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Time and energy allocation of female sea otters (*Enhydra lutris*) with pups in Alaska

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ABSTRACT

The behavior of sea otters (*Enhydra lutris kenyoni*) with dependent pups was observed between May and August of 2005–2010 in Simpson Bay, Alaska using focal follows and instantaneous sampling. Six behaviors (foraging, grooming, resting, swimming, swimming slowly and interacting) were recorded during four, 6-h time periods (dawn [05:00–11:00], day [11:00–17:00], dusk [17:00–23:00] and night [23:00–05:00]) to create a 24-h activity budget. Overall, 1190 focal follows were conducted for a total of 595 h. Females with dependent pups spent the greatest percentage of the day resting (42%), about equal percentages foraging (18%), grooming (15%), swimming (15%), swimming slowly (8%) and interacting (2%). Field Metabolic Rate (FMR) was estimated by using the oxygen consumption (ml O_2 min^{-1} kg^{-1}) for each behavior for captive otters (Yeates et al., 2007). The estimated FMR for females with a dependent pup was 12.69 MJ day^{-1} with the following absolute and percentage allocations for each behavior: foraging 2.38 (19%), grooming 2.70 (21%), resting 3.42 (27%), swimming 2.64 (21%), swimming slowly 1.25 (10%) and interacting 0.3 (2%). The estimated weight specific FMR was 601 kJ day^{-1} kg^{-1}, similar to that reported for territorial males in the same area. The sea otter population in Simpson Bay has been stable for at least the last 12 years. It would follow then that the time spent foraging might be similar to other areas where the population is stable, but this is not the case. In Simpson Bay, the time spent foraging is more similar to areas that have been recently occupied. The relatively small amount of time spent foraging may indicate that geographic differences (structure of the near-shore community: substrate, water depth, kelp canopy, prey assemblage, and competitors) may play a greater role in determining the amount of time spent foraging than population status.

1. Introduction

1.1. Background

Studies of sea otter (*Enhydra lutris*) behavior have been conducted in Alaska, California and Washington using different methods with considerable variability in activity budgets, which were first proposed to assess the status of marine mammal populations (Eberhardt and Siniff, 1977).

As sea otters have large energy requirements due to an elevated metabolic rate (Costa and Kooyman, 1984), previous studies focused on foraging behavior. Estes et al. (1986) suggested that time spent foraging may be the best indicator of populations status, as food is commonly the limiting resource (Kenyon, 1969). Foraging time would be expected to increase as a population grows and approaches equilibrium density (Eberhardt and Siniff, 1977), although not all studies have found consistent results. Some of the disparities may be attributed to the use of various methods (observation vs. tagging), constraints of study design (sample size, period of data collection) and uncertainty about population status (Bodkin et al., 2007). Population studies of marine mammals are difficult for a variety of reasons. Among the fur bearing marine mammals, counts during the breading season when they gather on land or some sort of mark/tagging are common. None of these techniques work well for sea otters as they do not consistently spend time on land, capturing them in the water is difficult, and they readily remove tags attached to their fur or hind flippers. Fortunately, sea otters are relatively easy to observe as most of their time is spent at the surface. Behavior is usually divided into 3–5 categories: foraging, grooming, swimming and resting are the most common. Several studies have used radio transmitters and/or abdominally implanted archival time-depth recorders (TDRs) to compile time budgets from a small number of animals in California and Alaska (Estes et al., 1986; Garshelis et al., 1986; Ralls and Siniff, 1990; Gelatt et al., 2002; Bodkin et al., 2007). Foraging dives deeper than 2 m are easily distinguished, and data is gathered continuously for months. The disadvantage of this approach is that behavior can only be classified as foraging, resting or other (very shallow forging dives are indistinguishable from travel or grooming), so some visual observations are usually taken to validate

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the recorded data. At the other extreme are studies that employ scan-sampling to observe as many animals as possible (Altmann, 1974; Estes et al., 1982, 1986; Walker et al., 2008). However, this method is limited by access to suitable locations that can be reliably scanned from shore. Spatial distribution may bias samples (Gelatt et al., 2002), as some behaviors are more conspicuous than others (resting and grooming vs. foraging and swimming). In addition, the sex of the otters is often unknown.

1.2. Previous studies of female sea otter activity patterns

1.2.1. Radio telemetry

Garshelis et al. (1986), Ralls and Siniff (1990), and Gelatt et al. (2002) used radio telemetry to determine the activity budgets of sea otters. Activities were usually categorized as foraging, resting or swimming based on the frequency, duration and interruptions of the radio signal.

Garshelis et al. (1986) conducted their study at Green Island (central Prince William Sound, Alaska) and Nelson Bay, and concluded that, over a 24-h period, solitary females and females with pups allocated 37% of their time to foraging, 51% to resting and 12% to swimming. Gelatt et al. (2002) conducted their study around Amchitka Island, Alaska. Adult female sea otters allocated 38% of their time to foraging, 48% to resting and 14% to other activities. In California, Ralls and Siniff (1990) found that, over a 24-h period, females with dependant pups ($n = 6$) foraged 40% of the time, rested 44.7%, and spent 15.7% in other behaviors.

1.2.2. Time-depth recorders (TDR)

Bodkin et al. (2007) conducted their study near Cross Sound, located in southeastern Alaska. Activities were categorized as foraging, resting, and other (swimming, grooming, and interacting). Females allocated 40% of their time to foraging and 52% to resting, although the authors admit that non-diving behavior may have been underrepresented.

