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Article *in* Marine Biology · August 2018
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https://doi.org/10.1007/s00227-018-3382-3

ORIGINAL PAPER

Constrained by consistency? Repeatability of foraging behavior at multiple timescales for a generalist marine predator

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Received: 9 February 2018 / Accepted: 2 July 2018

Abstract

Marine predators frequently exhibit consistency in foraging behaviors despite the dynamic nature of marine ecosystems, which has the potential for ecological and evolutionary implications depending on the timescale at which it persists. We examined behavioral consistency in movements and diving behavior of adult female California sea lions (*Zalophus californianus*), which are abundant, generalist central-place foragers inhabiting an ecosystem characterized by small- and broad-scale oceanographic variability. We used biologging devices to measure repeatability of behavior within a season and stable isotope analysis of whiskers to quantify behavior across a 2-year period associated with anomalous environmental conditions that affected prey availability. Sea lions were significantly repeatable in all variables across multiple timescales ($R_{adj} = 0.26–0.82$), although repeatability estimates were generally higher for variables related to characteristics of individual dives (e.g., dive depth) than those that described dive bouts (e.g., bout duration) or spatial use (e.g., volume of 3D utilization distribution). These differences may result from the fact that diving behaviors vary with prey type, whereas spatial use and bout variables may reflect the foraging success within prey patches or movement among patches. There was variation in how predictable individual sea lions were in their diving behaviors, which was largely unrelated or negatively related to foraging site fidelity. The strength of behavioral consistency decreased with time yet persisted across the 2-year period, suggesting that while sea lions alter their behavior in response to environmental change, the behavioral flexibility of individuals may ultimately be constrained by consistency.

Introduction

Foraging behavior affects the survival and reproductive success of organisms, and has the potential to shape community and ecosystem structure through a myriad of mechanisms (Croll et al. 2005; Hughes et al. 2013; Ripple et al. 2014; Roman et al. 2014). Intraspecific variability in foraging behavior has become a major focus for ecologists in recent decades, as it is increasingly recognized that individual variation in diet is both widespread and ecologically important (Bolnick et al. 2003; Araújo et al. 2011; Ceia and Ramos 2015). The occurrence and persistence of 'individual specialization' or 'behavioral consistency' may arise due to a multitude of ecological, morphological, physiological, and behavioral processes, and can encompass a broad array of foraging behaviors that also describe habitat use and how individuals find, capture, and consume prey (Bolnick et al. 2003; Tinker et al. 2008; Knudsen et al. 2010; Araújo et al. 2011; Patrick and Weimerskirch 2014b). Within the foraging ecology literature, behavioral consistency is typically evaluated in an ecological framework, where the focus is on describing the heterogeneity of resource use within populations not attributable to age, sex, or morphology and the ecological consequences of this individual niche specialization (Bolnick et al. 2003). The field of animal behavior provides an alternate framework that largely focuses on explaining the limited behavioral flexibility of some individuals and the persistence of behavioral consistency through time and

Responsible Editor: Y. Cherel.

Reviewed by K. H. Elliott, A. Lowther and an undisclosed expert.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00227-018-3382-3) contains supplementary material, which is available to authorized users.

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Published online: 09 July 2018

across contexts ('animal personalities'; Sih et al. 2004; Réale et al. 2007; Bell et al. 2009). These two approaches share a commonality as they converge on the concept that individual variation in behavior is of ecological and evolutionary interest (Dall et al. 2012).

The foraging behavior of central-place foragers, such as colonially breeding seabirds and otariids, is constrained by the need to return to the rookery in a timely manner to deliver prey or milk to dependent offspring. Foraging behavior is critical during this energetically expensive time period, as energy shortfalls can adversely affect offspring growth and lead to reproductive failure, even at very short timescales (Costa et al. 1989; Davoren and Montevecchi 2003; Costa 2008; Ballance et al. 2009). Dietary specialization and foraging site fidelity are common among central-place foragers, with populations often comprised of behavioral 'generalists' that have a broad niche and consume an array of prey resources and 'specialists' whose diet is often an ordered and predictable subset of the diet of generalists (Hamer et al. 2001; Woo et al. 2008; Ratcliffe et al. 2013; Harris et al. 2014; Patrick and Weimerskirch 2014b; Baylis et al. 2015a; Patrick et al. 2015; Wakefield et al. 2015; Kernaléguen et al. 2016). Diving behavior often reflects diet and/or habitat use, leading to the assumption that diet and/or foraging site fidelity dictates consistency in dive behavior (Staniland et al. 2004; Tinker et al. 2008; Elliott et al. 2008; Villegas-Amtmann et al. 2008; Woo et al. 2008; Kuhn et al. 2014; Arthur et al. 2016). Site fidelity does not always drive consistency in diving behaviors of central-place foragers (Wakefield et al. 2015), and given the influence of diving behavior on energy expenditure (Arnould et al. 1996; Costa and Gales 2000; McHuron et al. 2018), further study is warranted to quantify the relationships between consistency in the different components of foraging behavior.

