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Activity Budgets and Prey Consumption of Sea Otters (*Enhydra lutris kenyoni*) in Washington

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Abstract

Northern sea otters (*Enhydra lutris kenyoni*) were extirpated from the Washington coast in the early 1900s. Reintroductions of sea otters from Amchitka Island, Alaska, occurred in 1969 and 1970. By 2005, 814 sea otters occupied a range from Destruction Island north to Makah Bay. The focus of this study was to investigate diurnal activity budgets and variability in prey consumption at four locations in the current Washington sea otter range to test hypotheses concerning population growth potential and local impact of sea otters on prey availability. Overall, sea otters primarily spent their daylight hours resting (62.3%), grooming (19.7%), and feeding (7.6%). These activities varied by location. Diet consisted predominantly of crabs, clams, and sea stars. In each study area, one main prey item comprised 33.4 to 64.4% of the total prey consumed; however, the main prey item differed among locations. Of the foraging dives observed, 81.4% were successful. Average dive duration was 35.6 s; however, this varied among locations as well. The study locations were utilized differently—some as resting sites and others as feeding sites. The low diurnal feeding activity found in this study indicates that food availability was high, suggesting that this Washington population of sea otters is currently below equilibrium density.

Key Words: activity budgets, sea otter, *Enhydra lutris kenyoni*, foraging success, population growth, prey consumption, Washington State

Introduction

Sea otters (*Enhydra lutris*) were common along the Washington coast until they were extirpated during the fur trade (Scheffer, 1940; Riedman & Estes, 1990). The current Washington State sea otter population was founded from sea otters translocated from Amchitka Island, Alaska. Two groups of translocated sea otters were introduced

in 1969 and 1970, resulting in a total of 59 otters (41 females and 18 males) being released into Washington waters over these two years (Bowlby et al., 1988). It is believed that the current population was reestablished from no more than 43 otters, possibly as few as 10 (Jameson et al., 1982).

Between 1977 and 1989, records indicate that the Washington State population increased from 19 to 208 otters (Jameson, 1998; Lance et al., 2004). Since 1989, the Washington Department of Fish and Wildlife (WDFW) observed continued growth to a total of 604 animals by 1999 (Lance et al., 2004). Growth rates following translocation through about 1990 were approximately 21.0% in Washington (Bodkin et al., 1999). Jameson & Jeffries (2005) reported an average annual rate of increase of 8.2% since 1989. In the July 2005 census, 814 sea otters were counted, a 10.0% increase from 2004 (Jameson & Jeffries, 2005), indicating a positive growth phase, but with a rate of increase that is slowing over time. Telemetry studies conducted on sea otters in Washington have shown extensive movement and interchange throughout their known range, with the largest movement between Destruction Island and Cape Alava, a distance of approximately 60.0 km (Jeffries, 2004; Figure 1). One objective of the present study was to look for correlates of growth capacity in prey consumption and observed feeding activity in the expanding sea otter population in Washington.

Sea otter population growth, range expansion, and associated dietary changes have been well-documented in other areas (Garshelis et al., 1986; Estes, 1990). According to Krebs' (1978) optimal foraging theory, an increase in time spent foraging is correlated with decreases in the abundance and quality of prey items. More specifically, Garshelis et al. (1986) proposed a relationship between the amounts of time sea otters spent foraging and food availability and that one could use time budget data to assess the availability of prey in different parts of a population's range. Lower foraging

