

Activity Budgets Derived From Time–Depth Recorders in a Diving Mammal

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ABSTRACT We describe a method to convert continuously collected time–depth data from archival time–depth recorders (TDRs) into activity budgets for a benthic–foraging marine mammal. We used data from 14 TDRs to estimate activity-specific time budgets in sea otters (*Enhydra lutris*) residing near Cross Sound, southeast Alaska, USA. From the TDRs we constructed a continuous record of behavior for each individual over 39–46 days during summer of 1999. Behaviors were classified as foraging (diving to the bottom), other diving (traveling, grooming, interacting), and nondiving (assumed resting). The overall average activity budget (proportion of 24-hr/d) was 0.37 foraging (8.9 hr/d), 0.11 in other diving (2.6 hr/d), and 0.52 nondiving time (12.5 hr/d). We detected significant differences in activity budgets among individuals and between groups within our sample. Historically, the sea otter population in our study area had been expanding and sequentially reoccupying vacant habitat since their reintroduction to the area in the 1960s, and our study animals resided in 2 adjacent yet distinct locations. Males ($n = 5$) and individuals residing in recently occupied habitat ($n = 4$) spent 0.28–0.30 of their time foraging (6.7–7.2 hr/d), 0.17–0.18 of their time in other diving behaviors (4.1–4.3 hr/d), and 0.53–0.54 of their time resting (12.7–13.0 hr/d). In contrast, females ($n = 9$) and individuals residing in longer occupied habitat ($n = 10$) spent 0.40 of their time foraging (9.6 hr/d), 0.08–0.09 of their time in other diving behaviors (1.9–2.2 hr/d), and 0.51–0.52 of their time resting (12.2–12.5 hr/d). Consistent with these differences, sea otters residing in more recently occupied habitat captured more and larger clams (*Saxidomus* spp., *Protothaca* spp., *Macoma* spp., *Mya* spp., *Clinocardium* spp.) and other prey, and intertidal clams were more abundant and larger in this area. We found that TDRs provided data useful for measuring activity time budgets and behavior patterns in a diving mammal over long and continuous time periods. Fortuitous contrasts in time budgets between areas where our study animals resided suggest that activity time budgets estimated from TDRs may be a sensitive indicator of population status, particularly in relation to prey availability. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):2034–2044; 2007)

DOI: 10.2193/2006-258

KEY WORDS Alaska, behavior, diving, *Enhydra lutris*, population assessment, population status, sea otter, TDR, time budget, time–depth recorders.

Population status typically describes the abundance of a population relative to the environment's theoretical carrying capacity. Yet because both true population abundance and theoretical carrying capacity are inherently difficult to determine, indices intended to reflect population status are common tools in wildlife management. Indices of population status may include physiological (body composition and condition, disease prevalence, parasitism), life history (fecundity, survival), and habitat (food availability) variables, as well as behavioral attributes (e.g., time budgets; Eberhardt and Siniff 1977).

Time budgets describe the allocation of time to specific behaviors such as resting, grooming, foraging, or social interactions. A fundamental premise is that food resources frequently limit population abundance, that the proportion of time individuals allocate to foraging reflects food availability (Gelatt et al. 2002), and as the population approaches carrying capacity the average time spent foraging should increase. The utility of time budgets as a tool to assess population status has been demonstrated for a variety of seabirds (Cairns 1988, Burger and Piatt 1990, Monaghan et al. 1994, Zador and Piatt 1999, Litzow et al. 2002), waterfowl (Mallory et al. 1999), pinnipeds (Costa et al. 1989, Hood and Ono 1997, Boyd 1999), and primates (Watts 1988, Gursky 2000).

Since 1969 sea otter (*Enhydra lutris*) activity budgets have

been estimated at 7 different locations and during 13 different time periods, including populations that were increasing, stable, and decreasing (Gelatt et al. 2002). Despite this breadth of research, conclusions about the utility of time budgets as a measure of sea otter population status have been inconsistent (Shimek and Monk 1977; Estes et al. 1982, 1986; Garshelis et al. 1986; Ralls and Siniff 1990). Some of the divergence in results and conclusions stems from differences in the accuracy and precision produced by various methods (visual vs. telemetry), sampling designs (e.g., day vs. day and night, and variable sample sizes), uncertainty in population status relative to carrying capacity at the time of study, and the sometimes overwhelming influence of sampling variance (including within-individual variation across time, as well as variation among individuals, sexes, and age cohorts). However, if we assume that time budgets reflect energy availability, reducing methodological sources of uncertainty and increasing the precision of estimates should lead to an improved ability to discriminate among or within populations that vary in status.

Archival time–depth recorders (TDRs) are suitable for gathering large quantities of continuous dive-related behavioral data in air-breathing diving vertebrates. Interpreting dive data in a behavioral context requires identifying specific dive types (feeding, traveling, interacting, etc.) based on dive profiles, which can then be used to produce a continuous activity profile where time blocks of similar

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activity types can be identified and grouped. Specific dive types have been identified from TDR dive profiles for sea otters (Bodkin et al. 2004), and continuous recordings of dive activity should provide accurate and standardized measures of time budgets. Our objective was to provide a model for using archival TDR technology to estimate activity time budgets in a benthic-foraging diving mammal. As this was the first use of this technology on sea otters, our original intent did not include actually testing the hypothesis that activity time budgets reflect population status relative to food availability. However, the serendipitous postcapture movement and segregation of our study animals allowed us to test the effect of sex and area on estimated time budgets. To capitalize on this situation, we visually estimated foraging success, diet composition, and prey sizes, and directly estimated density and size distributions of intertidal clams (*Saxidomus* spp., *Protothaca* spp., *Macoma* spp., *Mya* spp., *Clinocardium* spp., *Hiatella* spp., *Pseudopythina* spp.) to evaluate prey availability according to the spatial separation of our study animals. These data allowed us to contrast and compare time budgets among individuals by sex and area, and relative to independent measures of prey availability and foraging success.

STUDY AREA

The sea otter population in southeast Alaska, USA, originated from 412 animals translocated from Amchitka and Prince William Sound during 1965 to 1969 (Jameson et al. 1982). Release sites in southeast Alaska included 2 locations near Cross Sound. Following translocations, sea otters colonized Port Althorp around 1975 and Idaho Inlet around 1988 (Fig. 1; Pitcher 1989, Bodkin et al. 2004), although portions of Idaho Inlet were colonized as recently as 1996.

