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Comparison of foraging patterns between northern fur seal (Callorhinus ursinus) pups and adult females from San Miguel Island, California using stable isotope analysis

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Comparison of foraging patterns between northern fur seal (*Callorhinus ursinus*) pups and adult females from San Miguel Island, California using stable isotope analysis

A Thesis submitted in partial satisfaction of the requirements for the degree Master of Science

in

Biology

by

Tanner James Howard

Committee in charge:

Professor Carolyn Kurle, Chair
Professor Lin Chao
Professor James Nieh

2018
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Chair

University of California, San Diego

2018
EPIGRAPH

The harder the conflict, the more glorious the triumph.

-Thomas Paine

A ship in a harbor is safe, but that is not what ships are built for.

-John Shedd
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This study, in full, is currently being prepared for submission for publication of the material. Howard, Tanner; Orr, Anthony. Tanner Howard was the primary investigator and author of this material.
ABSTRACT OF THE THESIS

Comparison of foraging patterns between northern fur seal (*Callorhinus ursinus*) pups and adult females from San Miguel Island, California using stable isotope analysis

by

Tanner James Howard

Master of Science in Biology

University of California, San Diego, 2018

Professor Carolyn Kurle, Chair

Ecogeochemistry has become a useful tool in studying foraging ecology of marine mammals and other consumers. Ratios of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in consumer tissues can reflect foraging history over longer time spans than traditional methods of dietary analysis. To better understand overall foraging patterns and potential stable isotope relationships between individuals from different age groups within the same population, I
measured stable isotope values from unrelated northern fur seal (*Callorhinus ursinus*) pups and post-parturient adult females from San Miguel Island, California. Fur seals at San Miguel Island can be severely impacted by climate events such as the El Niño Southern Oscillation, increasing the need to further understand their foraging ecology. I analyzed sequential $\delta^{13}C$ and $\delta^{15}N$ values along single whiskers from five pups and five adult females, estimated pup and *in utero* whisker growth rates, and reconstructed stable isotope profiles over time for each vibrissa. I then performed correlation tests on the stable isotope profiles to compare mean $\delta^{13}C$ and $\delta^{15}N$ values from pups and adult females. Pups had significantly lower $\delta^{13}C$ values and significantly higher $\delta^{15}N$ values than adult females over an overlapping 50-day period prior to tissue collection. Stable isotope profiles for pups were significantly correlated, but there were no correlations among adult female stable isotope profiles. My results suggest large inter-individual variation among adult female foraging patterns, no significant relationship between stable isotope values from unrelated pups and adult females, and potentially distinct stable isotope minima indicating the birth event for pups.
Introduction

Ecogeochecmy, the analysis of stable isotope ratios from organismal tissues, has become increasingly used for reconstructing food webs, assigning trophic niche partitions within certain sections of a population, and determining overall foraging ecology on a variety of spatial and temporal scales (Newsome et al. 2010; Lowther and Goldsworthy 2011; Ben-David and Flaherty 2012). More traditional methods of reconstructing animal diets, such as stomach-content analysis, are limited in that they only provide data for recent feeding patterns, require a dead specimen, and are difficult to perform on larger animals (Kurle and Worthy 2001). Even scat analyses, while non-intrusive, still only provide data for recent feedings. In addition, monitoring cryptic marine mammals during their at-sea migration phases can be challenging (Kurle and Worthy 2001; Cherel et al. 2009; Newsome et al. 2010; Van Blaricom et al. 2013). To overcome these difficulties, tissues from marine vertebrates that breed, haul-out, or otherwise spend some amount of time on shore, can be sampled and subsequently analyzed for their biogeochemical signatures, allowing for potentially long-term reconstructions of their trophic ecology and habitat use (Kurle and Gudmundson 2007; Newsome et al. 2007; Scherer et al. 2015; Turner Tomaszewicz et al. 2017, 2018).

Frequently, the ecological application of stable isotope analysis utilizes measures of stable carbon ($^{13}\text{C}/^{12}\text{C}$ or $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$ or $\delta^{15}\text{N}$) isotope values within animal tissues to reconstruct animal foraging dynamics. A consumer’s stable isotope values reflect those of its prey along with any predictable changes caused by the physiological processes of prey utilization (Ben-David and Flaherty 2012). Therefore, consumer tissues contain a record of foraging history that varies in time scale depending upon the protein turnover time of the sampled tissue (Kurle 2009). Tissues with faster protein turnover times (plasma, liver) reflect an
animal’s most recent diet (Kurle 2009), whereas inert tissues such as bone, teeth, and vibrissae (whiskers) incorporate stable isotope values from consumer diets over much longer periods of time (Newsome et al. 2007; Scherer et al. 2015; Turner Tomaszewicz et al. 2016). Stable carbon isotope values in consumer tissues reflect carbon processes at the base of a food web, and are often applied to marine vertebrate studies to categorize animal habitat use and indicate the location at which an individual has been feeding (Hobson 1999; Post 2002; Newsome et al. 2012). Stable nitrogen isotope values in consumer tissues are consistently higher with increasing trophic levels, and are used to indicate both trophic position and habitat use (Ben-David and Flaherty 2012; Turner Tomaszewicz et al. 2018).

