



Behavioral Ecology (2016), 00(00), 1–15. doi:10.1093/beheco/arw089

Original Article

Trade-offs between energy maximization and parental care in a central place forager, the sea otter

N.M. Thometz,^a M.M. Staedler,^b J.A. Tomoleoni,^c J.L. Bodkin,^d G.B. Bental,^{a,b,c} and M.T. Tinker^c

^aLong Marine Laboratory, Department of Ecology and Evolutionary Biology, University of California at Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, USA, ^bMonterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940, USA, ^cU.S. Geological Survey, Western Ecological Research Center, Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, CA 95060, USA, and ^dU.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA

Received 8 December 2015; revised 20 May 2016; accepted 25 May 2016.

Between 1999 and 2014, 126 archival time–depth recorders (TDRs) were used to examine the foraging behavior of southern sea otters (*Enhydra lutris nereis*) off the coast of California, in both resource-abundant (recently occupied, low sea otter density) and resource-limited (long-occupied, high sea otter density) locations. Following predictions of foraging theory, sea otters generally behaved as energy rate maximizers. Males and females without pups employed similar foraging strategies to optimize rates of energy intake in resource-limited habitats, with some exceptions. Both groups increased overall foraging effort and made deeper, longer and more energetically costly dives as resources became limited, but males were more likely than females without pups to utilize extreme dive profiles. In contrast, females caring for young pups (≤ 10 weeks) prioritized parental care over energy optimization. The relative importance of parental care versus energy optimization for adult females with pups appeared to reflect developmental changes as dependent young matured. Indeed, contrary to females during the initial stages of lactation, females with large pups approaching weaning once again prioritized optimizing energy intake. The increasing prioritization of energy optimization over the course of lactation was possible due to the physiological development of pups and likely driven by the energetic deficit incurred by females early in lactation. Our results suggest that regardless of resource availability, females at the end of lactation approach a species-specific ceiling for percent time foraging and that reproductive females in the central portion of the current southern sea otter range are disproportionately affected by resource limitation.

Key words: diving, *Enhydra lutris*, optimal foraging, reproductive constraints, resource availability, TDR.

INTRODUCTION

Consumer foraging strategies are dependent on a variety of biological and environmental factors that influence and ultimately shape foraging behavior. For instance, differences in sex, age, body size, and level of parental investment result in distinct foraging strategies between demographic groups in a wide array of terrestrial (Main et al. 1996; Ruckstuhl 1998; Shannon et al. 2006; Greenleaf et al. 2007) and marine (Stewart 1997; González-Solís et al. 2000; Phillips et al. 2004; Page et al. 2005) species. The relative abundance and spatial distribution of prey resources within a species' range can also influence intraspecific foraging strategies across heterogeneous landscapes (West 1986; Werner and Sherry 1987; Tollit

et al. 1998). Other extrinsic factors, such as weather, disturbance, and the presence/absence of predators or competitors, can also influence individual foraging strategies (Caraco 1980; Caraco et al. 1980; Stephens 1981; Clark and Mangel 1986), although which of these factors are most important in shaping behavior is species and context specific. Foraging theory predicts that consumers are strongly selected to balance trade-offs between multiple factors in a way that maximizes fitness. All else being equal, for an energy-limited predator this means that individuals should behave in such a way as to maximize rates of energy intake (Charnov 1976; Houston and McNamara 1985; Ydenberg et al. 1994; Ydenberg and Hurd 1998), and empirical support for this prediction has been found for a wide range of taxa (Krebs et al. 1974; Kacelnik et al. 1986; Paulissen 1987; Tamm 1989; Jones 1990; Doniol-Valcroze et al. 2011; Hazen et al. 2015).

Address correspondence to N.M. Thometz. E-mail: nthometz@ucsc.edu.

The relative abundance of important prey species is one of the primary determinants of foraging behavior (Charnov 1976). When per-capita prey abundance is low, as occurs when predators deplete their preferred prey species or feeding habitats, individuals must adjust their foraging behavior to maximize rates of energy intake under suboptimal conditions. Some common behavioral responses to density-dependent resource limitation include increasing search time and overall foraging effort (Andersson 1981; Houston and McNamara 1985; Kirkwood and Arnould 2011), adopting riskier foraging strategies (Caraco 1980, 1981; Stephens 1981), and individual diet specialization (Werner and Sherry 1987; West 1988; Beauchamp et al. 1997; Bolnick et al. 2003; Layman et al. 2015). Although maximizing net energy intake in the face of reduced prey abundance is an important driver of foraging behavior, individuals must also balance other components of fitness such as reproductive success (e.g., finding mates or caring for offspring) and predator avoidance (Mangel and Clark 1986). Indeed, a number of studies examining the behavior of central place foragers have shown that individuals may prioritize energy delivery to a brood, limiting time away from offspring, or avoiding predators, over maximizing individual rates of energy intake (Kacelnik 1984; Huntly et al. 1986; Bowers et al. 1993; Hughes and Ward 1993; Naef-Daenzer 2000; Kryštofková et al. 2006).

Sea otters (*Enhydra lutris*), like other marine mammals, behave as central place foragers moving between 2 critical resources—air and food. Sea otters primarily capture prey at depth within benthic foraging patches, but must return to the surface (the “central place”) to consume acquired prey and replenish oxygen stores before diving back down to resume searching for more prey. This cycle repeats itself many times within an individual foraging bout (Kenyon 1969; Bodkin et al. 2004). Due in part to their exceptionally high energy demands (Costa and Kooyman 1982; Yeates et al. 2007; Thometz et al. 2014) and the rather high site fidelity of individuals (Tarjan and Tinker 2016), sea otters are able to relatively quickly deplete preferred prey species within a given area (Kenyon 1969; Riedman and Estes 1990). This key aspect of sea otter ecology, coupled with their ongoing recovery from near extirpation during the fur trade of the 18th and 19th centuries (Kenyon 1969; Riedman and Estes 1990), has resulted in an ideal experimental framework for examining the effects of prey abundance on foraging strategies. Within their current range in the North Pacific Ocean, sea otters occur in a patchwork of populations of varying densities: Long-occupied sites support high densities of otters foraging in prey-limited habitats, whereas newly occupied sites contain low densities of otters foraging in prey-abundant habitats (Riedman and Estes 1990; Tinker et al. 2008).

Prey resource availability is generally believed to be the most important factor limiting sea otter population growth (Kenyon 1969; Riedman and Estes 1990; Monson et al. 2000; Bodkin et al. 2007; although there are some exceptions: e.g., Estes et al. 1998), and resource limitation has been suggested as one of the reasons for the reduced rate of growth of sea otter populations off the central coast of California (Estes, Hatfield, et al. 2003; Tinker et al. 2008; Johnson et al. 2009). It has been well established that for sea otters, resource-limited habitats are associated with increased foraging effort (Estes et al. 1982; Gelatt et al. 2002; Bodkin et al. 2007; Tinker et al. 2008), depressed rates of energy intake, reduced body condition (Monson et al. 2000; Tinker et al. 2013), and increased individual diet specialization (Tinker et al. 2008, 2012; Newsome et al. 2015). In particular, diet specialization acts to reduce competition between individuals and increase rates of energy intake

for those that specialize (Estes, Riedman, et al. 2003; Tinker et al. 2007). Diet specialization is especially pronounced among females (Elliott Smith et al. 2015), apparently reflecting their high degree of site fidelity and the increased energy demands associated with reproduction (Thometz et al. 2014; Thometz et al. forthcoming).

Adult female sea otters typically give birth once a year and care for dependent young for approximately 6 months (Jameson and Johnson 1993; Riedman et al. 1994). Consequently, females spend nearly their entire adult lives either pregnant or lactating. Lactation is the most energetically taxing life-history stage across mammalian species (Millar 1977; Oftedal et al. 1987), and this is especially true for sea otters (Thometz et al. 2014). Daily energy demands reach twice prepartum levels by 3-month postpartum, and females must manage these exceptional demands until weaning occurs (Thometz et al. forthcoming). In resource-limited areas where female sea otters exhibit reduced body condition and have limited energetic reserves (Chinn et al. 2016), the increased energetic costs associated with lactation (Thometz et al. forthcoming) and the demands of pup care (Payne and Jameson 1984; Riedman et al. 1994; Staedler 2011; Thometz et al. 2014) likely act together to influence female foraging strategies and dive behavior. In particular, the extensive time investment required to care for a small pup may constrain the ability of mothers to behaviorally respond to resource limitation in a manner that would maximize energy intake.

In contrast with females, male sea otters do not provide parental care to their offspring; thus, male reproductive costs are limited to locating, competing for access to, and mating with females (Kenyon 1969; Payne and Jameson 1984; Riedman and Estes 1990). Male and female sea otters also differ in their movement patterns, with most males exhibiting higher degrees of mobility than females (Loughlin 1980; Riedman and Estes 1990; Tarjan and Tinker 2016), and sexual dimorphism contributes to differences in diving capacities between the sexes (Kenyon 1969; Kooyman 1989; Thometz et al. 2015). Differences in diving ability, movement patterns, degree of prey specialization, and parental investment likely contribute to distinct diving and foraging strategies between males and females. Although general differences in diving behavior by sex have been documented in northern sea otters (*Enhydra lutris kenyoni*) (Bodkin et al. 2004, 2012; Esslinger et al. 2014), comparable data have not been published for southern sea otters (*Enhydra lutris nereis*). In addition, we lack a strong understanding of how diving and foraging behavior are influenced by the combined effects of prey availability, sex, and parental investment.

Here, we examine how prey availability and reproductive constraints together influence foraging behavior and habitat use in sea otters. Foraging theory posits that when food is abundant, the most profitable strategy for a central place forager is to utilize prey patches having the shortest travel times and thus the lowest associated metabolic costs (Orians and Pearson 1979; Houston and McNamara 1985); hence, we predict that sea otter dive depths should be relatively shallow at sites where prey is abundant. As prey become depleted, we predict that otters will make more frequent use of deeper patches where travel time to/from the bottom (and thus metabolic costs) are proportionately greater. With longer travel times, the marginal value theorem would predict longer patch residency time (Orians and Pearson 1979; Mori 1998; Thompson and Fedak 2001; Olsson et al. 2008), which for sea otters means longer dives with more time spent at the bottom searching for and acquiring prey. Given the difference in size and physiological capabilities between male and female sea otters (Kenyon 1969; Riedman and Estes 1990; Thometz et al. 2015), we hypothesize that males will

show a greater absolute range of dive depths and durations, as was demonstrated for sea otters in Alaska (Bodkin et al. 2004); however, after accounting for these differences, we predict that both sexes should respond to reduced food availability in similar ways, so as to maximize energy return. Alternatively, reproductive demands of pup care might place additional constraints on the dive behavior of females with pups, as longer and deeper dives could increase the risk of pup loss because females must leave pups unattended at the surface when diving. If pup care is a significant factor constraining the diving and foraging behavior of females, then we would expect females with very small pups to deviate most from the expected responses to food limitation. To test these predictions, we analyzed data from 126 time–depth recorders (TDRs) implanted in wild southern sea otters over a 15-year period and across multiple study sites spanning a wide range of prey availability.