METHODS

In May 1999, we captured 21 sea otters in Port Althorp and surgically implanted them with very high frequency (VHF) radiotransmitters (Advanced Telemetry Systems, Isanti, MN) and archival TDRs (Mark VII; Wildlife Computers, Redmond, WA) following the methods described in Bodkin et al. (2004). We tagged each individual on the hind flippers with color-coded tags to allow for visual recognition and identify each individual with an abbreviated code for those colors (e.g., red–white = re–wh; Table 1). We also extracted a premolar tooth to estimate age (Bodkin et al. 1997). We programmed each TDR to record depth, with 0.25-m accuracy, at 2-second intervals for 46 days (i.e., the memory capacity of the TDR). We searched for instrumented animals daily both from shore and from vessels using standard telemetric techniques and recorded precise locations (using Global Positioning System [GPS]) and behavior (resting, foraging, traveling, grooming, or interacting) at the time of detection (Riedman and Estes 1990). Continuous observations of active study animals allowed the identification of a subset of dives of known function (i.e., foraging, traveling, grooming) that we recorded by the date and time of the start of the dive. We then identified

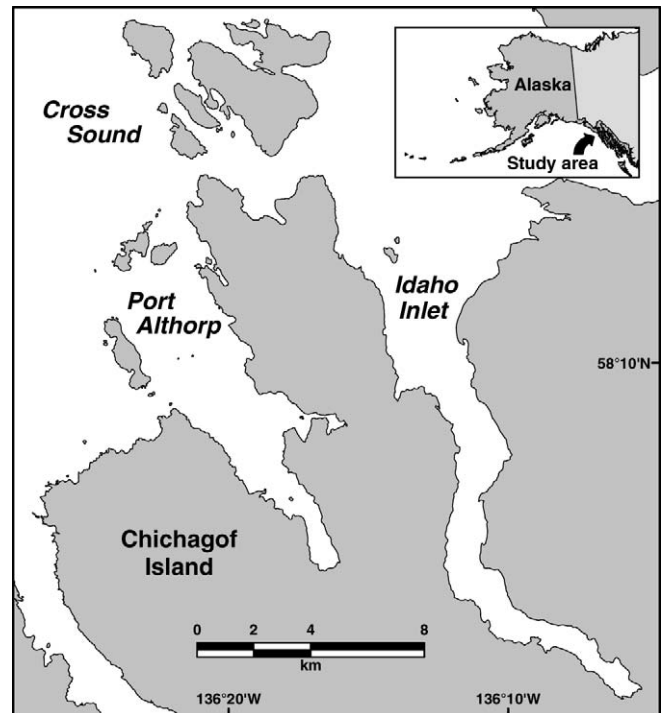


Figure 1. Location in southeast Alaska, USA, where sea otters were instrumented with time–depth recorders (TDRs). Figure includes the range of all known locations during May–July 1999. All animals were instrumented in Port Althorp and a sub-set of those, mostly males, spent some or most of their time in Idaho Inlet.

observations of dives of known function in the archival TDR record once we recovered it.

Capture, handling, monitoring, and surgical procedures were approved by the Animal Care and Use Committee of the United States Geological Survey, Alaska Science Center under Federal Permit DMA-766818.

Data Analysis

We downloaded and processed archived TDR data with zero offset software (Wildlife Computers) to calibrate depth readings relative to the sea surface (Hooker and Baird 2001). We then processed individual depth readings by compiling those into distinct dives using the software program Dive Analysis (Wildlife Computers). Foraging dives are easily identified through prey consumption at the surface, and we identified a sample of 1,251 dives through direct visual observation that we classified with certainty by function as either forage diving (i.e., prey were consumed following a dive), or other diving behavior (i.e., traveling, grooming, interacting). We then located these 1,251 dives of known function in the TDR records and used their attributes (duration, bottom time, ratio of bottom time to dive time, and descent and ascent rates) to parameterize a dichotomous logistic model. We then used these parameter values to classify all remaining dives in the TDR records as either foraging or other diving (for details see Bodkin et al. 2004). Because of instrument error and the location of the instrument in the abdomen, we restricted our analyses to dives with maximum depth of ≥ 2 m (Bodkin et al. 2004).

Table 1. Identification (ID), sex, age, weight at initial capture (wt change between captures), length, and condition (g/cm of total length [TL]) of sea otters sampled in southeast Alaska, USA, May–July 1999. Means are by sex.

Otter ID ^a	Age (yr)	Wt (kg)	Wt difference (kg)	TL (cm)	Wt/TL (g/cm)
F					
aq–aq	2	21.6	–4.1	118.5	182
re–wh	2	22.9	+0.4	126.3	181
lb–lb	2	20.4	+1.8	118.8	172
ch–ch	2	19.2	+0.2	121.0	159
lb–wh ^b	3	22.7	–5.9	125.0	181
pi–wh	6	24.5	+2.8	127.5	192
pu–pu	9	21.4	+0.2	125.0	171
si–si	11	25.3	–2.0	127.0	199
go–wh ^c	16	22.7		118.0	192
\bar{x}	5.9	22.3	–0.1 ^d	123.0	181
M					
or–or	5	39.0	0.0	140.0	279
ye–ye	6	38.8	+0.4	135.5	286
re–re	7	41.0	–1.3	140.8	292
ch–wh	7	37.9	–0.5	133.0	285
wh–wh	10	40.5	+2.0	142.3	285
\bar{x}	7.0	39.4	+0.1	138.3	285

^a Identification refers to color combinations of flipper tags used to identify individuals (e.g., aq = aqua, lb = light blue, ch = chartreuse, one tag/flipper).

^b Wt and wt/TL based on recapture wt only because of undetected pregnancy at initial capture.

^c Based on initial capture as no wt or TL at recapture (i.e., harvested).

^d Does not include lb–wh.

Time Activity Analysis

Sea otters are a benthic forager and must dive to the bottom to retrieve food; thus, we can safely assume foraging time will always be accompanied by diving activity. Moreover, because sub-surface traveling is less energetically expensive than surface swimming (Williams 1989); we assume that periods of travel will include some diving activity. We observed several extended periods of traveling (>20 min) during the monitoring period, and we always observed intermittent diving during this activity. Activity levels during nondiving time are less certain. Based on many years of observing sea otter behavior, we feel comfortable assuming extended periods of nondiving are likely resting or periods of low activity, but also acknowledge that assuming all nondiving time is resting may overestimate resting time to some degree. This is particularly true for females with small pups as they often travel without diving while carrying their pups on their chest. This was generally not an issue for this study.

With the above assumptions we compiled individual dives into a continuous activity record for each animal by identifying contiguous blocks of time (bouts) spent in 1 of 3 behaviors: 1) foraging, 2) other diving (including traveling, grooming, or interacting), or 3) nondiving, which we considered to be resting. We identified activity bouts through a step-wise process.

