lactating northern fur seals calculated for the same tracks shown in Figures 1 and 2. The top panel shows the FPTs calculated for GPS interpolated tracks while the bottom panel shows the FPTs calculated for the reconstructed pseudotrack. GPS interpolated FPTs were calculated for a radius of 12 km. The reconstructed pseudotrack FPTs were calculated for a 480 m radius, a value determined from the peak of the night time St. Paul Off-shelf graph shown in Figure 3. Spaces in the reconstructed pseudotracks are from sections of the track between GPS locations where either resting occurred or the tag failed to record data for a portion of that section.

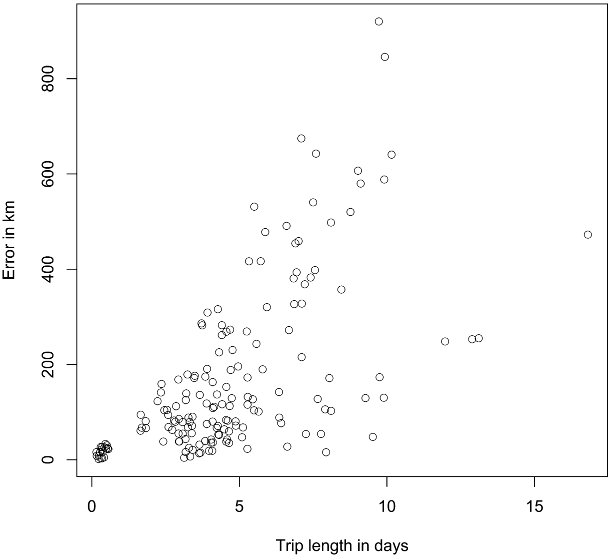

Figure 5. Error in final location of pseudotracks for complete unconstrained foraging trips of lactating northern fur seals. Data are for 117 trips from Bogoslof Island and 51 trips from St. Paul Island.

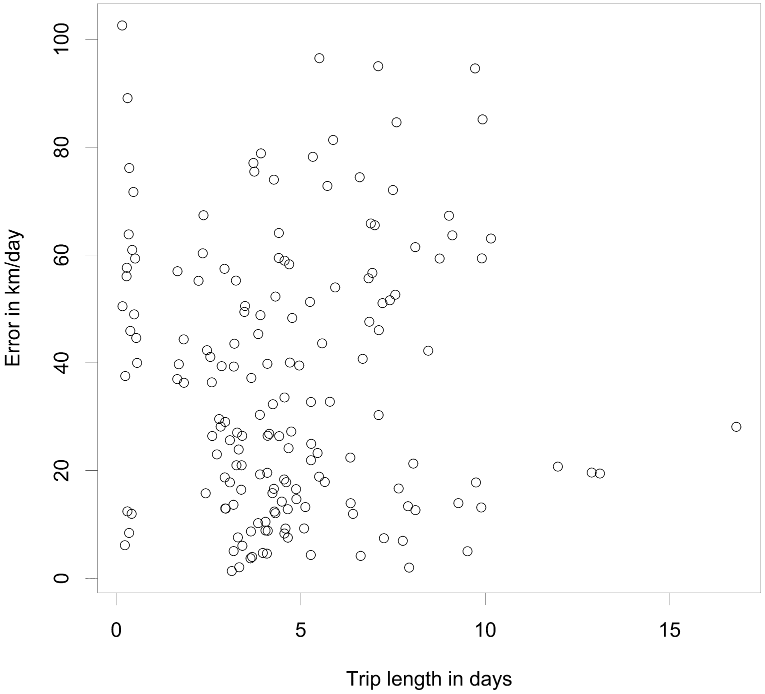

Figure 6. Error in final location of pseudotracks for complete unconstrained foraging trips divided by the length of the foraging trip. Data are for 117 trips from Bogoslof Island and 51 trips from St. Paul Island.

become obvious at about one-tenth the scale, and even more striking at the smallest scale where single seconds are plotted for the pseudotracks (Figs. 1, 2). Little similarity remains in areas of high tortuosity, though differences in areas of low tortuosity are minimal. Such differences are particularly important when calculating the amount of energy fur seals expend and require (overall dynamic body acceleration or doubly labeled water methods) given that an animal swimming on average between 55 and 75 km/d 2.3–3.1 km/h) expends considerably more energy moving through its environment than one that only moves 55% as far and as fast.