METHODS

Study animals and TDR implantation

Between 1999 and 2014, 291 free-ranging sea otters were captured, tagged, and implanted with intra-abdominal VHF radio transmitters (160g; Advanced Telemetry Systems Inc., Isanti, MN) and TDRs (27 g, Wildlife Computers, Redmond, WA) off the coast of California. Individuals were captured and surgically implanted following standardized procedures (Williams and Siniff 1983; Ames et al. 1986; Monson et al. 2001). Two colored plastic flipper tags (Temple Tags, Temple, TX) were attached in the webbing of each animal's hind flippers for visual identification in the field (Ames et al. 1986). Sea otters were primarily observed from shore, and behavioral data were collected by direct observation utilizing a 50×80 spotting scope (Questar, Inc., New Hope, PA); however, in rare cases, when coastal access was limited, individuals were observed by boat with binoculars. In general, TDRs were retrieved after 1 or more years of deployment by recapturing study animals and removing instruments using standardized procedures, or recovered during routine necropsy after a study animal had died and its carcass was found and retrieved from the study area.

TDRs were deployed in 5 different locations along the California coast (Figure 1): Monterey, Big Sur, San Luis Obispo County, Santa Barbara Channel, and San Nicolas Island (Figure 1). These locations spanned almost the entire extent of the southern sea otter range and included both long-established, high-density populations (Monterey, Big Sur, and San Luis Obispo County) and more recently established, low-density sea otter populations (Santa Barbara Channel and San Nicolas Island). Based on the geographic patterns of population recovery (Lafferty and Tinker 2014), recent population trends (Tinker and Hatfield 2015), and a variety of other biological indices (Tinker et al. 2008, 2013; Newsome et al. 2015), we inferred that sea otters at Monterey, Big Sur, and San Luis Obispo County were at or near carrying capacity and largely prey resource limited, whereas sea otters at Santa Barbara Channel and San Nicolas Island were well below carrying capacity with access to abundant prey resources.

Across all sites, sea otters were known to feed on over 80 different species of benthic invertebrates (Riedman and Estes 1990). When classifying sites by resource availability, we did not assume that sea otters reduced all prey species equally. Nor did we presume that sea otter predation was the only factor influencing the distribution and abundance of prey, because many other factors (e.g., recruitment, weather, and disease) also influence the abundance and distribution of benthic invertebrates. Ultimately, sea otter populations are

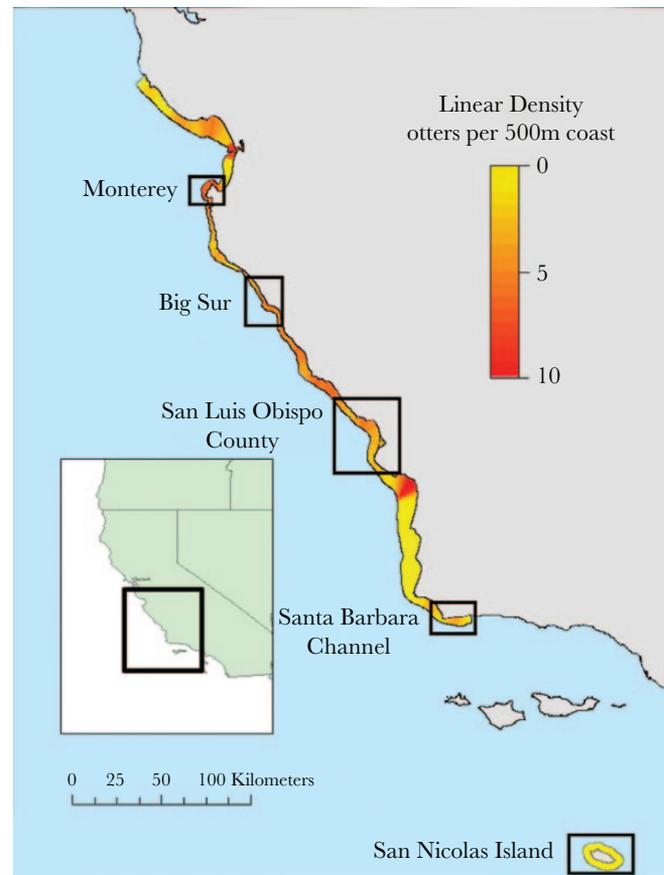


Figure 1

Map of the current southern sea otter (*Enhydra lutris nevis*) subspecies range along California with study areas denoted by black boxes. Variation in sea otter population density (measured as number of sea otters per 500 m of coastline) is represented by color coding, with warmer colors representing higher densities.

limited by density-dependent variation in per-capita availability of preferred prey, which leads to a broadening of their diets to include a wider range of less-preferred prey (Estes, Riedman, et al. 2003; Tinker et al. 2008). The reduction in per-capita availability of preferred prey occurs because sea otters significantly deplete preferred prey species (e.g., sea urchins), and also reflects behavioral responses of certain prey (e.g., abalone moving into crevices) and the fact that there are more otters sharing the same amount of prey. Therefore, the realized foraging success of individuals in recently established, low-density populations has been shown to be substantially higher than that of individuals in high-density, long-established populations (Tinker et al. 2008, 2013). Thus, we compared these 2 groups (high-density, resource-limited vs. low-density, resource-abundant) to examine the impact of resource availability on sea otter foraging behavior.

TDRs recorded diving behavior for an average of 1–2 years. During the period of TDR data logging, many females in the study gave birth to and raised until weaning 1 or more pups. For the purposes of this study, we classified females into one of 4 groups based on the presence and age of a dependent pup: with no pup, with a very small pup (pup ≤ 3 weeks old), with a small pup (pup $> 3 \leq 10$ weeks old), and with a large pup (pup > 10 weeks old). Data sets for each female were divided into the appropriate category based on their reproductive status on each day of TDR data logging, and we treated each of these data sets as an independent record for statistical analyses

(although individual ID was included in statistical models as a random effect, to account for individual differences). Male sea otters have no role in caring for dependent young; thus, male data were not divided or categorized by reproductive stage as were female data. Accordingly, we classified the data from our study animals into one of 5 distinct demographic groups (male, female without pup, female with very small pup, female with small pup, and female with large pup), which we treated as a categorical fixed effect in statistical analyses.

TDR analyses

Raw TDR data were downloaded from the TDR instruments and preprocessed using the software “Instrument Helper” (version 3.0; Wildlife Computers, Redmond, WA) to correct depth readings for drift from the zero mark and to compile the depth readings (at 2-s intervals) into distinct dives and contiguous surface intervals. For each identified dive, a series of 6 descriptive parameters were calculated (all depths in meters and all time durations in seconds): maximum dive depth (DEP), duration of the subsurface interval (DT), duration of time spent at the bottom of the dive (BT, = time spent at 90% of the maximum dive depth and thus not necessarily on the ocean floor), duration of the postdive surface interval (PDI; the number of seconds elapsed until the next dive), descent rate (DRT; vertical swim-speed from surface to bottom), and ascent rate (ART; vertical swim-speed from bottom to surface). These parameters were used to classify dives as feeding or nonfeeding dives (i.e., dives conducted during grooming, traveling, or social behavior), following previously published methods (Bodkin et al. 2004, 2007). Due to the location of the TDR implanted within the body cavity of each sea otter and limitations with instrument accuracy (0.25 m), dives <2 m could not always be reliably distinguished and so were excluded from analyses. Following established methods (Bodkin et al. 2004), binomial logistic regression was used to classify each recorded dive based on a combination of the above-described parameters:

$$\log\left(\frac{P}{1-P}\right) = \beta_1 + \beta_2(DT) + \beta_3(BT / DT) + \beta_4(ART) + \beta_5(DT)(ART) + \beta_6(BT / DT)(DRT) \quad (1)$$

where β_i ($i = 1-6$) is a vector of parameters fit to concurrent observational data using maximum likelihood methods, and all dives with $P > 0.5$ were classified as feeding dives. Equation 1 was initially fit to a subsample of 5000 confirmed dives (dives made by study animals for which an observer was able to visually confirm as either 1 = feeding or 2 = nonfeeding), and then validated by application to a second subsample of 1000 confirmed dives, to ensure a classification accuracy of >99%. Best-fit values for β_i were (-5.115, 0.258, 0.487, -0.210, 0.063, 3.543).

We applied Equation 1 to each TDR record to classify all dives and then subdivided the entire TDR record into contiguous “bouts” of similar activity states (inactive/resting, feeding, and active other) following methods described by Bodkin et al. (2004).

For every 24-h period of each TDR record, we calculated a time-activity budget by summing the cumulative time spent in each of the 3 activity states (inactive/resting, feeding, and active other). Foraging effort, defined as the percent of each day spent feeding, was then summarized for all study animals, and for each demographic group and location. As the main focus of this research was foraging behavior, nonfeeding dives were excluded from further analyses and all dive attributes reported herein refer only to foraging dives. Because individual dives within a feeding bout tended to be autocorrelated with respect to some dive parameters (e.g., depth and duration), we

used averages within feeding bouts as the basic statistical unit in all further analyses, to ensure independence (because feeding bouts are usually separated by several hours of resting behavior). For each distinct feeding bout, we calculated a series of 12 statistics (attributes) with MATLAB 8.0 programming software (Mathworks, Natick, MA): 1) number of dives per bout, 2) foraging bout duration (in minute), 3) mean dive depth (in meter), 4) mean dive duration (in second), 5) mean postdive interval (in second), 6) variance in postdive interval (in second), 7) mean bottom time (in second), 8) mean ratio of bottom time to dive time, 9) maximum dive depth (in meter), 10) maximum dive duration (in second), 11) mean descent rate (minute per second), and 12) mean ascent rate (minute per second).