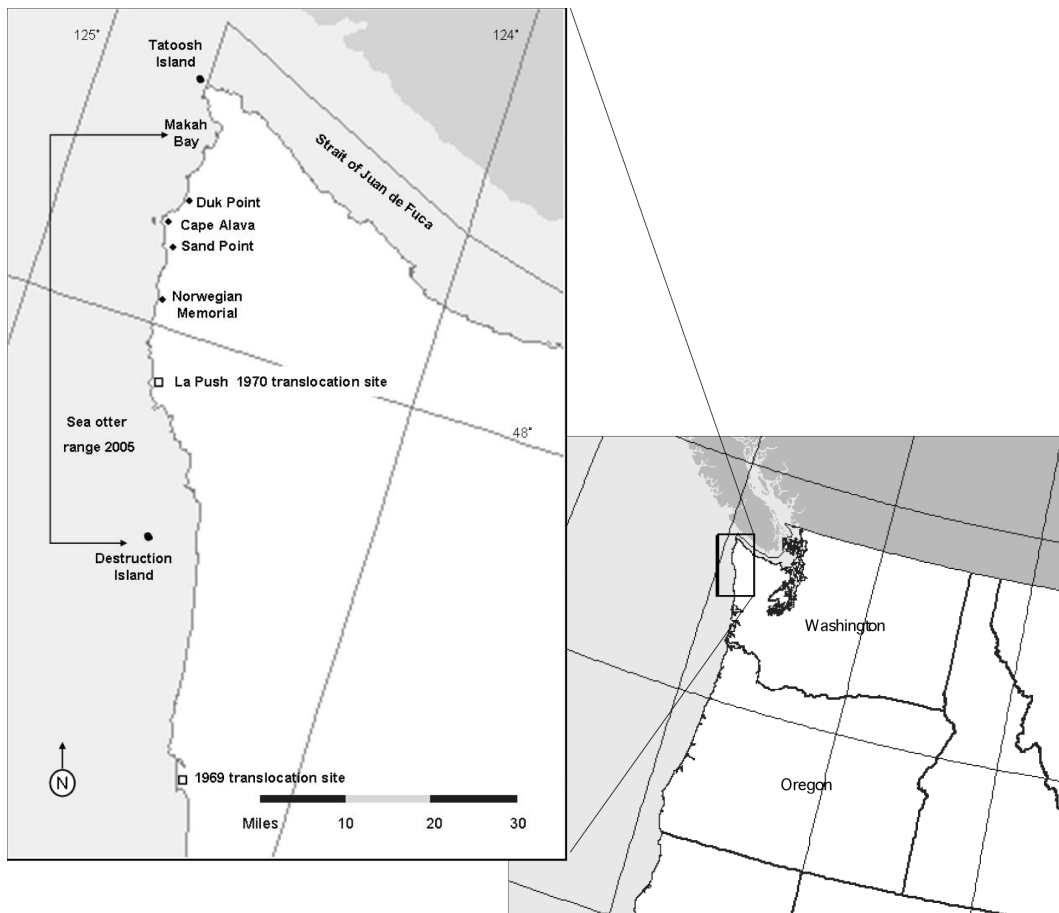


Figure 1. Study locations, current range, and release sites of the translocated Washington sea otter population; map created using *Map Maker: National Atlas of the United States*, March 24, 2006 (<http://nationalatlas.gov>).

activity percentages are believed to occur in areas where sea otter populations are below equilibrium density as a consequence of still abundant sessile prey (Estes et al., 1982, 1986; Garshelis, 1983). To test whether time spent foraging supported the hypothesis that the translocated sea otter population in Washington was still below equilibrium density and in an active growth phase, the authors investigated foraging activities and prey consumption in this population for comparison relative to values obtained from other sea otter populations (Estes et al., 1982, 1986; Estes, 1990) and to earlier studies conducted in Washington (Bowlby et al., 1988; Laidre & Jameson, 2006). Based on the observed average annual rate of increase, it was predicted that sea otter foraging activity should be low, indicating that prey is still plentiful in the area.

In addition to activity budget considerations, prey availability changes over time have been shown to be correlated with overall length

of occupancy (Estes et al., 1978; Ostfeld, 1982; Garshelis, 1983). In particular, benthic communities in Washington, particularly sea urchin densities, have changed over time, which may be related to the growing population of sea otters (Kvitek et al., 1998). For the sea otter population in Washington, Bowlby et al. (1988) presented 1986-1987 data on sea otter abundance, distribution, and activity budgets for specific locations along the outer Washington coast. Laidre & Jameson (2006) presented 1993 to 1999 data on foraging patterns and prey selection, but from unspecified localities on the outer coast of Washington and in the Strait of Juan de Fuca. The present study aimed to compare site-specific prey consumption differences with the Bowlby et al. (1988) study in addition to looking at general shifts in overall prey consumption compared with Laidre & Jameson (2006). With the growth of the Washington sea otter population since the initial studies in 1986-1987, the authors predicted that

there would have been local changes in prey consumption despite prey abundance throughout the area remaining high enough to support continued population growth. Changes in local prey availability as reflected by consumption, if present, represent an especially important factor for development of area management policy.

