



Research Article

# Temporal Patterns in the Foraging Behavior of Sea Otters in Alaska

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**ABSTRACT** Activity time budgets in apex predators have been proposed as indicators of population status relative to resource limitation or carrying capacity. We used archival time-depth recorders implanted in 15 adult female and 4 male sea otters (*Enhydra lutris*) from the northernmost population of the species, Prince William Sound, Alaska, USA, to examine temporal patterns in their foraging behavior. Sea otters that we sampled spent less time foraging during summer (females 8.8 hr/day, males 7.9 hr/day) than other seasons (females 10.1–10.5 hr/day, males 9.2–9.5 hr/day). Both sexes showed strong preferences for diurnal foraging and adjusted their foraging effort in response to the amount of available daylight. One exception to this diurnal foraging mode occurred after females gave birth. For approximately 3 weeks post-partum, females switched to nocturnal foraging, possibly in an effort to reduce the risk of predation by eagles on newborn pups. We used multilevel mixed regression models to assess the contribution of several biological and environmental covariates to variation in the daily foraging effort of parous females. In the random effects only model, 87% of the total variation in foraging effort was within-otter variation. The relatively small among-otter variance component (13%) indicates substantial consistency in the foraging effort of sea otters in this northern population. In the top 3 models, 17% of the within-otter variation was explained by reproductive stage, day length, wind speed, air temperature and a wind speed  $\times$  air temperature interaction. This study demonstrates the potential importance of environmental and reproductive effects when using activity budgets to assess population status relative to carrying capacity. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** activity budget, Alaska, diving, *Enhydra lutris*, foraging behavior, multilevel model, population status, predator, sea otter, time-depth recorder.

Foraging effort is a density-dependent behavioral response that has been used to assess predator population status relative to carrying capacity—as predator density increases, prey availability declines and predators must increase time spent foraging to meet energy requirements (Eberhardt 1977, Fowler and Siniff 1992). Consistent with this hypothesis, many studies have demonstrated that foraging effort (time spent foraging), a major component of activity budgets, varies inversely with prey availability across a broad spectrum of top predators (Garshelis et al. 1986, Mori and Boyd 2004, Green et al. 2005, Harding et al. 2007, Gesquiere et al. 2008). However, it also has been demonstrated that predators adjust their activity budgets in response to changes in reproductive status, environmental conditions, and predation risk (Garshelis et al. 1986, Beck et al. 2003, Ronconi and Burger 2008). Because these and other density-independent factors likely affect predators on a regular basis and vary at multiple

temporal scales, understanding how much variation in foraging effort is due to physiological and environmental factors is necessary before activity budgets can be interpreted reliably and used to inform population status assessments.

The sea otter (*Enhydra lutris*) is well-suited for the study of how activity patterns are linked to the population status of a top predator because 1) they live typically near shore in an open marine environment, where they can be directly observed consuming prey and conducting other behaviors on the water surface, and 2) it has been shown that their populations are typically limited by food abundance over most of their range (Estes et al. 1982, but see Estes et al. 1998). Several observational studies have demonstrated that sea otter activity budgets vary in response to prey availability (Estes et al. 1986, Garshelis et al. 1986, Gelatt et al. 2002). Sea otters also have been shown to modify their activity patterns based on weather conditions, day length, season, and reproductive status (Garshelis 1983, Gelatt et al. 2002). Nonetheless, the extent to which these factors modify sea otter activity patterns remains unclear. Accounting for variability caused by environmental factors, such as water temperature and season, and individual factors, such as

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sex and reproductive status, should improve the reliability of activity budget comparisons across populations.

Three attributes make sea otters particularly ideal for examining how environmental variation affects activity. First, their high metabolic rate and lack of blubber as a long-term energy reserve suggest their behavior reflects short-term energy demands (Gelatt et al. 2002). Second, their dependence on benthic prey ensures that their diving behavior directly relates to foraging effort (Bodkin et al. 2007). Third, they are non-migratory with relatively small home ranges (Garshelis and Garshelis 1984) within which they must adapt their behavior in response to seasonal environmental changes. Given that sea otters living at northern latitudes experience a greater degree of seasonal variation in temperature and daylight than otters at southern latitudes, their activity budgets are more likely to vary seasonally.

Activity studies that include the effects of environmental conditions on sea otters at lower latitudes are lacking, but anecdotal observations suggest that wind waves disrupt resting and possibly cause an increase in foraging activity (Estes et al. 1986). For sea otter populations in Alaska, winter is generally perceived as the most energetically demanding season based on evidence of increased foraging effort (Garshelis et al. 1986), elevated mortality (Kenyon 1969), and greater thermoregulatory costs associated with colder ambient temperatures (Esslinger 2011). However, little is known about the relative influence of reproduction and environmental conditions on activities of Alaska sea otters during winter because reduced daylight and stormy weather make collection of activity budget data using traditional observation and radiotelemetry methods particularly challenging.

Time-depth recorders (TDRs) are electronic instruments capable of logging sea otter diving activity and body temperature ( $T_b$ ) data continuously for extended periods, regardless of environmental conditions or distance from shore. When these data are paired with observed dives from a focal animal, dive function can be assigned to all unobserved dives in the TDR record and a continuous activity budget can be constructed (Bodkin et al. 2004, 2007). Using surgically implanted TDRs, Bodkin et al. (2004, 2007) found biologically significant differences in the diving behavior and activity budgets of sea otters in southeast Alaska and attributed some of the variation to individuals, sexes, and study areas. However, Bodkin et al. (2007) were unable to determine how much variation was due to changes in environmental conditions and reproductive status because of the relatively short TDR deployment period (39–46 days). Assuming year-round TDR-derived activity budget data are available, influential physiological and environmental factors should be identifiable if appropriately modeled.

Our objective was to describe temporal patterns in sea otter foraging behavior and assess the effects of environmental conditions and reproductive status on activity budgets. For this paper, we analyzed year-round TDR data from free-ranging sea otters in Alaska to determine 1) how foraging effort varies across time, 2) how much daily variation in

foraging effort is within versus among individuals, and 3) whether environmental covariates explain a significant portion of variation in the daily foraging effort of parous females. First, we used descriptive statistics to summarize the behavior of our study animals to facilitate comparisons to previously published studies. Next, we used multilevel mixed regression models (Singer and Willet 2003, Breton et al. 2008) to quantify how foraging effort varies with biological and environmental factors. Based on previous studies of sea otter activity in Alaska (Garshelis et al. 1986, Gelatt et al. 2002), we suspected that foraging effort would be greater during winter when energetic demands of the environment are greater and when females are rearing large (older) pups.