Statistical analyses

Prior to statistical analyses, all 12 foraging dive attributes were \log_{10} transformed, with the exception of the bottom time to dive time ratio, which was arcsine square-root transformed to normalize distributions. Foraging dive attributes were first analyzed using a 4-factor multivariate analysis of variance (MANOVA), with demographic group (5 levels: male, female without pup, female with very small pup, female with small pup, and female with large pup), resource availability (2 levels: abundant and limited), and age class (2 levels: subadult and adult) as fixed effects, and the interaction between demographic group and resource availability as a fourth factor. Age class and the interaction between demographic group and resource availability were not statistically significant and were dropped from subsequent analyses. We then used a 2-factor MANOVA to test for differences in dive attributes by demographic group and resource availability. For all MANOVA analyses, Pillai’s trace was used to determine significance. MANOVA analyses do not report which specific dive attributes contribute to the significant variation observed between groups. Therefore, we subsequently performed univariate analyses of variance (Anovas) to examine differences in specific foraging dive attributes by demographic group and resource availability. Site and otter ID were included as random effects in all univariate analyses by nesting otter ID within site. When fixed effects were found to be significant, we used Tukey’s Honestly Significant Difference (HSD) post hoc comparisons to examine specific differences in diving attributes by demographic group and Student’s *t*-tests to examine differences by resource availability. Percent time foraging was arcsine square-root transformed to ensure normality, and differences in percent time foraging were analyzed using a 2-factor Anova with demographic group and resource availability as fixed effects and otter ID and site included as random effects. A Tukey’s HSD post hoc comparison was made to examine specific among-group differences in percent time foraging and a student’s *t*-test was used to examine differences by resource availability. We tested for a functional relationship between dive depth and bottom time by fitting linear and nonlinear regressions to data points representing the mean depths and mean bottom times for individual study animals. We compared both a linear model (fit using least squares) and a power model ($f[x] = a \times x^b$, fit using maximum likelihood) and selected the most appropriate function by comparing adjusted r^2 values. We then fit curves separately to each demographic group, to evaluate how the functional relationship between depth and bottom time varied by sex and reproductive status. All MANOVA and Anova analyses were completed using JMP®11.0.0 statistical software program (SAS Institute Inc., Cary, NC). Linear and power functions were fit using MATLAB Statistics Toolbox. All means are reported \pm standard error, and results were considered significant if $P < 0.05$.

RESULTS

Of 291 TDRs deployed, 126 were recovered in which the archival data were able to be retrieved and processed successfully (Table 1; 91 females; 35 males). Of the 91 study females, 15 were younger than 3.5 years old when implanted and were classified as subadults at time of capture (Kenyon 1969; Riedman and Estes 1990; Jameson and Johnson 1993; Tinker et al. 2006). Individual data sets were available for each of the 5 subpopulations along the California coast (Figure 1): Monterey (56 females; 13 males), Big Sur (9 females; 2 males), San Luis Obispo County (20 females; 13 males), Santa Barbara Channel (4 females; 3 males), and San Nicolas Island (2 females; 4 males). The duration of archived data from TDRs was dependent on an individual otter's survival as well as the battery life of each TDR, and ranged from 40 to 1094 days. A total of 857 162 h of recorded data were processed and analyzed for use in this study, which included 202 140 feeding bouts composed of 8943 758 individual foraging dives.

Overall patterns in diving behavior

The mean dive depth determined for male and female sea otters in California was 8.32 ± 0.28 m, with individual mean dive depths ranging from 2.30 to 28.57 m. The maximum dive depth recorded for any individual was 88 m, performed by a 9-year-old male sea otter in San Luis Obispo County. The 15 deepest-diving individuals (70–88 m) in this study were all males from the center of the range (San Luis Obispo County: $n = 7$; Big Sur: $n = 2$; Monterey: $n = 6$). The deepest dive by a female sea otter was 69 m and was made by a female without a pup from Monterey. Furthermore, the 5 deepest-diving females (66–69 m) were all without pups and from Monterey. The mean dive duration for male and female sea otters in California was 61.52 ± 1.20 s, but mean dive durations varied considerably across individuals, ranging from 25.78 to 132.57 s. The maximum dive duration recorded for any individual was 472 s (7.9 min). This prolonged dive was performed by a 10-year-old male sea otter in Monterey. The maximum number of dives performed in a single bout was 297 with a corresponding foraging bout duration of 504.37 min or 8.4 h. This foraging bout was performed by a primiparous 3-year-old female sea otter in Monterey while she had a very small pup, and it is notable that she subsequently lost the pup.

Key factors influencing foraging dive attributes

We found that foraging dive attributes (Table 2) differed significantly by demographic group ($F_{48,884} = 5.00$, $P < 0.0001$) and resource availability ($F_{12,218} = 7.28$, $P < 0.0001$), but not by age class ($F_{12,218} = 1.42$, $P = 0.16$), and the interaction between demographic group and resource availability was also not significant

($F_{48,884} = 1.06$, $P = 0.36$). Subsequent inclusion of subadult female data into the “female without pup” group did not change overall patterns or any results reported here. It should be noted that we lacked comparable sample sizes of subadults across all study locations to robustly test for differences in foraging behavior due to age class across sites. In the reduced model, demographic group ($F_{48,904} = 9.74$, $P < 0.0001$) and resource availability ($F_{12,223} = 7.83$, $P < 0.0001$) remained highly significant.

Univariate tests performed on each dive attribute revealed nuanced differences in the diving behavior of sea otters by demographic group and resource availability (Table 3). Demographic group was highly significant for all dive attributes examined. The number of dives made per bout ($F_{4,168} = 39.50$, $P < 0.0001$) was greatest for females with large pups and females without pups and was smallest for females with very small pups. Females without pups exhibited the shallowest mean foraging depths, whereas females with very small pups had the shortest mean foraging dive durations (Table 3). Maximum depths ($F_{4,183} = 74.62$, $P < 0.0001$) differed greatly by demographic group with males exhibiting the greatest maximum depths, followed by females without pups, then females with large pups, and lastly females with small and very small pups. A similar pattern was observed for maximum dive durations ($F_{4,179} = 76.41$, $P < 0.0001$); however, males and females without pups were not significantly different. Descent and ascent rates were greatest for females with small and very small pups (Table 3).

Resource availability had a significant impact on over half of the dive parameters (Table 3). Foraging bout durations ($F_{1,135} = 7.76$, $P = 0.0061$) and the mean number of dives per bout ($F_{1,135} = 7.92$, $P = 0.006$) were higher in resource-limited areas compared with resource-abundant areas. For both males and females without pups, foraging bout durations increased by an average of 34-min longer in resource-limited areas. For females with very small pups, foraging bout durations were on average 47-min longer in resource-limited areas (Table 2). Variation in postdive intervals ($F_{1,147} = 4.45$, $P = 0.037$) was highest in resource-abundant areas (Table 3). In general, bottom times ($F_{1,130} = 5.39$, $P = 0.022$) were highest in resource-limited areas, although for females without pups and females with large pups mean bottom times were similar in both resource-abundant and resource-limited habitats (Table 2). Lastly, maximum depths ($F_{1,147} = 5.82$, $P = 0.017$) and bottom time to dive time ratios ($F_{1,125} = 6.11$, $P = 0.015$) were generally greater in resource-limited areas than in resource-abundant areas; although, for females with pups, maximum dive depth did not appear to differ by resource availability (Table 2).

Distribution of foraging depths and dive durations

Although mean foraging depths did not differ by resource availability (Table 3), the shape of the frequency distributions of dive

Table 1

Summary information for TDRs recovered and processed from animals examined in this study

Site	Resource availability	TDRs (<i>n</i>)	Age range (year)	Median age (year)	Years of deployments	Duration of TDR recording (days; minimum–maximum)
Monterey	Limited	56 F, 13 M	2.5–12	5.5	2001–2012	47–1106
Big Sur	Limited	9 F, 2 M	2.5–9	8	2008–2011	86–1094
San Luis Obispo County	Limited	20 F, 13 M	1–12	7	2001–2013	77–357
Santa Barbara Channel	Abundant	4 F, 3 M	6–10	8	2012–2014	40–371
San Nicolas Island	Abundant	2 F, 4 M	5–12	10	2003–2005	138–722

Age estimates for study animals were made at time of TDR implantation.

Table 2
Summary data of mean foraging dive attributes for southern sea otters in resource-abundant ($n = 13$) and resource-limited ($n = 113$) habitats as determined via archival TDRs (mean \pm standard error)

Demographic group	Mean dives per bout (#)	Mean bout duration (min)	Mean dive depth (m)	Mean dive duration (s)	Maximum dive depth (m)	Maximum dive duration (s)	Mean positive interval (s)	Variance in positive interval (s)	Descent rate (m/s)	Mean bottom time (s)	Ascent rate (m/s)	Bottom time:dive time
Resource-abundant habitat												
Male ($n = 7$)	28.72 \pm 2.59	83.91 \pm 5.69	8.04 \pm 0.63	54.08 \pm 3.40	48.57 \pm 4.12	276.29 \pm 14.86	108.14 \pm 5.56	104.52 \pm 4.80	0.69 \pm 0.03	29.77 \pm 3.66	-0.67 \pm 0.04	0.47 \pm 0.03
Female, no pup ($n = 6$)	32.60 \pm 3.31	87.11 \pm 7.03	6.16 \pm 0.60	60.30 \pm 4.00	30.00 \pm 4.25	259.00 \pm 16.11	113.74 \pm 8.77	110.06 \pm 8.65	0.64 \pm 0.03	34.46 \pm 4.01	-0.59 \pm 0.04	0.51 \pm 0.05
Female, very small pup ($n = 2$)	9.49 \pm 0.63	34.45 \pm 1.54	10.49 \pm 2.07	46.59 \pm 5.54	21.50 \pm 4.50	135.00 \pm 29.00	149.12 \pm 7.02	135.31 \pm 6.56	0.84 \pm 0.03	24.50 \pm 2.75	-1.04 \pm 0.05	0.47 \pm 0.02
Female, small pup ($n = 3$)	33.01 \pm 16.20	79.08 \pm 24.59	7.47 \pm 2.01	46.48 \pm 4.68	20.33 \pm 3.71	163.33 \pm 33.91	100.47 \pm 27.43	93.88 \pm 22.80	0.76 \pm 0.08	24.68 \pm 2.93	-0.83 \pm 0.12	0.47 \pm 0.01
Female, large pup ($n = 2$)	44.41 \pm 9.10	119.93 \pm 11.26	9.22 \pm 1.45	69.22 \pm 0.63	35.00 \pm 6.00	229.00 \pm 5.00	96.76 \pm 10.51	90.89 \pm 14.78	0.71 \pm 0.07	40.67 \pm 0.11	-0.81 \pm 0.04	0.50 \pm 0.03
Resource-limited habitat												
Male ($n = 28$)	41.06 \pm 3.92	118.25 \pm 9.39	11.36 \pm 0.98	72.38 \pm 3.56	67.52 \pm 2.31	279.79 \pm 10.85	105.79 \pm 3.81	92.45 \pm 3.00	0.69 \pm 0.03	43.04 \pm 2.40	-0.72 \pm 0.03	0.53 \pm 0.01
Female, no pup ($n = 85$)	52.30 \pm 2.24	120.92 \pm 4.36	7.19 \pm 0.38	60.13 \pm 1.83	40.13 \pm 1.49	248.78 \pm 5.66	91.40 \pm 2.36	86.20 \pm 1.95	0.64 \pm 0.02	35.81 \pm 1.35	-0.64 \pm 0.02	0.56 \pm 0.01
Female, very small pup ($n = 47$)	33.05 \pm 5.92	81.68 \pm 9.90	8.35 \pm 0.60	57.17 \pm 2.47	21.87 \pm 1.57	156.43 \pm 6.84	109.16 \pm 6.07	101.52 \pm 4.89	0.77 \pm 0.03	36.15 \pm 1.87	-0.95 \pm 0.04	0.60 \pm 0.01
Female, small pup ($n = 34$)	41.01 \pm 2.82	105.01 \pm 6.50	8.93 \pm 0.90	63.72 \pm 3.88	24.68 \pm 1.97	160.94 \pm 6.21	93.79 \pm 6.20	85.76 \pm 3.94	0.81 \pm 0.03	42.23 \pm 2.85	-0.93 \pm 0.05	0.63 \pm 0.01
Female, large pup ($n = 25$)	58.52 \pm 4.87	134.92 \pm 10.19	8.18 \pm 1.00	63.53 \pm 4.28	33.56 \pm 2.50	188.80 \pm 7.37	73.33 \pm 4.25	68.79 \pm 2.74	0.72 \pm 0.03	41.71 \pm 3.10	-0.77 \pm 0.05	0.63 \pm 0.01

Data from individual females may be included in 1–4 female groups depending on the reproductive status of a female throughout the duration of TDR recording.