1.2.3. Scan sampling

Estes et al. (1986) used the scan-sampling method to determine the activity budget of sea otters in a rocky reef and kelp forest habitat in central California. Behavior was categorized as foraging, resting or other by sampling a group of otters in an area at 30 min intervals with binoculars. Due to low light and poor visibility, they could not use this method at night. The study concluded that the otters allocated 24% of their time to foraging, 59% to resting and 17% to other behaviors. Walker et al. (2008) used scan sampling to determine the activity budget of translocated sea otters in rocky coastal habitat along the Olympic Peninsula in Washington State, an area known to be below equilibrium density. Their study found that sea otters allocated 62% of their time to resting, 20% to grooming, 8% to foraging, 8% to swimming and 2% to other behaviors.

1.2.4. Individual follows and instantaneous sampling

Pearson and Davis (2005) and Finerty et al. (2009) conducted their studies in Simpson Bay, Alaska, the same location as this study. Activities for territorial male otters only were categorized as foraging, grooming, interacting with other otters, swimming, patrolling, and resting. Pearson and Davis (2005) concluded that during *daylight hours*, male otters allocated 30% of their time to foraging, 15% to grooming, 11% to interacting with other otters, 17% to patrolling, 18% to resting, and 9% to swimming. Finerty et al. (2009) produced a *24-h* activity budget and observed the following allocation of time: foraging 14%, grooming 19%, interacting 5%, patrolling 9%, resting 27% and swimming 26%.

In the current study, we used we used focal follows (Mann, 1999) with instantaneous behavioral samples (Altmann, 1974; Lehner, 1996; Mann, 1999; Pearson and Davis, 2005) to compile a detailed 24-h activity budget for female sea otters with pups during the summer (June to August), a period when many pups are ca. 1–3 months in age. Field Metabolic Rate (FMR) was than estimated using metabolic rates for each behavior that were measured in captive otters (Yeates et al., 2007). This FMR will be somewhat elevated from normal as the female is caring for a pup. The cost of lactation and pup grooming will be examined in subsequent studies (Cortez, in review). For the sake of brevity, the term population refers to animals in Simpson Bay with the understanding that this is a subset of the animals in Prince William Sound, and the daily and monthly movements of some animals likely encompass a much larger area.

2. Methods

2.1. Study site

Simpson Bay (ca. 60.6° N, 145.9° W), located in northeastern Prince William Sound, Alaska (Fig. 1), was used as the study site because of its protection from rough seas, reliable presence of sea otters and easy access. It is approximately 21 km^2 in area; 7.5 km long in the northern and western bays, 5 km long in the eastern bay, and 2.5 km wide at the entrance of the bay.

The study area has an average water depth of 30 m (maximum depth 125 m) and a benthos primarily of soft sediments (mud and mud/gravel) with some rocky reefs (Gilkinson, 2004; Noll et al., 2005). None of the large-bodied kelps (e.g., Nereocystis) that form canopies are present, but large fronds of sugar (*Laminaria saccharina*), split (*Laminaria bongardiana*), and sieve (*Agarum clathratum*) kelp cover the benthos in many areas of the bay from the subtidal to a depth of approximately 10 m (R. W. Davis, pers. obs.). The bay was re-colonized by male sea otters in 1977, and females moved into the area between 1983 and 1985 (Garshelis, 1983; Rotterman and Simon-Jackson, 1988; VanBlaricom, 1988). Since 2002, it has been used during the summer (June–August) by an average of 124 ± 14.7 sea otters, including adults and subadults (93 ± 8.7) and pups (31 ± 6.9) with an average summer density of 5.9 otters km^{-1} (Wolt et al., 2012). During the winter, the number of otters in the bay decreases to ca. 50, although where they disperse to is poorly understood. This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.

2.2. Focal observations

The behavior of sea otters with dependent pups was observed from a skiff from late May to mid-August of 2005–2010. Age of the pups could not be determined, but they were newborn up to ca. three months. The high latitude made visual observations possible for nearly all 24-h which was divided into four, 6-h time periods corresponding to astronomical dawn (05:00–11:00), day (11:00–17:00), dusk (17:00–23:00) and night (23:00–05:00). Because of the latitude of the study site, the light level during night observations varied over the summer. From late June to mid-July, there was adequate light for observations throughout the night. However, by early August, it was too dark to make observations around 02:00, which is astronomical midnight for this location in Alaska. As a result, we worked during periods of the night that allowed observations and avoided the darkest periods. The study area was divided into three parts (North Bay, West Bay and East Bay, Fig. 1), but no systematic vessel track was followed because the otters congregated in different locations depending on weather and other factors that are not completely understood. Instead, the skiff (with at minimum a driver and recorder/spotter) approached otters opportunistically on a search path that minimized the possibility of observing an individual otter more than once during a 3–4 h session. When an individual was sighted, the skiff was maneuvered close enough (ca. 100 m) to observe behavior with the aid of binoculars. If the individual's behavior remained unchanged once the skiff was in position, a 30 min focal follow (Mann, 1999) with 31 instantaneous