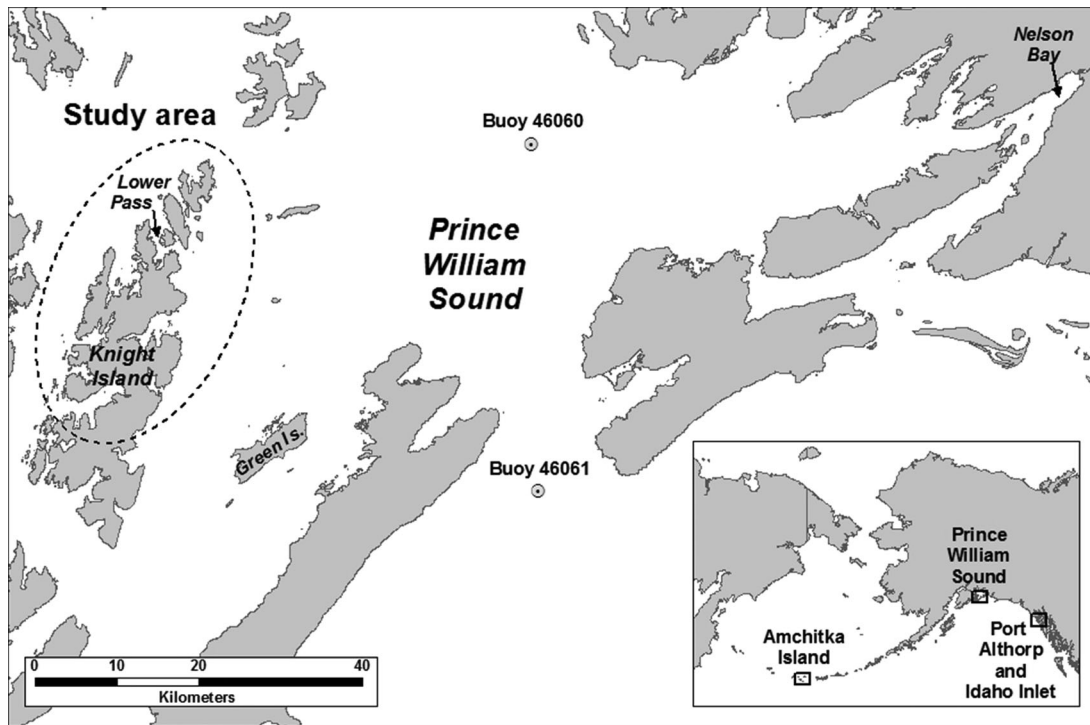
## STUDY AREA

We conducted this study at northern Knight Island (60°26'N, 147°40'W) in Prince William Sound (PWS), Alaska (Fig. 1). Sea otter habitat surrounding Knight Island is characterized by bays up to 240 m in depth, lined with steep, rocky shorelines largely devoid of surface, canopy-forming kelps (<http://alaskafisheries.noaa.gov/shorezone/>). From late November through early March, sea ice was common and covered up to 50% of the large bays where sea otters resided (A. P. Kearney, Cordova Air Service, personal communication). Sea otters at Knight Island foraged primarily on clams in unconsolidated substrates (Dean et al. 2002) and rested in open water or hauled-out on shore (J. L. Bodkin, U.S. Geological Survey, unpublished data). With the exception of Lower Pass (Fig. 1), the potential for disturbance from vessel traffic was low in summer and nearly non-existent in winter. Areas of PWS such as Knight Island were also ideal for studying seasonal activity patterns because they were the most northerly location in the sea otter's range and presented the broadest variation of photoperiod and temperature extremes encountered by the species (Fig. 2). The sea otter population in this region suffered substantial mortality during the 1989 *Exxon Valdez* oil spill and the data used in this study were part of a larger effort to examine the intertidal foraging behavior of sea otters living at Knight Island before the population had fully recovered to pre-spill abundance (Bodkin et al. 2012).

## METHODS

### Instrument Deployment and Recovery

We captured 30 adult sea otters using diver-operated Wilson traps (Ames et al. 1986) and surgically implanted each individual with a very high frequency (VHF) radio transmitter (Advanced Telemetry Systems, Isanti, MN) and an archival TDR (model Mk 9; Wildlife Computers, Redmond, WA) during the summers of 2003 ( $n = 21$ ) and 2004 ( $n = 9$ ; Bodkin et al. 2012). The Animal Care and Use Committee of the United States Geological Survey, Alaska Science Center, and the United States Fish and Wildlife Service, under Permit 740507, approved the capture and handling protocol. We programmed the TDRs to record

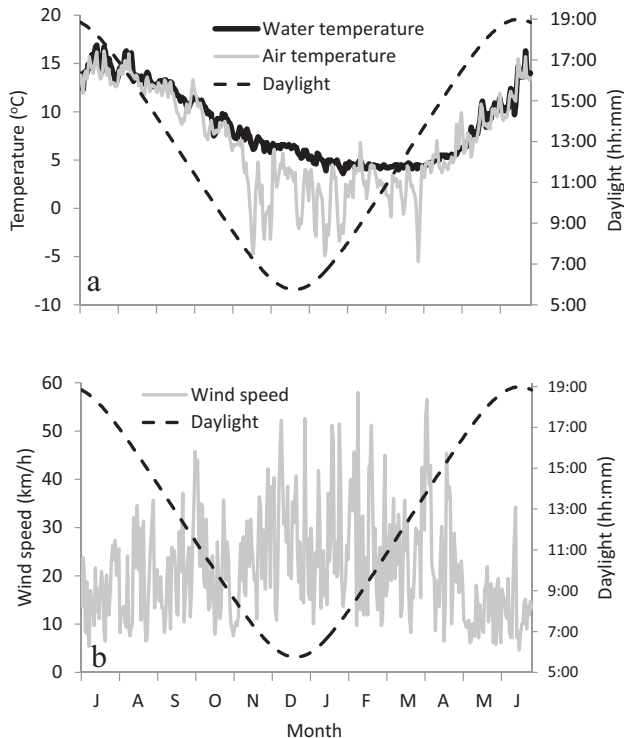


**Figure 1.** Location of sea otter study area surrounding Knight Island relative to weather buoys in Prince William Sound, Alaska, USA, 2003–2005. Locations of earlier sea otter activity studies conducted at Green Island (Garshelis et al. 1986), Nelson Bay (Garshelis et al. 1986), Amchitka Island (Gelatt et al. 2002), Port Althorp (Bodkin et al. 2007), and Idaho Inlet (Bodkin et al. 2007), referenced in the text, are also provided.

depth with 0.5-m resolution every 2 seconds for 1 year (Bodkin et al. 2012).

To visually document sea otter behavior (resting, foraging, traveling, grooming, or interacting) and reproductive status

of females (no pup, small pup, or large pup), we attempted to locate study animals during spring and summer on a weekly basis using a combination of boat- and shore-based radiotelemetry equipment and 50–80× telescopes (Questar Corporation, New Hope, PA). We defined pup size as small or large based on the distinction that small pups have natal pelage and an inability to dive proficiently (Payne and Jameson 1984). In addition to the ground-based observations, a pilot using radiotelemetry from a fixed-wing aircraft tried to locate instrumented otters at least once every 10 days, year round, to monitor survival and pup status. We later used these focal observations ( $n=563$ ), ranging from a few minutes to several hours, to ground truth dive data recorded by the TDRs and construct female reproductive histories (see below).



**Figure 2.** Day length relative to (a) mean daily water and air temperatures and (b) mean daily wind speed in Prince William Sound, Alaska, USA, 2003–2004.