Table 3
Results of 2-way Anovas for detailed dive attributes and percent time foraging

Dive attributes:	P value	Student's <i>t</i>		Tukey's HSD				
		Resource availability		Demographic group				
		Abundant	Limited	M	F	F _{VS}	F _{SM}	F _{LG}
Number of dives per bout								
Resource availability	0.0056	B	A					
Demographic group	<0.0001			BC	AB	D	C	A
Bout duration								
Resource availability	0.0061	B	A					
Demographic group	<0.0001			AB	AB	C	B	A
Mean depth								
Resource availability	ns	ns	ns					
Demographic group	<0.0001			A	C	AB	AB	B
Mean duration								
Resource availability	0.0465	B	A					
Demographic group	0.0002			A	BC	C	ABC	AB
Postdive interval								
Resource availability	ns	ns	ns					
Demographic group	<0.0001			AB	B	A	B	C
Variation in postdive interval								
Resource availability	0.0366	A	B					
Demographic group	<0.0001			AB	B	A	B	C
Bottom time								
Resource availability	0.0218	B	A					
Demographic group	0.0001			AB	B	B	A	A
Maximum depth								
Resource availability	0.0171	B	A					
Demographic group	<0.0001			A	B	D	D	C
Maximum duration								
Resource availability	ns	ns	ns					
Demographic group	<0.0001			A	A	C	C	B
Descent rate								
Resource availability	ns	ns	ns					
Demographic group	<0.0001			AB	B	A	A	B
Ascent rate								
Resource availability	ns	ns	ns					
Demographic group	<0.0001			BC	C	A	A	B
Bottom time:dive time								
Resource availability	0.0148	B	A					
Demographic group	<0.0001			B	B	A	A	A
Percent time foraging								
Resource availability	0.0023	B	A					
Demographic group	<0.0001			AB	BC	D	C	A

In all Anova analyses, fixed effects included resource availability and reproductive status, with site and otter ID included random effects. P values are provided for significant results, whereas ns indicates not significant. Student's *t* and Tukey's HSD post hoc comparisons were used to distinguish detailed differences within fixed effect levels. In post hoc comparisons, levels not connected by the same letter(s) are significantly different. In addition, letters indicate relative values with A distinguishing the highest value(s) and D distinguishing the lowest value(s). F = females without pups; F_{LG} = females with large pups; F_{SM} = females with small pups; F_{VS} = females with very small pups; M, males.

depths did, with a greater concentration of dives around an intermediate depth range between 2 and 15 m when resources were abundant (Figure 2a). For example, in resource-abundant habitats, 99% of dives made by male sea otters occurred in waters shallower than 25 m, compared with only 85% in resource-limited habitats (Figure 2). This pattern was less dramatic for females without pups. In resource-abundant habitats, females without pups made 99% of dives to depths shallower than 20 m, compared with 96% in resource-limited habitats. On average, males made deeper dives than females without pups and this difference was most apparent in resource-limited habitats (Figure 2b).

The effect of resource abundance on dive depth distributions of females with pups was more complex (Figure 2). In resource-abundant areas, dive depths of females with young pups differed greatly from females without pups. Females without pups in these areas

made 54% and 25% of their dives to 2–5 and 6–10 m, respectively. In contrast, females with very small pups made only 3% of dives to 2–5 m and greatly increased their proportion of dives within the 6–10 m (52%) and 11–15 m (29%) depth ranges (Figure 2). In both resource-abundant and resource-limited areas, females with small and very small pups made a greater proportion of dives in the 6- to 15-m range and limited very shallow dives (2–5 m) compared with females without pups. In resource-abundant areas, females with large pups made a greater proportion of moderately deep dives (16–25 m) than did all other groups, including males (Figure 2); however, when resources were limited, females with large pups, those without pups, and those with small pups all made a similar proportion of their dives to 16–25 m. Notably, females with large pups made a greater proportion of dives in the 6- to 10-m depth range in resource-limited areas compared with resource-abundant areas.

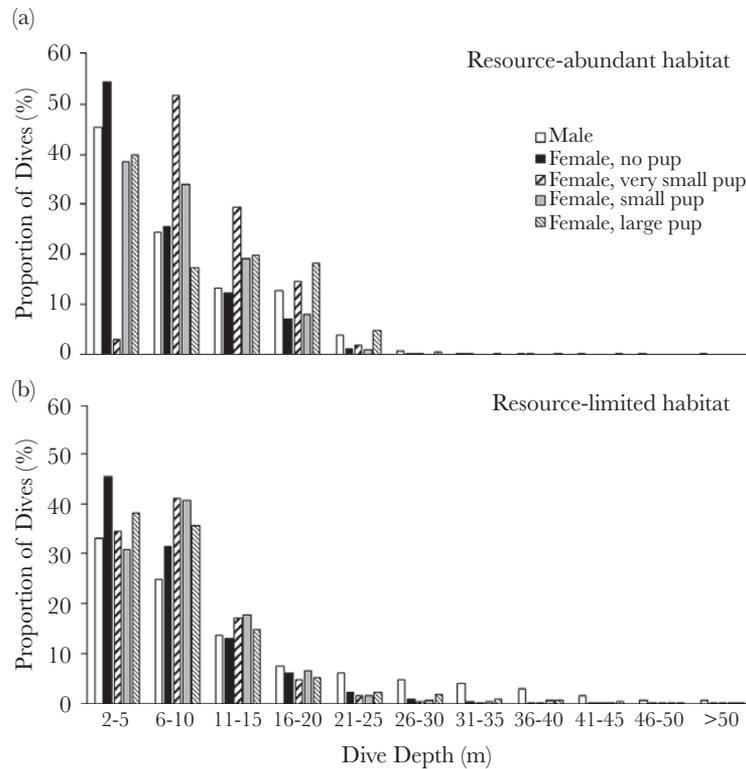


Figure 2

Frequency distributions of foraging dive depths for southern sea otters across a range of demographic groups living in (a) resource-abundant and (b) resource-limited habitats. Vertical bars display the mean proportion of foraging dives that occurred across a range of depths for sea otters in each of 5 demographic groups: males (white), females without pups (black), females with very small pups (thick striped), females with small pups (gray), and females with large pups (thin striped).

Frequency distributions of dive durations (Figure 3) also varied as a function of resource availability, although patterns deviated slightly from those described for dive depths. For males, there was a strong shift toward longer dives when resources were limited: Only 9% of dives made by males in resource-abundant habitats were longer than 2 min, compared with 23% in resource-limited habitats. Similarly, when food was abundant a greater proportion of male dives were very short in duration: 62% of dives in resource-abundant habitats were 21–60 s in duration, compared with only 39% in resource-limited habitats (Figure 3). In contrast, females without pups exhibited comparable proportions of dives greater than 1 min in both resource-abundant (46%) and resource-limited habitats (50%; Figure 3).

We found that variation in the frequency distributions of dive durations of females with pups were dependent on pup age. In resource-abundant habitats, 72% of dives made by females with very small pups lasted 21–60 s in duration, as compared with 51% for females without pups (Figure 3a). In resource-limited habitats, changes in routine dive durations following pup birth were much less pronounced (Figure 3b). In both resource-abundant and resource-limited habitats, the proportion of dives greater than 1 min increased progressively with pup age. In resource-abundant areas, 56% of dives made by females with large pups were longer than 1 min, compared with 30% of dives for females with small pups (Figure 3a). In resource-limited areas, the difference between these 2 groups was less pronounced (only 3%). This was likely due to the fact that females with large pups in resource-limited habitats made fewer dives >1.5 min compared with those in resource-abundant habitats (Figure 3). Regardless of resource availability, females made few extended-duration dives (>1.5 min) when caring

for very small and small pups, and increased their proportion of extended-duration dives when supporting large pups close to weaning (Figure 3).

There was a positive relationship between mean dive depth and mean bottom time (patch residence time) across all study sites and individual sea otters (Figure 4). The relationship was best fit by a power function and explained a high proportion of variation in bottom time for males ($r^2 = 0.80$; Figure 4a) and females without pups ($r^2 = 0.82$; Figure 4b). Bottom time also tended to increase with depth for females with very small pups; however, the relationship explained much less variation ($r^2 = 0.34$; Figure 4d), and many individuals exhibited shorter bottom times for a given dive depth than was predicted by the best-fit curve for females without pups. A stronger relationship between depth and bottom time re-emerged as pups grew older ($r^2 = 0.65$ and $r^2 = 0.78$ for females with small pups and large pups, respectively; Figure 4e and f), converging on the same functional form observed for males and females without pups. Because there were consistently strong correlations between dive depth and total travel time per dive ($r^2 = 0.98$, $P < 0.0001$) and between dive duration and bottom time ($r^2 = 0.98$, $P < 0.0001$), the functional relationships described above could also be expressed as dive depth versus dive duration, or as travel time versus patch residency time.