I used stable isotope analysis of sequentially segmented whiskers collected from unrelated pup and adult female northern fur seals (Callorhinus ursinus) on San Miguel Island, California to compare their foraging ecology over time and assess the degree to which the isotope values in whiskers from pups reflect those from adult, post-parturient females. Otariids (fur seals and sea lions) retain their whiskers over multiple years; thus, successive segments reflect the stable isotope values of the animal’s diet from a particular time period (Rea et al. 2015; McHuron et al. 2016). However, acquisition of whisker samples from adult otariids requires specialized and time-intensive techniques, since adults are large in size and can exhibit aggressive behavior (C.M. Kurle, personal communication). Therefore, I examined stable isotope values from pups and adult females to determine the viability of using stable isotope data from whiskers of randomly selected pups as proxies for the foraging history of mothers in the same population, which would potentially eliminate the need for difficult sampling from adult otariids. Additionally, I recreated time series of stable isotope data from fur seal whiskers to determine if these data supported previous research documenting seasonal and yearly oscillations in otariid
diets and habitat use, and if certain isotopic patterns reflect the timing of important physiological events such as birth and weaning. Furthermore, while my study was limited to a specific region, new methods supported by my findings can be applied to pinniped population and foraging studies and their conservation research regardless of species or geographic location.
Materials and Methods

Northern Fur Seals

Stable isotope analysis has been used to decipher otariid foraging ecology in past studies, including northern fur seals, Australian sea lions (*Neophoca cinerea*), Steller sea lions (*Eumetopias jubatus*), and Antarctic fur seals (*Arctocephalus gazella*) (e.g., Kurle and Worthy 2001, 2002; Kurle and Gudmundson 2007; Zeppelin and Orr 2010; Lowther and Goldsworthy 2011; Rea *et al.* 2015; Kernaléguen *et al.* 2016). Northern fur seals were designated as depleted in 1988 under the Marine Mammal Protection Act and are listed as vulnerable by the International Union for Conservation of Nature (IUCN). The population has largely been declining since the 1950’s, but has shown signs of stabilizing since 2010 (Orr *et al.* 2016). About half of the world’s northern fur seals breed in the United States and range from San Miguel Island in the Channel Islands, California, to the Pribilof Islands in the eastern Bering Sea (Orr *et al.* 2016). Fur seals breed on land from June to November largely on the Pribilof Islands, but with smaller colonies on San Miguel Island and Bogoslof Island in the Aleutian archipelago, Alaska (Gentry 1998; Orr *et al.* 2016). The reproductive cycle for the San Miguel northern fur seals begins approximately two weeks earlier than that for fur seals on the Pribilof Islands (DeLong and Melin 2000), with a mean of median pupping dates on 5 July (Orr *et al.* 2016). As a species, northern fur seals consume primarily fish and squid during both their breeding seasons and migration phases (Antonelis *et al.* 1990; Kurle and Worthy 2001, 2002).

The San Miguel colony of northern fur seals likely originated in the late 1950’s (DeLong 1982), but archaeological records indicate they bred throughout coastal California as far back as the middle Holocene up until ~1,000 BP (Burton *et al.* 2001). As of 2014, the San Miguel population represented less than 17% of the total northern fur seal stock in North America (Orr *et
Oceanographic conditions near the Channel Islands produce cold, nutrient-rich waters and cool weather patterns that provide suitable living conditions for northern fur seal breeding colonies (DeLong 1982; Orr et al. 2016). However, periodic climate events such as the El Niño-Southern Oscillation (ENSO) can alter these conditions along the California coast, resulting in higher sea surface temperatures, diminished upwelling strength, and reduced productivity (Arntz et al. 1991). Especially pronounced ENSO events in 1983 and 1997 reduced primary production in waters off southern California, decreasing prey availability in the region and increasing the mortality rate of northern fur seals in the Channel Islands (DeLong and Antonelis 1991). The San Miguel colony is continuing to recover from the 1997 ENSO event, with pup production in 2014 setting the colony’s second highest mark in recorded existence (Orr et al. 2016). However, territorial bull counts are still lower than those of 1997, and the colony remains at risk in face of future ENSO events (Orr et al. 2016). Since smaller populations like the San Miguel colony are more susceptible to large-scale environmental perturbations, it is necessary to monitor individuals within those populations to record their foraging and migration patterns for conservation purposes (Sterling and Ream 2004).

Tissue Selection

Researchers from NOAA’s Marine Mammal Laboratory and the University of California, San Diego’s Division of Biological Sciences collected a single mystacial whisker from 5 adult females and 5 pups \((n = 10)\) from the Adams Cove rookery on San Miguel Island (Figure 1; Table 1). Pinniped whiskers are especially useful for reconstructing animal foraging ecology and habitat use since whiskers are keratinous and therefore metabolically inert once formed (Ben-David and Flaherty 2012; Rea et al. 2015). Otariid whiskers grow continuously and do not shed
(Scheffer 1962; Hirons et al. 2001; Cherel et al. 2009; McHuron et al. 2016), meaning an undamaged whisker can reflect dietary information for an individual’s entire life span, with the most recent data at the root (proximal end) of the whisker and the oldest data at the tip (distal end) (Rea et al. 2015; Scherer et al. 2015). The diet consumed by a pregnant mammal directly contributes to the formation of her fetus (Gluckman et al. 2007) and otariid whiskers start to form during in utero development (Scheffer 1962), so a pup’s whisker will reflect the diet of its mother during gestation (Lowther and Goldsworthy 2011; Scherer et al. 2015; Baylis et al. 2016). When collecting whiskers for isotopic analysis, whiskers are typically plucked from the tissue bed or cut off near the base of the whisker, although the latter method leaves behind the subcutaneous tissue that contains isotopic data from the animal’s most recent foraging periods (Rea et al. 2015). To best interpret the temporal scale represented by the stable isotope data along the length of a whisker, it is necessary to determine whisker growth rates for each age group of the targeted species, as these rates can vary between different age classes (Zhao and Schell 2004; Tyrrell et al. 2013; Rea et al. 2015).