1. We examine all forage dives in the record (i.e., removing nonforage dives)—the first forage dive initiates a forage bout, which continues as long as surface intervals between dives are ≤ 20 minutes. Any surface interval > 20 minutes results in a new forage bout beginning at the start of the next forage dive following this surface interval. Nonforage dives are then reintegrated, and any dives falling within identified forage bouts are considered

part of the forage bout (i.e., they do not become a separate sub-bout within the forage bout). However, we can identify nonforage time within forage bouts by summing nonforage dive times and their respective surface intervals. We then divided the final 20-minute surface interval depending on what follows:

- A. If no diving occurs within the 20-minute surface interval, then 10 minutes is assigned to the forage bout (from the start of the last forage dive to allow for handling of the final prey item) and 10 minutes is assigned to other activity (to allow for typical surface swimming and grooming behaviors that may not entail diving prior to resting). At that point, a resting bout begins 20 minutes after the beginning of the last forage dive.
 - B. If a nonforage dive falls within the final 20-minute surface interval following a final forage dive the total surface interval up to the start of the nonfeeding dive is assigned to the forage bout, and a nonforaging other activity bout begins at the start of the nonforage dive.
2. Next, we examine all nonfeeding dives not already assigned to forage bouts, and again, contiguous dives with surface intervals ≤ 20 minutes are combined into sequentially numbered other activity bouts. The final 20-minute surface interval of the other activity bout is again divided depending on what follows:
 - A. If no diving occurs within the 20-minute surface interval following the last other dive then, 10 minutes is assigned to the other activity bout (from the start of the last dive), and at this point, a resting bout begins 10 minutes after the beginning of the last nonforage dive.
 - B. If a feeding dive falls within the final 20-minute surface interval following an other dive, the total

surface interval up to the start of the feeding dive is assigned to the other activity bout, and a feeding bout begins at the start of the forage dive. Because forage bouts have already been identified, short forage bouts (usually 1 or 2 forage dives) may occur within the newly identified other activity bouts, these become sub-bouts of foraging activity.

3. We assign extended surface intervals (i.e., no recorded dives for >20 min) to nondiving or resting bouts. Any diving activity lasting >20 minutes makes a break in the resting bout and we assigned the next extended surface interval as the new resting bout. However, short bouts of diving activity lasting <20 minutes (usually 1 or 2 dives) do not cause a break in the resting bout, and are assigned as a sub-bout of activity within the extended resting bout. Our 20-minute cut-off for foraging bouts reflected the maximum observed surface prey-handling time of 16 minutes, measured during 10,000 recorded surface intervals in southeast Alaska (J. L. Bodkin, United States Geological Survey, unpublished data). When summing activity times, we subtracted time in sub-bouts of alternative behavior and we added those times to the appropriate behavior type. We incorporated the bout definitions described above into code allowing for automated classification of behaviors.

Finally, we summed the total time for each activity category for the entire TDR record, making any necessary adjustments for nested sub-bouts, to compute an overall activity budget for each individual during the period of data collection. We next used the underlying bout information to create an activity record for every 10-minute interval of the TDR record that would be analogous to, and directly comparable with the instantaneous, focal-animal sampling data traditionally collected through VHF telemetry and direct observation in past behavior studies (Estes et al. 1986, Garshelis et al. 1986, Ralls and Siniff 1990, Garshelis and Johnson 2001, Gelatt et al. 2002). Thus, each 24-hour day contained 144 data points with activity assigned according to the underlying activity assignments. We used the 10-minute interval data to provide confidence intervals around the computed overall time budgets in the sense of a daily mean activity budget. That is, because there is no variance estimate from the continuous activity record (it is simply the sum of all the time within the TDR record) it gave no sense of the individual daily variation in time activity budgets. We obtained variance estimates associated with the mean daily time budgets based on the 144 daily activity data points for each individual in our sample.

We used *t*-tests to compare male and female activity patterns, and activity patterns between areas using individuals as the sampling unit (i.e., $n = 9$ F and 5 M or $n = 10$ from Port Althorp and 4 from Idaho Inlet), when data met tests of normality and equal variances. When data assumptions were not met, we used the Mann-Whitney rank sum to compare sex and area effects and test results are reported as median values in the text. We interpreted

statistical significance at $P < 0.05$. Because we had only one male that was resident only at Port Althorp and no females that were resident only at Idaho Inlet, we were unable to test potential interactions between sex and area in time allocations. We performed all data manipulations and analysis with Excel (Microsoft Corp., Redmond, WA), SigmaStat (Systat Software, Inc., San Jose, CA) and SAS (SAS Institute, Inc., Cary, NC) software.

Sea Otter Diet and Foraging Success

We measured sea otter foraging success and prey composition and size using focal animal foraging observations and activity scan sampling techniques (Altmann 1974) adapted for sea otter work in past studies (Calkins 1978, Estes et al. 1981, Doroff and DeGange 1994, Dean et al. 2002). We used high-power telescopes (Questar, New Hope, PA) and 10× binoculars to record forage success and prey type, number, and size during foraging bouts of focal animals at sites within Port Althorp and Idaho Inlet. We identified prey to the lowest taxa possible that occasionally resulted in classification of prey above the species level (e.g., we considered clams, crabs [*Telmessus* spp., *Cancer* spp., *Paralithodes* spp.], and urchins [*Strongylocentrotus* spp.] as single prey types). We estimated prey sizes as categorical values using the average sea otter forepaw width of 52 mm as a reference (J. L. Bodkin, unpublished data). Size categories ranged from <26 mm (≤ 0.5 paw width) to 234 mm (>4 paw widths) in 26-mm intervals, representing 9 categories. We used the mid-point of each of the 9 categories (in mm) to calculate mean sizes by prey species or type. We made foraging observations of both marked and unmarked animals from 1996 through 1999. We categorized forage bouts by prey type to allow computing of success rates by prey type (e.g., we classified a bout consisting of predominantly or exclusively clams as a clam bout). We used the chi-square statistic to evaluate differences in the proportions of prey consumed by sea otters, and we used the *t*-test to evaluate differences in the number and mean sizes of prey consumed by sea otters in Port Althorp and Idaho Inlet.

Prey Abundance

To estimate infaunal bivalve prey availability we sampled randomly selected unconsolidated sheltered intertidal habitats at Port Althorp and Idaho Inlet during May–July 2000. We used a handheld GPS to navigate to coordinates identifying each sampling location. At each site, we positioned a 200-m transect parallel to the shoreline at the zero tide level (\bar{x} lower-low water). We chose a random starting meter and excavated 10 0.25-m² quadrats placed 20 m apart to a depth of 25 cm. We sieved all sediments through a 10-mm-mesh screen, identified all clams to the lowest possible taxa, and counted and measured each clam to the nearest mm using dial calipers. For each site sampled we calculated, by species and in aggregate, the mean density of clams per 0.25 m², mean biomass (g/0.25 m²), and the size-class distribution of clams.