Differences between islands in the ratio of pseudotrack length and GPS interpolated track length likely reflect differences in the number of GPS points taken per day. Such ratios could potentially be used to estimate average pseudotrack distances over the course of a trip given similar frequencies of GPS fixes. The difference in the number of GPS fixes from each island may be due to how the Mk-10F tags were prepared for deployment, where tags used on Bogoslof had a white cloth tape covering the GPS receiver while those from St. Paul did not. The cloth tape prevents the shedding of water from the surface of the tag which inhibits the GPS. Although tags were programmed to take a fix every 15 min, differences between the actual and programmed times likely reflect a combination of deployment approaches, tag placement, individual tag differences, individual seal behavior, satellite locations, and weather.

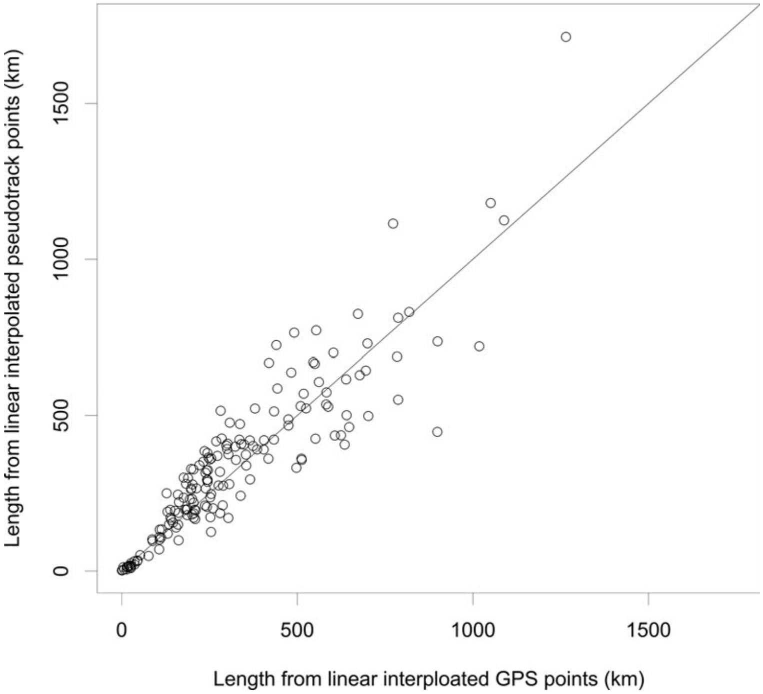

Figure 7. Length of constrained (start and end points only) pseudotracks for complete foraging trips of lactating northern fur seals as calculated by interpolation between points in time when GPS locations were taken plotted against length calculated by interpolation between GPS locations.

First Passage Time Analysis

We had expected the optimal foraging search radius (scale) to be similar for fur seals from St. Paul Island and Bogoslof Island that primarily foraged in the deep basin waters. However, the off-shelf St. Paul Island animal optimal scale (500 m) was an order of magnitude larger than that of the Bogoslof animals (50 m). Both estimates were significantly smaller than the foraging areas calculated from GPS interpolated data (12 km for St. Paul and 6 km for Bogoslof; Nordstrom *et al.* 2013). The same general trends were observed using either data set (Fig. 4); however, FPT was longer for the GPS interpolated data (as more time is generally required to move through a larger area). This underlines the importance of scale when interpreting first passage time values. Hierarchically, it is probable that the coarser resolution location data outlines large scale patches, which contain patches within patches (Fauchald and Tveraa 2006, Suryan *et al.* 2006). In this instance it would appear that the higher resolution pseudotrack data better reflects the sizes and distributions of prey patches targeted by the fur seals (Benoit-Bird *et al.* 2013).

Dietary analyses suggest that these two deep basin foragers targeted different prey species with the St. Paul animals primarily targeting juvenile walleye pollock and squid and the Bogoslof animals primarily targeting northern smooth tongue and