### TDR Data Reduction: Dive Type Classification and Activity Bouts

To exclude potentially abnormal behavior from the analyses, we removed the first 3 days post-surgery (and, in the case of the only TDR recovered from a mortality during this study, 3 days before time of death) from each archive. For each recovered TDR, we used the manufacturer’s software (Instrument Helper 0.0.0.750, Wildlife Computers, Redmond, WA) to surface-calibrate and convert depth data into individual dives following methods described in Bodkin et al. (2012). We completed all subsequent data manipulation using SAS 9.2 (SAS Institute, Cary, NC). Using a set of 1,311 dive events for which we had both TDR data for dive duration (s), bottom time (s), and ascent rate (m/s) and visual observations that indicated whether the otter was foraging

(766 foraging and 545 non-foraging), we derived a binary logistic regression that predicted dive type using a probability threshold of 0.5 (Bodkin et al. 2004, 2012). We used this model to classify the remaining 2,051,752 unobserved dives as either foraging or non-foraging with a classification accuracy of 93% for known dives (Bodkin et al. 2012).

We identified bouts of foraging, other diving, and resting activity using the method of Bodkin et al. (2007), which we briefly summarize here. A foraging bout began with an initial foraging dive and ended either 1) 10 minutes after the last foraging dive when 20 minutes had elapsed with no diving, or 2) at the beginning of the next non-foraging dive when 20 minutes had elapsed with no foraging dives. Foraging bouts often include non-foraging dives because sea otters often travel, groom, or interact while foraging. Thus, we defined foraging effort as the amount of time spent in foraging bouts expressed in hours/day or as a proportion of the day or hour. We considered bouts that contained dives associated only with traveling, grooming, or interacting behavior as other diving. Other diving bouts began with a non-foraging dive and ended either 1) 10 minutes after the last non-foraging dive when 20 minutes had elapsed with no diving, or 2) at the beginning of the next foraging dive. We classified surface intervals lasting >20 minutes as resting periods.

### Female Reproductive Histories

We used reproductive histories to partition females into 6 reproductive stages (no pup, early gestation, late gestation, small pup, large pup, and unknown) for subsequent descriptive and statistical analyses. We constructed female reproductive histories from visual observations, body temperature ( $T_b$ ) patterns in the TDR archive, pup size at capture, and pup growth rates from the literature. Parous female sea otters show a gradual decline in  $T_b$  during gestation, followed by a rapid increase in  $T_b$  at parturition (Tinker et al. 2008). Some females also display a marked increase in  $T_b$  approximately 200 days pre-partum thought to be an estrus signature (Tinker et al. 2008). When possible, we used these patterns to infer the timing of estrus, gestation, and parturition.

We used the gestation periods from 5 recaptured females with clear  $T_b$  estrus signatures to estimate a mean gestation length of 195 days (SD = 11 days), which is similar to sea otter gestation periods estimated in other studies (6 months; Jameson and Johnson 1993, 201–218 days; Monson et al. 2000). We used this estimate (195 days) to designate gestation for the other 7 females in our study. We also used the timing of estrus as determined by  $T_b$  to inform pup presence or absence because the pilot had trouble visually confirming pups during winter. In this case, we assumed that initiation of estrus approximated date of a previous pup loss or weaning (Monson et al. 2000).

In conjunction with the  $T_b$  patterns, we used pup growth rates from Monnet et al. (1991) to back calculate pregnancy and pup dependency when we obtained pup weights during capture or recapture of females. We assumed a period of pup

dependency of 169 days based on an average estimated from radio-implanted pups in PWS (Monnet et al. 1991) and split these periods into small and large pup stages at 85 days, which roughly coincides with the age at which pups are able to dive proficiently (Payne and Jameson 1984). In the absence of visual observations or clearly discernible reproductive events in the TDR archive, we designated female reproductive status as unknown.

### Environmental Parameters

We obtained environmental measurements from a variety of sources. We downloaded sunrise and sunset times for the Port Audrey tide station on Knight Island (Fig. 1) from the United States Naval Observatory ([www.usno.navy.mil/USNO/astronomical-applications](http://www.usno.navy.mil/USNO/astronomical-applications), accessed 25 Feb 2008) to define variables day, night, day length, and day trend. Day trend was a binary variable used to indicate whether day length was increasing or decreasing. We obtained wind speed and air and water temperature from the NOAA National Data Buoy Center ([www.ndbc.noaa.gov/](http://www.ndbc.noaa.gov/), accessed 1 Jan 2011). The nearest marine weather buoy, West Orca Bay 46060, approximately 50 km northeast from the center of the study area, provided 75% of the 2003–2005 weather data. When data from this buoy were unavailable, we used data from the next closest buoy, Seal Rocks 46061 (Fig. 1), because daily means for air and water temperature at the 2 buoys were nearly identical ( $r^2 = 0.99$ , and  $0.97$ , respectively). Wind speed was not as well predicted ( $r^2 = 0.67$ ) so we obtained the values via a simple linear regression of mean daily wind speed from Buoy 46060 on Buoy 46061 ( $\beta_0 = 0.755$ ,  $\beta_1 = 0.694$ ). Although environmental conditions measured at exposed buoy locations may differ from conditions sea otters experience, we assumed wind velocity and temperature were reliable indicators of overall weather conditions.

### Temporal Patterns in Activity Budgets and Foraging Effort

To assess seasonal changes in diel activity, we plotted months with similar activity patterns on a diel scale. We used these groupings of similar diel activity budgets to define 4 seasons for subsequent descriptive and statistical analyses: fall (Aug–Sep), winter (Oct–Feb), spring (Mar–Apr), and summer (May–Jul). Also on a diel scale, we plotted the proportion of time spent foraging by females with newborn pups as a function of pup age to investigate whether the transitory increases in nocturnal foraging time reported by Gelatt et al. (2002) occurred in PWS. To examine temporal variation in foraging effort in parous females, we plotted mean foraging effort relative to date of parturition. To quantify seasonal variation in individual activity budgets, we calculated average hours per day spent in each activity for each sea otter. This part of our analysis is descriptive (based only on our sample); we did not perform statistical tests of differences.

### Statistical Modeling of Daily Foraging Effort

We used multilevel mixed models to analyze the fixed effects of various biological and environmental factors on foraging effort while at the same time partitioning variance due to the

random effects of within-otter variation (the repeated measures effect, equivalent to the residual variance) and among-otter variation (Breton et al. 2008). Consistent with Singer and Willet (2003), we refer to the residual within-otter variation as level 1 variance and variation among-otters as level 2 variance. We assessed the assumption that values of foraging effort were normally distributed using normal probability and standardized residual plots, and the assumption of homoscedasticity in the residuals by plotting residuals of foraging effort against predictors at each level (Singer and Willet 2003). We removed 12 extreme outliers of daily foraging effort, representing <0.2% of the data, prior to analysis. For models including reproductive stage, we excluded all records where the stage was unknown. We included both within- and among-otter random effects in each model to account for residual autocorrelation, another benefit of our multilevel mixed model approach (Singer and Willet 2003). We fitted all models using the full information maximum likelihood (FIML) method, which allowed models with different fixed effects to be compared (Singer and Willet 2003) using an information-theoretic approach (Burnham and Anderson 2002). We used PROC MIXED in SAS 9.2 to perform all model fitting and estimate variance components and Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ; Burnham and Anderson 2002).