Table 2. Sea otter identification (ID) and number of days of time–depth recorder (TDR) data collected in southeast Alaska, USA, May–July 1999. All animals residing in primarily Port Althrop were females except ch–wh, which is included in Althrop and male means. All animals residing in primarily in Idaho Inlet were males. For each activity category the average bouts per day (b/d), mean bout duration (Dur [hr]), and summed proportion of time (P time) are for the entire TDR record.

Otter ID	Time TDR data collected (d)	Foraging				Other diving				Resting			
		b/d	Dur	P time	SD ^a	b/d	Dur	P time	SD	b/d	Dur	P time	SD
Althrop													
aq–aq	46	6.2	1.4	0.37	0.10	8.0	0.36	0.12	0.09	4.8	2.6	0.52	0.13
re–wh	44	5.1	2.3	0.48	0.10	7.0	0.25	0.07	0.05	4.0	2.7	0.45	0.12
lb–lb	46	6.3	1.6	0.43	0.06	10.9	0.22	0.10	0.03	5.5	2.1	0.47	0.05
ch–ch	43	6.2	1.5	0.39	0.07	9.1	0.31	0.11	0.04	4.6	2.6	0.49	0.07
lb–wh	39	5.8	1.3	0.33	0.06	9.4	0.28	0.10	0.04	4.9	2.8	0.57	0.09
pi–wh	41	3.7	2.8	0.43	0.09	5.0	0.22	0.04	0.03	3.1	4.1	0.53	0.09
pu–pu	46	6.0	1.5	0.38	0.07	8.0	0.24	0.08	0.03	4.5	2.9	0.54	0.08
si–si	42	4.4	2.0	0.36	0.06	7.0	0.23	0.07	0.03	3.9	3.5	0.58	0.08
go–wh	39	4.9	2.2	0.45	0.07	6.4	0.19	0.05	0.03	4.4	2.8	0.50	0.07
ch–wh M	44	7.2	1.3	0.40	0.03	10.7	0.26	0.12	0.03	4.8	2.5	0.48	0.05
\bar{x}	F	5.4**	1.9**	0.40**	0.05	7.9**	0.26*	0.08	0.03	4.4*	2.9	0.52	0.04
	Althrop	5.6*	1.8**	0.40**	0.05	8.1**	0.26*	0.09	0.03	4.4*	2.9	0.51	0.04
Idaho													
or–or	46	9.1	0.8	0.30	0.08	14.9	0.50	0.30	0.13	6.9	1.5	0.40	0.14
ye–ye	44	7.1	1.0	0.30	0.06	12.0	0.35	0.17	0.11	5.2	2.5	0.53	0.12
re–re	46	7.4	0.9	0.27	0.07	12.2	0.36	0.18	0.12	5.8	2.3	0.55	0.10
wh–wh	46	5.8	1.0	0.23	0.08	9.4	0.25	0.10	0.04	4.8	3.4	0.67	0.08
\bar{x}	M	7.3	1.0	0.30	0.06	11.8	0.34	0.17	0.08	5.5	2.4	0.53	0.08
	Idaho	7.4	0.9	0.28	0.03	12.1	0.36	0.18	0.09	5.7	2.4	0.54	0.09

^a We calculated SD of P time by breaking the TDR record into daily units using 10-min sub-samples and we based significance tests on that sub-sampling. Asterisks indicate significance level of area (Althrop vs. Idaho) and sex differences.

* $P < 0.05$.

** $P < 0.01$.

RESULTS

We recovered TDRs from 15 individuals (5 M and 10 F) consisting of 2 groups. One group included 10 individuals (9 F and 1 territorial M) that largely remained residents of Port Althrop. The other group consisted of 5 adult males that resided predominantly in Idaho Inlet but on occasion returned approximately 20 km to Port Althrop. One female (re–wh) spent 8 days at Idaho Inlet with the rest of the time spent at Port Althrop (Fig. 1). Females were generally younger ($\bar{x} = 5.9$ yr) than males ($\bar{x} = 7.0$ yr) and weighed significantly less per unit length (181 g/cm) than males (285 g/cm, $t = -12.7$, $P < 0.001$; Table 1). We obtained 46 days of continuous data from 6 of the recovered instruments, and 39–44 days for the remaining 8 (Table 2).

Time–Activity Budgets

Activity–time budgets varied among individuals, sexes, and areas (Althrop and Idaho; Table 2). The mean proportion of time allocated to foraging among all individuals over all days was 0.37 (SE = 0.02; 8.9 hr/d, SE = 29 min) and ranged from 0.23 to 0.48 (5.5–11.5 hr/d). Females allocated on average 2.4 hours per day more toward foraging (9.6 hr/d) than males (7.2 hr/d; Table 2). Among individuals residing in Port Althrop, the average allocation of time to foraging was also 9.6 hours per day, which was 2.9 hours per day greater than the 6.7 hours per day average among individuals residing in Idaho Inlet (Table 2). Sea otters in Port Althrop and females had significantly fewer forage bouts per day than those in Idaho Inlet (5.6 and 5.4 vs. 7.4

and 7.3, respectively; Table 2). Mean forage bout duration was 1.8 hours in Port Althrop and 1.9 hours among females, and included an average of 16 minutes of other dive activity within the forage bout. In contrast, individuals residing primarily in Idaho Inlet and males had feeding bout durations that averaged about 1 hour less than at Port Althrop (0.9–1.0 hr), and included an average of 11 minutes of other dive activity. Median maximum forage–bout duration among individuals in Port Althrop was 7.0 hours, which was significantly greater than the 4.0 hours in Idaho Inlet ($T = 10.0$, $P = 0.007$). The maximum continuous forage–bout duration was 8.6 hours for a female at Port Althrop and 4.4 hours for a male in Idaho Inlet. Average daily minimum and maximum allocation to foraging was nearly 3 hours more at Port Althrop (5.5 hr/d vs. 2.8 hr/d and 13.6 hr/d vs. 10.9 hr/d; Table 3).

Sea otters residing in Port Althrop engaged in other diving behaviors nearly 3 hours per day less (0.09, SE = 0.01 hr/d or 1.2 hr/d) on average compared to otters residing primarily in Idaho Inlet (0.18, SE = 0.04 hr/d or 4.1 hr/d), but the sex effect was not significant (Table 2). Sea otters in Port Althrop and females had significantly fewer other activity bouts per day than in Idaho Inlet and males (8.1 vs. 12.1 by area and 7.9 vs. 11.8 by sex; Table 2). The mean duration of other diving bouts was significantly less at Port Althrop than at Idaho Inlet (15 min vs. 22 min, $t_1 = -2.79$, $P = 0.016$) and among females compared to males (16 min vs. 20 min, $t_1 = -2.23$, $P = 0.045$). Maximum durations of continuous other diving bouts were 3.8 hours by a female in Port Althrop and

Table 3. Daily mean minimum and mean maximum allocations of time (proportion of 24-hr d) to activity categories for individual sea otters at Port Althorp and Idaho Inlet, southeast Alaska, USA, and for areas combined, May–July 1999.