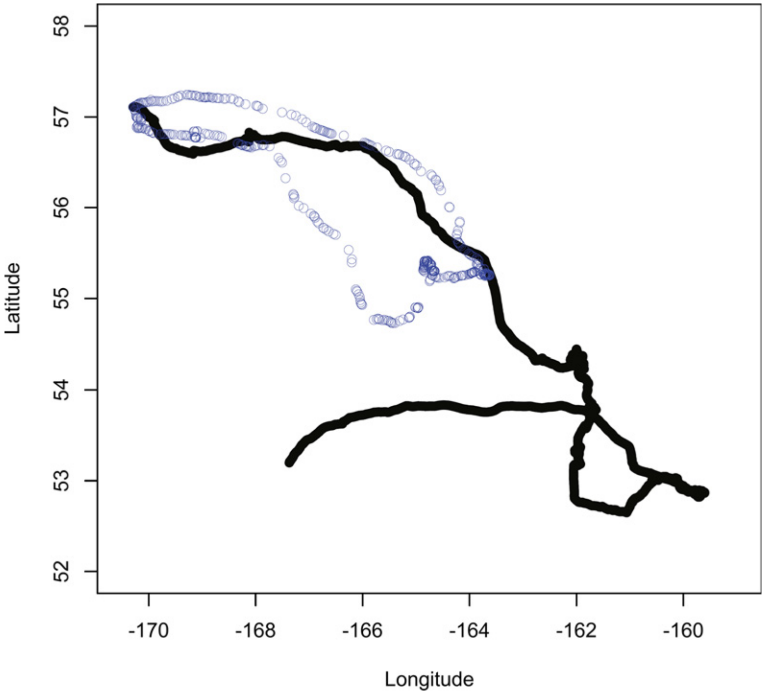

Figure 8. Complete unconstrained pseudotrack (black) of a lactating northern fur seal plotted over GPS locations (Blue) taken for the same foraging trip, our longest (~16 d) trip.

squid. The patch dynamics and schooling behavior of these prey species and the age classes targeted by the northern fur seals may have differed between islands which would account for the differences in optimal scale (50 m *vs.* 500 m). However, it is not clear what portion of the scat samples found on the rookeries contain prey remains from off-shelf because it takes the off-shelf foragers a day to traverse the shelf to return to St. Paul. Gut evacuation rates of the females returning from foraging off-shelf is unknown.

In contrast to the off-shelf St. Paul foragers (500 m), the optimal scale for differentiating behavior of St. Paul fur seals that feed on-shelf (50 m) was similar to that of the Bogoslof animals that fed in the deep basin (50 m). However, during daytime, the optimal scale of behavior of St. Paul fur seals fell to about 50 m over the deep basin. This similarity in behavior among all forager types does not mean that the seals were engaged in the same behaviors during day and night, but more likely reflects that different behaviors were occurring within a similar scale. The combination of surface-grooming and transiting behavior during the day may coincidently occur at the same scale as generalized searching, area restricted search and foraging behavior. Constant surface rolling behavior (Battaile *et al.* 2015) during daytime may not look that different from area restricted search for prey through the summarizing filter of FPT mathematics at these fine scales. Auxiliary data, such as depth data, may need to be employed to more certainly assign behaviors to ARS metrics.

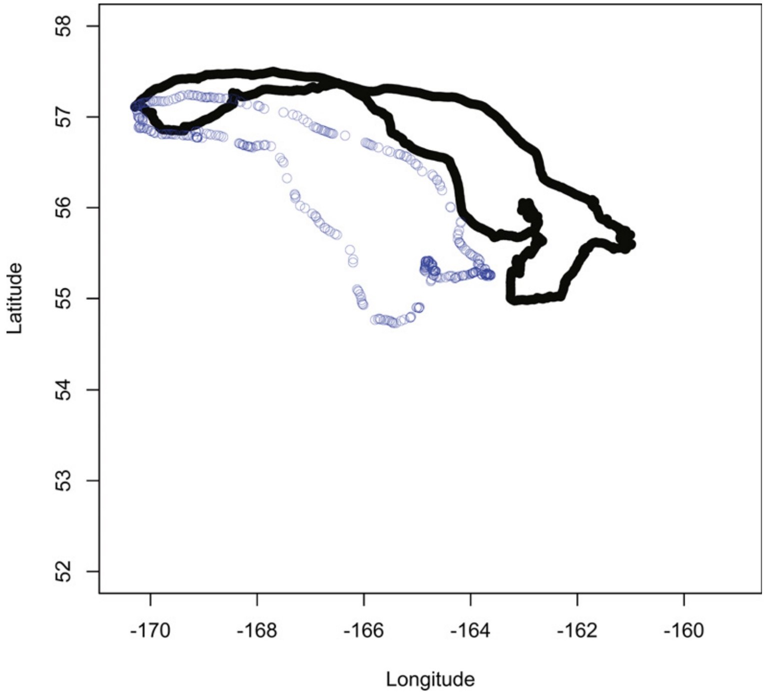

Figure 9. Complete constrained (start and end points only) pseudotrack of a lactating northern fur seal plotted over GPS locations (blue) taken for the same foraging trip. Same trip as Figure 8.