**Stable Isotope Analysis**

My collaborator and I removed all debris and lipids from the whiskers by placing them in separate glass test tubes with aerated lids and filled with enough petroleum ether to fully cover the whisker. The tubes were placed in a rack and submerged in deionized (DI) water in a sonicator at 60°C for five minutes, after which the whiskers were removed, rinsed with ultra-pure DI water, sonicated again in a test tube filled with ultra-pure DI water at 60°C for ten minutes, then dried, weighed, and measured for length.
We divided each whisker into multiple 1 mm segments using a 1 mm biopsy punch, starting at the proximal end and progressing longitudinally towards the distal end. The biopsy punch had a chamber designed to capture each divided segment to reduce the risk of losing a segment. Since an otariid whisker tapers towards the distal end (Rea et al. 2015), some 1 mm segments were not heavy enough to satisfy the 0.5-1 milligram range required for isotope ratio mass spectrometry (IRMS). Following previously established protocols, adjacent segments were combined to fulfill that mass requirement when necessary (Rea et al. 2015). IRMS mass requirements also limited the portion of total whisker length eligible for stable isotope analysis, so only the most recent portion of growth in utero is represented in δ^{13}C and δ^{15}N profiles. The segments were packaged in tin capsules and sent to the Stable Isotope Lab at the University of California, Santa Cruz (UCSC-SIL, http://es.ucsc.edu/~silab/index.php). Samples were analyzed for their δ^{13}C and δ^{15}N values by a Carlo Erba 1108 elemental analyzer coupled to a Thermo-Finnigan Delta Plus XP isotope ratio spectrometer (EA-IRMS).

The ratios of carbon and nitrogen stable isotopes are expressed in delta (δ) notation, such that

\[ \delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000, \]

and R=^{13}C/^12C or ^{15}N/^14N. The units are parts per thousand (per mil, ‰) deviations from the Vienna Pee Dee Belemnite standard for δ^{13}C and atmospheric air standard for δ^{15}N (Ben-David and Flaherty 2012). I calculated the average precision for these data as the SD of δ^{13}C and δ^{15}N values from a set of standards (acetanilide), and precision was 0.01‰ and 0.04‰, respectively. I separated stable isotope time series into pup time series and adult female time series, and calculated point-wise means to produce an average δ^{13}C and δ^{15}N time series for both pups and adult females. I then averaged those means over the most recent overlapping 50-day period to
generate a mean $\delta^{13}$C and $\delta^{15}$N value for pups and adult females over that time span. Due to isotopic fractionation processes that occur during nutrient consumption, breakdown, and utilization, the $\delta^{15}$N values in consumers are higher than those of their food by a predictable value called a trophic discrimination factor or TDF (Kurle et al. 2014). TDF’s are also expressed in delta notation, such that

$$\Delta X = \delta_{\text{tissue}} - \delta_{\text{diet}}$$

and X is $^{13}$C or $^{15}$N (Turner Tomaszewicz et al. 2017).

**Determination of Whisker Growth Rates and Temporality**

I determined the growth rates of northern fur seal pup and adult female whiskers to best estimate the temporal scale reflected by each whisker segment and place the stable isotope data within a reconstructed timeline. This resulted in a stable carbon and nitrogen “isotope profile” over time for each whisker (Figure 5, 6, 7, 8). Previous work demonstrated that otariid whisker growth rates differed among age groups, with whiskers growing fastest during the pup stage, slowest in adulthood, and at an intermediate rate during development in utero (Rea et al. 2015; McHuron et al. 2016). I calculated average whisker growth rates for pups and fur seals in utero using methods from Rea et al. (2015), in which the time duration in days from 5 July (mean of median pupping dates) and 28 September (collection date) represents the postnatal portion of each whisker. The range of total whisker lengths for adult females did not reflect the relatively wider variability of their respective ages, likely due to physical wear at the tip of certain whiskers, making it impossible to assess the time frame of their whisker growth with certainty. For this reason, I used the average whisker growth rate of adult Steller sea lions from Rea et al.
(2015) as a proxy for the average whisker growth rate of adult northern fur seals, since northern fur seals and Steller sea lions are both otariids and are thus closely related species.

First, since some of the segments I analyzed were longer than 1 millimeter to accommodate IRMS mass requirements, I converted the isotope values for each whisker segment into isotope values per millimeter. Using calculated average whisker growth rates for pups and an average whisker growth rate for adults reported by Rea et al. (2015), I then converted these corrected isotope values per millimeter into isotope values per day. By combining these time corrections with the known collection dates for each whisker, I estimated a time series for the stable isotope analysis values from each sequential segment from each entire whisker.