	Foraging				Other diving				Resting			
	Min.	Dur ^a	Max.	Dur	Min.	Dur	Max.	Dur	Min.	Dur	Max.	Dur
Althorp	0.23 ^b	5.5	0.57 ^b	13.6	0.03 ^b	0.63	0.20 ^b	4.9	0.33	7.9	0.71	17.1
SE	0.03		0.03		0.005		0.02		0.02		0.03	
Idaho	0.11	2.8	0.45	10.9	0.05	1.13	0.46	11.0	0.28	6.8	0.74	17.8
SE	0.03		0.04		0.008		0.08		0.08		0.03	
\bar{x}	0.20	4.7	0.53	12.8	0.03	0.77	0.28	6.6	0.32	7.6	0.72	17.3
SE	0.02		0.03		0.005		0.04		0.03		0.02	

^a Duration (hr).

^b Indicates significance level ($P < 0.05$) of area (Althorp vs. Idaho) effect. Significance tests based on 10-min sub-sampling of each individual's complete daily record.

5.5 hours by a male in Idaho Inlet. Average daily minimum allocations of time to other diving was about 30 minutes less at Port Althorp compared to Idaho Inlet (43 min and 72 min, respectively). Maximum daily allocations of time to other diving was 6.1 hours less at Port Althorp compared to Idaho Inlet (4.9 hr and 11.0 hr, respectively; Table 3).

Individuals spent an average of 0.52 (SE = 0.02; 12.5 hr/d \pm 23 min) of their time resting. Mean values did not differ significantly by area or sex (Table 2). However, the mean number of resting bouts per day was significantly greater in Idaho Inlet (5.5 vs. 4.4). Mean duration of resting bouts was 2.7 hours, and the mean maximum resting bout duration was 12.4 hours and did not differ between areas. However, animals at Port Althorp tended to rest about 30 minutes longer during each rest period (\bar{x} = 2.9 hr vs. 2.4 hr). Maximum continuous resting bout duration was 20.1 hours for a female at Port Althorp, and 14.1 hours for a male in Idaho Inlet. The average daily minimum time allocated to resting was 7.7 hours and the average daily maximum was 17.3 hours among all individuals, and neither differed between areas.

Individual and Daily Variation in Time Budgets

The mean allocation of time to the behavior categories we defined was fairly uniform over the duration of the study within areas (Table 2). However, variation in daily time budgets was evident within and between areas (Fig. 2) and within individuals over time (Fig. 3). Daily minimum and maximum mean allocations of time to foraging were significantly greater at Port Althorp (min. = 5.5 hr vs. 2.8 hr, and max. = 13.6 hr vs. 10.9 hr, respectively; Table 3). Daily minimum and maximum mean allocations of time to other diving behaviors were greater at Idaho Inlet (min. = 38 min vs. 68 min, and max. = 4.9 hr vs. 11.0 hr, respectively; Table 3). There was no difference in the mean minimum or mean maximum proportions of time allocated to resting behaviors between areas.

The difference between individual daily minimum and maximum proportion of time allocated to foraging or resting activities did not differ between areas (\bar{x} Δ = 0.33 hr or 7.9 hr, and 0.40 hr or 9.6 hr for foraging and resting, respectively). In contrast, the difference between daily maximum and minimum time allocated to other diving

behaviors differed by both sex and area. At Port Althorp the average difference was 0.17 (4.1 hr) versus 0.41 (9.8 hr) at Idaho Inlet ($t_1 = -4.17$, $P < 0.001$), and 0.18 (4.3 hr) for females versus 0.36 (8.7 hr) for males ($t_1 = -2.73$, $P = 0.018$).

Although our sample of individuals precludes separation of the potentially confounding effects of sex and area, suggestions of the relative contribution of these 2 factors in the differences we detected are evident in our data. The single territorial male (ch-wh) that resided only in Port Althorp had an activity budget very similar to Port Althorp

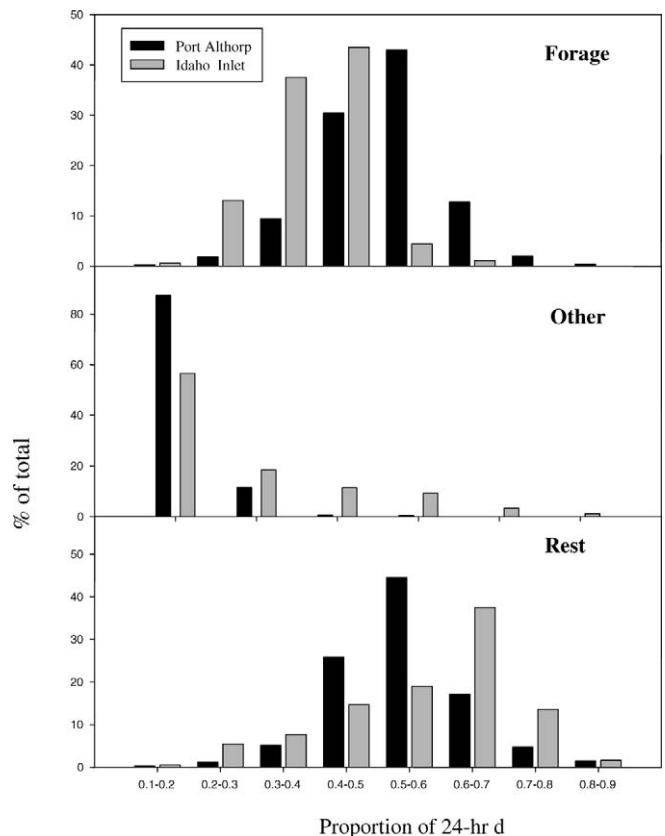


Figure 2. Daily variation in the distribution of time allocated to foraging, other, and resting behaviors for 10 sea otters residing in Port Althorp and 4 in Idaho Inlet, southeast Alaska, USA, during May–July 1999. Estimates based on sub-sampling of entire data set at 10-minute intervals. Each interval = 2.4 hours.