Our model selection procedure for our 3 statistical analyses (Assessment of Variance Components; Estimates of Foraging Effort; and Assessment of Explanatory Predictors) was carried-out as follows: 1) we fit the full set of models for each respective analysis to the data; 2) based on rough-rules-of-thumb provided by Burnham and Anderson (2002; see table on page 70), we discarded all models with  $\Delta AIC_c$  values >6 and considered all remaining models top models (equally supported based on  $\Delta AIC_c$ ); 3) we further refined selection of top models for estimating parameters using evidence ratios of model weights,  $w_i/w_j$ , where  $w$  refers to the  $AIC_c$  model weight of model  $i$  and model  $j$  (Burnham and Anderson 2002; see table on page 78), and model effect sizes including their 95% confidence intervals. We considered effect sizes statistically significant when 95% confidence intervals did not overlap 0 and assessed biological significance by interpreting the magnitude of the effect sizes.

*Assessment of variance components.*—For this analysis, we fit a model with a fixed intercept and both random effects (unconditional means model sensu Singer and Willet 2003) and a model with the level-2 random effects removed. We used the best model to 1) estimate the within- and among-otter variance components, and 2) to represent the base (null) model before adding any predictor variables in subsequent analyses.

*Estimates of foraging effort.*—To provide estimates of foraging effort that could be directly compared with published estimates, we separately assessed the fixed effects of study year, season, day versus night, and reproductive stage in 4 identical analyses each containing 3 models. For each analysis, we fit models with and without sex and compared them against each other and the null model from our assessment of variance components.

*Assessment of explanatory predictors.*—To assess the contribution of explanatory predictors to temporal variation in foraging effort in parous females, we used a combination of field experience and literature-based predictions to specify a list of 20 a priori candidate models including the null model from our assessment of variance components. In this analysis, we specified foraging effort as the continuous response variable and then assessed the effects of reproductive stage and 5 environmental covariates: day trend (length increasing or decreasing), day length, wind speed, air temperature, and water temperature. We specified reproductive stage as a categorical variable (intercepts) and environmental covariates as continuous variables (slopes). A preliminary examination of the raw data suggested a third-order polynomial relationship between foraging effort and day length, and a linear relationship for all others. With the exception of day length, day trend, and water temperature, we modeled all possible combinations of the biological and environmental predictors. We fit day length and trend together as additive effects, excluding water temperature from composite models because it was highly correlated ( $r^2 = 0.84$ ) with air temperature and showed less daily variation.

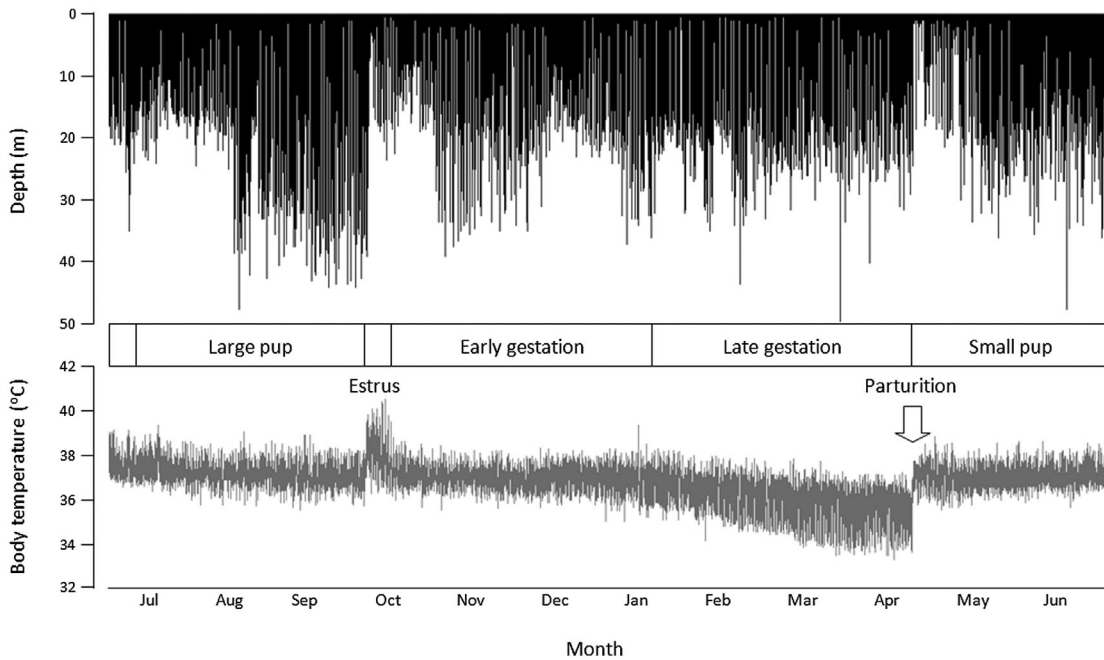
## RESULTS

We located instrumented sea otters an average of once every 19 days (range, 1–297 days). We recaptured 17 live individuals for surgical TDR extraction during the summers of 2004 ( $n = 8$ ), 2005 ( $n = 7$ ), and 2008 ( $n = 1$ ), and the spring of 2006 ( $n = 1$ ). We recovered 2 TDRs from carcasses (winter 2004, spring 2008), bringing the total sample size for this study to 15 females and 4 males (see , available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). Due to sea otter mortality or TDR battery failure during deployment, 5 TDR archives were <1 year ( ).

The  $T_b$  archives from 12 females showed clear signs of reproductive events, but only 5 individuals showed clear estrus signatures (Fig. 3). The timing of pregnancies was staggered throughout the year, but all 12 parous females were pregnant in late December and gave birth between late December and early July ( ).

### Temporal Patterns in Activity Budgets and Foraging Effort

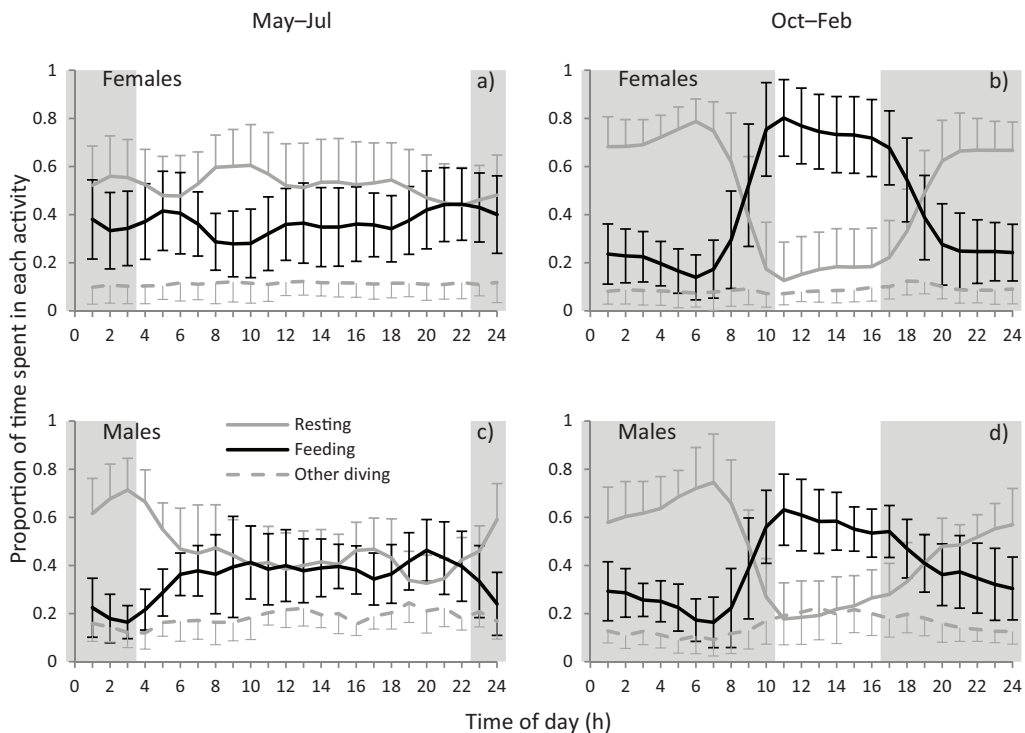
On average, females in our sample spent 48% of their overall activity budget resting (SD = 0.04; 11.6 hr/day, SD = 61 min), 41% foraging (SD = 0.04; 9.9 hr/day, SD = 55 min), and 10% other diving (SD = 0.04; 2.5 hr/day, SD = 53 min). Males spent 46% of their time resting (SD = 0.03; 11.1 hr/day, SD = 47 min), 38% foraging (SD = 0.02; 9.0 hr/day, SD = 28 min), and 5% other diving (SD = 0.05; 3.9 hr/day, SD = 69 min). Temporal patterns were apparent in the seasonal means of daily activity for individuals with yearlong TDR data (see , available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). Based on the individuals in our sample, females spent about 1.6 hours per day less time foraging during summer than during all other seasons (fall: 10.3, SD = 1.4; winter: 10.4, SD = 0.7; spring: 10.6, SD = 1.1; summer: 8.8, SD = 1.4). The only exceptions to this pattern were 2