Foraging effort

The cumulative effect of variation in dive attributes was generally consistent with the variation observed in percent time foraging, which differed by both demographic group ($F_{4,180} = 79.31$, $P < 0.0001$) and resource availability ($F_{1,142} = 9.67$, $P = 0.0023$). Tukey's HSD post hoc comparisons revealed that of all demographic

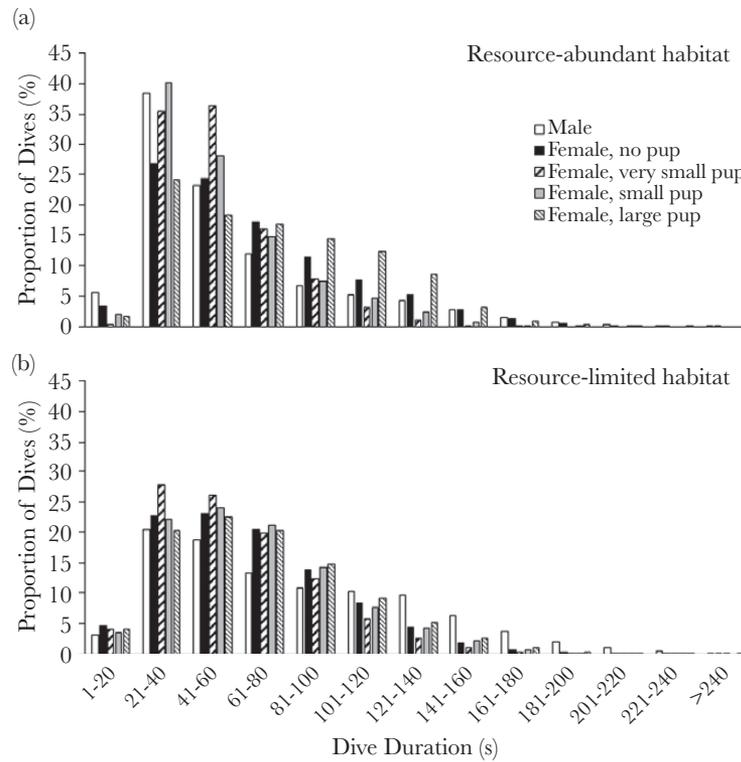


Figure 3

Frequency distributions of foraging dive durations for southern sea otters across a range of demographic groups living in (a) resource-abundant and (b) resource-limited habitats. Vertical bars display the mean proportion of foraging dives that occurred across a range of dive durations for sea otters in each of 5 demographic groups: males (white), females without pups (black), females with very small pups (thick striped), females with small pups (gray), and females with large pups (thin striped).

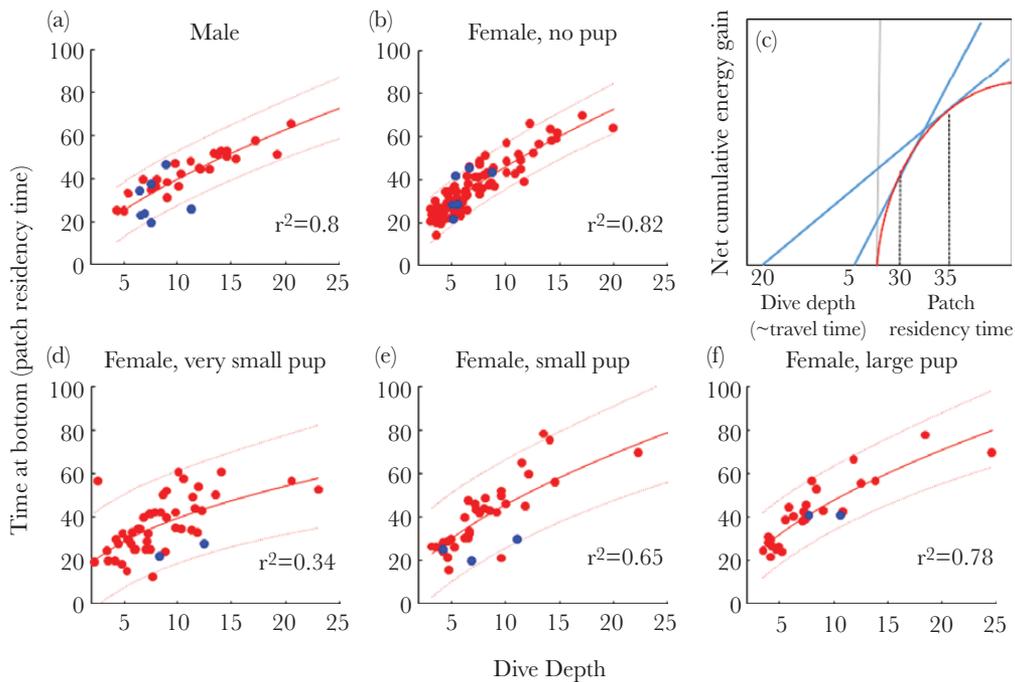


Figure 4

Scatterplots of dive depth versus dive bottom time (patch residency time) for 5 sea otter demographic groups [(a) male; (b) female, no pup; (d) female, very small pup; (e) female, small pup; (f) female, large pup]. Each dot represents the mean bottom time in relation to the mean dive depth for an individual study animal. Data for individuals from resource-abundant (blue dots) and resource-limited (red dots) habitats are shown on the same figure. Best-fit power functions and associated 95% confidence limits for each function, as well as corresponding r^2 values, are displayed for each demographic group. (c) A graphical representation of the expected relationship based on the marginal value theorem as applied to a prey-loading, central place forager.

groups, females with large pups exhibited the greatest foraging effort, followed by males, although these 2 groups were not statistically different from one another (Table 3). Females with very small pups significantly differed from all other groups, exhibiting the lowest percent time foraging in both resource-abundant and resource-limited habitats (Tables 3 and 4). A student's *t*-test revealed that individuals in resource-limited habitats foraged for a significantly greater proportion of each day when compared with individuals in resource-abundant areas (Table 3). The greatest differences were observed for females with very small and small pups, in which percent time foraging was approximately 10% greater in resource-limited habitats compared with resource-abundant habitats (Table 4). Although males and females without pups differed in their overall values for percent time foraging, they exhibited similar increases in percent time foraging when in resource-limited habitats compared with resource-abundant habitats. Females with large pups had the highest foraging effort of all demographic groups, regardless of resource availability, yet showed very little difference in percent time foraging between resource-abundant and resource-limited locations (Table 4).

DISCUSSION

This large-scale study of diving behavior in southern sea otters, which spanned a 15-year period and the entire subspecies range, has resulted in a comprehensive picture of how this apex predator responds to reductions in food availability through changes in habitat utilization and foraging tactics. In general, the behavioral responses we report are consistent with predictions of foraging theory for a predator where energy maximization is the primary determinant of fitness; however, our results also demonstrate striking differences in diving behavior between the sexes and between females with and without pups. In particular, we show that females with young pups do not exhibit predicted patterns of depth usage and dive durations for an energy-maximizing predator, as was found for males and females without pups. The discrepancies between predicted (based on foraging theory) and observed dive behavior for females with pups suggest that foraging tactics are constrained by the requirements of pup care, and females face a trade-off between ensuring offspring survival and optimizing individual energy intake.

Although one of the smallest marine mammals (Reynolds and Rommel 1999), sea otters are known to be capable divers. For example, sea otters in Alaska have been reported to make dives to depths as great as 100 m (Bodkin et al. 2004). The sea otters we report on here exhibited similar diving capabilities to their northern counterparts, with the deepest dive measured at 88 m and the longest dive lasting 7.9 min. In spite of their notable physiological

capacities, most individual otters only used a small portion of available dive depths and foraging strategies. Our findings show that multiple metrics of dive behavior varied across study animals (Table 2), with much of the variation attributable to differences between sexes, between females with and without pups, and to variation in the relative abundance of prey resources (Table 3). The latter factor explained a great deal of variation in dive behavior and foraging effort across sites, although different demographic groups responded to resource limitation in distinct ways.

In the case of males and females without pups, the differences we found between resource-abundant and resource-limited study sites, in terms of dive behavior (dive depth, dive duration, bottom time, PDI) and foraging effort (proportion of time feeding, forage bout length, and number of dives per bout), were generally supportive of predictions for an energy-maximizing single-prey loading central place forager (Andersson 1981; Houston and McNamara 1985; Costa 1991; Mori 1998; Thompson and Fedak 2001). When resources were abundant, both of these groups made most of their foraging dives to relatively shallow prey patches, exhibited short dive durations and bottom times, had relatively short feeding bouts, and spent less than 40% of their time feeding. At sites with depleted prey resources, these same demographic groups spent more time foraging (Table 4), exhibited longer foraging bouts (Table 3), and made more dives to deeper habitats (Figure 3), with males exhibiting greater maximum dive depths and durations than females (Table 2). Feeding bouts with deeper dives were associated with greater dive durations and longer times at bottom. The strong functional relationship between travel time (which was proportional to dive depth) and patch residency time (corresponding to bottom time) is a key prediction of the marginal value theorem (Figure 4a–c) as applied to a central place forager (Charnov 1976; Orians and Pearson 1979; Olsson et al. 2008).

An underlying assumption of the predicted relationship between travel time and patch residency time is that patch residency is characterized by a declining utility function, that is, the longer the time spent within a patch on a given trip (for sea otters, the longer the bottom time on a given dive), the lower the rate of increase in cumulative net energy gain (Figure 4c). For some central place, prey-loading foragers, a declining utility function occurs due to greater costs associated with load size (DeBenedictis et al. 1978; Schmid-Hempel et al. 1985; Kacelnik et al. 1986; Tamm 1989; Cuthill and Kacelnik 1990), whereas in other cases, there may be declining prey capture rates as feeding patches become depleted (Krebs et al. 1974; Charnov 1976; Orians and Pearson 1979; Chapman et al. 1989; Olsson et al. 2008). Both of these mechanisms could conceivably apply to sea otters utilizing benthic prey patches; however, a potentially more important factor contributing to a declining utility function in this species is the energetic cost associated with diving against a high degree of positive buoyancy.

Table 4
Mean percent time foraging for individuals in each demographic group by resource availability

Demographic group	Percent time foraging (%)	
	Resource-abundant habitat	Resource-limited habitat
Male	39.56 ± 1.53	45.63 ± 0.97
Female, no pup	34.86 ± 1.98	41.60 ± 0.72
Female, very small pup (pup ≤ 3 weeks)	16.57 ± 1.59	27.30 ± 1.65
Female, small pup (3 weeks < pup ≤ 10 weeks)	29.41 ± 2.59	39.28 ± 1.13
Female, large pup (pup > 10 weeks)	47.71 ± 1.63	48.20 ± 1.21

Values represent mean percent time foraging over a 24-h period.