Quantitative ecological inferences can only be made at a multiple of the finest scale at which data are collected, and this is true when describing foraging behavior (Pinaud 2008). While data can be subsampled or scaled up to look at larger-scale processes, the opposite is not possible. On the other hand, finer-scale data may not always be desirable. The technological ability to collect data outpaces the ability to derive effective ways to analyze the ever-larger resulting databases. Nonetheless, the scale at which tag data is collected does not allow for inference of ecological processes at a finer scale, which may be more ecologically relevant than the smallest detectable scale allowed by the data. A companion study (Benoit-Bird *et al.* 2013) comparing the foraging behavior of northern fur seals with oceanographic acoustic data would not have been possible with GPS data alone.

Pseudotrack Measures of Error

Because it would be rare to not know the point at which tracking tags are deployed and recaptured, the metrics with anchor points at either end are probably the most useful. Nonetheless, the error measures are still large relative to distances traveled using the GPS point interpolations (Figs. S9, S10)—again illustrating the magnitude of potential error in unconstrained tracks and pitfalls in using the data in analyses of absolute measures in space. This seems especially

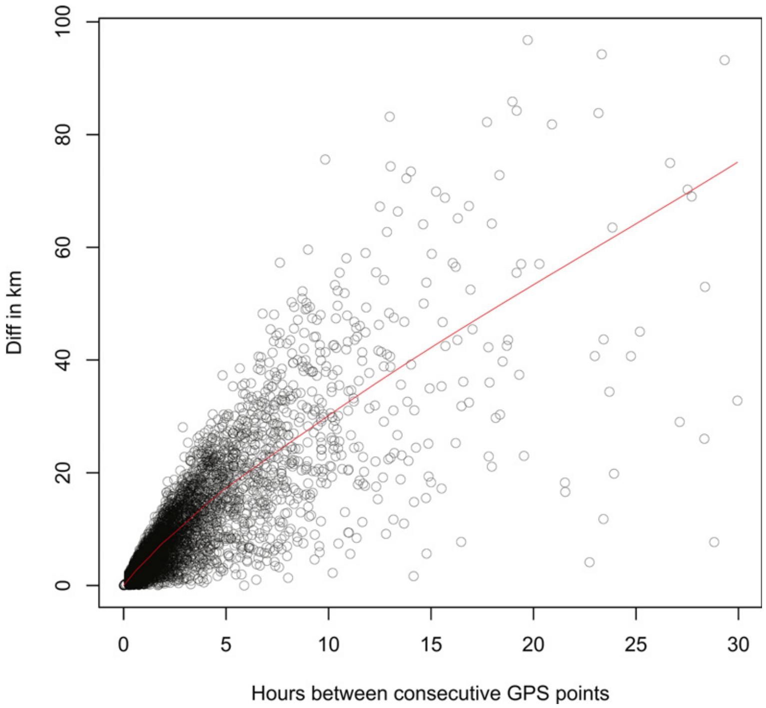

Figure 10. Error in final location of unconstrained pseudotracks of lactating northern fur seals calculated between consecutive GPS locations, plotted against the time between consecutive GPS locations. Data are for 117 trips from Bogoslof Island and 51 trips from St. Paul Island for a total of 13264 points.

true given the increased effort of calculating pseudotracks relative to simply interpolating between GPS points and the scale at which the pseudotrack data becomes more informative than the GPS data. The smoother in Fig. 12 and Figs. S9, S10 could be translated into 50% confidence interval errors (with some effort) around the georeferenced pseudotrack with respect to the distance to the nearest GPS anchor point, which is why we used distance instead of time for this error metric. In practice, GPS points are likely to be taken relatively frequently, reducing the magnitude of error.

Consideration of Fine-scale Positional Data

While tri-axial accelerometer and magnetometer estimated relocations are based on the mature discipline of navigation, the instrumentation we were able to deploy necessitated a number of tradeoffs be made between battery life, available technology, and size of the tags in order to collect adequate data to estimate a pseudotrack between two known positions.