The timescale at which measurements are collected influences the strength of behavioral consistency, which can result from sampling bias or reflect the different underlying processes driving consistency (or lack thereof) at multiple timescales (Bolnick et al. 2002; Woo et al. 2008; Harris et al. 2014; Novak and Tinker 2015; Wakefield et al. 2015; Kernaléguen et al. 2016; Camprasse et al. 2017). Because variation in resource use affects an individual's internal state and how it interacts with the environment, complementary methods that provide estimates of consistency at different timescales are important to understand the ecological implications that may arise from this variation. Biologging devices are commonly used to quantify the foraging behavior of marine species, resulting in fine-scale measurements of behavior such as at-sea locations, diving behavior, and associations with oceanographic features (Hazen et al. 2012). These measurements are typically limited to very short timescales (hours to < 1 year), requiring the use of alternate techniques to quantify foraging behavior of individual animals across multiple years. For otariids, stable isotope analysis of whiskers has been instrumental in this regard because whiskers are slow growing (0.05–0.19 mm day^{-1}) with retention times up to 8+ years (Cherel et al. 2009; Kernaléguen et al. 2015; Rea et al. 2015; McHuron et al. 2016b), and isotope values remain unchanged once incorporated into the tissue. Whiskers can thus be sub-sectioned to provide a longitudinal record of foraging behavior across a substantial proportion of an individual's lifespan, allowing researchers to address questions related to ontogeny, niche specialization, and temporal variation in individual behavior (Cherel et al. 2009; Lowther et al. 2011, 2013; Baylis et al. 2015a; Kernaleguen et al. 2016).

The goal of this study was to examine consistency in a suite of foraging behaviors at multiple timescales for adult female California sea lions (*Zalophus californianus*), an abundant and generalist central-place forager inhabiting coastal and offshore environments of the California Current System (CCS). Adult females use multiple diving strategies to target a diversity of prey species (Orr et al. 2011; McHuron et al. 2016a), indicating that individuals may have considerable flexibility to behaviorally adapt to environmental changes. Although this population is believed to be at or near carrying capacity (Laake et al. 2018), there has been a steady decrease in pup growth rates over the last decade that has been attributed to a decline in energy-rich forage fish (McClatchie et al. 2016a), raising questions about how sea lions will adapt to environmental variability and change. We combined data from biologging devices and stable isotope analysis of whiskers to determine (1) the strength and persistence of individual variation in foraging behavior at multiple timescales (weeks to years), (2) whether behavioral consistency varied among different behavioral categories (diving, spatial use, bout characteristics) and timescales, and (3) whether individuals varied in the strength of behavioral predictability and which factors might drive this variation. Here we define consistency as occurring when individuals within a population differ from each other but exhibit relatively low within-individual variability in a given behavior that is largely irrespective of the contribution of extrinsic or intrinsic factors to this pattern (Wilson 2018).

Materials and methods

Adult female California sea lions were captured in November of 2005–2008 at San Nicolas Island (32.2°N, 119.5°W) using custom hoop nets. San Nicolas Island is one of the two largest California sea lion rookeries, with upwards of 20,000 pups born each year (Lowry et al. 2017). Once captured, females were sedated with gas anesthesia using a portable field vaporizer (Gales and Mattlin 1998). Satellite tags that collected either ARGOS or GPS-quality locations,

time-depth recorders, and a VHF tag were attached to the dorsal midline of each animal using a quick setting epoxy. Time-depth recorders were programmed to collect depth and temperature data at 1-, 2-, or 4-s intervals (depending on the year). Tags were mounted on a neoprene base and attached to mesh netting with zip-ties. Standard length and mass were also measured at initial capture. Sea lions were released and subsequently recaptured after approximately 2 months to recover instruments and archived data.

Whiskers were collected from ten adult females captured at San Nicolas Island in November of 2014 as part of an unrelated study using the methods described above (McHuron et al. 2018). A single whisker (typically one of the longest) was plucked from the whisker bed while the sea lion was under gas anesthesia. Whisker samples were stored in paper envelopes at room temperature until analysis.

Dive and movement behavior

Location data were processed with a speed and angle filter to remove erroneous locations (12 km h^{-1} and 160º, IKNOS toolbox, Y. Tremblay unpublished). Hourly at-sea locations were interpolated using either a correlated random walk (R package *crawl*, Johnson et al. 2008; ARGOS locations) or linear interpolation (GPS locations). The majority of ARGOS locations (> 85%) were of class A or better, corresponding to error estimates of < 5 km (Costa et al. 2010). Dive data were subsampled to 4-s intervals to standardize across years and processed using a custom Matlab program (IKNOS toolbox, Y. Tremblay unpublished) to obtain summary statistics for each dive, including environmental data associated with each dive [temperature at surface (SST) and thermocline depth]. Interpolated locations were used to identify dive locations using a custom Matlab script (P. Robinson unpublished). California sea lions exhibit periods of intensive diving while at sea (diving bouts), which can be associated with either transit or foraging behavior. We used a modification of the method described in Boyd et al. (1994) to identify these bouts and exclude potential transiting dives (R. Beltran unpublished; McHuron et al. 2016a). The minimum criterion for a bout was a minimum of five dives with a maximum surface interval of 10 m or less between dives. Bouts were excluded from analysis if the mean dive depth of the bout was less than 8 m (Melin et al. 2008).

The location and dive data were used to calculate 15 variables that described the foraging behavior of sea lions on each foraging trip to sea. A foraging trip was defined as any trip to and from San Nicolas Island that lasted a minimum of 1 day. This criterion was chosen for two reasons: (1) to ensure that each trip encompassed both day and night so that all behaviors were represented for each foraging trip per sea lion, and (2) because trips < 1 day often had very few satellite locations associated with them, resulting in inaccurate representations of spatial use. Trips < 1 day occurred infrequently for most sea lions; 78% of sea lions had ≤ 2 short trips that comprised an average of < 5% of all foraging trips per individual.