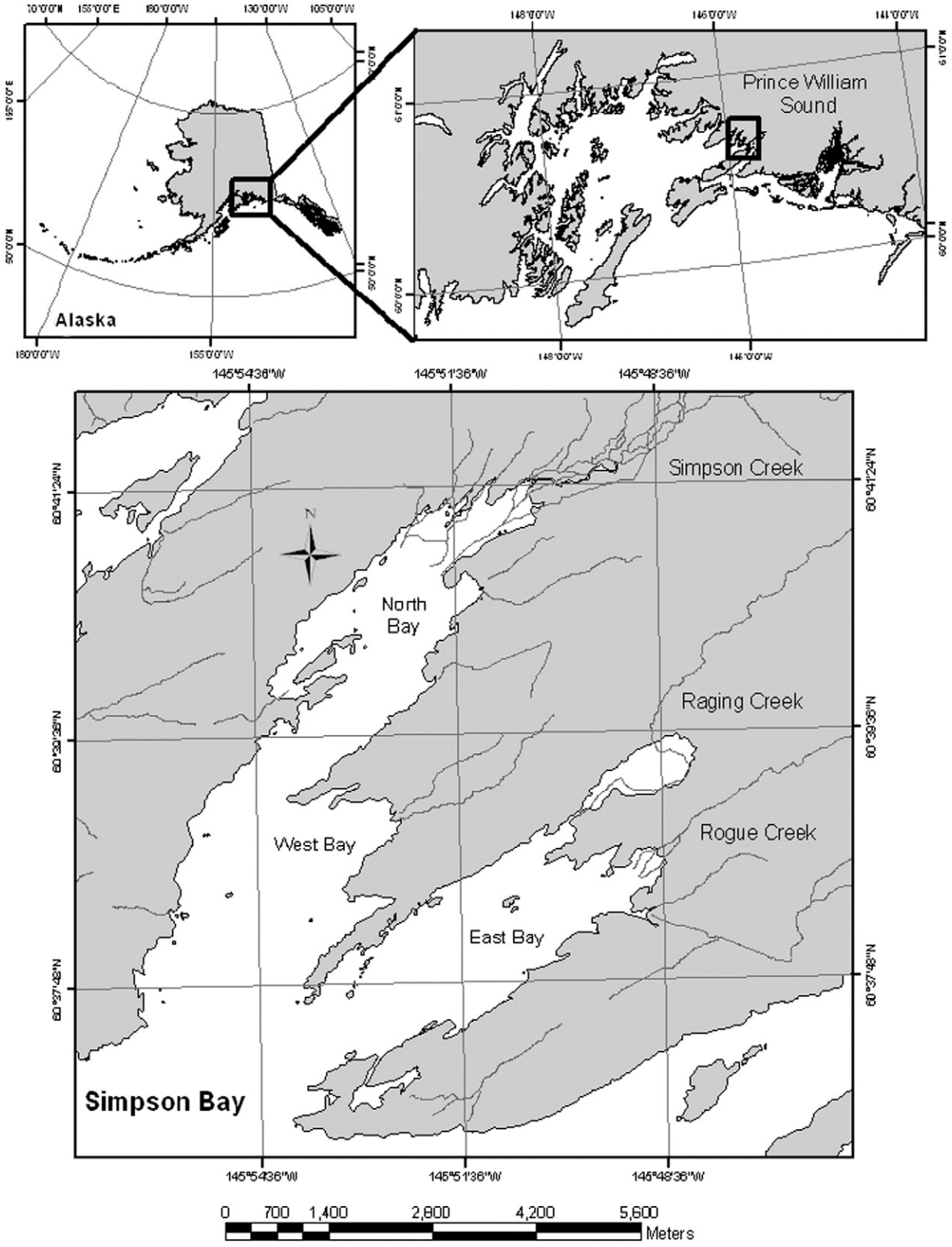

Fig. 1. Simpson Bay, Prince William Sound, Alaska (Noll et al., 2005).

samples (Altmann, 1974; Lehner, 1996; Mann, 1999; Pearson and Davis, 2005) was conducted. Behaviors, based on descriptions by Packard and Ribic (1982) included foraging, grooming (including pup grooming), resting (including nursing), swimming, swimming slowly and interacting. GPS locations were taken at the beginning and the end of each observation. After the focal follow, photo-identification based on nose scars was attempted when possible at a distance ≥30 m (Finerty et al., 2007). Since there are on average 31 female and pup pairs in the study area at any given time it is likely that some individuals were sampled more than once. We were careful not to observe the same animal in a 3–4 h session and as individual identification is impossible in most cases we treated each observation individually.

2.3. Field Metabolic Rate (FMR)

FMR was estimated by using the oxygen consumption (ml O_2 min^{-1} kg^{-1}) for resting (13.3), feeding (21.6), grooming (29.4), swimming (29.6), and interacting (24.5) for captive otters (Yeates et al., 2007) with the activity budget for the otters in this study. Yeates et al. (2007) determined oxygen consumption in captive otters under four conditions: 1) resting on the surface, 2) grooming, 3) after serial foraging dives, and 4) after single non-foraging dives Study animals were trained to dive to the bottom of a 9.1-m deep, 4-m diameter seawater tank with a metabolic dome at the surface of the water. A rocky substrate along with 3–5 kg of live crabs (*Cancer* spp.) and mussels (*Mytilus edulis*) were placed at the bottom of the tank to simulate foraging conditions in the wild. Each otter was allowed to forage by making repeated dives to the bottom to collect prey after which it surfaced beneath the metabolic dome while handling and consuming the prey. All measurements followed the methods of Williams et al. (2004b) using open-flow respirometry for aquatic mammals (Yeates et al., 2007).