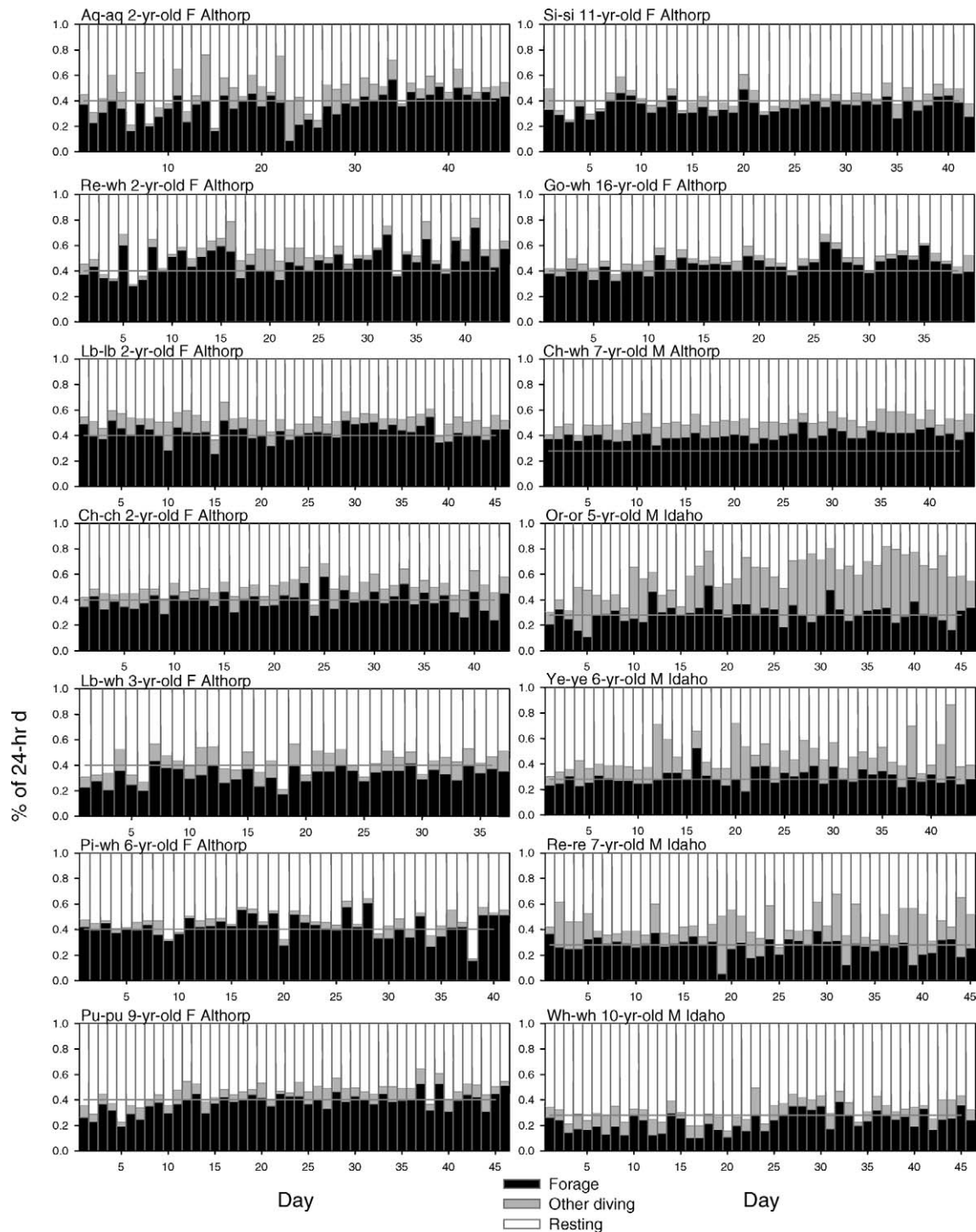


Figure 3. Individual variation in the proportion of time allocated to behavior categories by 14 sea otters over 42–46 days in southeast Alaska, USA, May–July 1999. Solid lines represent mean feeding proportions at Port Althorp and Idaho Inlet, respectively. Data based on sub-sampling of entire data set at 10-minute intervals.

females including a relatively high proportion of time spent foraging (0.40, or 9.6 hr/d). In contrast, the single male that resided only in Idaho Inlet had the lowest mean foraging time among all individuals (0.23, or 5.5 hr/d) and the highest mean resting time (0.67, or 16.2 hr/d) of all animals during the study. Individuals that used both Port Althorp and Idaho Inlet appeared to change their activity budget depending on the area of residence. The 3 males that

traveled from Port Althorp to Idaho Inlet significantly increased their average foraging time while at Idaho Inlet (7.3 hr/d) compared to their foraging time while residing in Port Althorp (6.0 hr/d, $t_1 = -4.92$, $P = 0.008$; Table 4). Males from Idaho Inlet also increased their average daily allocation to other diving behaviors from 4.2 hours per day to 6.3 hours per day while in Port Althorp, although this difference was not significant, and one male actually spent

Table 4. Mean allocation of time to activity categories by area for 4 individual sea otters that spent time in both Port Althorp and Idaho Inlet, southeast Alaska, USA, May–July 1999, and for the days they traveled between areas.

Otter ID	Sex	Location	Time spent (d)	Foraging	Other diving	Resting
re-wh	F	Althorp	35	0.49	0.05	0.46
		Idaho	6	0.40	0.14	0.46
		Travel	3	0.47	0.16	0.37
or-or	M	Althorp	5	0.25	0.42	0.33
		Idaho	25	0.31	0.22	0.47
		Travel	16	0.29	0.38	0.33
ye-ye	M	Althorp	11	0.27	0.11	0.63
		Idaho	32	0.31	0.18	0.51
		Travel	1	0.28	0.44	0.28
re-re	M	Althorp	8	0.23	0.25	0.52
		Idaho	30	0.29	0.12	0.58
		Travel	8	0.24	0.30	0.46

less time in other diving while at Port Althorp. Time allocated to resting was similar for these 3 males at both locations (11.8–12.5 hr/d). The opposite pattern occurred for the single female that resided at both locations as she decreased her foraging time (9.7 hr/d vs. 11.9 hr/d) and increased other activities (3.4 hr/d vs. 1.2 hr/d) when she was in Idaho Inlet compared to when she resided in Port Althorp. These contrasting patterns of change are actually consistent with a general finding of more food available at Idaho Inlet when viewed with some knowledge of sea otter social structure (see Discussion). On days when the 4 animals that used both locations traveled between locations, they generally spent less time foraging and resting and more time in other diving behaviors (M \bar{x} = 0.37 or almost 9 hr/d), likely related to traveling (Table 4).