Sea otters are unusual among diving marine mammals in that they are positively buoyant over the majority of feeding depths they utilize, a consequence of the insulating air layer contained in their fur, their unusually large lung capacity, and the fact that they dive with inflated lungs (Cashman 2002; Thometz et al. 2015). Thus, feeding dives are relatively costly in this species because individuals must expend a considerable amount of energy fighting positive buoyancy to stay down at depth while searching for and capturing prey (Yeates et al. 2007), contrary to other marine mammals that can utilize neutral or negative buoyancy to reduce foraging costs at depth (Williams et al. 2000). It has been hypothesized that sea otters may adjust the amount of air they take down on a given dive so as to carry an optimal amount of air for an anticipated dive depth and duration (Thometz et al. 2015), similar to what has been reported for some penguin species (Sato et al. 2002, 2006). This means that dive costs per unit time will be lower for shorter dives and increase for longer dives when sea otters need to carry more air in their lungs and thus, increase positive buoyancy. Consequently, even if the rate of prey acquisition at the bottom were constant, the net rate of energy gain for longer dive times will necessarily decrease because of increased metabolic costs. This factor (possibly in addition to other factors such as prey load size; Kacelnik et al. 1986; Tamm 1989) will generally lead to a declining utility curve as sea otters spend longer times at depth. Thus, the tight relationship between dive depth and bottom time seen for males (Figure 4a) and females without pups (Figure 4b) in this study is consistent with the marginal value theorem (Figure 4c) and suggests that these groups are behaving so as to maximize the net rate of energy gain while feeding at different depths. Another adaptive response of sea otters to reduced food abundance is the emergence of diet specialization, such that different individuals utilize different suites of prey (Estes, Riedman, et al. 2003; Tinker et al. 2007, 2012). Interestingly, the functional relationship between dive depth and bottom time appeared to be identical for all animals, irrespective of what prey taxa they specialized on, if they specialized at all; further supporting the hypothesis that the declining utility curve is more a function of physiological costs, rather than any specific feature of prey load size or prey patch depletion.

The foraging behavior of females with pups differed in a number of ways from the behavior of females without pups, although the specifics of these differences varied with pup age and prey resource availability. When prey resources were abundant, females with very small pups showed a relatively narrow range of dive depths, with reduced utilization of the shallowest feeding habitats (relative to females without pups) and more feeding activity within the 6–15 m depth range (Figure 2). This pattern likely reflected increased use of areas with canopy-forming giant kelp, as kelp beds are most common within the 6–15 m range (McLean 1962; Jackson 1987). Staedler (2011) reported that females with very small pups switched to foraging in areas of high kelp cover and that such a switch was often accompanied by changes in diet. Females with young pups may preferentially forage in areas of high kelp cover to minimize the chances of a pup drifting away while a female is underwater or to reduce predation risk. Similarly, they may avoid foraging in very shallow areas because high-energy waves close to shore can lead to the physical harm of a young pup and increase the likelihood of a mother–pup pair becoming separated (Figure 5c). Thus, foraging habitat selection by this demographic group appears to be driven more by ensuring pup survival than optimizing foraging success of the mother. Consistent with this inference is the fact that females with very small pups spent the least amount of time feeding (Table

4), consistently made shorter dives than other demographic groups (Figure 3) and had longer and more variable surface interval times (Table 2) between feeding dives, during which time they spent nursing, grooming, and otherwise attending to a pup.

As pups transitioned from the very small to the small age class, females increased their percent time feeding (though they still spent less time feeding than females without pups; Table 4) and broadened the range of foraging depths they utilized (Figure 2). Increased foraging effort and flexibility of dive depths were likely the result of the increasing physiological capacities of dependent young during this stage of development (Thometz et al. 2015). By 8–10 weeks of age, pups have shed their natal pelage and transitioned to adult coats, which reduces overall positive buoyancy and marks the initiation of extended-duration diving attempts (Payne and Jameson 1984). Over this period females progressively increased foraging effort (Table 4), such that females with large pups exhibited the longest average foraging bout durations, the greatest number of dives per bout, the shortest mean postdive intervals, and the greatest proportion of time spent foraging of all groups in this study (Table 3). Ultimately, females with large pups must work particularly hard during late lactation to keep pace with their own basal metabolic requirements, the increasing demands of their offspring, and to recover from the energetic deficit likely accrued during earlier stages of lactation when foraging activity was reduced.

The progressive changes in dive behavior described above suggest that the unique requirements of nurturing a young pup collectively represent the predominant factor limiting feeding behavior of adult females early in lactation, while maximizing energy return becomes an increasingly important driver as pups near weaning. These trade-offs exist regardless of resource availability, but with some key differences between females in resource-abundant and resource-limited habitats. In resource-limited areas, females with very small pups expanded the range of depths they utilized by making greater use of the shallowest depth ranges (Figure 2), an adjustment in behavior that increases risk to young pups (Figure 5c). This shift suggests a response to reduced prey availability within the preferred depth range (Figure 5b), driven by the fact that females in resource-limited populations enter pup dependency in poorer body condition (Chinn et al. 2016), and thus are less able to sustain reduced foraging success. Females with larger pups also increased the range of depths used when prey was limiting, although these animals tended to make more dives in deeper habitats. Time at the surface between dives decreased for all demographic groups when food was scarce (Table 2), likely reflecting both reduced size and numbers of prey captured on each dive, but also a greater premium on maximizing foraging efficiency. The overall percent time feeding increased in resource-limited habitats for females with very small and small pups (Table 4), but for females with large pups, the difference in foraging effort was minimal (48% in resource-limited areas vs. 47% in resource-abundant areas), suggesting that these animals are already at their limit in terms of daily foraging effort, and thus further increases would be difficult to impossible.

Even as females with pups increased the range of depths utilized in resource-limited areas, their ability to extend dive durations on deeper dives appeared more constrained than for females without pups. In particular, the relationship between dive depth (and thus travel time) and time spent at the bottom on each dive was less evident for females with pups than for males and females without pups (Figure 4). For females with very small pups, the relationship was almost nonexistent (Figure 4d), reflecting a higher frequency of shorter-than-expected bottom times on deeper dives.

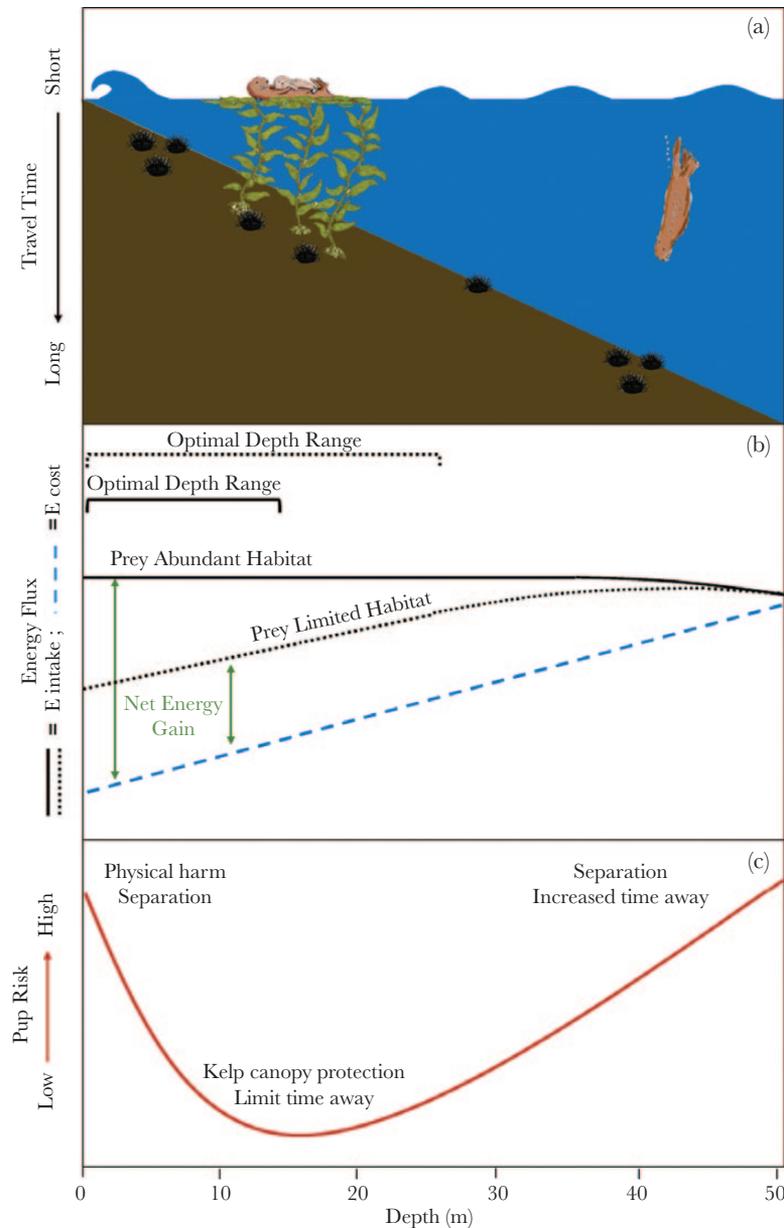


Figure 5

Conceptual model of foraging constraints and trade-offs for sea otters. (a) A visual representation of the inherent correlation between dive depth and travel time, which leads to greater dive costs for deeper dives. In addition, it illustrates the depth range at which canopy-forming kelp is most likely to occur. A mother-pup pair is depicted in the 10- to 20-m depth range within the protection of the kelp canopy, whereas a male sea otter is depicted foraging in the 40- to 45-m depth range. (b) The relationship between rates of energy intake in resource-abundant (solid black line) and resource-limited (black dotted line) habitats, the energetic cost of foraging at different depths (blue dashed line), and the resulting relative net energy gain (green lines and arrows) when foraging at different depths in both resource-abundant and resource-limited habitats. Theoretical optimal foraging depth ranges are depicted for resource-abundant (solid black bracket) and resource-limited (dotted black bracket) habitats. In resource-limited habitats, as a result of disproportionate depletion of prey in shallow depths, there is a broader range of optimal depths offering equivalent net feeding benefits despite the fact that deeper dives are more costly. (c) The relative risk to a young pup (≤ 10 weeks) when its mother forages at various depths. When foraging at very shallow depths, there is a high risk of physical harm to a pup and separation from its mother due to increased sea swell energy and wave action close to shore. Foraging at intermediate depths, where there is a higher likelihood of canopy-forming kelp, limits risk to a pup due to the relatively short amount of time a female is away while foraging and due to the protection provided by canopy-forming kelp from wave action and drift. When foraging at deeper depths outside the protection of canopy-forming kelp, pups are at increased risk of separation due to the fundamental increase in foraging time, and thus time apart, combined with the effects of sea swell and open ocean drift.

Thus, these mothers did not adhere to the predicted pattern for energy-maximizing central place foragers, and instead curtailed dive times in order to limit time away from their pups. As pups grew older, females likely had greater flexibility to make longer dives, and thus the relationship between dive depth and bottom

time became stronger for females with small pups (Figure 4c), and for females with large pups, the functional relationship was almost identical to that seen for females without pups (Figure 4f).