The Washington State sea otter population is currently protected under the Marine Mammal Protection Act of 1972 and under endangered species legislation in the State of Washington. As sea otters continue to increase in Washington, oil spill and anthropogenic contaminant risks, shellfish fisheries conflicts, and the effects of sea otters on the coastal marine ecosystem structure and dynamics become of increasing concern (Lance et al., 2004). Ecological data on time and activity budgets and prey consumption need to be documented to aid management in these possible future conflicts. These data can be used to support the WDFW Sea Otter Recovery Plan (Lance et al., 2004), which is aimed at ensuring that a self-sustaining population of sea otters will eventually exist in Washington.

Prey consumption data is of special significance because of the concerns surrounding recent mortalities. Environmental contaminants such as butyltins, PCBs, and organochlorine pesticides are being evaluated in the Washington sea otter population (Brancato et al., 2008) and are known to be involved in sea otter mortality in California (Kannan et al., 2004). Recent necropsy findings in Washington have revealed the presence of acanthocephalan peritonitis, protozoal encephalitis (caused by the protozoal parasite *T. gondii* and/or *S. neurona*), and leptospirosis (Lance et al., 2004). Sea otters captured for transmitter implantation in Washington in 2000 and 2001 have also shown positive titers to morbillivirus (Lance et al., 2004; Brancato et al., 2008). With the possibility that protozoal parasites and morbillivirus, as well as industrial and agricultural compounds, are being transported into sea otter tissues via trophic transfer (Brancato et al., 2008), it is critical to monitor prey consumption trends.

In this study, data on prey consumption, dive success rates and durations, and diurnal activity patterns for sea otters in Washington were collected at four locations along the Olympic Peninsula to support our hypothesis on population equilibrium and to assess changes in local prey consumption and site utilization. These findings provide data for U.S. Fish and Wildlife Service toxicological and epidemiological studies, which are attempting to establish links between prey consumption, general health, and recent mortality events in the Washington sea otter population.

Materials and Methods

Study Site

Research was conducted in the Olympic Coast National Marine Sanctuary on the Washington State Olympic Peninsula in the Olympic National Park during the spring and summer of 2003 and 2004 with the permission of the National Park Service. This was a land-based observation study, which used coastal viewing areas accessible by backcountry trails and four-wheel drive vehicles to observe rafts of sea otters. Four locations were selected for concentrated survey efforts: (1) Duk Point, (2) Cape Alava, (3) Sand Point, and (4) Norwegian Memorial (Figure 1). Based on previous habitat characterizations and nautical charts, sea otter habitats at these locations were classified as rocky coastal and subtidal substrates (Laidre et al., 2002). All observations occurred in areas between the coastline and the 20-m depth contour. These sites were chosen to provide comparisons over time with the Bowlby et al. (1988) study as well as to complement current contaminant and epidemiological studies being conducted in the area by the U.S. Fish and Wildlife Service.

Data Collection

The study design was based on methods used by Estes et al. (1982) in which an effort was made to evenly distribute observations across time periods for all locations in an attempt to reduce the effects of spatial segregation bias due to point-in-time sampling.

Sea otter activity was initially observed from the coast by scanning the water using Cabela Alaskan Guide 10 × 40 binoculars (Cabela, Sidney, Nebraska, USA). An AT-80 high definition Swarovski spotting scope (Swarovski Optik, Cranston, Rhode Island, USA) was then used to facilitate closer observations of prey consumption and behavioral activities. Every 30 min during each observation period (lasting from approximately dawn to dusk), a systematic scan was conducted. Date, time, location, and observable tidal cycle (i.e., high, mid, and low) were recorded. Since visual scans were the method for data collection, our observations were limited during periods of poor viewing conditions (i.e., intense rain or fog) or inclement weather, which occurred sporadically throughout the study.