Foraging behaviors were classified into one of three general categories: spatial use, characteristics of individual dives (hereafter referred to as diving behavior), and bout characteristics. Spatial variables included the duration of each foraging trip (identified using the wet–dry sensor on the time-depth recorder; days), the maximum straight-line distance traveled from the rookery (km), and three-dimensional 50 and 95% kernel density utilization distributions (3D-UD, km^3) of hourly mean dive depths and their spatial location using a two-stage plug-in method (R package *ks,* Duong 2018) as described in Simpfendorfer et al. (2012) and Cooper et al. (2014). Dive behaviors were calculated by averaging all dives across a foraging trip and included the percentage of time spent diving, maximum day and night dive depths (m), the percentage of time spent diving during the day and night, the percentage of dives that were within the water column and < 200 m (epipelagic) or ≥ 200 m (mesopelagic; McHuron et al. 2016a), and a diel index that described the change in day–night dive depth (McHuron et al. 2016a). Bout characteristics included the mean inter-bout interval (h), mean bout duration (h), and mean number of bouts per day.

Isotope analysis of whiskers

Whiskers were sonicated for 15 min in de-ionized water and rinsed with petroleum ether to remove any exogenous debris. The total length of whiskers was measured before sectioning each whisker into ~ 3-mm segments starting at the base. Subsections from the proximal end of each segment were weighed into tin boats (0.5 ± 0.05 mg) and analyzed for C and N stable isotopes using a Carlo-Erba NE2500 CHNS-O Analyzer coupled to a Thermo Finnigan DELTAplus XP Isotope Ratio Mass Spectrometer via a Thermo Finnigan ConFlo III at the University of California Santa Cruz Stable Isotope Laboratory. Results are presented in delta (δ) notation in per mil (‰) relative to either Vienna-Pee Belemnite Limestone (C) or atmospheric N_2 (N). Precision of an internal laboratory standard was 0.05‰ for $\delta^{13}C$ and 0.07‰ for $\delta^{15}N$.

Individual whisker growth rates were estimated as described in ESM1 and used to determine the amount of foraging time integrated into each segment, which ranged from 25 to 47 days. We excluded the first whisker segment from all analyses because initial plots of $\delta^{13}C$ and $\delta^{15}N$ values revealed that isotope values in the segment closest to the base were noticeably different from nearby whisker segments, a pattern that has also been found in whiskers of other pinnipeds (Zhao et al. 2006; Hückstädt et al. 2012).

We used biologging data and stable isotope values in plasma collected across a single foraging trip from sea lions tagged in 2014 as part of an unrelated study (McHuron et al. 2018) to understand how variation in whisker isotope values was related to behavioral variables (ESM2).

Population-level behavioral consistency

The repeatability of each behavioral variable (R) was calculated using the following equation:

$$R = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{\varepsilon}^2},$$

where σ_{α}^2 is the between-individual variability and σ_{ε}^2 is the residual error (within-individual variability; Dingemanse and Dochtermann 2013). We used the R package *rptR* to calculate the repeatability of each behavior, including the significance of repeatability estimates using permutation tests and bootstrapped 95% confidence intervals (Stoffel et al. 2017). Separate models were run for each variable, with year as a fixed factor and individual as a random effect. Because of the inclusion of year as a fixed effect, the resulting repeatability estimates are considered adjusted repeatabilities (R_{adj}), representing the repeatability as if all measurements were taken at a fixed time (Nakagawa and Schielzeth 2010). The repeatability of whisker δ^{13}C and δ^{15}N values were estimated using the same approach, but instead of including time as a fixed effect, we limited our analyses to include isotope values within the 2 years prior to collection to ensure the behavior of individuals was represented by similar time periods. Repeatability measurements range from 0 to 1, with greater repeatability as values approach one. We also assigned a qualitative measure of repeatability based on numerical values as described in Harris et al. (2014); behaviors with values from 0 to 0.25 had low repeatability, values of 0.25–0.5 were considered repeatable, values of 0.5–0.75 were moderately repeatable, and behaviors with values > 0.75 were considered strongly repeatable.

To examine temporal changes in repeatability, we recalculated the repeatability of each behavior using the first 3 (~ 2 weeks), 6 (~ 1 month), and 10 (~ 2 months) foraging trips to sea. Because sea lions varied in their number of foraging trips, we limited our estimates of repeatability for this analysis to the 16 sea lions that were tracked across at least 10 trips to sea. We used linear mixed effects models to evaluate whether the number of foraging trips influenced the repeatability of behavioral traits (R package *lme4*, Bates et al. 2015). The number of trips (3, 6, or 10), the behavioral category (spatial, dive, bout), and the interaction between the two were included as fixed factors, and each behavior was treated as a random effect to account for the non-independence of repeatability estimates within a behavior. The significance of the number of observations was assessed using F tests and the Kenward–Roger approximation of degrees of freedom (R package *afex*, Singmann et al. 2018). Multiple comparisons were made using Tukey's HSD tests (R package *multcomp*, Hothorn et al. 2008).

Individual-level behavioral consistency

Individual repeatability estimates were calculated for each behavioral variable using the equation

$$R'_{\text{adj}.i} = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{i}^2},$$

where σ_{α}^2 is the between-individual variability and σ_{i}^2 is the residual variance for individual i. In addition, we calculated the individual repeatability of SST and thermocline depth as indicators of environmental consistency. Because there were often large differences in mean behavioral values among sea lions, we natural log transformed all dive and movement variables so that the residual variance represented a relative instead of an absolute change from each sea lion's behavioral mean.