Overall, the behavioral responses of sea otters to reduced prey availability are consistent with previous reports of sea otters as

energy-limited predators that are strongly selected to optimize rates of energy intake (Ostfeld 1982; Estes, Riedman, et al. 2003; Bodkin et al. 2007; Tinker et al. 2008, 2012; Elliott Smith et al. 2015). Our work builds on previous studies by showing that sea otters increase their use of deeper depths as prey resources become depleted and make additional modifications to dive behavior (such as increased patch residence time) to accommodate increased travel times and corresponding energetic costs. At the same time, we show that the demands of pup rearing place additional behavioral constraints on females, particularly those with very young pups. The suite of behavioral responses and trade-offs described here can be envisioned as a simple conceptual model (Figure 5), in which the predicted range of depths used by sea otters in a given habitat (Figure 5a) is based on maximizing energy intake relative to energetic costs (Figure 5b). In addition, females with young pups (≤ 10 weeks) must concurrently balance trade-offs associated with the level of risk posed to pups when foraging at different depths (Figure 5c). As depicted in Figure 5, an increase in the range of depths used by males and females without pups occurs as a result of disproportionate depletion of prey in shallow depths, which broadens the depth range offering equivalent net feeding benefits (despite the fact that deeper dives are always more costly). Ultimately, because females with pups adjust their behavior in order to maximize the likelihood of pup survival, they are considerably restricted in their ability to respond to reductions in prey in a manner that would optimize rates of energy intake.

Trade-offs between energy maximization and parental investment have been documented in a wide range of taxa. For instance, Kacelnik (1984) showed that starlings (*Sturnus vulgaris*), while provisioning their nest, maximize energy gain to their offspring over total yield or foraging efficiency. In painted hunting dogs (*Lycan pictus*), small pack size results in a major trade-off between pack hunting success (i.e., energy intake) and amount of pup-guarding (i.e., likelihood of pup survival) (Courchamp et al. 2001). And for otariids (sea lions and fur seals), which are income breeders that give birth and nurse their young on land, but forage at sea, there is a trade-off between time spent foraging and time away from dependent pups (Boness and Bowen 1996). When prey resources are limited, females must increase their time spent foraging at sea and this results in a higher incidence of pup mortality (Trillmich and Dellinger 1991; Soto et al. 2004). Although balancing trade-offs between energy maximization and parental investment is not unique to sea otters, the energetic and behavioral constraints imposed on females of this species during lactation are particularly substantial (Thometz et al. 2014; Thometz et al. forthcoming), a fact that is strongly supported by the data presented here and reflected in published patterns of mortality and demographic trends for southern sea otters (Tinker et al. 2006, 2008; Chinn et al. 2016).

In conclusion, this study revealed that sea otters behave as energy-maximizing foragers and conform to predictions based on single-prey loading central place foragers. Males and females without pups generally responded to reductions in prey in similar ways. We found that females with very small and small pups prioritized pup care over energy maximization, but did so less efficiently when food was limited. Indeed, females in resource-limited areas behaved in ways that increased risk to young pups by foraging over a larger range of depths, a behavioral response likely necessitated by prey depletion at preferred depths and differences in female body condition at parturition between resource-abundant and resource-limited habitats. A progressive increase in pup diving capacities throughout ontogeny allowed females with large pups to once again

prioritize energy rate maximization during the later stages of lactation. Females with large pups, regardless of resource availability, devoted a very high proportion of their activity budget to foraging. The limited ability of females with large pups to increase foraging effort suggests that they may be pushing their physiological limits in terms of foraging effort. Thus, our results provide further evidence that this demographic group is most sensitive to resource limitation.

FUNDING

This work was supported by the U.S. Geological Survey, Western Ecological Research Center and Alaska Science Center; Monterey Bay Aquarium; California Department of Fish and Wildlife; California Coastal Conservancy; Bureau of Ocean Energy Management; and the National Science Foundation (Award 1210591).

The authors would like to thank dozens of collaborating researchers and volunteers who contributed to fieldwork activities, including sea otter captures and instrumentation, collection of observational and radio telemetry data, and TDR recovery. We thank 2 anonymous reviewers for providing thoughtful and constructive reviews. We are grateful to J. Ames, B. Ballachey, F. Batac, E. Dodd, S. Espinosa, G. Esslinger, J. Fujii, M. Harris, B. Hatfield, L. Henkel, D. Jessup, A. Johnson, A. Kage, M. Kenner, K. Kloecker, N. LaRoche, M. Miller, D. Monson, M. Murray, T. Nicholson, Z. Randell, J. Stewart, B. Weitzman, L. Yeates, C. Young, M. Young, and a substantial number of volunteers from the Monterey Bay Aquarium, U.S. Geological Survey, and UC Santa Cruz who participated throughout various stages of this project. We thank P. Raimondi, J. Estes, and T. Williams who provided helpful comments on earlier versions of this manuscript. Wild animal work was conducted under US Fish and Wildlife permits PRT-766818 to J.L.B. and MA672624 to M.T.T. All animal care use protocols were evaluated and approved by the Institutional Animal Care and Use Committee at the University of California Santa Cruz. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US government.

Handling editor: David Stephens

REFERENCES

- Ames J, Hardy RA, Wendell FE. 1986. A simulated translocation of sea otters, *Enhydra lutris*, with a review of capture, transport and holding techniques. Mar Resour Tech Rep. 52:1–17.
- Andersson M. 1981. Central place foraging in the whinchat, *Saxicola rubetra*. Ecology. 62:538–544.
- Beauchamp G, Giraldeau L-A, Ennis N. 1997. Experimental evidence for the maintenance of foraging specializations by frequency-dependent choice in flocks of spice finches. Ethol Ecol Evol. 9:105–117.
- Bodkin JL, Ballachey BE, Coletti HA, Esslinger GG, Kloecker KA, Rice SD, Reed JA, Monson DH. 2012. Long-term effects of the “Exxon Valdez” oil spill: sea otter foraging in the intertidal as a pathway of exposure to lingering oil. Mar Ecol Prog Ser. 447:273–287.
- Bodkin JL, Esslinger GG, Monson DH. 2004. Foraging depths of sea otters and implications to coastal marine communities. Mar Mamm Sci. 20:305–321.
- Bodkin JL, Monson DH, Esslinger GG. 2007. Activity budgets derived from time–depth recorders in a diving mammal. J Wildl Manag. 71:2034–2044.
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulseley CD, Forister ML. 2003. The ecology of individuals: incidence and implications of individual specialization. Am Nat. 161:1–28.
- Boness DJ, Bowen WD. 1996. The evolution of in maternal care pinnipeds. Bioscience. 46:645–654.
- Bowers MA, Jefferson JL, Kuebler MG. 1993. Variation in giving-up densities of foraging chipmunks (*Tamias striatus*) and squirrels (*Sciurus carolinensis*). Oikos. 66:229–236.
- Caraco T. 1980. On foraging time allocation in a stochastic environment. Ecology. 61:119–128.