An ethogram, modeled after the behavioral classifications defined by Packard & Ribic (1982), was constructed, and activity budget data were collected. Activity budget categories included resting, grooming, foraging, traveling, playing, nursing, and other (e.g., copulating, startled). Only pups were classified in the nursing category as adult

females were often witnessed grooming while the pup nursed/suckled. A scan sample method (Estes et al., 1982) was employed to record instantaneous accounts of behavior. Scans were conducted with a spotting scope to determine the total number of sea otters concentrated in one location and their individual activity. Age classification (adult or pup) and the number of sea otters per group at each location were recorded. One minute was spent in each field of view visible through the spotting scope so as not to exclude sea otters that were under water. This was based on an average reported dive time for sea otters of 1 min. During every scan, each sea otter observed was classified into one of the seven behavior categories. A scan was repeated every 30 min, with the total time at each study location being distributed as equally as possible.

Prey consumption data was collected by direct observation of individual sea otters feeding. Once a foraging sea otter (eating or engaged in foraging dives) was located, data collection would begin. Once an individual was no longer actively foraging or moved out of sight, the feeding observation was terminated. Location, time of day, and tidal cycle were recorded for all feeding observations, along with sex and age, if identifiable. Sex of the adults was determined by the presence of either a penile or testicular bulge on the male's lower abdomen or the presence of abdominal teats on the female (Riedman & Estes, 1990). Pups were not sexed because of difficulties in distinguishing reproductive anatomy in young animals. Age was categorized as adult or pup (approximately 0 to 24 wks old).

During a feeding observation, the authors noted (1) the total number of successful dives (prey item captured and brought to the surface) and unsuccessful dives (no prey item upon surfacing), (2) the duration of each observed foraging dive (in s), (3) the number of prey brought to the surface after a foraging dive, and (4) the identification of the prey item. The authors recognize that prey size would allow for calculation of energy consumption rates; however, because of the distance the sea otters were located from shore, it was not possible to estimate prey size with complete confidence. Taxonomic classification of prey species was determined to the lowest possible taxon. If there was difficulty in classifying an individual prey species, then the major taxonomic group was indicated (i.e., crab, clam, sea star, mussel, etc.). Average dive time was calculated from foraging dives witnessed in 2004 at Duk Point, Sand Point, and Norwegian Memorial. Dive duration data for Cape Alava were not included in subsequent analyses due to a low dive duration sample size.

Observations were made during the daylight hours to allow for assessments of behavior and

prey capture. Data collection occurred on subsequent days, and due to the nature of observing unmarked individuals, the sea otters monitored were not distinguishable from previous observation days and, therefore, may be overrepresented. Because of a low number of radio-implanted sea otters in the area, telemetry studies could not be conducted; therefore, nocturnal foraging activities are not represented in the current study. Gelatt et al.'s (2002) study on sea otters at Amchitka Island, Alaska, with telemetry showed that animals also dove (presumably to forage) at night, but no data are available to assess day/night difference in prey choice. The current study can only be more directly compared with the diurnal-only time budget studies of Estes et al. (1982, 1986) and Bowlby et al. (1988) during which direct observation of sea otter activity was obtained through scan sampling methods.

Statistical Methods

The percentage of animals in each activity was calculated at each location to get an overall index of relative activity for the seven categories (Table 1). Chi square contingency 2×4 tables were used to examine whether each activity varied among the four locations. Chi square contingency tables were also used to examine whether prey consumption varied among locations (2×4 tables) and by gender (2×2 tables).

Differences in dive durations among locations were tested using one-way analysis of variance (ANOVA), with tidal cycle included as a covariate in the model, followed by a Tukey post hoc comparison. The effects of gender and of females with pups on dive duration were also tested using a one-way ANOVA.