The primary issue with processing tri-axial magnetometer and accelerometer data from marine animals is determining the angle of the tag relative to the earth. The angle must be known to determine heading because the tri-axial magnetometers will

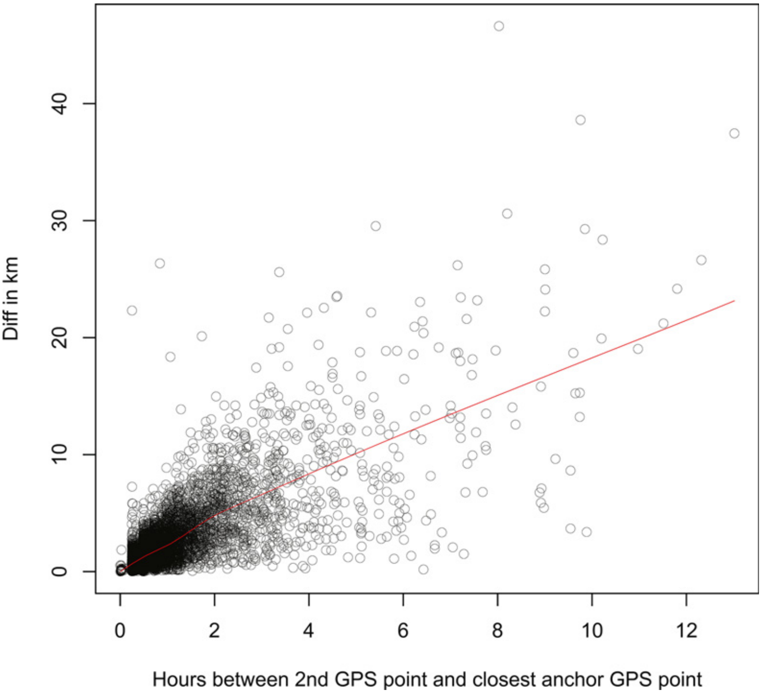

Figure 11. Error of pseudotrack of a lactating northern fur seal calculated at 2nd GPS location of pseudotracks constrained between 1st and 3rd GPS location, plotted against the shortest time between 1st and 2nd or 2nd and 3rd GPS locations. Data are for 117 trips from Bogoslof Island and 51 trips from St. Paul Island for a total of 13,264 points.

individually record different magnitudes of the earth's magnetic field in the same location given different tag angles. Given the declination and inclination of the magnetic field and tag angle, heading can be resolved. Accelerometers can be used to determine angle perfectly in a tag that is not accelerating. However, a tagged animal that creates acceleration signals *via* movement on an order similar or greater to gravity considerably confounds the ability to differentiate acceleration from gravity (static acceleration) or animal movement (dynamic movement) and hence tag angle and consequently heading. This problem is likely to become antiquated as tags are now being tested that contain gyroscopes that can differentiate between the static and dynamic forms of acceleration.

We adopted the "pseudotrack" terminology that is becoming the norm for biologging researchers engaged in track reconstruction from tri-axial accelerometer and magnetometer data. The pseudotrack term emphasizes the estimated nature of the tracks and implies there are proper and improper ways to use these reconstructions for further analysis and ecological interpretation. Our pseudotracks should be interpreted as estimated paths that have a higher degree of resolution and detail than the linear interpolations between GPS or ARGOS fixes. Unfortunately, no algorithm is available yet to estimate errors surrounding pseudotrack track reconstruction, making it difficult to assess how accurate the calculated locations actually are. However, making relative comparison of positions over time is a valid means to differentiate