- Caraco T. 1981. Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). *Behav Ecol Sociobiol.* 8:213–217.
- Caraco T, Martindale S, Whittam TS. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Anim Behav.* 28:820–830.
- Cashman ME. 2002. Diving in the southern sea otter, *Enhydra lutris nereis*: morphometrics, buoyancy, and locomotion [Masters thesis]. [Santa Cruz (CA)]: University of California Santa Cruz.
- Chapman CA, Chapman IJ, McLaughlin RL. 1989. Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia.* 79:506–511.
- Charnov EL. 1976. Optimal foraging, the marginal value theorem. *Theor Popul Biol.* 9:129–136.
- Chinn SM, Miller MA, Tinker MT, Staedler MM, Batac FI, Dodd E, Henkel LA. 2016. The high cost of motherhood: end-lactation syndrome in southern sea otters (*Enhydra lutris nereis*) on the Central California Coast, USA. *J Wildl Dis.* 52:307–318.
- Clark CW, Mangel M. 1986. The evolutionary advantages of group foraging. *Theor Popul Biol.* 30:45–75.
- Costa DP. 1991. Reproductive and foraging energetics of high latitude penguins, albatrosses, and pinnipeds: implications for life history patterns. *Am Zool.* 31:111–130.
- Costa DP, Kooyman GL. 1982. Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Can J Zool.* 60:2761–2767.
- Courchamp F, Rasmussen GSA, Macdonald DW. 2001. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behav Ecol.* 13:20–27.
- Cuthill I, Kacelnik A. 1990. Central place foraging: a reappraisal of the “loading effect.” *Anim Behav.* 40:1087–1101.
- DeBenedictis PA, Gill FB, Hainsworth FR, Pyke GH, Wolf LL. 1978. Optimal meal size in hummingbirds. *Am Nat.* 112:301–316.
- Doniol-Valcroze T, Lesage V, Giard J, Michaud R. 2011. Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behav Ecol.* 22:880–888.
- Elliott Smith EA, Newsome SD, Estes JA, Tinker MT. 2015. The cost of reproduction: differential resource specialization in female and male California sea otters. *Oecologia.* 178:17–29.
- Esslinger GG, Bodkin JL, Breton AR, Burns JM, Monson DH. 2014. Temporal patterns in the foraging behavior of sea otters in Alaska. *J Wildl Manag.* 78:689–700.
- Estes JA, Hatfield BB, Ralls K, Ames J. 2003. Causes of mortality in California sea otters during periods of population growth and decline. *Mar Mamm Sci.* 19:198–216.
- Estes JA, Jameson RJ, Rhode EB. 1982. Activity and prey election in the sea otter: influence of population status on community structure. *Am Nat.* 120:242–258.
- Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. *J Anim Ecol.* 72:144–155.
- Estes JA, Tinker MT, Williams TM, Doak DF. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science.* 282:473–476.
- Gelatt TS, Siniff DB, Estes JA. 2002. Activity patterns and time budgets of the declining sea otter population at Amchitka Island, Alaska. *J Wildl Manag.* 66:29–39.
- González-Solis J, Croxall JP, Wood AG. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos.* 90:390–398.
- Greenleaf SS, Williams NM, Winfree R, Kremen C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia.* 153:589–596.
- Hazen EL, Friedlaender AS, Goldbogen JA. 2015. Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Sci Adv.* 1:e1500469.
- Houston AI, McNamara JM. 1985. A general theory of central place foraging for single-prey loaders. *Theor Popul Biol.* 28:233–262.
- Hughes JJ, Beard D. 1993. Predation risk and distance to cover affect foraging behaviour in Namib Desert gerbils. *Anim Behav.* 46:1243–1245.
- Huntly NJ, Smith AT, Ivins BL. 1986. Foraging behavior of the pika (*Ochotona princeps*), with comparisons of grazing versus haying. *J Mamm.* 67:139–148.
- Jackson GA. 1987. Modelling the growth and harvest yield of the giant kelp *Macrocystis pyrifera*. *Mar Biol.* 95:611–624.
- Jameson J, Johnson AM. 1993. Reproductive characteristics of female sea otters. *Mar Mamm Sci.* 9:156–167.
- Johnson CK, Tinker MT, Estes JA, Conrad PA, Staedler M, Miller MA, Jessup DA, Mazet JA. 2009. Prey choice and habitat use drive sea otter pathogen exposure in a resource-limited coastal system. *Proc Natl Acad Sci USA.* 106:2242–2247.
- Jones G. 1990. Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? *Anim Ecol.* 59:587–602.
- Kacelnik A. 1984. Central place foraging in starling (*Sturnus vulgaris*). I. Patch residence time. *J Anim Ecol.* 53:283–299.
- Kacelnik A, Houston AI, Schmid-Hempel P. 1986. Central-place foraging in honey bees: the effect of travel time and nectar flow on crop filling. *Behav Ecol Sociobiol.* 19:19–24.
- Kenyon KW. 1969. The sea otter *Enhydra lutris* in the Eastern Pacific Ocean. *North Am Fauna.* 68:1–352.
- Kirkwood R, Arnould JPY. 2011. Foraging trip strategies and habitat use during late pup rearing by lactating Australian fur seals. *Aust J Zool.* 59:216–226.
- Kooyman GL. 1989. *Diverse divers*. New York: Springer-Verlag.
- Krebs JR, Ryan JC, Charnov EL. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Anim Behav.* 22:953–964.
- Kryštofková M, Exnerová A, Porkert J. 2006. Parental foraging strategies and feeding of nestlings in common redstart *Phoenicurus phoenicurus*. *Ornis Fenn.* 83:49–58.
- Lafferty KD, Tinker MT. 2014. Sea otters are recolonizing southern California in fits and starts. *Ecosphere.* 5:1–11.
- Layman CA, Newsome SD, Gancos Crawford T. 2015. Individual-level niche specialization within populations: emerging areas of study. *Oecologia.* 178:1–4.
- Loughlin TR. 1980. Home range and territoriality of sea otters near Monterey, California. *J Wildl Manag.* 44:576–582.
- Main MB, Weckerly FW, Bleich VC. 1996. Sexual segregation in ungulates: new directions for research. *J Mamm.* 77:449–461.
- Mangel M, Clark CW. 1986. Towards a unified foraging theory. *Ecology.* 67:1127–1138.
- McLean J. 1962. Sublittoral ecology of kelp beds of the open coast area near Carmel, California. *Biol Bull.* 122:95–114.
- Millar JS. 1977. Adaptive features of mammalian reproduction. *Evolution (NY).* 31:370–386.
- Monson DH, Estes JA, Bodkin JL, Siniff DB. 2000. Life history plasticity and population regulation in sea otters. *Oikos.* 90:457–468.
- Monson DH, McCormick C, Ballachey BE. 2001. Chemical anesthesia of northern sea otters (*Enhydra lutris*): results of past field studies. *J Zoo Wildl Med.* 32:181–189.
- Mori Y. 1998. Optimal choice of foraging depth in divers. *J Zool Lond.* 245:279–283.
- Naef-Daenzer B. 2000. Patch time allocation and patch sampling by foraging great and blue tits. *Anim Behav.* 59:989–999.
- Newsome SD, Tinker MT, Gill VA, Hoyt ZN, Doroff A, Nichol L, Bodkin JL. 2015. The interaction of intraspecific competition and habitat on individual diet specialization: a near range-wide examination of sea otters. *Oecologia.* 178:45–59.
- Oftedal OT, Boness DJ, Tedman RA. 1987. The behavior, physiology, and anatomy of lactation in the pinnipedia. In: Genoways HH, editor. *Current mammalogy*. Vol. 1. New York: Plenum Publishing Corporation. p. 175–245.
- Olsson O, Brown JS, Helf KL. 2008. A guide to central place effects in foraging. *Theor Popul Biol.* 74:22–33.
- Orians GH, Pearson NE. 1979. On the theory of central place foraging. In: Horn DJ, Mitchell RD, Straits GR, editors. *Analysis of ecological systems*. Athens (OH): Ohio University Press. p. 154–177.
- Ostfeld RS. 1982. Foraging strategies and prey switching in the California sea otter. *Oecologia.* 53:170–178.
- Page B, McKenzie J, Goldsworthy S. 2005. Inter-sexual differences in New Zealand fur seal diving behaviour. *Mar Ecol Prog Ser.* 304:249–264.
- Paulissen MA. 1987. Optimal foraging and intraspecific diet differences in the lizard *Cnemidophorus sexlineatus*. *Oecologia.* 71:439–446.
- Payne SF, Jameson RJ. 1984. Early behavioral development of the sea otter, *Enhydra lutris*. *J Mamm.* 65:527–531.
- Phillips RA, Silk JRD, Phalan B, Catry P, Croxall JP. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc Biol Sci.* 271:1283–1291.
- Reynolds JE, Rommel SA, editors. 1999. *The biology of marine mammals*. Washington (DC): Smithsonian Institution Press.
- Riedman ML, Estes JA. 1990. The sea otter (*Enhydra lutris*): behavior, ecology, and natural history. *Biological Report 90 (14)*. Washington (DC): U.S. Fish and Wildlife Service. p. 126.
- Riedman ML, Estes JA, Staedler MM, Giles AA, David R. 1994. Breeding patterns and reproductive success of California sea otters. *J Wildl Manag.* 58:391–399.

- Ruckstuhl KE. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Anim Behav*. 56:99–106.
- Sato K, Naito Y, Kato A, Niizuma Y, Watanuki Y, Charrassin JB, Bost CA, Handrich Y, Le Maho Y. 2002. Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? *J Exp Biol*. 205:1189–1197.
- Sato K, Watanuki Y, Naito Y. 2006. The minimum air volume kept in diving Adelle penguins: evidence for regulation of air volume in respiratory system. *Coast Mar Sci*. 30:439–442.
- Schmid-Hempel P, Kacelnik A, Houston AI. 1985. Honeybees maximize efficiency by not filling their crop. *Behav Ecol Sociobiol*. 17:61–66.
- Shannon G, Page BR, Duffy KJ, Slotow R. 2006. The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia*. 150:344–354.
- Soto KH, Trites AW, Arias-Schreiber M. 2004. The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *J Zool Lond*. 264:419–428.
- Staedler MM. 2011. Maternal care and provisioning in the southern sea otter (*Enhydra lutris nereis*): reproductive consequences of diet specialization in an apex predator [Masters thesis]. [Santa Cruz (CA)]: University of California Santa Cruz.
- Stephens DW. 1981. The logic of risk-sensitive foraging preferences. *Anim Behav*. 29:628–629.
- Stewart BS. 1997. Ontogeny of differential migration and sexual segregation in northern elephant seals. *J Mamm*. 78:1101–1116.
- Tamm S. 1989. Importance of energy costs in central place foraging by hummingbirds. *Ecology*. 70:195–205.
- Tarjan LM, Tinker MT. 2016. Permissible home range estimation (PHRE) in complex habitats: a new general algorithm and an evaluation for sea otters (*Enhydra lutris*). *PLoS One*. 11:e0150547.
- Thometz NM, Kendall T, Richter B, Williams TM. Forthcoming. The high cost of reproduction in sea otters necessitates unique physiological adaptation. *J Exp Biol*.
- Thometz NM, Murray MJ, Williams TM. 2015. Ontogeny of oxygen storage capacity and diving ability in the southern sea otter (*Enhydra lutris nereis*): costs and benefits of large lungs. *Physiol Biochem Zool*. 88:311–327.
- Thometz NM, Tinker MT, Staedler MM, Mayer KA, Williams TM. 2014. Energetic demands of immature sea otters from birth to weaning: implications for maternal costs, reproductive behavior and population-level trends. *J Exp Biol*. 217:2053–2061.
- Thompson D, Fedak MA. 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim Behav*. 61:287–296.
- Tinker MT, Bentall G, Estes JA. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proc Natl Acad Sci USA*. 105:560–565.
- Tinker MT, Costa DP, Estes JA, Wieringa N. 2007. Individual dietary specialization and dive behaviour in the California sea otter: Using archival time–depth data to detect alternative foraging strategies. *Deep Sea Res Part II Top Stud Oceanogr*. 54:330–342.
- Tinker MT, Doak DF, Estes JA. 2008. Using demography and movement behavior to predict range expansion of the southern sea otter. *Ecol Appl*. 18:1781–1794.
- Tinker MT, Doak DF, Estes JA, Hatfield BB, Staedler MM, Bodkin JL. 2006. Incorporating diverse data and realistic complexity into demographic estimation procedures for sea otters. *Ecol Appl*. 16:2293–2312.
- Tinker MT, Guimarães PR, Novak M, Marquitti FMD, Bodkin JL, Staedler M, Bentall G, Estes JA. 2012. Structure and mechanism of diet specialization: testing models of individual variation in resource use with sea otters. *Ecol Lett*. 15:475–483.
- Tinker MT, Hatfield BB. 2015. Southwest U.S. Southern sea otter annual range-wide census results: U.S. Geological Survey data release. Available from: <http://dx.doi.org/10.5066/F7F47M5C> (Accessed 31 May 2016).
- Tinker MT, Tomoleoni JA, Weitzman BP, Staedler M, Jessup D, Murray M, Miller M, Burgess T, Bowen E, Miles K, et al. 2013. Sea otter population biology at Big Sur and Monterey, California: investigating the consequences of resource abundance and anthropogenic stressors for sea otter recovery. DRAFT Final Report to California Coastal Conservancy and U.S. Fish and Wildlife Service.
- Tollit DJ, Black AD, Thompson PM, Mackay A, Corpe HM, Wilson B, Van Parijs SM, Grellier K, Parlange S, Parijs SM. 1998. Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *J Zool*. 244:209–222.
- Trillmich F, Dellinger T. 1991. The effects of El Niño on Galapagos pinnipeds. In: Trillmich F, Ono KA, editors. Pinnipeds and El Niño. Responses to environmental stress. Heidelberg (Germany): Springer Verlag, p. 66–74.
- Werner TK, Sherry TW. 1987. Behavioral feeding specialization in *Pinaroloxias inornata*, the “Darwin’s Finch” of Cocos Island, Costa Rica. *Proc Natl Acad Sci USA*. 84:5506–5510.
- West L. 1986. Interindividual Variation in prey selection by the snail *Nucella (= Thais) emarginata*. *Ecology*. 67:798–809.
- West L. 1988. Prey selection by the tropical snail *Thais melones*: a study of interindividual variation. *Ecology*. 69:1839–1854.
- Williams TD, Siniff DB. 1983. Surgical implantation of radiotelemetry devices in the sea otter. *J Am Vet Med Assoc*. 183:1290–1291.
- Williams TM, Davis RW, Fuiman LA, Francis J, Le Boeuf BJ, Horning M, Calambokidis J, Croll DA. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. *Science*. 288:133–136.
- Ydenberg R, Hurd P. 1998. Simple models of feeding with time and energy constraints. *Behav Ecol*. 9:49–53.
- Ydenberg RC, Welham CVJ, Schmid-Hempel R, Schmid-Hempel P, Beauchamp G. 1994. Time and energy constraints and the relationships between currencies in foraging theory. *Behav Ecol*. 5:28–34.
- Yeates LC, Williams TM, Fink TL. 2007. Diving and foraging energetics of the smallest marine mammal, the sea otter (*Enhydra lutris*). *J Exp Biol*. 210:1960–1970.