Behaviors in our study that did not fall into one of the classifications of Yeates et al. (2007) were categorized as 'other' (e.g., interacting and swimming slowly). Swimming slowly was considered to be energetically the same as "other" (24.5 vs. 29.6 ml O_2 min^{-1} kg^{-1} for swimming) as only a single hind flipper or both intermittently were being used to propel the animal. The weight specific FMR (kJ day^{-1} kg^{-1}) was estimated as the sum of the energetic cost of each activity, the number of minutes per day spent in each activity (i.e., proportion of day in each activity times 1440 min day^{-1}), and a conversion factor of 2.0083×10^{-2} kJ ml^{-1} O_2 (Schmidt-Nielsen, 1997). The total FMR (MJ day^{-1}) was calculated as the product of the weight specific FMR and the mean body mass (21.1 kg) of adult female Alaskan sea otters (Kenyon, 1969) divided by 1000 to convert kJ to MJ.

2.4. Data analysis

A complete 24-h time and energy budget was created, as well as for each of the four 6-h time periods. Multivariate analysis of variance (MANOVA) was used to test for differences in the relative amount of time and energy female otters spent performing each of the six behaviors (dependent variables) among the four time periods (independent variables). If a significant difference was found, an analysis of variance (ANOVA) was used to determine the source, and a multiple comparison test run by plugging the formula into Excel. MANOVA and ANOVA were conducted in JMP (Version 10. SAS Institute Inc., Cary, NC, 1989–2010). In addition, a canonical correspondence and canonical variants analysis were conducted using CANOCO (Version 4.5) to simultaneously quantify the relative influences of multiple characteristics associated with each observation. These included 6-h period, total time (min) spent in each behavior and year (e.g., using time of day to explain variations in behavior or the variation in behavior to explain time of day). This uses a weighted averaging procedure similar to a discriminate function analysis (Lepš and Šmilauer, 2003).

3. Results

3.1. Research effort

Overall, 1190 focal follows (31 min each) were conducted for a total of 595 h; 25% (N = 291) during the dawn (05:00–11:00 h), 28% (N = 330) during the day (11:00–17:00 h), 25% (N = 303) during the dusk (17:00–23:00 h) and 22% (N = 266) during the night (23:00–05:00 h).

3.2. Activity budget

A combined (all four time periods) 24-h activity budget showed that females with dependent pups spent the greatest percentage of the day resting (42%), about equal amounts of time feeding (18%), grooming (15%) and swimming (15%), and the remainder swimming slowly (8%) and interacting (2%) (Fig. 2). An average 30-minute observation would then look as follows: resting (12.4 ± 11.0 min), foraging (5.4 ± 9.6 min), grooming (4.5 ± 5.9 min), swimming (4.4 ± 6.7 min), swimming slowly (2.5 ± 4.9 min), and interacting (0.6 ± 1.7 min). A similar allocation of time occurred among the four 6-h periods, although there were some differences (Table 1). Females spent a significantly greater percentage of their time resting during the dawn (52%) and less time (32%) during the day. In contrast, females spent a significantly greater percentage of their time foraging during the day (27%) and less time during the dawn (13%) and night (13%). In addition, females spent more time swimming during the night (20%) and less time during the dawn (9%). The percentage of time grooming (18–23%), interacting with other sea otters (2–3%) and swimming slowly (9–11%) did not differ significantly among the time periods (Fig. 3).

A MANOVA showed that there was a significant difference in the percentage of time spent in at least one of the behavioral categories among the four, 6-h time periods (Table 1). Using an ANOVA, each behavior was tested individually to identify significant differences in the amount of time spent performing each behavior among time periods (Table 3). Foraging, resting and swimming were found to have significant differences among time periods so ANOVAs and Tukey–Kramer multiple comparisons tests were run to identify which time periods differed significantly (Table 4). Foraging was significantly different among all time periods except dusk. Although resting and swimming were significantly different among all time periods according to the multiple comparisons, the ANOVAs failed to find a significant difference among all time periods (Table 4).

The canonical correspondence analysis showed resting to be most closely associated with dawn, foraging and interacting with day, and swimming with night.

The percentage of time spent grooming and swimming-slow varied the least among time periods and did not distinguish among them. While significant (p-value = 0.002), the total variation explained by time period (and year, run as a covariable) was only 4.7%, with time of day accounting for 2.4%. Canonical variants analysis (similar to the CCA but using behavior to explain time of day) showed that the greatest variation in behavior occurred during the day (4.67%) followed by dawn (3.88%), night (2.55%) and dusk (0.54%) with 3% of the total variation explained by the 6-h time period.