**Figure 3.** Example of a yearlong archive of dive depth and body temperature data downloaded from a time depth recorder (TDR) deployed in a female sea otter in Prince William Sound, Alaska, USA, July 2003–July 2004 with identifiable reproductive events noted. In addition to marked changes in diving behavior and body temperature during estrus and parturition, the timing of reproductive events were consistent with visual sightings of this female and published estimates of gestation length and pup growth rates.

females (PuCh and YeGr) that were rearing large pups during summer. The 4 males in our sample foraged approximately 1.3 hours less per day during summer and fall than during winter and spring (fall: 8.1, SD = 0.7; winter:

9.5, SD = 0.4; spring: 9.6, SD = 0.9; summer: 8.4, SD = 1.2). Based on our sample, both sexes increased time spent in other diving during summer and fall; most females increased time spent resting during summer, but males



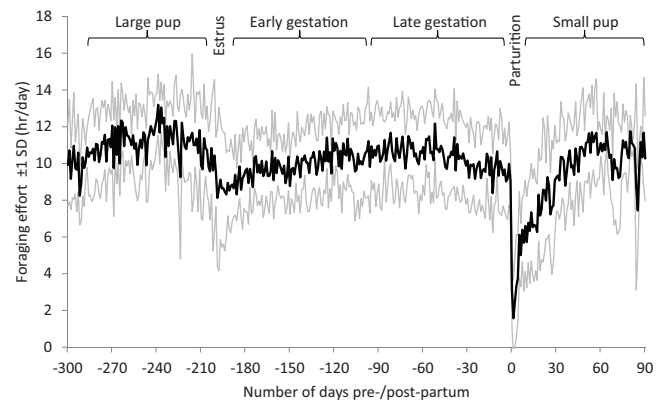
**Figure 4.** Seasonal changes in the diel activity patterns, resting, feeding, and other diving of female ( $n = 15$ ) and male ( $n = 4$ ) sea otters at Knight Island, Prince William Sound, Alaska, USA, 2003–2005. Shaded regions indicate approximate hours of darkness based on sunrise and sunset at summer (May–Jul) and winter (Oct–Feb) solstice. Error bars represent  $\pm 1$  standard deviation of the mean.

showed no clear pattern (see , available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

Sea otters in our sample clearly responded to changes in day length by structuring the timing of foraging to coincide with daylight (Fig. 4). Females transitioned from diel foraging with slight crepuscular peaks during summer (Fig. 4a) to strongly diurnal foraging during winter (Fig. 4b). Compared to females, the diurnal foraging pattern for males was stronger during summer (Fig. 4c) and less pronounced during winter (Fig. 4d). Diel changes in foraging were closely mirrored by reciprocal changes in resting and time spent in other diving activities remained at a relatively low level throughout the day and in all seasons. The absence of a strong diurnal foraging pattern in the activity budgets of adult females during summer is likely due to the fact many females had small pups during this time of the year and rapidly switched from a diurnal foraging mode to a nocturnal foraging mode for 3 weeks following parturition (Fig. 5). This nocturnal switch occurred regardless of season, and foraging effort was reduced to low levels during the first 3 weeks with a newborn pup (Fig. 6).

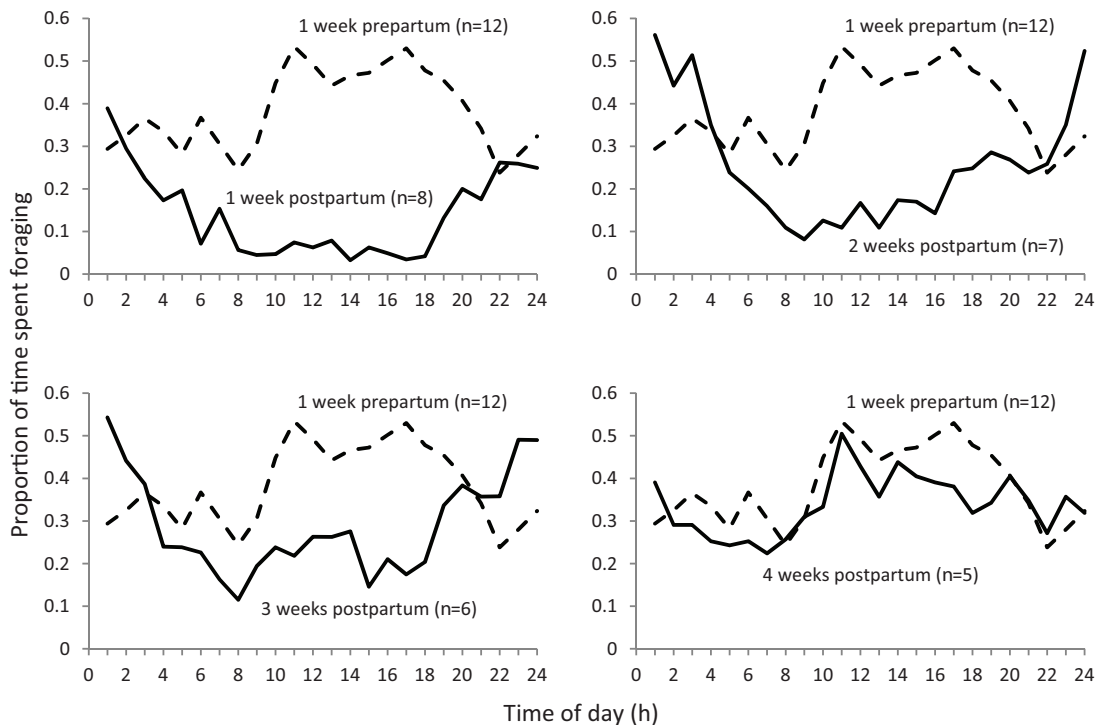
### Daily Foraging Effort

*Assessment of variance components.*—The model with both the within-otter (level-1) and among-otter (level-2) random effects acquired exclusive support;  $\Delta AIC_c$  for the model with only the within-otter random effects (residual errors) was 694.8. From the only supported model, 13% of the variation in foraging effort was among otters and 87% was within otters (i.e., daily variation).