In addition, ontogenetic shifts in pups from growth in utero to ingestion of their mother’s milk are marked by minimized nitrogen isotope values preceding a steep rise in the δ¹⁵N value along an otariid whisker (Rea et al. 2015; Kelleher 2016). These minimized δ¹⁵N values were spread across a 2 mm interval in each pup whisker after correcting for length. I therefore designated the middle of each interval as that pup’s birth event, at which point in utero growth rates switched to pup growth rates for temporal determination. Pinniped whisker development likely begins 6-7 months before parturition (Scheffer 1962; Hewer and Backhouse 1968), so I assigned the onset of whisker development in utero at 6.5 months (with 30 days per month) prior to the mean of median pupping dates. I then calculated the distance from the point on the whisker marking the designated birth event to the distal end of the whisker, and divided that length by the 6.5-month duration to calculate the in utero whisker growth rate.
Statistical Analysis

Since curves generated from stable isotope values per whisker segment were nonparametric, I used the Spearman rank-order correlation coefficient ($r_s$) to test for significant similarity between stable isotope profiles. To maintain a consistent sample size among pairwise correlations, I performed correlation analysis on the number of whisker segments that corresponded with the number of segments in the smallest analyzed whisker portion ($n = 8$). Starting at the proximal end of each whisker, I calculated pairwise correlation coefficients among pup profiles, among adult female profiles, and between pup and adult female profiles. Using the Fisher $z$-transformation to reduce statistical bias (Corey et al. 1998; Zar 2005), I converted pairwise correlation coefficients to $z$-scores, averaged the $z$-scores, and back-converted the average $z$-score to a correlation coefficient ($r_s'$). I repeated this process to generate $r_s'$ values representing the collective similarity among pup profiles, among adult female profiles, and between pup and adult female profiles, with $r_s'$ considered significant at $p < 0.05$. In addition, I used the Student $t$-test to compare $\delta^{13}C$ and $\delta^{15}N$ values between sampled pups and adult females over the most recent overlapping 50-day period, with results considered significant at $p < 0.05$ and reported as mean ($\pm$SD). I reconstructed stable isotope profiles and conducted statistical analyses using R version 3.4.1.
Results

Plucked whiskers ranged from 4.6-6.3 cm and 8.2-12.8 cm for pups and adult females, respectively. Analyzed portions of these whiskers ranged from 16-34 mm for pups and 30-112 mm for adult females, with means (±SD) of 23.8 ± 6.9 mm and 79.6 ± 34.0 mm, respectively (see Appendix). Calculated whisker growth rates for pups and fur seals in utero were 0.21 mm/day and 0.19 mm/day, respectively, which are both slower than previous estimated growth rates for those age groups (Table 2). Whisker growth rates for adult Steller sea lions from Rea et al. (2015) averaged 0.15 mm/day. Estimated portions of in utero whisker development captured with our stable isotope analyses ranged from 10-29% of a pup’s whisker length, with a mean of 17 ± 7%.

Over an estimated 50-day period prior to whisker collection, adult females had mean δ¹³C and δ¹⁵N values of −15.8 ± 0.4‰ and 16.9 ± 0.3‰, respectively. The mean δ¹³C value from pups (−16.5 ± 0.3‰) was significantly lower than that of adult females (t-test, p < 0.001), whereas the mean δ¹⁵N value from pups (18.3 ± 0.6‰) was significantly higher than that of adult females (t-test, p < 0.001) (Figure 2).

The results from the Spearman rank-order correlation coefficient analyses indicated that the δ¹⁵N profiles among the five pups were significantly similar between pup individuals ($r_s' = 0.61, p < 0.05$) (Figure 3). The δ¹³C profiles among all five pups were also significantly similar ($r_s' = 0.53, p < 0.05$) (Figure 4). The δ¹³C and δ¹⁵N profiles compared among the five adult females across the same time span were not significantly similar ($\delta^{13}C r_s' = 0.01, p = 0.24; \delta^{15}N r_s' = -0.11, p = 0.30$) (Figures 3, 4). In addition, δ¹³C and δ¹⁵N profiles were not significantly similar between pups and adult females ($\delta^{13}C r_s' = 0.12, p = 0.20; \delta^{15}N r_s' = -0.16, p = 0.33$) (Figures 3, 4).
The $\delta^{15}$N profiles from pups exhibited their lowest values at around 17‰ followed by a steep rise to around 19‰ (Figure 5). The $\delta^{13}$C profiles from pups showed a similar pattern, with minima at approximately −17 to −17.5% followed by a steep rise to around −16.5 to −16‰ (Figure 6). In reconstructed stable isotope profiles fit to timelines based on our estimated pup whisker growth rates, the lowest stable isotope values for each pup coincided with June/July, with the exception of the $\delta^{15}$N values from pup SM1276SML, which were lowest in mid-May (Figure 5D).