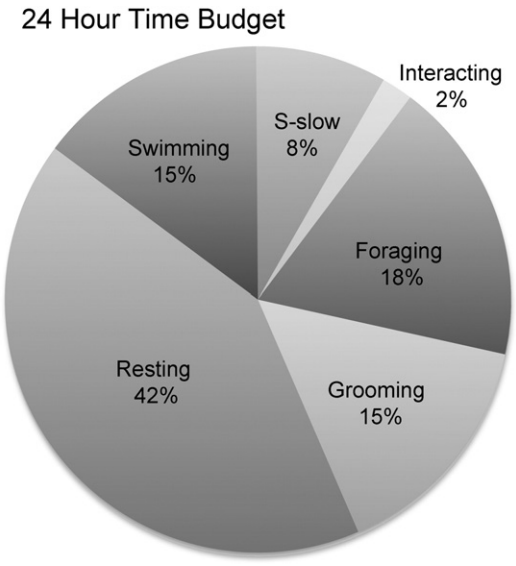

Fig. 2. Twenty-four hour activity budget for adult female sea otters with dependent pups in Simpson Bay, Alaska during summers (May to August).

Table 1
Activity budget by time period.

Activity Budget	Foraging	Grooming	Resting	Swimming	S-slow	Interacting
Dawn	13%	15%	52%	9%	9%	2%
Day	27%	13%	32%	17%	8%	3%
Dusk	19%	16%	42%	13%	8%	2%
Night	13%	16%	40%	20%	9%	2%
24-h	18%	15%	42%	15%	8%	2%

3.3. Estimated Field Metabolic Rate (FMR)

The estimated FMR for a female sea otter with a dependent pup was 12.69 MJ day^{-1} with the following contribution of each behavior: foraging 2.38 (19%), grooming 2.70 (21%), resting 3.42 (27%), swimming 2.64 (21%), swimming slowly 1.25 (10%) and interacting 0.3 (2%) (Table 5).

A MANOVA showed that dusk was the only time period that did not differ significantly. Foraging was significantly different between dawn and night (14 and 13%, respectively) compared with day (27%). The energy expended while resting differed significantly between day (20%) and dawn (36%), and for swimming between dawn (14%) and night (27%) (Tables 6 & 7).

3.4. Hourly time budget

The 24-h activity budget plotted hour-by-hour showed an overall consistency in behavior (Fig. 4). Although there was not much periodicity, the most notable change was the gradual decrease in resting towards the afternoon with a corresponding increase in foraging. Traveling increased during the night, but swimming slowly and grooming remained fairly constant throughout the 24-h cycle.

4. Discussion

4.1. Sampling methods

Shore-based scan sampling is the most common means of collecting time budget data for sea otters when animal-borne instrumentation is not possible, although this method has some distinct disadvantages because some behaviors are less easily identifiable visually. Estes and Jameson (1988) found that the probability of sighting a resting otter was 0.99, but only 0.77 for foraging otters. Spatial distribution of otters may also bias scan samples. Gelatt et al. (2002) found that activity was not consistent across ages and sexes and, since there is some degree of sexual segregation, a particular location will only reflect the cohort occupying that area. Scans are only possible during daylight hours depending on latitude and season, making comparisons between studies with and without night problematic. Even in areas that are in close geographic proximity (Green Island and Nelson Bay which are ca. 100 km apart), sea otters have been found to forage more during the day in one location (Green Island) and at night in another (Nelson Bay) (Garshelis et al., 1986), skewing any results that assume that behavior is consistent during a 24-h period. In recently occupied areas of Prince William Sound, scan sampling showed that otters spent 16% of their time foraging while with telemetry that number increased to 37%. In areas of longer occupation, scan sampling showed 62% while telemetry indicated 48% (Garshelis et al., 1990) of time spent foraging. Given that the data was collected at the same time of year in roughly the same locations and all within a 10 year span (most of it was much closer together in time), scan-sampling appears to be the least accurate of the two methods. Garshelis et al. (1990) concluded that scan sampling was misleading and should be abandoned.

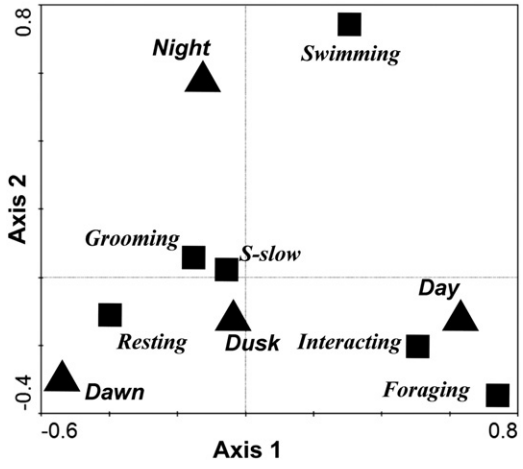

Fig. 3. Canonical correspondence analysis of all behaviors and time of day.

Table 2
MANOVA Testing if the relative amounts of time spent in each behavior differed by Time Period.

MANOVA		
Across all behaviors	F-value	p-Value
All 4 time periods	11.82	<0.0001
Dawn	8.21	<0.0001
Day	8.96	<0.0001
Dusk	1.18	0.32
Night	5.10	<0.0001

4.2. Results from this study

4.2.1. Activity budget

Focal animal sampling used in the current study was the same as that used by Pearson and Davis (2005) and Finerty et al. (2009) in the same study area, extending their observations to include night and portions of dawn and dusk. Focal animal sampling (Altmann, 1974; Lehner, 1996) differs from group-follows or scan sampling. In our study, we conducted "individual follows" where observers monitored a single individual regardless of whether it was solitary or in a group, which differs from a "group-follow" where an entire group of animals is monitored (Mann, 1999). In addition, we conducted "instantaneous sampling" whereby an observer recorded an individual's behavior at preselected times (i.e., every minute for 30 min). In contrast, "scan sampling" involves taking one instantaneous sample of an individual's behavior at regular intervals before moving on to the next animal, often in a group (Altmann, 1974; Mann, 1999). Scan sampling is valuable for determining behavior when individual follows are not possible or if the researcher wishes to keep track of group activities. Individual follows and the instantaneous sampling technique are better for determining time budgets (Altmann, 1974; Mann, 1999).