We ran a principal components analysis on the individual repeatability estimates to create a reduced set of uncorrelated variables that described suites of behavioral repeatabilities (R package *FactoMineR*, Le et al. 2008). Varimax rotation was used on axes with eigenvalues > 1 to clarify the contribution of variables to each principal component. Pearson's correlations were used to determine the relationships between each principal component and the original variables, with Bonferroni corrections applied to adjust for multiple comparisons. Linear models were used to examine whether foraging site fidelity, consistency in SST or thermocline depth, year, or mass explained any of the variability in principal component scores. The foraging site fidelity of each sea lion was estimated by quantifying the pairwise overlap in the 95% kernel density utilization distributions among foraging trips using Bhattacharyya's affinity (Fieberg and Kochanny 2005). Utilization distributions were created using the *adehabitatHR* package with the ad hoc smooth parameter and default grid size (Calenge 2006). Pairwise overlap estimates were averaged to create a single index of foraging site fidelity per sea lion. We ran all possible combinations of models without interactions (separate models were run for each variable) and used Akaike Information Criterion corrected for small sample (AIC_c) to inform model selection. We considered all models that were within two ΔAIC_c values of the top model.

All statistical analyses were run using R version 3.4.1 (R Core Team 2017). No comparisons were made between individual repeatabilities of short- and long-term behaviors

because these two datasets were collected from different individuals. Means are presented ± SD.

Results

A total of 32 adult female California sea lions were tracked across at least six foraging trips to sea (ESM3—Table S2). The mean tracking duration was 62.2 ± 12.0 days, with an average of 10 ± 3 trips per sea lion. The total number of trips varied among individuals despite similar tracking durations because the duration of each trip varied (ESM3—Table S2). Stable isotope values in whiskers across the 2-year period ranged from − 14.4 to − 16.3‰ for δ^{13}C and 16.1–18.0‰ for δ^{15}N. Variation in δ^{13}C values was largely explained by how far sea lions foraged from the mainland coast (higher values closer to the mainland), whereas variation in δ^{15}N was in part explained by diving behavior, mainly the percentage of epipelagic dives (higher values with less epipelagic dives; ESM2).

Population-level repeatability

Repeatability estimates for all variables representing short-term behavior were significant, but the strength of repeatability varied widely among behaviors (R_{adj} = 0.26–0.82, P < 0.01; Fig. 1). Variables characterizing diving behavior were generally more repeatable across foraging trips than those describing spatial use or bout characteristics. Behavior was also repeatable across longer temporal scales, as evidenced by the moderate repeatability of δ^{15}N (R = 0.63, P < 0.01) and δ^{13}C (R = 0.52, P < 0.01) values (Fig. 1).

The strength of repeatability decreased as the number of foraging trips included in the analysis increased, but the magnitude and specific differences among the discrete periods (3, 6, or 10 foraging trips) were affected by the behavioral category (interaction term: F (4, 28) = 10.08, P < 0.01; Fig. 2). Repeatability estimates of diving behavior were significantly different between 3 vs. 10 foraging trips (P < 0.01) but not 3 vs. 6 trips (P = 0.20) or 6 vs. 10 trips (P = 0.36). In contrast, repeatability estimates of spatial behavior and bout characteristics differed between 3 vs 6 and 3 vs. 10 foraging trips (P < 0.01) but not 6 vs. 10 foraging trips (P = 0.88).

Individual-level repeatability

There was considerable variation in estimates of individual repeatability for all short-term behavioral variables, indicating that some sea lions were more predictable in their behavior than others (ESM3—Fig. S4). Individual repeatability estimates of isotope values showed similar trends across the entire 2-year period (δ^{13}C: 0.28–0.75, δ^{15}N: 0.47–0.92), although values of sequential whisker segments tended to cluster together in isospace for all sea lions (Fig. 3). There was no correlation between individual repeatability estimates of δ^{13}C and δ^{15}N (r = 0.22, P = 0.55). Individual variation in short-term repeatability estimates could be described along five principal components primarily associated with spatial use (PC 1), night diving behavior (PC 2), bout characteristics (PC 3), day diving behavior (PC 4), and the percentage of deep dives (PC 5; Table 1). Significant correlations between mean values of each behavioral variable and the principal components were only present for PC 2; these correlations indicated

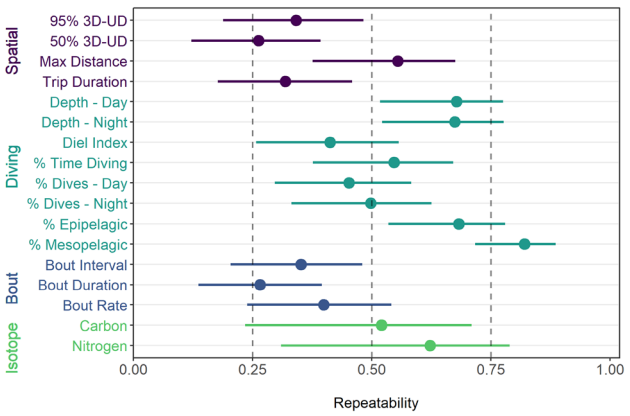

Fig. 1 Repeatability estimates of behavioral traits of adult female California sea lions with 95% CI. Behaviors are color coded by category (spatial, individual dive characteristics, bout characteristics, isotopes), with the 1st three categories representing short-term consistency (2 months; n = 32 sea lions) and the final category representing long-term consistency (2 years; n = 10 sea lions). Cutoff values for qualitative assessments of the strength of repeatability are shown with dashed gray lines, corresponding to low, repeatable, moderately repeatable, and strongly repeatable behaviors