The $\delta^{13}$C and $\delta^{15}$N profiles for adult females were more variable among individuals. Female A1292WAF exhibited a consistent oscillation in $\delta^{15}$N values, with maxima during summer and winter seasons (Figure 7A), indicating regular, potentially seasonally-related shifts in nitrogen isotope values. However, the $\delta^{13}$C values for female A1292WAF exhibited less consistent oscillations (Figure 8A). Both females A1338WAF and A4760PRT showed a steep drop in $\delta^{13}$C and $\delta^{15}$N values around April 2011 and July 2011, respectively, which were not observed in the other three adult females (Figures 7, 8). All females demonstrated oscillating $\delta^{13}$C and $\delta^{15}$N values over time, but recurrent highs and lows did not coincide with the same time periods as indicated by the reconstructed timelines estimated from adult whisker growth rates previously determined by Rea et al. (2015) (Figures 7, 8).
Discussion

I measured stable carbon and nitrogen isotope signatures from successive segments of whiskers collected from pup and adult female northern fur seals, then reconstructed stable isotope profiles over time for each seal using estimated pup whisker growth rates that I calculated and estimated adult whisker growth rates from the literature (Rea et al. 2015; McHuron et al. 2016). I detected patterns of stable isotope minima in the pups’ whiskers coincident with approximate pupping dates for fur seals on San Miguel Island, supporting previous research indicating such patterns marked birth events in other otariids (Rea et al. 2015; Kelleher 2016). I evaluated whether stable isotope signatures in whiskers from pups could be used as proxies for those from unrelated, post-parturient adult females, and found they could not. Stable isotope data from both pups and adult females indicate significant variability in diet and habitat use among individuals, as no single pattern emerged for isotope values along the reconstructed timelines.

When estimating whisker growth rates for pinnipeds and reconstructing stable isotope profiles, temporal estimations involve multiple potential sources of error (Rea et al. 2015). Fur seal pups on San Miguel Island are typically born between mid-June and mid-July (Orr et al. 2016), and since we did not know the exact birth date of pups sampled in this study, my estimates using the mean pupping date may over- or underestimate individual pup whisker growth rates. For example, the minimum stable isotope values that indicate the birth event for pup SM1276SML coincide with a mid-May birth date, which is two or more weeks earlier than the earliest fur seal births observed on San Miguel Island during that year (Orr et al. 2013). This could also indicate that the practice of matching minimum stable isotope values with birth events in otariid pup whiskers is not valid; however, stable isotope minima from the remaining four
pups fall close to the mean of median pupping dates and previous work further details this phenomenon in fur seal pups from the Pribilof Islands (Rea et al. 2015). Whisker growth rates are also affected by factors such as age, sex, diet, seasonal progression, and, in the case of fetal growth rates, maternal nutritional status (Trites 1991; Gluckman et al. 2007; R.R. Ream, personal communication). Despite the potential for error, the methods I used for estimating pup and fetal whisker growth rates follow established protocols (Rea et al. 2015) and are sufficient for temporal analysis of fur seal pup and adult female isotope values.

My calculated whisker growth rates are slower than previously determined whisker growth rates for otariids (Rea et al. 2015). This may be due to the smaller body size of northern fur seals compared to other otariid species. However, a slower whisker growth rate in utero compared to postnatal growth is consistent with previous studies, and is attributed to a metabolic focus on internal organ development in utero (Rea et al. 2015). There was no correlation between adult female age and length of respective sampled whisker, possibly due to breakage at the tip of some adult female whiskers. Therefore, I was unable to determine the growth rate of the adult fur seals in my study, so I used the average whisker growth rate determined for adult Steller sea lions from Rea et al. (2015).

Lower δ\(^{13}\)C and higher δ\(^{15}\)N values for pups compared to adult females are consistent with previous studies on trophic discrimination in pinnipeds (Zeppelin and Orr 2010; Rea et al. 2015). The higher δ\(^{15}\)N values occur because pups are nursing on their mothers’ milk, and mammalian milk contains higher δ\(^{15}\)N values than prey consumed by adult females (Hobson and Sease 1998). Maternal milk is high in lipids, which contain lower δ\(^{13}\)C values than protein (Hobson and Sease 1998; Post et al. 2007) and is the likely cause of the lower δ\(^{13}\)C values in pup whiskers compared to those from the adult females.
Birth events indicated by the stable isotope minima and my reconstructed timelines based on growth rates were within reasonable range of the mean pupping date for four of the five pups, and all pup stable isotope profiles followed similar trends. However, those trends were not reflected in the isotope values from adult females. I therefore rejected my hypothesis that stable isotope values collected from pups can be used as proxies for stable isotope values from unrelated, post-parturient adult females from the same population. There was also no relationship between adult females for either $\delta^{13}C$ or $\delta^{15}N$ values, indicating a large variation in foraging history among adult females. The temporal stable isotope profile of each female exhibited oscillation over time, but the temporal placement of stable isotope minima and maxima varied by individual and did not reflect any uniform seasonality or other pattern. While a pup’s isotope values can reflect isotope values from its mother during gestation and nursing (Rea et al. 2015), there is too much inter-individual variation in foraging behavior of adult females to extrapolate that methodology for use with unrelated pups and mothers across an entire population.