The percentage of time spent foraging (18%) in this study was on the low end of values reported in other studies. However it was similar to other studies of increasing populations: 15–18% (Estes et al., 1982),

Table 3
ANOVA testing each behavior individually to see if there was a significant difference in the amount of time spent performing each behavior between time periods.

ANOVA	F-value	p-Value
	All 4 time periods	
Foraging	13.98	<0.0001
Grooming	1.49	0.22
Resting	16.85	<0.0001
Swimming	12.35	<0.0001
S-slow	0.87	0.45
Interacting	1.98	0.11

Table 4
Tukey–Kramer multiple comparisons & ANOVAs comparing each time period against all others individually for behaviors found to have a significant difference in Table 2 (y = significant, n = not significant).

Tukey-Kramer multiple comparisons					ANOVAs				
significant at α 0.05									
Foraging	Dawn	Day	Dusk	Night	Foraging	Dawn	Day	Dusk	Night
Dawn		y	y	n	Dawn		0.000	0.03	0.877
Day	y		y	y	Day	0.000		0.00	0.000
Dusk	y	y		y	Dusk	0.034	0.000		0.023
Night	n	y	y		Night	0.877	0.000	0.02	

Tukey-Kramer multiple comparisons					ANOVAs				
significant at α 0.05									
Resting	Dawn	Day	Dusk	Night	Resting	Dawn	Day	Dusk	Night
Dawn		y	y	y	Dawn		0.00	0.00	0.000
Day	y		y	y	Day	0.000		0.00	0.005
Dusk	y	y		y	Dusk	0.000	0.00		0.6
Night	y	y	y		Night	0.000	0.01	0.60	

Tukey-Kramer multiple comparisons					ANOVAs				
significant at α 0.05									
Swimming	Dawn	Day	Dusk	Night	Swimming	Dawn	Day	Dusk	Night
Dawn		y	y	y	Dawn		0.00	0.02	0.00
Day	y		y	y	Day	0.000		0.05	0.09
Dusk	y	y		y	Dusk	0.019	0.05		0.00
Night	y	y	y		Night	0.000	0.09	0.00	

Table 6
MANOVA testing if the relative amounts of energy spent per behavior differed by time period.

MANOVA		
Across all behaviors	F-value	p-Value
All 4 time periods	11.82	<0.0001
Dawn	8.21	<0.0001
Day	8.96	<0.0001
Dusk	1.17	0.32
Night	5.10	<0.0001

11% (Bowlby et al., 1988), 21–28% (Estes et al., 1986), and 24% (Shimek and Monk, 1977) and to one decreasing population, 21–52% (Gelatt et al., 2002). The locations of those studies were typically exposed, high-energy coasts with rocky benthos. In southeast Alaska, where the habitat and diet are similar to those of Simpson Bay, Bodkin et al. (2007) reported that sea otters foraged 37% of the day (range 23–48%) using time-depth recorders. Radio transmitters were used by Garshelis et al. (1986) in Simpson and Nelson Bays from 1980 to 1981. They found that otters foraged 37% of the day, but that study was conducted partly during the winter when the time spent foraging appears to increase.

For the 24-h period, territorial male otters in our study area spend 14% of the day foraging (Finerty et al., 2009), which was similar to that for females with pups (18%) at the same time of year. In a multivariate analysis, Finerty et al. (2009) observed that foraging was more closely associated with day (11:00–17:00 h) than any other time period. Similarly, we found an increase in foraging during the day (27% versus 19% for dusk and 13% for night and dawn), although there were small peaks in foraging activity at 5:00 h and 14–15:00 h.

The number of otters in Simpson Bay during the summer has remained consistent during the summer (June–August) over the past 12 years (Wolt et al., 2012), which indicates that equilibrium density has been reached. However the time spent foraging is more similar to other areas known or thought to be below equilibrium density. It should be noted that the number of sea otter in Simpson Bay falls by almost half, to about 50 animals, during the winter (Davis and Weltz, unpub. obs.). This means that the average annual population of sea otters in Simpson Bay is ca. 60 adults. If a factor besides food limitation is keeping the sea otter population at its current density, that factor has not yet been identified. Predation is a possibility, however no predation event has ever been witnessed in Simpson Bay and the otters show little response to killer whales. If immigration/emigration is the cause, it will require tagging for confirmation.

We believe that our boat-based observations did not affect otter behavior. To test this, the behavior of females with pups was recorded from five shore locations and compared to the boat-based time budget. We found no significant biological effect of the skiff on sea otter behavior. The shore-based method recorded a small decrease in resting (42% vs. 50%) and a small increase in swimming (20% vs. 14%). If the skiff were affecting the otter's behavior (i.e., the otter was avoiding the skiff), we would expect the opposite result. The percentage of time spent foraging remained exactly the same (19%) between the two methods. Overall, there was no biological or statistical indication that boat-based observations from a distance of ca. 100 m significantly altered the otters' behavior or gave different results from shore-based methods. Furthermore, the boat-based method provided more detailed behavioral observations and could be used under lower light levels that enabled 24-h activity budgets (Cortez et al., 2014 in review).