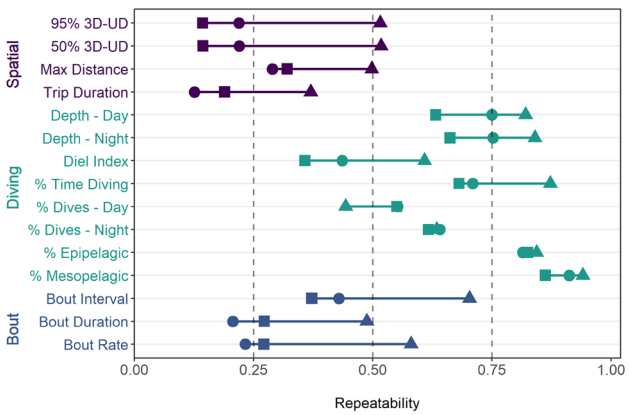

Fig. 2 Repeatability estimates of behavioral traits for 16 adult female California sea lions using three (triangle), six (circle), and ten (square) foraging trips to sea. Cutoff values for qualitative assessments of the strength of repeatability are shown with dashed gray lines, corresponding to low, repeatable, moderately repeatable, and strongly repeatable behaviors

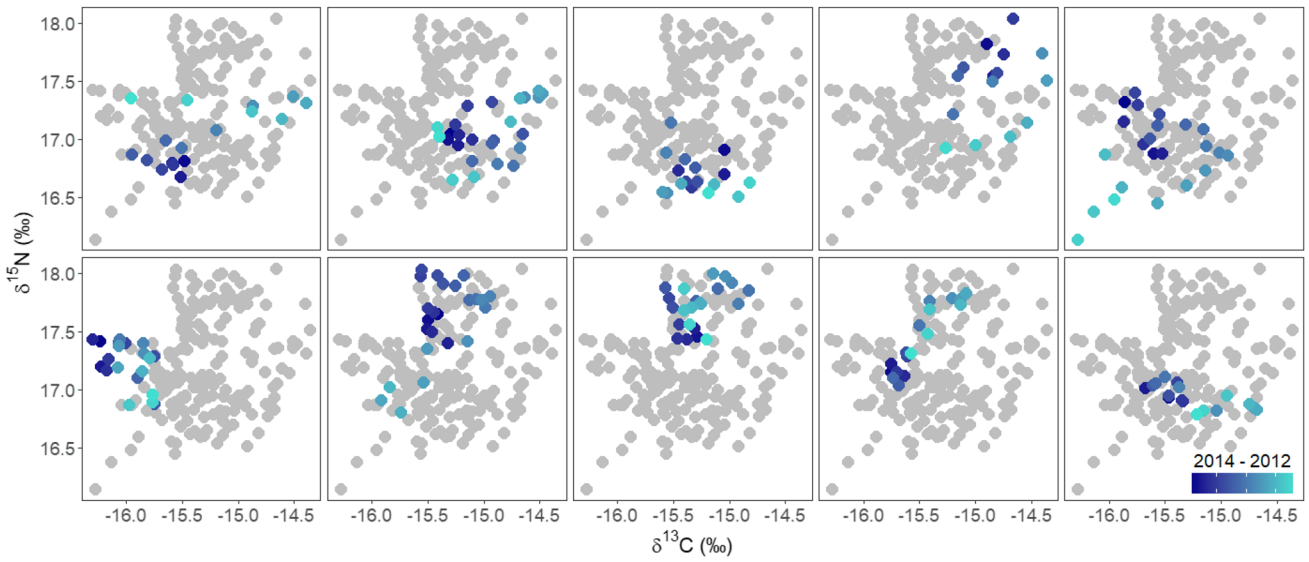

Fig. 3 Isotope values of δ^{15}N and δ^{13}C in sequential whisker segments of adult female California sea lions, incorporating approximately 2 years of foraging behavior. Each subplot represents a different individual, with darker colors indicative of more recent growth. The position of all sea lions in isospace is depicted by gray circles in each subplot

Table 1 Principal component loadings with the greatest contribution (>0.5) to axes that describe individual variation in repeatability estimates of foraging behavior (top) and correlations between each principal component and the original behavioral variables (bottom). Loadings or the correlation coefficient (*r*) are shown in parentheses following each variable. The proportion of variability explained by each axis is shown in parentheses following each component header

PC 1 (36.5%)	PC 2 (18.4%)	PC 3 (11.3%)	PC 4 (7.6%)	PC 5 (6.5%)
Loadings				
50% UD volume (0.92)	% night dive (0.90)	# bouts per day (0.86)	Diel index (0.77)	% mesopelagic (0.86)
95% UD volume (0.91)	Night depth (0.80)	Bout interval (0.76)	% day dive (0.75)	Day depth (0.53)
Max distance (0.88)	% dive (0.58)	Bout duration (0.71)	Day depth (0.67)	
Trip duration (0.63)			% epipelagic (0.57)	
Correlations				
None	% mesopelagic (−0.75)	None	None	None
	Night depth (−0.74)			
	Bout interval (−0.67)			
	Day depth (−0.64)			
	% dive (0.62)			
	# bouts per day (0.60)			
	Trip duration (0.54)			

that lower repeatability in night diving behavior was associated with deep-diving sea lions (Table 1). Linear models indicated site fidelity was important in explaining individual variation in repeatability for PC 1 and PC 2; however, the direction of these relationships was not the same for each principal component (Table 2). Sea lions with high site fidelity were more repeatable in trip duration, maximum distance traveled from the rookery, and the volume of space use than more wide-ranging individuals (PC 1). In contrast, individual repeatability in night diving behaviors decreased with increasing site fidelity (Fig. 4). Year was also included in all top models for PC 2. Overall, most of the variation in individual repeatability estimates remained unexplained, as there were no relationships between our explanatory variables and the remaining principal components and models for PC 1 and PC 2 explained only about 40% of the variability in our data.