Hirons et al. (2001) found that stable isotope oscillations observed from sequential segments of pinniped whiskers primarily reflected changes in diet and feeding location rather than endogenous shifts in physiological processes. While we observed variation in the oscillation patterns of the $\delta^{15}N$ values among adult females, minimized $\delta^{15}N$ values were consistently observed during periods of late winter and early spring, concurrent with high levels of seasonal upwelling in the California Current and matching observations in $\delta^{15}N$ values from phytoplankton in the Southern California Bight (Kurle and McWhorter 2017). Lack of similarity in oscillations over time for both $\delta^{13}C$ and $\delta^{15}N$ values in adult females could be reflective of spatial and temporal variation in oceanographic conditions within the Southern California Bight (Gelpi and Norris 2008; Dong et al. 2009; Kurle and McWhorter 2017). Sea surface temperature,
upwelling strength, and eddy currents within the Southern California Bight follow interannual, seasonal, and intraseasonal trends, which can affect productivity and prey availability (Dong et al. 2009). Additionally, adult females travel outside of the Southern California Bight during the non-breeding season (approximately December to May) from northern California to as far north as Vancouver Island, Canada (A.J. Orr, personal communication). Utilization of different foraging destinations along the North American coast likely contributes to the variations I observed among oscillation patterns from the adult females, including anomalous dips observed in patterns from two adult females. Aside from those anomalies, ranges of $\delta^{13}$C and $\delta^{15}$N values in all five adult females were highly constrained in months previous to collection date (roughly $-17\%\text{o}$ to $-15\%\text{o}$ and $15.5\%\text{o}$ to $17.5\%\text{o}$, respectively), likely indicating minimal diet shifts in trophic level and/or foraging locations. Therefore, even if females are utilizing different regions and/or feeding on different prey from one another, which are reflected in the whisker stable isotope values, their movements and trophic niches are still relatively narrow. This is consistent with data demonstrating that San Miguel northern fur seals do not undertake long-range annual migrations between low and high latitudes with their conspecifics breeding at the Pribilof Islands, but rather stay near the California coast year-round (DeLong and Melin 2000; Orr et al. 2016; C.M. Kurle, personal communication).

In summary, I reconstructed stable carbon and nitrogen profiles using estimated whisker growth rates along with stable isotope data generated from whiskers collected at San Miguel Island, California to compare foraging patterns of pups and unrelated, post-parturient adult females. This method has been previously established by Rea et al. (2015) and other previous studies, and is sufficient for temporal estimations despite containing multiple potential sources of error. For future studies, methods that account for whisker tapering with greater precision will
enable more accurate temporal placement of stable isotope values generated from the distal end of otariid whiskers. Using estimated age-specific growth rates from the same species in the absence of calculated growth rates can maintain consistency between different age groups, and recording birth dates of sampled pups can enhance temporal accuracy for minima signifying the birth event within stable nitrogen profiles. While one estimated birth date was placed outside of the range of observed birth events in the year of collection, all five pups exhibited stable isotope patterns consistent with estimations previous otariid studies. However, large inter-individual variation among adult female stable isotope profiles prevents the use of pup stable isotope values as proxies for stable isotope values of unrelated, post-parturient adult females, indicating a need to continue sampling from adult otariids for population studies despite the higher difficulty and greater risk in safety. I found that pups had lower $\delta^{13}\text{C}$ values and higher $\delta^{15}\text{N}$ values than adult females, likely due to their consumption of mothers’ milk. Finally, I determined that variation among stable carbon and nitrogen profiles for adult females can stem from oceanographic trends within and outside of the Southern California Bight, and can reflect changes in diet or foraging location over time in response to changing environmental conditions.

This study, in full, is currently being prepared for submission for publication of the material. Howard, Tanner; Orr, Anthony. Tanner Howard was the primary investigator and author of this material.
FIGURES

Figure 1. Study site where whiskers were collected from northern fur seal pups and adult females, located at Adams Cove on San Miguel Island, California.

Figure 2. $\delta^{15}\text{N}$ values in pup whiskers were higher than $\delta^{15}\text{N}$ values in adult female whiskers over the most recent overlapping 50-day period, whereas $\delta^{13}\text{C}$ values in pup whiskers were lower than $\delta^{13}\text{C}$ values in adult female whiskers over the same time period.
Figure 3. Correlations of $\delta^{15}$N isotope profiles among pups were higher than those among adult females. Increasing circle size corresponds with increasing correlation.
**Figure 4.** Correlations of $\delta^{13}$C isotope profiles among pups were higher than those among adult females. Increasing circle size corresponds with increasing correlation.
Figure 5. Stable nitrogen profiles among pups showed similar patterns over time.
Figure 6. Stable carbon profiles among pups showed similar patterns over time.
Figure 7. Oscillations were widely variable among stable nitrogen profiles in adult females, but the range of mean values was constrained to approximately $2\%$. 

23
Figure 8. Oscillations were widely variable among stable carbon profiles in adult females, but the range of mean values was constrained to approximately 2‰.
### TABLES

**Table 1.** Northern fur seal sample identification and collection date.

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**Table 2.** Otariid whisker growth rates featured in this study, with growth rates presented as mean (±SD).

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<td>In utero</td>
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<td><em>E. jubatus</em></td>
<td>Rea et al. (2015)</td>
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<td>0.15 ± 0.05</td>
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<td>Rea et al. (2015)</td>
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APPENDIX

Table 3. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for adult female A1292WAF, along with total analyzed whisker length and mean (±SD) stable isotope values.

<table>
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Table 3, continued. δ\textsuperscript{13}C and δ\textsuperscript{15}N values per whisker segment for adult female A1292WAF, along with total analyzed whisker length and mean (±SD) stable isotope values.

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Table 4. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for adult female A1338WAF, along with total analyzed whisker length and mean (±SD) stable isotope values.