**Figure 6.** The mean and standard deviation of foraging effort for 12 parous female sea otters, Prince William Sound, Alaska, USA, 2003–2005.

*Foraging effort.*—In the model set used to assess study year, all 3 models acquired top model support (Table 1, model set 1). Despite this uncertainty, the top-ranked model, study year + sex, was favored 5:1 over the study-year-only model and 8:1 over the null model. Sex and study year effect sizes were also statistically significant in the top-ranked model: the sex effect indicated females foraged an average of 1.00 (CI: 0.21, 1.79) hour per day longer than males and the year effect indicated sea otters spent 0.77 (CI: 0.08, 1.46) hours more per day foraging in study year 2003–2004 than in 2004–2005 (Table 2). Our results suggest that model selection uncertainty was likely due to sample size constraints rather than lack of genuine effects of sex and study year.



**Figure 5.** Diel changes in time spent foraging proportional to other activities (resting, other diving) of female sea otters relative to the age of their newborn pups at Knight Island, Prince William Sound, Alaska, USA, 2003–2005. The dotted lines indicate the mean proportion of time spent foraging 1 week prepartum and are provided as a reference in all 4 panels. The solid line in each panel represents the proportion of time spent foraging during a given postpartum week.

**Table 1.** Model sets, information criteria, and other results used to estimate the foraging effort (hours per day) of sea otters in Prince William Sound, Alaska, USA, 2003–2005 by study year, season, day versus night, and reproductive stage by sex: Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>); change in AIC<sub>c</sub> relative to the top ranked model ( $\Delta$ AIC<sub>c</sub>); Akaike weight ( $w_i$ ); log likelihood (LL); and number of parameters ( $K$ ).

Model set	Fixed effects <sup>a,b</sup>	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$	LL	$K$
1	Study year, sex	27,582.4	0	0.76	-13,786	5
	Study year	27,585.8	3.4	0.14	-13,789	4
	(Intercept-only)	27,586.5	4.1	0.10	-13,790	3
2	Season, sex	27,145.1	0	0.71	-13,566	7
	Season	27,146.9	1.8	0.29	-13,567	6
	(Intercept-only)	27,586.5	441.4	0.00	-13,790	3
3	Day_night, sex	44,908.5	0	0.55	-22,449	5
	Day_night	44,908.9	0.4	0.45	-22,450	4
	(Intercept-only)	48,281.9	3,373.4	0.00	-24,138	3
4	Stage <sup>c</sup>	17,564.8	0.0	1.00	-8,775	7
	(Intercept-only)	23,599.8	6,035.0	0.00	-11,797	3

<sup>a</sup> All models include a population intercept as a fixed effect.

<sup>b</sup> All models include observation and otter as random effects.

<sup>c</sup> Reproductive stage (no pup, early gestation, late gestation, small pup, large pup).

In the model set used to assess the effect of season, the null model acquired no support ( $\Delta$ AIC<sub>c</sub> = 441.4), the remaining two models acquired equal support (Table 1, model Set 2). Despite this uncertainty, the top-ranked model, season + sex, was favored 3:1 over the season-only model and the sex effect was statistically significant: females spent 0.92 (CI: 0.04, 1.81) more hours per day foraging than males. As above, model selection uncertainty in this analysis was likely due to sample size constraints rather than lack of a genuine effect of sex. Based on estimates from the season + sex model, foraging effort was lowest in the summer and highest in the spring (Table 3).

The model contrasting foraging effort during day versus night was strongly supported over the null model ( $\Delta$ AIC<sub>c</sub> = 3373.4; Table 1, model set 3). The model with sex (top-ranked model) and the model without sex ( $\Delta$ AIC<sub>c</sub> = 0.04) were equally supported. Consistent with this result, the sex effect in the top-ranked model was not significant (0.37 [CI: -0.08, 0.82]). However, the 95% confidence interval associated with the sex effect strongly favored a positive effect, that is, that females foraged longer on average than males just like in our analyses of study year and season. The statistical significance of sex in this analysis, as with the previous 2 analyses, was likely affected by small sample size. From the day versus night model (without sex), sea otters spent an average of 2.68 (CI: 2.60, 2.77) more hours per day foraging than at night.

For parous females only, the reproductive stage model acquired exclusive support (Table 1, model set 4) and none of

the stage effect sizes in this model overlapped 0 (no pup: -2.15 [CI: -2.66, -1.64]; early gestation: -1.76 [CI: -2.02, -1.50]; late gestation: -1.29 [CI: -1.55, -1.03]; small pup: -2.75 [CI: -3.03, -2.47]). Females with large pups spent more time foraging than any other reproductive stage (Table 4). When males were added to the stage model, the model failed to converge on an estimate of the sex effect (not shown in Table 1, model set 4), likely because the sex effect was close to 0 (i.e., males and females without pups spent about equal amounts of time foraging per day).

*Explanatory predictors (parous females only).*—Data from this analysis supported 3 top models (Table 5, models 1–3), all other models had  $\Delta$ AIC<sub>c</sub> values >6 (not supported); all models in this analysis included a fixed intercept as well as within- and among-otter random effects. The top-ranked model (Table 5, model 1) included reproductive stage, day trend, day length (cubic function), wind speed, air temperature, and a wind speed × air temperature interaction. Despite this long list of effects, 83% of the within-otter variance in the top-ranked model remained unexplained (Table 6, column 5) indicating that daily variation in foraging effort was largely driven by unknown factors. The top-ranked model was favored 7:1 (evidence ratio) over the second best model (model 2; Table 5), which excluded air temperature and the wind speed × air temperature interaction, and 20:1 over the third best model (model 3; Table 5)

**Table 3.** Estimates of sea otter foraging effort by sex and season from the top-ranked model (Table 1, model set 2), Prince William Sound, Alaska, USA, 2003–2005.

Sex	Season	Mean foraging effort (hr/day)	SE	95% CI	
				Lower	Upper
Female	Fall	10.09	0.22	9.66	10.51
	Winter	10.28	0.21	9.87	10.69
	Spring	10.46	0.22	10.03	10.89
	Summer	8.78	0.21	8.36	9.20
Male	Fall	9.16	0.41	8.37	9.96
	Winter	9.35	0.40	8.56	10.14
	Spring	9.53	0.41	8.74	10.33
	Summer	7.85	0.41	7.06	8.65

**Table 2.** Estimates of sea otter foraging effort by study year and sex from the top-ranked model (Table 1, model set 1), Prince William Sound, Alaska, USA, 2003–2005.

Year	Sex	Mean foraging effort (hr/day)	SE	95% CI	
				Lower	Upper
2003–2004	Female	10.22	0.22	9.79	10.65
	Male	9.22	0.37	8.50	9.94
2004–2005	Female	9.45	0.30	8.86	10.03
	Male	8.45	0.44	7.58	9.32



**Table 4.** Estimates of sea otter foraging effort by reproductive stage from the top-ranked model (Table 1, model set 4), Prince William Sound, Alaska, USA, 2003–2005.