Females with new born pups spend surprisingly little time (2–9%) foraging (Sandegre et al., 1973; Hanson et al., 1993, Cortez, in review). However, as this period only lasts a week or two, it probably did not affect our results. The percentage of time spent foraging in the current study (18%) was an average based on females with pups that varied in age from newborn to a several months. As pups mature, that energy requirements increase, so females spend more time foraging (Cortez, unpub. obs.).

Resting averaged 42% of the time, ranging from 32% during the day to 52% at dawn. This is similar to or slightly below what was found in previous studies. In general, resting varied inversely with foraging (i.e., as foraging time increased resting decreased).

Grooming (13–16%), interacting (2–3%) and swimming slowly (8–9%) were relatively constant across all time periods. As fur is the otters' only source of thermal insulation, frequent grooming to maintain the air layer adjacent to the skin is essential and represents a significant

Table 5
Daily activity budget and estimated Field Metabolic Rate (FMR) for female sea otters with dependent pups in Simpson Bay.

Behavior	Activity budget		Field Metabolic Rate		
	% of day	Minutes	(kJ min^{-1} kg^{-1})	(MJ day^{-1} kg^{-1})	(MJ day^{-1})
Foraging	18.19	261.87	0.43	0.113	2.38 (18.74%)
Grooming	15.08	217.22	0.59	0.128	2.70 (21.33%)
Resting	41.64	599.66	0.27	0.162	3.42 (26.94%)
Swimming	14.70	211.72	0.59	0.125	2.64 (20.79%)
S-slowly	8.39	120.83	0.49	0.059	1.25 (9.85%)
Interacting	1.99	28.70	0.49	0.014	0.3 (2.34%)
Total	100	1440	2.86	0.60	12.69

Table 7
ANOVA testing if there was a significant difference in the amount of energy spent per each behavior (over each 30 min observation) between time periods.
Tests between time periods were conducted running each against the other three (eg. if dawn was significantly different from day, dusk & night).

ANOVA	F-value	p-Value
	All 4 time periods	
Foraging	13.98	<0.0001
Grooming	1.49	0.22
Resting	16.85	<0.0001
Swimming	12.35	<0.0001
S-slow	0.87	0.45
Interacting	1.98	0.11

percentage of daily activity compared to marine mammals that use subcutaneous fat for thermal insulation.

Photoperiods vary greatly at this latitude, so it may not be surprising that light level (i.e. time of day) did not have a strong influence on behavior. As foraging otters frequently dive below the depth of light penetration and stir up clouds of soft sediment while excavating prey, it is unlikely that they are using vision to locate food. Unlike many other mammals at this latitude, they do not hibernate and must perform all required activities in diminished light for extended periods during the winter.

Swimming slowly may be, at least in part, a response to the large tidal changes (−2.5 to +13 ft is not uncommon, NOAA tide predictions) and flow of water in and out of the bay. As there are no canopy-forming kelps in which to wrap themselves while resting, low energetic swimming may be their best means of resisting tides and currents.

Swimming averaged 15% of the time, ranging from 9% (dawn) to 20% (night). This is well below that reported for territorial males (26%) in Simpson Bay (Finerty et al., 2009) but similar (14%) to what Garshelis et al. (1986) reported, although the method of data collection was different (visual vs. telemetry). Other non-visual based studies cannot distinguish among swimming, grooming and interacting and so behaviors that are not resting or foraging are lumped together as "other".

4.2.2. Estimated Field Metabolic Rate (FMR)

The weight specific FMR for otters in our study was 601 kJ day^{-1} kg^{-1}, and the total FMR was 12.69 MJ day^{-1} (Table 3). This is similar to the predicted FMR based on the allometric regression from other marine mammals including sea lions, fur seals and true seals (Williams et al., 2004a, 2004b). It is a little less than estimated by Yeates et al. (2007) for sea otters in California (15.7 ± 2.7 MJ day^{-1}), and for adult male otters in Simpson Bay (19.04 MJ day^{-1} [Finerty et al., 2009]), but this may be because the animals in those studies were male and somewhat larger than a typical Alaskan female sea otter (21.1 kg, Kenyon, 1969). The smallest animal in California (22 kg) had an FMR of 12.73 MJ day^{-1} similar to our estimate. Our activity budget differed from Yeates et al. (2007) in that our animals spent less time foraging and resting and much more time grooming and swimming.

If swimming and swimming slowly are taken together, they represent 38% of the FMR at night, more than any other category in any time period. Swimming by itself (27% of the FMR during the night) is equivalent to foraging during the day. Finerty et al. (2009) also found a large percentage of the male activity budget devoted to swimming (26% of the time and 43% of the FMR), and this was separate from territorial patrolling. It is unclear why otters in Simpson Bay spend so much time moving around. For example, during one 3-h shore-based observation (with no possibility of our influencing the female's behavior with the presence of a boat), we observed a female with a pup swim for the entire period only to end up right back where she was when we began the observation (Cortez and Wolt, personal observation).