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Table 5, continued. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for adult female A2177PRT, along with total analyzed whisker length and mean (±SD) stable isotope values.

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Table 6. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for adult female A4760PRT, along with total analyzed whisker length and mean (±SD) stable isotope values.

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Table 6, continued. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for adult female A4760PRT, along with total analyzed whisker length and mean (±SD) stable isotope values.

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</table>
Table 7. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for adult female A4790PRT, along with total analyzed whisker length and mean (±SD) stable isotope values.

<table>
<thead>
<tr>
<th>Segment Number</th>
<th>Length (mm)</th>
<th>$\delta^{13}$C (‰)</th>
<th>$\delta^{15}$N (‰)</th>
</tr>
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<tbody>
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<td>1</td>
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<td>−15.45</td>
<td>16.95</td>
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<td>−15.18</td>
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<td>−15.45</td>
<td>17.40</td>
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<td>1</td>
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<td>−16.07</td>
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<td>1</td>
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<td>−15.48</td>
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<td>19</td>
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<td>−15.81</td>
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<td>−16.70</td>
<td>16.39</td>
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<td>30</td>
<td>−15.80 ± 0.53</td>
<td>16.87 ± 0.50</td>
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Table 8. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for pup SM1128SML, along with total analyzed whisker length and mean (±SD) stable isotope values.

<table>
<thead>
<tr>
<th>Segment Number</th>
<th>Length (mm)</th>
<th>$\delta^{13}$C (‰)</th>
<th>$\delta^{15}$N (‰)</th>
</tr>
</thead>
<tbody>
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<td>1</td>
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<td>−16.42</td>
<td>18.55</td>
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<td>2</td>
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<td>7</td>
<td>1</td>
<td>−16.68</td>
<td>18.02</td>
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<td>1</td>
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<td>2</td>
<td>−16.94</td>
<td>17.18</td>
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<tr>
<td>19</td>
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<td>−16.77 ± 0.19</td>
<td>17.78 ± 0.61</td>
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</tbody>
</table>

Table 9. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for pup SM1233SML, along with total analyzed whisker length and mean (±SD) stable isotope values.

<table>
<thead>
<tr>
<th>Segment Number</th>
<th>Length (mm)</th>
<th>$\delta^{13}$C (‰)</th>
<th>$\delta^{15}$N (‰)</th>
</tr>
</thead>
<tbody>
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<td>1</td>
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<td>2</td>
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<td>−16.58</td>
<td>18.82</td>
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<td>4</td>
<td>2</td>
<td>−16.67</td>
<td>18.57</td>
</tr>
<tr>
<td>5</td>
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<tr>
<td>7</td>
<td>2</td>
<td>−16.43</td>
<td>17.59</td>
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<tr>
<td>8</td>
<td>2</td>
<td>−16.63</td>
<td>16.92</td>
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<td>9</td>
<td>2</td>
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<tr>
<td>12</td>
<td>2</td>
<td>−17.02</td>
<td>17.22</td>
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<tr>
<td>24</td>
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<td>17.98 ± 0.85</td>
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</tbody>
</table>
Table 10. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for pup SM1244SML, along with total analyzed whisker length and mean (±SD) stable isotope values.

<table>
<thead>
<tr>
<th>Segment Number</th>
<th>Length (mm)</th>
<th>$\delta^{13}$C (‰)</th>
<th>$\delta^{15}$N (‰)</th>
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<td>1</td>
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<td>$-16.06$</td>
<td>$18.80$</td>
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<td>$-15.94$</td>
<td>$18.64$</td>
</tr>
<tr>
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<td>2</td>
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<td>$18.57$</td>
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<td>2</td>
<td>$-16.28$</td>
<td>$18.49$</td>
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<td>5</td>
<td>2</td>
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<td>$18.88$</td>
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<tr>
<td>6</td>
<td>2</td>
<td>$-16.67$</td>
<td>$18.53$</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>$-16.83$</td>
<td>$18.40$</td>
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<td>2</td>
<td>$-16.90$</td>
<td>$18.03$</td>
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<td>9</td>
<td>2</td>
<td>$-17.13$</td>
<td>$17.44$</td>
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<tr>
<td>10</td>
<td>2</td>
<td>$-16.93$</td>
<td>$17.23$</td>
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<tr>
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<td>2</td>
<td>$-16.94$</td>
<td>$17.23$</td>
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<td>$17.44$</td>
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<tr>
<td>13</td>
<td>2</td>
<td>$-16.83$</td>
<td>$18.12$</td>
</tr>
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</table>

| 26             | $-16.61 \pm 0.39$ | $18.14 \pm 0.61$ |

Table 11. $\delta^{13}$C and $\delta^{15}$N values per whisker segment for pup SM1276SML, along with total analyzed whisker length and mean (±SD) stable isotope values.