Sea Otter Diet and Foraging Success

We observed 92 forage bouts averaging 14 dives per bout at Althorp, and 14 bouts averaging 5 dives per bout at Idaho (Table 5). Among forage dives with known outcomes, the success rate was essentially 1.0 at Idaho Inlet for all prey types (1.0 for clams, crabs, urchins, and other prey types [primarily gastropods, chitons, and stars]). Foraging success was lower at Port Althorp (0.93, 0.83, 0.85, 0.78 for clams, crabs, urchins, and other prey types, respectively). Although prey composition differed between areas ($\chi^2 = 42.48$, $P < 0.001$; Table 5), clams were the dominant prey in both areas (0.83 at Port Althorp and 0.69 at Idaho Inlet), with other prey (mussels, snails, sea stars, and urchins) equaling <0.10 of other identified prey items. Crabs were 0.29 of the diet at Idaho Inlet, compared to only 0.02 at Port Althorp. Sea otters at Idaho Inlet retrieved significantly more clams per dive than otters at Port Althorp ($\bar{x} = 3.3/\text{dive}$ vs. $2.2/\text{dive}$,

respectively; $t_1 = -2.40$, $P = 0.018$), but the number retrieved per dive was not different for any other prey types, averaging 1.1 for crabs, 2.9 for urchins, and 1.2 for other prey. The mean size class of all prey types was significantly larger at Idaho Inlet, with clams averaging only 50 mm (26–52-mm size class) at Port Althorp, compared to 78 mm (78–104-mm size class) at Idaho Inlet ($t_1 = -8.54$, $P < 0.001$). In Port Althorp, the helmet crab (*Telmessus cheiragonus*) was most common species (0.60 of identified crabs) and the mean size was 72 mm (52–78-mm size class) carapace width. In Idaho Inlet, we most commonly observed Dungeness (*Cancer magister*) and king crab (*Paralithodes* sp.; 0.67 and 0.33, respectively), averaging 136 mm (130–156-mm size class) in carapace width. Urchins (*Strongylocentrotus* sp.) averaged 48 mm (26–52-mm size class) at Port Althorp and we did not observe them in the diet at Idaho Inlet, and other prey averaged 90 mm (78–104-mm size class) at Port Althorp, compared to 104 mm (104–130-mm size class) at Idaho Inlet. The smaller number and sizes of prey retrieved at Port Althorp likely contributed to sea otters having shorter average dive and surface times compared to Idaho Inlet for each prey type (Table 5).

Prey Availability

We sampled intertidal clam populations at 12 sites (120 quadrats) in Port Althorp and 14 sites (140 quadrats) in Idaho Inlet. In aggregate and for each species encountered, clams were more abundant in Idaho Inlet than in Port Althorp (Fig. 4), although only for species of *Macoma* were the differences significant. There were no differences in mean sizes of any clam species sampled between areas. Estimated intertidal clam biomass was nearly twice as great

Table 5. Sea otter prey composition and mean dive time plus surface time of forage dives for sea otters at Port Althorp and Idaho Inlet, southeast Alaska, USA, 1996–1999.

Location	Prey composition ^a				\bar{x} dive + surface times (sec)				
	Clam	Crab	Urchin	Other	Clam	Crab	Urchin	Other	None
Althorp	0.83	0.02	0.08	0.08	158	212	134	154	104
Idaho	0.69	0.29	0.00	0.02	224	271		207	

^a Species of clam included *Saxidomus*, *Protothaca*, *Macoma*, *Mya*, and *Clinocardium*. Species of crab included *Telmessus* at Port Althorp and *Cancer* and *Paralithodes* at Idaho Inlet. Urchins were *Strongylocentrotus* sp., and other includes unidentified gastropods, chitons, and echinoderms (stars).

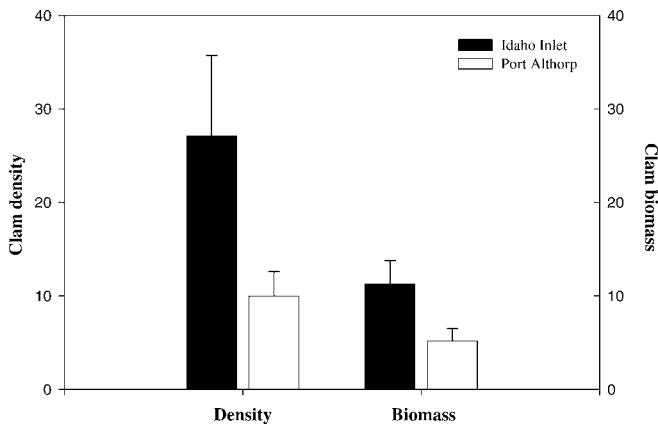


Figure 4. Densities (no./0.25 m²) and biomass (g ash-free dry wt/0.25 m²) estimates of intertidal clams (*Protothaca staminea*, *Saxidomus gigantea*, *Macoma* sp., *Mya* sp., *Hiatella* sp., *Pseudopythina* sp., and *Clinocardium* sp.) from Port Althorp and Idaho Inlet, southeast Alaska, USA, May–July 2000. Biomass estimates based on length–weight relations (Wacasey and Atkinson 1987, Dean et al. 2002).

in Idaho Inlet for all species, although again, the differences were only significant for *Macoma* species.

DISCUSSION

Time–Activity Budgets

Using uninterrupted records of behaviors derived from archival time–depth recorders over relatively long periods, we provide a new method to estimate time budgets in air-breathing, diving vertebrates. Our estimates of time allocated to diving and nondiving behaviors were sufficiently precise to detect significant differences among individuals, sexes, and areas where study animals resided. Our independent estimates of foraging success and prey availability suggest that where prey were more abundant, sea otters allocated less time to foraging and more time to other behaviors, primarily reproductive. Conversely, where prey was less abundant, more time was spent foraging and less time in other behaviors.

As a consequence of their polygynous reproductive system, sea otter populations are generally segregated into areas occupied by reproductive females and territorial males, and areas occupied by high-density aggregations of bachelor males that must travel to gain access to females (Kenyon 1969, Riedman and Estes 1990). In expanding populations, bachelor males tend to aggregate at and extend the boundary of the occupied habitat, presumably taking advantage of the abundant food resources available there (Riedman and Estes 1990). Occupied for >25 years, Port Althorp, where we captured our study animals, was a female area at or near carrying capacity relative to food, whereas Idaho Inlet, where most of our males study animals resided, was occupied for 3–9 years, was considered to be well below carrying capacity, and was occupied almost exclusively by males (Bodkin et al. 2004). Thus, male reproductive opportunities are almost nonexistent in Idaho Inlet.

The motivation for males to travel from Idaho Inlet, where prey were more abundant, to Port Althorp, where females

were more abundant but prey were not, appears largely related to reproductive opportunities. We base this conclusion on contrasting several of our results. 1) Males that traveled between areas tended to increase feeding and resting time while residing at Idaho Inlet (i.e., replenishing energy reserves), but then decreased feeding time and increased other activities while at Port Althorp (i.e., expending reserves for reproductive opportunities; Table 4). In fact, we regularly observed or–or and re–re, in particular, consorting with adult females while in Port Althorp. In contrast, the oldest male (wh–wh; Table 1), a 10-year-old animal, was observed only in Idaho Inlet after the initial capture, allocated the least amount of time toward foraging and the most toward resting, with relatively little investment in other activities. This animal also gained the most weight between captures of any animal in the study. 2) Female re–wh was the only female that moved between areas, but unlike the males, she decreased her forage time while at Idaho Inlet compared to her forage time while in Port Althorp (Table 4). It appears this move may have represented a significant energy savings in terms of foraging effort, as her time allocated to feeding while in Port Althorp was much higher than any other female residing at Port Althorp, and only while at Idaho Inlet did she lower her feeding time to a level similar to the other females. In contrast to the males that traveled between areas, the other male reproductive strategy (territoriality) exhibited by ch–wh (Table 2) resulted in a time budget indistinguishable from females residing in Port Althorp, but presumably in more reproductive opportunities and less energy spent in travel time. Thus, it appears that time budgets may reflect social and behavioral constraints in addition to reflecting prey availability.