The estimated daily prey consumption for a female with a FMR of 12.69 MJ day^{-1} and an all clam diet with an energy content of 3.36 MJ kg^{-1} clam (Cortez, in review) was 3.78 kg day^{-1}. This would require that females capture 3.56 clam dive^{-1} assuming: 1) an average dive duration of 1.69 min, 2) a success rate of 87% (Wolt et al., 2012), 3) 18% of the day spent foraging, 4) the average mass of a clam to be 10.2 g (Cortez, in review), and 5) an average interdive interval of 30 s. Although there a several assumptions in this estimate, it is consistent with our observations of the capture of multiple prey items per dive.

4.2.3. Conclusions

Our study enabled us to examine behavior on a 24-h basis similar to telemetry studies, but without any of the assumptions about intermittent signals. As we visually observed the animals, there was no question about behavior, and our data represent an unprecedented number of observations with such high resolution. The otters in Simpson Bay show a surprising degree of homogeneity with regard to behavior throughout the 24-h period. There was a slight crepuscularity to their foraging, as has been seen to a greater degree in other locations (Estes et al., 1986; Ralls and Siniff, 1990). While behavior may differ significantly among the 6-h time periods, the total variation explained by time of day was only 2.4–3%.

Our estimated Field Metabolic Rate (12.69 MJ day^{-1}) was similar to that previously reported, with a small difference attributable to differences in body mass (male vs. female, and Alaska vs. California otters) and time budgets.

Time spent foraging has been the focus of most time budget studies because of its implications for population status (Eberhardt and Siniff, 1977; Estes et al., 1986; Ralls and Siniff, 1990), although this has been questioned. While the theory behind it may be sound, there are likely many confounding variables that make comparisons among different habitats difficult (Table 8). Garshelis et al. (1990) suggested that

Table 8
Previous sea otter activity budgets.

Location	Source	Pop. Status	Method	Behavior, % of time[a]		
				Foraging	Resting	Swimming
Prince William Sound, AK	Finerty et al. (2009)[c]	Stable	Visual — 24 h	14	27	26
Washington State	Walker et al. (2008)	Increasing	Visual	8	62	8
Cross Sound, AK	Bodkin et al. (2007)	Increasing	TDR — 24 h	40	52	
San Simeon, CA	Yeates et al. (2007)[c]		Radiotelemetry — 24 h	36	40	8.5
Prince William Sound, AK	Pearson and Davis (2005)[c]	Stable	Visual	30	18	9
Amchitka, AK	Gelatt et al. (2002)[b]	Decreasing	Radiotelemetry — 24 h	38	49	
California	Ralls and Siniff (1990)	Increasing	Radiotelemetry — 24 h	41		
California	Estes et al. (1986)	Increasing	Visual	24	59	
Prince William Sound, AK	Garshelis et al. (1986)[c]	Stable/Inc.	Radiotelemetry — 24 h	47	50	3
California	Loughlin (1980)	Stable	Radiotelemetry — 24 h	34		

[a] Row totals do not all equal 100% due to the differing categories of activities in each study.
[b] Females only.
[c] Males only.

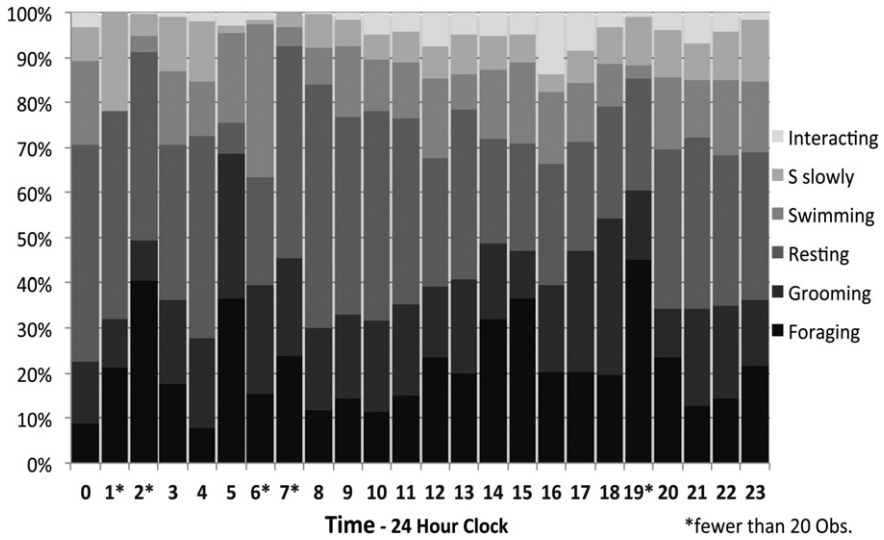

Fig. 4. Activity budget of female sea otter with dependant pups in Simpson Bay during the summer (June–August) shown by hour of the day.

geographic differences (structure of near-shore community: substrate, water depth, kelp canopy, prey assemblage, predators and competitors) play a larger role in determining the amount of time spent foraging than population status. In California, the percentage of time foraging was similar between four study areas (21–28%) despite differences in the length of time they were occupied (Estes et al., 1986), and success rate of prey capture differed <2% between prolonged and recently occupied areas (Estes et al., 1981). For the percentage of time spent foraging to be more meaningful or useful as a proxy for population status, a complete 24-h budget must be used and the type of habitat must be taken into account. We suggest that our time and energy budgets are a good bench-mark for a soft and mixed sediment benthos without canopy forming kelp during the summer for a population of otters whose diet is well known and whose numbers have remained consistent for at least 12 years (Wolt et al., 2012).

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