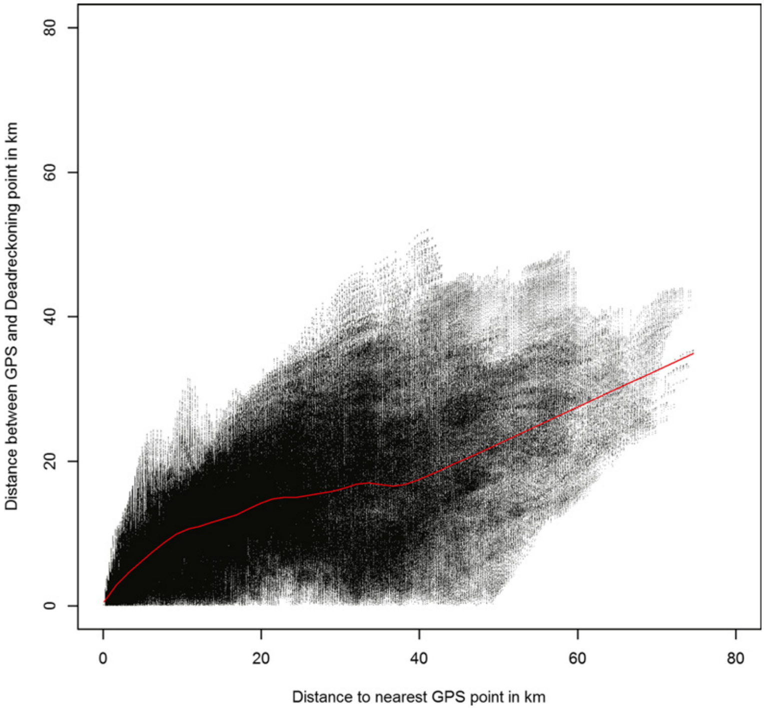

Figure 12. Difference between the GPS point and the anchored deadreckoned track using all possible window sizes and GPS points within the window for an entire foraging track. Bogoslof island example foraging track of a lactating northern fur seal.

between broad classes of behavior, such as when an animal is traveling in a relatively straight line to feeding grounds compared to when an animal is actively foraging or returning to land. Hence, ecological inferences dependent upon the reliability of the locations in space are probably dubious while analysis of the pseudotracks in a relative way is reasonable.

The new class of biologging tags that incorporate accelerometers and magnetometers have much to offer, but have limitations that warrant consideration when deciding on whether to invest in them. One primary concern is that analysis software is not yet commercially or freely available that can handle the large data files these tags create. At 16 Hz, a deployment will collect ~1.4 million lines of data every 24 h from animals that forage from weeks (fur seals) to months (elephant seals) at a time. Data files of this size mandate analysis in script-based programs (*e.g.,* Igor Pro, Matlab, or R) and will require programming expertise to ensure reasonable analysis times on even modern desktop hardware. While an R package dedicated to calculating pseudotracks and visualizing them is available from the authors, a dedicated program written in C++ or another low level programming language is probably needed. Analyses that further exploit the data generated by these tags are being developed and new analytical methods are needed to use them to their full potential. A second consideration is the scale and question the researcher is considering. GPS units can accurately record relatively high frequency data (on the scale of minutes) that can be remotely retrieved, while accelerometer data requires tag retrieval. Until such time that high-resolution data can be transferred through remote means, many ecological studies will have to wait to benefit from finer scale data.

Conclusions

Location data at the scale of 1 Hz provides a different picture of the foraging ecology of lactating northern fur seals than do locations derived from GPS only data at coarser scales. Calculations of swimming distance indicate that lactating fur seals are traveling much further and are consequently expending more energy to obtain food than previously recognized. The high-resolution data also shows that the scale at which fur seals are searching and foraging are one to two orders of magnitude below that previously determined with GPS data alone. This may indicate a hierarchical foraging strategy and provides better insight into the processes determining when and where fur seals feed.

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SUPPORTING INFORMATION

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12240/suppinfo.

Figure S1. Distribution of segment traveling speed of a lactating northern fur seal before and after removal of 5 outliers.

Figure S2. Distribution of diving speed data for lactating northern fur seals before and after square transformation to normalize data.

Figure S3. Residuals from most parsimonious dive distance model for lactating northern fur seals without modeling for heterogeneity in the variance.

Figure S4. Residuals from the most parsimonious dive distance model for lactating northern fur seals with heterogeneity in the variance modeled.

Figure S5. Residuals from the most parsimonious horizontal distance (sans depth) model for lactating northern fur seals without modeling for heterogeneity in the variance.

Figure S6. Residuals from the most parsimonious horizontal distance (sans depth) model for lactating northern fur seals with heterogeneity in the variance modeled.

Figure S7. Residuals from the most parsimonious total distance (horizontal + depth) model for lactating northern fur seals without modeling for heterogeneity in the variance.

Figure S8. Residuals from the most parsimonious total distance (horizontal + depth) model for lactating northern fur seals with heterogeneity in the variance modeled.

Figure S9. Difference between the GPS point and the anchored deadreckoned track using all window sizes and GPS points within the window for an entire foraging track. Pribilof island off-shelf example foraging track of a lactating northern fur seal.

Figure S10. Difference between the GPS point and the anchored dead reckoned track using all window sizes and GPS points within the window for an entire foraging track. Pribilof island on-shelf example foraging track of a lactating northern fur seal.