<table>
<thead>
<tr>
<th>Segment Number</th>
<th>Length (mm)</th>
<th>$\delta^{13}$C (‰)</th>
<th>$\delta^{15}$N (‰)</th>
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<td>$18.82$</td>
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<tr>
<td>2</td>
<td>2</td>
<td>$-15.77$</td>
<td>$18.93$</td>
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<td>3</td>
<td>2</td>
<td>$-16.02$</td>
<td>$18.83$</td>
</tr>
<tr>
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<td>2</td>
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<td>$18.87$</td>
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<td>5</td>
<td>2</td>
<td>$-16.46$</td>
<td>$18.89$</td>
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<td>2</td>
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<td>$18.60$</td>
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<td>2</td>
<td>$-16.56$</td>
<td>$18.27$</td>
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<td>8</td>
<td>2</td>
<td>$-16.85$</td>
<td>$17.99$</td>
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<tr>
<td>9</td>
<td>2</td>
<td>$-16.90$</td>
<td>$18.20$</td>
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<td>2</td>
<td>$-17.03$</td>
<td>$17.88$</td>
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<td>2</td>
<td>$-17.14$</td>
<td>$18.01$</td>
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<td>2</td>
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<td>$17.93$</td>
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<td>2</td>
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<td>$17.64$</td>
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<td>2</td>
<td>$-16.93$</td>
<td>$17.37$</td>
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<tr>
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<td>2</td>
<td>$-16.98$</td>
<td>$17.00$</td>
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<tr>
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<td>$17.17$</td>
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<tr>
<td>17</td>
<td>2</td>
<td>$-16.63$</td>
<td>$17.30$</td>
</tr>
</tbody>
</table>

| 34             | $-16.63 \pm 0.44$ | $18.10 \pm 0.65$ |
Table 12. $\delta^{13}C$ and $\delta^{15}N$ values per whisker segment for pup SM1289SML, along with total analyzed whisker length and mean (±SD) stable isotope values.

<table>
<thead>
<tr>
<th>Segment Number</th>
<th>Length (mm)</th>
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<th>$\delta^{15}N$ (%)</th>
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<tbody>
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<td>−16.57</td>
<td>17.20</td>
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<td>−17.08</td>
<td>17.54</td>
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<td>2</td>
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<td>17.95</td>
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<tr>
<td>8</td>
<td>2</td>
<td>−17.04</td>
<td>18.00</td>
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<td>17.84 ± 0.68</td>
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</table>

Table 13. $\delta^{15}N$ Spearman correlation coefficients for pups (SM1-) and adult females (A-).

<table>
<thead>
<tr>
<th></th>
<th>A1292WAF</th>
<th>A1338WAF</th>
<th>A2177PRT</th>
<th>A4760PRT</th>
<th>A4790PRT</th>
</tr>
</thead>
<tbody>
<tr>
<td>SM1128SML</td>
<td>−0.81</td>
<td>−0.76</td>
<td>0.86</td>
<td>−0.50</td>
<td>0.69</td>
</tr>
<tr>
<td>SM1233SML</td>
<td>−0.93</td>
<td>−0.71</td>
<td>0.89</td>
<td>−0.60</td>
<td>0.67</td>
</tr>
<tr>
<td>SM1244SML</td>
<td>−0.76</td>
<td>−0.71</td>
<td>0.55</td>
<td>−0.10</td>
<td>0.45</td>
</tr>
<tr>
<td>SM1276SML</td>
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<td>−0.62</td>
<td>0.54</td>
<td>0.00</td>
<td>0.76</td>
</tr>
<tr>
<td>SM1289SML</td>
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<td>−0.48</td>
<td>0.23</td>
<td>−0.74</td>
<td>−0.24</td>
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</table>
Table 14. $\delta^{15}N$ correlation probability values for pups (SMI-) and adult females (A-).

<table>
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<th>A1292WAF</th>
<th>A1338WAF</th>
<th>A2177PRT</th>
<th>A4760PRT</th>
<th>A4790PRT</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.87</td>
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<td>SM1233SML</td>
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<td>0.79</td>
<td>0.08</td>
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<td>0.99</td>
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<td>1.00</td>
<td>1.00</td>
<td>0.59</td>
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<td>1.00</td>
<td>1.00</td>
<td>0.66</td>
<td>1.00</td>
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</table>

Table 15. $\delta^{13}C$ Spearman correlation coefficients for pups (SMI-) and adult females (A-).

<table>
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<th>A1292WAF</th>
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<th>A2177PRT</th>
<th>A4760PRT</th>
<th>A4790PRT</th>
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</thead>
<tbody>
<tr>
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<td>−0.04</td>
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<td>0.32</td>
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<td>−0.43</td>
<td>0.00</td>
<td>−0.13</td>
</tr>
<tr>
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<td>−0.81</td>
<td>0.95</td>
<td>0.14</td>
<td>0.69</td>
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<tr>
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<td>−0.81</td>
<td>0.95</td>
<td>0.14</td>
<td>0.69</td>
</tr>
<tr>
<td>SM1289SML</td>
<td>−0.45</td>
<td>−0.64</td>
<td>0.95</td>
<td>0.00</td>
<td>0.71</td>
</tr>
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</table>

Table 16. $\delta^{13}C$ correlation probability values for pups (SMI-) and adult females (A-).

<table>
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<th></th>
<th>A1292WAF</th>
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<th>A2177PRT</th>
<th>A4760PRT</th>
<th>A4790PRT</th>
</tr>
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<td>SM1244SML</td>
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<td>0.01</td>
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<td>1.00</td>
<td>0.01</td>
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<td>0.95</td>
</tr>
<tr>
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<td>0.33</td>
<td>0.01</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
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References


Kurle, C.M. University of California, San Diego, 9500 Gilman Drive, La Jolla, California, 92093.