Reproductive stage	Mean foraging effort (hr/day)	SE	95% CI	
			Lower	Upper
No pup	9.52	0.31	8.90	10.13
Early gestation	9.91	0.26	9.41	10.42
Late gestation	10.38	0.26	9.88	10.88
Small pup	8.92	0.27	8.39	9.44
Large pup	11.67	0.27	11.13	12.21

which had no interaction between wind speed and air temperature.

## DISCUSSION

This study improves our understanding of sea otter behavior using detailed longitudinal data to describe activity patterns at several temporal scales and quantifies multiple sources of density-independent variation in foraging effort. Collectively, these findings suggest that sea otters in PWS modify their foraging effort at diel and seasonal timescales in response to factors such as day length, wind speed and, for females, reproductive status. Most of the variation in foraging effort was within-otter variation (level-1). Nonetheless, effects in our top models—reproductive stage, day length, wind speed, and air temperature—explained 17% of this variation. Despite that 83% of the variation was left unexplained in our analysis, likely due in part to variation in prey availability and/or quality, our results indicate that reproductive and environmental covariates should be considered when using foraging effort to assess the population status, and including

such factors would likely increase our understanding of differences observed among populations.

Our estimates of foraging effort for independent adult female sea otters (9.5–10.4 hr/day; Table 4) are similar to earlier estimates for independent adult females at Knight Island (9.9 hr/day; Dean et al. 2002) and summer estimates in Port Althorp, southeast Alaska (9.6 hr/day; Bodkin et al. 2007). In contrast, males living in Idaho Inlet (Fig. 1), an area with more abundant prey resources than Port Althorp (Bodkin et al. 2007), foraged an average of 1.1 hours per day less than males in our study during summer (7.85 hr/day; Table 3). A radiotelemetry study in PWS estimated that solitary adult females foraged 11.3 hours per day at Green Island, an area of prolonged sea otter occupation described as having relatively poor food resources, and only 8.8 hours per day at Nelson Bay (Fig. 1) where prey availability was greater (Garshelis 1983, Garshelis et al. 1986). Estimates of foraging effort from sea otters in California range from 6 hours per day in areas of high prey abundance to 12 hours per day in areas of low prey abundance (Ralls and Siniff 1990, Bentall 2005, Staedler 2011). These comparisons suggest sea otters have a wide range of flexibility in their activity budgets and support earlier studies (Bodkin et al. 2002, Dean et al. 2002) that indicated sea otters at Knight Island were not feeding at maximal effort and, therefore, below carrying capacity with respect to food resources. However, because our estimates of foraging effort are closer to the upper end of the range of published values for sea otters, this population may have been approaching food limitation.

This study found evidence of a seasonal pattern in foraging effort with sea otters spending an average of 1.7 hours more

**Table 5.** Model set, information criteria, and other results used to assess biological and environmental factors that might be affecting the foraging effort (hours per day) of parous female sea otters ( $n = 12$ ), Prince William Sound, Alaska, USA, 2003–2005: Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ); change in  $AIC_c$  relative to the top ranked model ( $\Delta AIC_c$ ); Akaike weight ( $w_i$ ); log likelihood (LL); and number of parameters ( $K$ ).

Model	Fixed effects <sup>a,b</sup>	$AIC_c$	$\Delta AIC_c$	$w_i$	LL	$K$
1	Stage <sup>c</sup> , day trend, day length, day length <sup>2</sup> , day length <sup>3</sup> , WS <sup>d</sup> , AT <sup>e</sup> , WS $\times$ AT	17,198.7	0	0.84	–8,585	14
2	Stage, day trend, day length, day length <sup>2</sup> , day length <sup>3</sup> , WS	17,202.7	4.0	0.11	–8,589	12
3	Stage, day trend, day length, day length <sup>2</sup> , day length <sup>3</sup> , WS, AT	17,204.7	6.0	0.04	–8,589	13
4	Stage, day trend, day length, day length <sup>2</sup> , day length <sup>3</sup> , AT	17,242.2	43.5	0	–8,609	12
5	Stage, day trend, day length, day length <sup>2</sup> , day length <sup>3</sup>	17,279.1	80.4	0	–8,629	11
6	Stage, day trend, day length, WS	17,302.4	103.7	0	–8,641	10
7	Stage, day trend, day length, WS, AT	17,304.4	105.7	0	–8,641	11
8	Stage, day trend, day length, AT	17,347.6	148.9	0	–8,664	10
9	Stage, wind speed, AT	17,366.8	168.1	0	–8,674	9
10	Stage, wind speed, AT, (WS $\times$ AT)	17,368.8	170.1	0	–8,674	10
11	Stage, day trend, day length	17,382.7	184.0	0	–8,682	9
12	Stage, WS	17,399.4	200.7	0	–8,692	8
13	Stage, AT	17,458.2	259.5	0	–8,721	8
14	Stage	17,564.8	366.1	0	–8,775	7
15	Day trend, day length, day length <sup>2</sup> , day length <sup>3</sup>	17,613.7	415.0	0	–8,800	7
16	Day trend, day length	17,733.9	535.2	0	–8,862	5
17	WS	17,742.2	543.5	0	–8,867	4
18	AT	17,832.9	634.2	0	–8,912	4
19	Water temperature	17,850.6	651.9	0	–8,921	4
20	(Intercept-only)	17,946.8	748.1	0	–8,970	3

<sup>a</sup> All models include a population intercept as a fixed effect.

<sup>b</sup> All models include observation and otter as random effects.

<sup>c</sup> Reproductive stage (no pup, early gestation, late gestation, small pup, large pup).

<sup>d</sup> Wind speed.

<sup>e</sup> Air temperature.

**Table 6.** Variance components ( $\pm$ SE), percent level-1 variation explained, and change in Akaike's Information Criterion corrected for small sample size ( $\Delta$ AIC<sub>c</sub>; relative to the top-ranked model) for the reference (null) model and the top models (Table 5, models 1–3) used to investigate biological and environmental covariates that might be contributing to variation in the foraging effort of parous female sea otters in Prince William Sound, Alaska, USA, 2003–2005.

Models	Observation, otter	Stage, day trend, day length, day length <sup>2</sup> , day length <sup>3</sup> , wind speed, air temperature, observation, otter	Stage, day trend, day length, day length <sup>2</sup> , day length <sup>3</sup> , wind speed, observation, otter	Stage, day trend, day length, day length <sup>2</sup> , day length <sup>3</sup> , wind speed, air temperature, wind speed $\times$ air temperature, observation, otter
Variance components				
$\hat{\sigma}_r^2 \pm \widehat{SE}^a$	5.494 (0.124)	4.563 (0.103)	4.563 (0.103)	4.554 (0.103)
$\hat{\sigma}_{otter}^2 \pm \widehat{SE}^b$	0.812 (0.317)	0.902 (0.352)	0.902 (0.351)	0.898 (0.350)
% Level-1 variation ( $\hat{\sigma}_r^2$ ) explained	0.0	16.9	16.9	17.1
$\Delta$ AIC <sub>c</sub>	748.1	6.0	4.0	0.0 <sup>c</sup>

<sup>a</sup> ( $r$ ) Residual variation at the observation level.