Table 2 Model output explaining individual variability in repeatability estimates for the two principal component axes where the intercept-only model was not one of the top models

Model	*k*	logLik	AIC_c	ΔAIC_c	*w*	r^2
PC 1						
Site fidelity + thermocline	4	−62.62	134.77	0.00	0.33	0.37
Site fidelity	3	−64.59	136.07	1.29	0.17	0.33
Intercept only	2	−70.81	146.06	11.28	< 0.01	0.00
PC 2						
Site fidelity + year	6	−50.03	115.56	0.00	0.26	0.40
Site fidelity + year + mass	7	−49.00	116.86	1.31	0.13	0.42
Site fidelity + thermocline + year	7	−49.24	117.35	1.79	0.11	0.41
Intercept only	2	−60.18	125.76	9.22	< 0.01	0.00

Model parameters are shown for all models within 2 ΔAIC_c of the top model. The intercept-only model is also shown for comparison. Adjusted r^2 values are presented when the model contained more than one variable

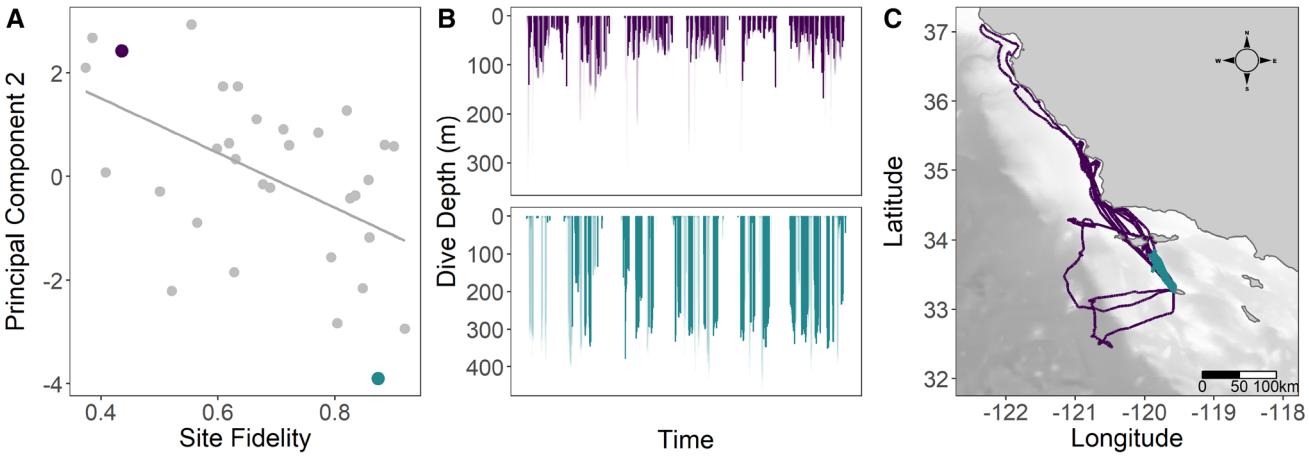

Fig. 4 The relationship between principal component 2 that primarily described variation in individual repeatability estimates of night diving behavior and foraging site fidelity (**a**). The dive profiles (**b**) and satellite tracks (**c**) for the two sea lions highlighted in **a** are shown to illustrate that deep-diving sea lions with high site fidelity were less predictable in behaviors related to dive depth and the percentage of dives occurring at night than shallower diving sea lions that were more predictable in their diving behavior but exhibited lower site fidelity. In **b**, a subset of six foraging trips is shown for esthetics, and darker and lighter shades depict night and day dives, respectively. In **c**, tracks are plotted on bathymetry ranging from 0 to 4000 m depth

Discussion

We detected consistency in foraging behavior across multiple timescales for adult female California sea lions, a central-place forager inhabiting a temporally and spatially dynamic ecosystem. Behaviors related to characteristics of individual dives, such as dive depth and the percentage of dives to specific zones within the water column, were generally more repeatable than behaviors related to spatial use or bout characteristics. While stable isotopes represent behavior at a much coarser resolution than obtained from biologging devices, $\delta^{15}N$ values were related to the percentage of dives in the epipelagic zone, suggesting that consistency in diving behavior persists to some extent across multiple years. Diving bouts represent periods of intensive diving and are believed to occur when sea lions encounter or move between prey patches (Feldkamp et al. 1989). Bout characteristics may thus be influenced by the specific characteristics of patches (e.g., size, density) as has been suggested for other air-breathing marine predators (Boyd 1996), as well as the immediate state of an individual (e.g., hunger level, energy needs). The persistence of individual prey patches in the marine environment occurs on the timescale of several weeks (Davoren et al. 2003; Sigler et al. 2017), which may have contributed to the reduced repeatability of bout and spatial use variables. Trip duration is affected by foraging location, but it also tends to increase during periods of reduced prey availability or increased energetic requirements (Boyd et al. 1997; Croxall et al. 1999); thus, flexibility in this variable is likely adaptive as it allows individuals to adjust to current environmental conditions and energy requirements.