The time budgets we calculated with TDRs from Port Althorp are similar to time budgets estimated using other methods from populations near or below equilibrium densities (Garshelis et al. 1986, Ralls and Siniff 1990, Gelatt et al. 2002). The time allocated to foraging by adult males in Idaho Inlet is less than reported from any population studied to date, including populations considered to be below equilibrium density, and the pattern of greater allocation to other behaviors by males is similar across studies (Gelatt et al. 2002).

Daily variation in time budgets were not equal among individuals, or consistent over time within each individual (Fig. 3). We have attributed a portion of the variation in activity budgets among individuals to location (food availability), sex differences, and social behaviors (accessing F). It is also likely that dietary differences are contributing to variation in time budgets among and within individuals. Estes et al. (2003) found significant and persistent variation in individual sea otter prey selection in long-occupied rocky substrate habitats in central California, USA. The role of dietary specialization in soft-sediment habitats remains unexplored but could contribute to the activity patterns among and within individuals displayed in Figure 3. For example, individuals with high daily variability in foraging

may be specializing in relatively large high-energy prey, which provide larger payoffs when found but also present a greater risk of negative energy balance on days when fewer prey items are recovered. In contrast, a specialist on smaller items may have a dependable consistent prey source which results in lower daily variation in foraging time but overall less energy per item and, thus, higher energy expenditure for the same caloric return. Relatively small sample sizes of diet on most individuals in this study precluded testing these ideas.

Because TDR-derived activity budgets rely entirely on diving to classify behaviors, activities that do not include diving may be underrepresented. For example, an individual's behavior while swimming on the surface without diving for periods >20 minutes would be classified as nondiving and interpreted as resting. This scenario may be particularly relevant for females with small pups that may spend significant amounts of time swimming at the surface while carrying and grooming their pup. We found only one female with a pup while instrumented, but it was lost within a few days of parturition and it did not influence her activity budget to a great degree. Inclusion of 10 minutes of foraging and other diving activity postforaging (e.g., grooming or interacting) was provided as compensation for this potential source of bias. A second type of behavior that may affect time-budget estimates using TDR data is foraging to depths <2 m (i.e., intertidal zones or in surface kelp canopies), where diving may not be detected with instruments used here. We rarely observed very shallow foraging in the intertidal zone for extended periods and the relatively infrequent (<20 min) requirement of a foraging dive >2 m is intended to minimize this potential bias. Also, kelp canopies in our study area were limited to relatively small beds of bull kelp (*Nereocystis luetkeanus*) and ribbon kelp (*Alaria fistulosa*) where canopy-foraging for epibenthic invertebrates such as snails and crabs was not observed. This bias may be more important in places where canopy-foraging in the giant kelp (*Macrocystis* sp.) is common. However, swimming and other activities generally result in some amount of diving behavior, and once a dive activity is initiated, the bout definition results in an activity bout ≥ 20 minutes if foraging (10 min of foraging time and 10 min of other activity) or 10 minutes for other diving. Despite the potential biases in both observational and TDR-derived activity budgets, the consistent pattern of greater allocation by males to other activities among studies suggests a generality among sea otter populations independent of methods or population status. Further, the differences we detected in time budgets using TDRs should reflect any potential sources of bias equally between sex and area.

The significantly greater allocation of time to other activities by males traveling between male aggregations in Idaho Inlet and the female area in Port Althorp can be attributed to reproductive behaviors. Further, the single male (ch-wh; Table 2) that maintained an exclusive breeding territory in Port Althorp allocated slightly more time toward other diving (including patrolling and defending his territory) than the average other diving behavior of

females in Port Althorp (0.11 vs. 0.08). Thus, either through long-distance travel or territory defense, males appeared to be allocating proportionately more effort into accessing females than the converse. This additional expenditure of effort may be a factor contributing to the generally higher mortality rates observed in male sea otters, as well as other sexually dimorphic and polygynous mammals (Siniff and Ralls 1991, Monson and DeGange 1995).

We intended to simply apply TDR technology to estimate time budgets in a single population of sea otters. Thus, our comparison of areas that differed in food resources is fortuitous even if sampling allocation was less than ideal. Acknowledging the confounding effects of sex on our area comparisons, contrasts of our findings of foraging and resting allocations with results from other studies supports the conclusion that the southeast Alaska population of sea otters we studied is below equilibrium density with respect to food resources, particularly in the more recently colonized Idaho Inlet. Our contrasts of foraging, other diving, and resting times at Idaho Inlet compared to Port Althorp further supports the conclusion that measures of activity budgets, estimated from continuous records of behavior as determined from archival TDRs, provide relatively sensitive estimates of population status relative to prey availability.

MANAGEMENT IMPLICATIONS

Effective conservation and management of wildlife will benefit from new approaches and additional tools to evaluate the status of populations relative to limiting resources. Specifically, approaches that provide evaluation of factors that are presently affecting vital rates and, thus, future population trends, are needed. Activity time budgets, as they reflect the effort required to obtain necessary energetic or nutritional resources, provide a way to measure the availability of food, one of the fundamental factors recognized to influence vital rates within populations. Activity time budgets as an approach for evaluating the status of populations has been validated across both avian and mammalian taxa. For birds and mammals that dive to obtain food, TDRs provide a powerful new tool to estimate time budgets over long and continuous time periods. These instruments are capable of recording nearly continuous records of diving behavior, and by inference, other behaviors, for periods of years. Such data will allow evaluation of an individual's ability to obtain food over the spatial and temporal scales that are most relevant to the critical demographic variables of reproduction and survival.

ACKNOWLEDGMENTS

This work was supported by the United States Geological Survey, Alaska Science Center; Purdue University; and the Monterey Bay Aquarium. Significant contributions to this work were provided by B. Ballachey, J. DeGroot, J. de la Bruere, A. Doroff, J. Estes, T. Gelatt, K. Kloecker, K. Miles, K. Oakley, P. Snyder, M. Staedler, T. Tinker, and G. Wrobel. A. DeGange, B. Ballachey, K. Oakley, L.

Holland-Bartels, T. Tinker, and 2 anonymous reviewers provided valuable comments on this paper.

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Associate Editor: Morrison.