<sup>b</sup> ( $otter$ ) Residual variation at the otter level.

<sup>c</sup> Top-ranked (best) model AIC<sub>c</sub> = 17,198.7.

per day foraging in spring than in summer. Only 2 other studies have examined seasonal variation in time spent foraging by sea otters. Radiotelemetry data from Green Island show that sea otters increased their foraging time by 5.1 hours per day to 16.6 hours per day (69%) in the winter (Garshelis et al. 1986). Conversely, foraging effort in adult females at Amchitka Island did not differ seasonally and adult males spent 2.6 hours less per day foraging during winter, apparently because of unusually high winter prey abundance in the form of an episodically available influx of spawning lumpfishes (*Aptocyclus ventricosus*; Gelatt et al. 2002). Comparisons thus far suggest that seasonal variation in foraging effort may be driven by seasonal differences in energetic demands at northern latitudes, but the magnitude of these differences may be influenced by spatial or temporal differences in prey availability and quality.

In addition to seasonal variation in the amount of foraging effort, sea otters at Knight Island structured their foraging effort around daylight hours. This finding is consistent with seasonal changes in diel foraging at Green Island, where sea otters also fed primarily on clams (Garshelis 1983). In contrast, males in Nelson Bay foraged nocturnally year-round on a crab-based diet (Garshelis 1983). Clearly capable of foraging diurnally or nocturnally, the diel activity patterns of sea otters in PWS are likely prey-dependent. Given the clam-based diet at Knight Island, daylight may confer some advantage to sea otters in locating, extracting, or handling clams.

Sea otters have long been considered tactile foragers (Riedman and Estes 1990) and the extent to which they rely on vision for foraging is unknown. Murphy et al. (1990) found sea otter vision to be well adapted for seeing underwater as well as in air so they may prefer diurnal foraging if they are more efficient at capturing certain prey types using visual cues. If nocturnal foraging is indeed less efficient for locating clams at Knight Island, then this reduced efficiency could partially explain why foraging effort is strongly focused to occur during daylight in winter when daylight can be limited to <6 hours (Fig. 4). Further, because

parous females forage part of the year for themselves and their pup, they have additional incentive to forage during more efficient daylight hours. Consistent with this hypothesis, females more closely aligned their foraging effort with daylight hours relative to males.

A major exception to diurnal foraging occurred when females were caring for small pups. During this time, females spent less time foraging than at any other reproductive stage and concentrated their foraging activity during the night. Shimek and Monk (1977) speculated that females with small pups might use nocturnal foraging as a means of avoiding pup depredation by bald eagles (*Haliaeetus leucocephalus*). Bald eagles at Amchitka Island have been observed preying on newborn sea otter pups left alone on the surface while their mothers were diving to gather food (Sherrod et al. 1975) and pup carcasses have been found in bald eagle ground nests throughout the western Aleutian Archipelago (Krog 1953, Gelatt 1996, Anthony et al. 2008). At Amchitka Island, Gelatt (1996) reported that parous females exhibited decreased diurnal foraging effort until pups weighed more than eagles could carry (approx. 3 weeks). Bald eagles commonly occur throughout PWS, but nest searches for prey remains have been limited as they usually nest in trees (P. F. Schempf, U.S. Fish and Wildlife Service, personal communication). Although bald eagles are the most obvious and likely predator of helpless and unattended sea otter pups, the behavioral pattern of females with neonates observed in this study could be an anti-predator response to any visual predator.

Consistent with findings from Amchitka (Gelatt et al. 2002), females with large pups in our study devoted more time to foraging than during any other reproductive stage. Although reproductive stages from Garshelis et al. (1986) were not directly comparable, females with dependent pups spent more time foraging than solitary adult females at Green Island. In California, 2 studies have addressed variation in female foraging effort related to reproduction. Ralls and Siniiff (1990) found no difference in foraging effort between adult females with and without pups based on

radiotelemetry-derived activity budgets; however, differences could have been masked by combining small and large pups. Staedler (2011) reported that TDR-instrumented female sea otters with large pups foraged more than any other reproductive stage at 12 hours per day, which is very similar to our estimate of 11.7 hours per day. The actual amount of time females spend foraging appears to vary spatially among populations, but behavioral studies conducted thus far suggest the large pup stage is the most expensive in terms of time and energy invested by females as she must acquire prey for herself, her pup and continue to lactate until weaning (Riedman and Estes 1990).

The relatively small among-otter variance component (13%) reveals a high-level of consistency in foraging effort among sea otters in this extreme northern population at any particular time. This among-otter consistency suggests that measuring foraging effort with high-resolution TDR data over yearlong timescales may provide a reliable indicator of population status even if sample sizes are small. To assess the prevalence of low among-otter variation and whether this consistency is due to strong environmental drivers, yearlong TDR data could be collected from sea otter populations at lower latitudes and analyzed using a multilevel model framework.

Most of the variation in daily foraging effort in this study was within-otter (daily) variation, with 17% explained by the combined effects of reproductive stage, day length, and wind speed. The large amount of within-otter variance is not surprising because many other factors likely affect daily foraging effort, such as social interactions, prey preferences, and energy recovery rates and these are difficult to distinguish in the TDR data and account for in the models. Based on the findings of many studies (Estes et al. 1986, Garshelis et al. 1986, Gelatt et al. 2002, Bodkin et al. 2007), spatial and temporal variation in prey availability and quality would presumably have been an influential source of variation in foraging effort. Further, assuming that sea otters confronted with low prey availability would be more responsive to reproductive and environmental constraints, these factors could explain a greater percentage of the variation in foraging effort in populations experiencing food limitation. Alternatively, the standard unit of a day for assessing variation in otter foraging effort may be too long or too short to detect influential sources of variation in the data. We propose that future research also consider varying the unit used in the analysis to scales not previously considered such as hours or combinations of days based on known or suspected biological rhythms.

## MANAGEMENT IMPLICATIONS

As humans continue to modify ecosystems, accurately interpreting activity budgets as indices of population status will require an understanding of the factors affecting the behavior of predators. Our results suggest that reproductive stage, day length, wind speed, and air temperature should be considered when using foraging effort to assess the population status of sea otters. However, caution must be exercised in applying these results to populations of differing status

relative to carrying capacity because the current study was not designed to assess the magnitude of the effects at varying levels of prey abundance. For example, if the population in this study had been more food limited, the seasonal differences in foraging effort could have been more pronounced (e.g., Green Island; Garshelis et al. 1986). Further, the fact that PWS sea otters live at the northern extent of the species range means the results of this study may not apply directly to populations in more southern areas with different habitats, and reinforces the need to collect data on environmental conditions and reproductive status in future studies of this type to determine whether these factors vary systematically among populations.

Since the completion of this study, TDR technology has advanced and devices are now capable of collecting 10-year archives and will soon record behavior over the entire life span of a sea otter (approx. 20 years). By measuring the spacing between successive reproductive cycles, TDRs have the potential to reveal long-term reproductive rates and pre-weaning survival of pups, hence providing additional insight into population status. The use of multilevel models to account for fixed and random effects facilitates the comparison of activity budgets and vital rates across different regions and times. As various other activity data-logging technologies improve, a multilevel analysis framework such as the one used in this study can account for multiple sources of variance and improve our ability to gauge the population status of sea otters and other species.

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