The diving behavior of marine predators often reflects characteristics of prey, such that individuals targeting different prey species, age classes, or functional groups exhibit distinctive differences in their dive profiles, particularly with respect to depth and the position within the water column (Tinker et al. 2007; Elliott et al. 2008; Hoskins et al. 2015). McHuron et al. (2016b) hypothesized that the presence of multiple co-occurring foraging strategies exhibited by adult female sea lions, which differed in many of the diving behaviors measured here, reflected different target species, such as pelagic forage fish, market squid (*Doryteuthis opalescens*), and Pacific hake (*Merluccius productus*). The repeatability of diving behavior may thus reflect individual prey preferences, although it is unknown what mechanisms might contribute to the occurrence and persistence of these preferences for this population. Intra-specific competition is a key factor that can contribute to dietary diversification and specialization in populations (Svanbäck and Bolnick 2007; Tinker et al. 2008; Newsome et al. 2015), and could be a contributing factor here given the current population size (Laake et al. 2018) and the high-energy demands and restricted range of females during lactation that may exacerbate resource limitation (McHuron et al. 2017). Cultural transmission and phenotypic differences are less likely explanations (but see Schakner et al. 2017), but age (Hoskins et al. 2015), classical personality traits (Patrick et al. 2017), and memory-based learning during the exploratory juvenile phase (Votier et al. 2017) are intrinsic factors that could contribute to behavioral consistency of sea lions and deserve further exploration.

Similar to previous studies, behavioral repeatability decreased as the measurement timescale increased (Woo et al. 2008; Harris et al. 2014; Novak and Tinker 2015; Kernaléguen et al. 2016; Camprasse et al. 2017), but the magnitude and timing of this decrease differed among behavioral categories. Repeatability of spatial use and bout characteristics decreased significantly when behavior was measured across more than three foraging trips, whereas repeatability of diving behaviors was relatively consistent across most of the tracking duration. These patterns may reflect the different underlying processes influencing these variables as mentioned previously, with bout/spatial variables related to prey patch characteristics and diving variables reflective of species composition that is likely to be relatively constant within a season. We hypothesize that sea lions exploit the same prey patch (or multiple patches nested within a larger area) at short timescales (weeks) but may be forced to move among patches at longer timescales, which is supported by the positive relationship between PC 1 and site fidelity. The timing in the reduction of repeatability estimates aligns well with studies on the duration of patch persistence (Davoren et al. 2003; Sigler et al. 2017), and as predicted by the marginal value theorem (MVT), may correspond to the time interval at which energy intake in a particular patch is equal to the environmental average (Charnov 1976). Empirical tests of the MVT are limited in marine species due to challenges associated with quantifying patch quality and often result in conflicting conclusions with respect to optimal foraging models (Mori and Boyd 2004; Doniol-Valcroze et al. 2011; Heaslip et al. 2014; Watanabe et al. 2014; Foo et al. 2016); however, there is evidence from fur seals that within a foraging trip individuals make decisions about leaving prey patches in accordance with the MVT (Mori and Boyd 2004).

The majority of studies reporting repeatability estimates for diving behavior of marine predators have largely focused on seabirds (Cook et al. 2006; Ratcliffe et al. 2013; Harris et al. 2014; Patrick et al. 2014; Baylis et al. 2015b; Potier et al. 2015; Wakefield et al. 2015; Camprasse et al. 2017) and not mammals (McIntyre et al. 2017), although there are numerous mammalian studies that have quantified niche variation using stable isotopes (Newsome et al. 2009; Arnould et al. 2011; Hückstädt et al. 2012; Kernaléguen et al. 2012; Rossman et al. 2015), which may reflect diving behavior. Similar to our findings, several studies reported that certain diving behaviors (e.g., depth) were more repeatable than trip metrics (Cook et al. 2006; Ratcliffe et al. 2013; Harris et al. 2014; Wakefield et al. 2015), but others found the opposite relationships (Patrick et al. 2014; Camprasse et al. 2017). There also appears to be variability among studies in the timescale at which repeatability in diving behavior persists; for some species or populations it has only been documented across relatively short timescales (e.g., days; Camprasse et al. 2017), whereas in others it appears to persist across much longer timescales (e.g., years; Woo et al. 2008; Wakefield et al. 2015; McIntyre et al. 2017). Camprasse et al. (2017) suggested that this lack of consensus across studies could be due to temporal consistency in the occurrence of prey species, with benthic foragers exhibiting greater behavioral consistency because benthic communities provide static navigational cues (e.g., bathymetric features) that individuals can use to repeatedly visit the same areas. Contrary to this hypothesis, our study indicates that pelagic foraging species can exhibit strong behavioral consistency, suggesting that the occurrence of behavioral consistency may be modulated at the population or even colony level, as many species experience variable oceanographic conditions throughout their range and exhibit colony-specific differences in foraging sites and diet (Grémillet et al. 2004; Suryan et al. 2006; Garthe et al. 2007; Baylis et al. 2008; Kuhn et al. 2014).

While most diving behaviors were moderately repeatable at the population level, there was variation among individuals in the strength of behavioral repeatability. This variation was either unrelated or negatively associated with foraging site fidelity, suggesting that there are multiple ways for female sea lions to exhibit behavioral specialization. Our findings are similar to those of Wakefield et al. (2015) for

northern gannets (*Morus bassanus*) but inconsistent with the assumption that site fidelity dictates consistency in diving behavior (Staniland et al. 2004; Kuhn et al. 2014; Arthur et al. 2016). The negative relationship between repeatability of night diving behaviors and site fidelity was associated with dive depth and the percentage of mesopelagic dives, with deeper diving sea lions exhibiting higher site fidelity yet lower predictability in their diving behavior across foraging trips than shallow divers. Deep-diving is a spatially explicit foraging strategy at San Nicolas Island, with foraging concentrated in a relatively small area along the continental shelf break (McHuron et al. 2016a). This relationship may arise because sea lions using this strategy forage on a variety of prey species that vary in their diel behavior, or because the proximity of their core foraging area to other habitats may provide female sea lions with a range of foraging opportunities, thereby reducing consistency in diving behavior. At the opposite end of the spectrum, the strong predictability exhibited by some shallow-diving sea lions with low site fidelity may still be attributable to foraging location; most of these sea lions foraged on the continental shelf, which may constrain the range of available behaviors. It also is possible that sea lions targeted similar or the same prey species despite foraging in different areas. Year was an important explanatory factor for PC 2, suggesting that prey availability may play a role in driving behavioral consistency in this species.

Studies investigating consistency in foraging behavior are key in understanding the strategies individuals use to cope with environmental variation and the potential for species to adapt to a rapidly changing environment. The CCS is a productive eastern boundary system characterized by seasonal, annual, and multi-year variability in oceanographic conditions, including seasonal upwelling, tropical El Niño Southern Oscillation forcing, and Pacific Decadal Oscillation (Checkley and Barth 2009). California sea lions are typically considered to be a flexible species with respect to foraging, as they consume a diversity of prey species (Orr et al. 2011) and alter their behavior during El Niño events or other anomalous periods of increased SST (Weise et al. 2006; Melin et al. 2008). For example, Melin et al. (2008) found that lactating females from San Miguel Island spent more time in offshore habitats and dived deeper during an El Niño event compared with non-El Niño conditions. Our study provides further insight into population- and individual-level behavioral responses to environmental change, as the whisker isotope data covered a temporal period associated with anomalously warm SST and multiple years of poor reproductive success (McClatchie et al. 2016a, b). We found that isotope values of both C and N were significant repeatedly across the 2-year period but that some sea lions were more predictable than others in their behavior. At the population level, California sea lions may be buffered to some extent from environmental change due to the wide range of behaviors present within the population; however, the behavioral flexibility of individual sea lions appears to operate within the constraints of behavioral consistency, which may limit the ability of individuals to successfully adapt to environmental change depending on the degree of mismatch between behavior and prey availability. While we cannot exclude the hypothesis that consistency is an emergent property of successful foraging and not indicative of the true flexibility of sea lions, this seems unlikely given that several of the sea lions in 2014 were not observed with a pup or had an underweight pup, suggesting that they were not successful enough with their current (or previous) foraging behavior to support the costs of reproduction (McHuron et al. 2018). Further investigation of these patterns is warranted given the relatively small sample size, representation of a single rookery, and lack of data from an "average" year for comparison.

Behavioral consistency has been a focus of both ecological and behavioral studies due to the ramifications that individual variation in resource use has for ecological and evolutionary processes (Bolnick et al. 2003; Wolf and Weissing 2012). Our study adds to a growing body of literature that indicates many populations of marine predators exhibit some degree of behavioral consistency with respect to foraging (Ceia and Ramos 2015; Carneiro et al. 2017). Behavioral consistency in female California sea lions may in part arise because individuals prey on different functional groups, species, or age classes; however, further research is necessary to provide support for this hypothesis and elucidate the mechanisms that give rise to this behavioral diversity. The decreasing strength of repeatability estimates with time indicates that sea lions alter their behavior in response to environmental changes, which is likely adaptive for a species that inhabits a dynamic environment where prey availability varies at multiple temporal and spatial scales. The tendency for some sea lions to be more predictable than others appeared partially driven by prey availability and prey behavior; however, the remaining unexplained variance raises questions about other factors that may contribute to this pattern (e.g., physiology, personality traits) and whether consistency in foraging behavior is part of a larger behavioral syndrome in this species. The presence of behavioral consistency indicates that the flexibility of sea lions to alter their behavior in response to environmental change may be tempered by consistency; however, because some sea lions were more predictable than others this effect is unlikely to be uniform across the population, which leads to the question of whether there are fitness advantages associated with different behavioral strategies. Studies on a variety of marine and terrestrial predators have produced conflicting results, and even when present, the strength and direction of fitness consequences appear to be modulated by environmental conditions (Votier

et al. 2004, 2017; Katzner et al. 2005; Woo et al. 2008; Whitfield et al. 2009; van de Pol et al. 2010; Patrick and Weimerskirch 2014a, b, 2017; Abrahms et al. 2018). Variation in diving behavior has energetic implications for sea lions across short timescales (McHuron et al. 2018), but future studies that couple measurements of sea lion foraging behavior with reproductive success and other behavioral traits are necessary for understanding the mechanisms that give rise to behavioral consistency and in predicting how environmental changes will shape the population dynamics and ecological impacts of this abundant and generalist species.

Acknowledgements We would like to acknowledge the US Navy and John Ugoretz for logistical support, S. Simmons, C. Kuhn, P. Robinson, M. Fowler, S. Peterson, L. Hückstädt, and the numerous field volunteers that helped with data collection. We also thank the reviewers whose comments improved the manuscript. Much of the data collection for this project was part of the Tagging of Pelagic Predators (TOPP) project, which was funded by Grants from the California Sea Grant Program, National Oceanographic Partnership Program, the Office of Naval Research, and the Moore, Packard, and Sloan Foundations. A Grant from the E & P Sound and Marine Life Joint Industry Programme (#22 07-23) to DPC and the Earl and Ethel Myers Oceanographic and Marine Biology Trust to EAM funded the remainder of this effort.

Funding This study was funded by the E & P Sound and Marine Life Joint Industry Programme, the California Sea Grant Program, National Oceanographic Partnership Program, the Office of Naval Research, and the Moore, Packard, and Sloan Foundations.

Compliance with ethical standards

Ethical approval Animal handling was permitted under appropriate permits (NMFS #87-1593, 1851, 17952) and approved by the University of California Santa Cruz Institutional Animal Care and Use Committee. All applicable, international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest The authors declare that they have no conflict of interest.

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