Logistic regression was performed to model the effects of location, gender of the sea otter, or the presence of a dependent pup on a foraging mother (categorical independent variables) on the successfulness or unsuccessfulness of foraging dives (dichotomous dependent variable). A Wald statistic was used to test the significance of the individual independent variables. All statistical tests were conducted using SPSS, Version 11.5 (SPSS, Inc., Chicago, IL, USA).

Results

Activity Budget Data

The combined time and activity budget data for 2003-2004, taken from 7,116 observations, showed that sea otters spent 62.3% of their daylight hours resting, with 7.6% of their time dedicated to feeding. While sea otters spent the majority of the daylight hours resting in all locations, the amount of time spent in resting, feeding, traveling, and "other" activities varied significantly

Table 1. Activity percentages for 2003 and 2004 by age and location

Location	No. of observations	Activity %						
		Feed	Groom	Rest	Play	Travel	Nurse	Other
Duk Point								
Adults	3,579	6.7	19.7	61.8	1.8	9.6	--	0.4
Pups	240	4.2	5.4	75.4	2.5	4.2	7.9	0.4
Total	3,819	6.5	18.8	62.7	1.9	9.2	0.5	0.4
Cape Alava								
Adults	1,026	3.1	20.1	72.1	0.8	3.4	--	0.5
Pups	119	4.2	6.7	73.1	3.4	5.0	7.6	0.0
Total	1,145	3.2	18.7	72.2	1.1	3.6	0.8	0.4
Sand Point								
Adults	1,484	12.6	23.5	53.4	2.4	8.0	--	0.1
Pups	168	6.6	5.9	74.4	0.6	4.2	8.3	0.0
Total	1,652	12.0	21.7	55.6	2.3	7.6	0.8	0.01
Norwegian Memorial								
Adults	429	11.7	24.0	55.5	0.9	5.6	--	2.3
Pups	71	8.5	5.6	77.5	2.8	2.8	2.8	0.0
Total	500	11.2	21.4	58.6	1.2	5.2	0.4	2.0
All locations								
Adults	6,518	7.8	20.9	61.1	1.7	8.0	--	0.5
Pups	598	5.4	5.8	74.9	2.1	4.2	7.4	0.2
Grand total	7,116	7.6	19.7	62.3	1.8	7.6	0.6	0.4

among locations ($\chi^2 = 83.09$, $p < 0.001$; $\chi^2 = 91.96$, $p < 0.001$; $\chi^2 = 44.50$, $p < 0.001$; $\chi^2 = 33.72$, $p < 0.001$, respectively). On the other hand, diurnal grooming, playing, and nursing activities were not significantly different among the four study sites ($\chi^2 = 7.74$, $p = 0.05$; $\chi^2 = 6.70$, $p = 0.08$; $\chi^2 = 4.91$, $p = 0.18$, respectively).

Diet Composition

Over the two seasons of data collection, 833 foraging dives were recorded. Sea otters were observed consuming crabs (Order Decapoda), including unidentified species and kelp crabs (*Pugettia producta*); clams (Order Bivalvia), including Pacific littleneck clams (*Protothaca staminea*) and unidentified bivalves; octopus (*Octopus dofleini*);

sea stars (*Pisaster* sp.), including Dawson's sea stars (*Solaster dawsoni*); sea cucumbers (*Cucumaria miniata*); mussels (*Mytilus* sp.); snails (Class Gastropoda); and red sea urchin (*Strongylocentrotus franciscanus*).

Overall, 82.0% of the prey consumed consisted of crabs, clams, and sea stars (Table 2). In each study area, one main prey type made up from 33.9 to 64.4% of the total consumption of all identifiable prey, but the main prey types differed among locations. The number of clams, crabs, sea stars, and mussels differed significantly among locations ($\chi^2 = 171.83$, $p < 0.001$; $\chi^2 = 18.09$, $p < 0.001$; $\chi^2 = 118.80$, $p < 0.001$; $\chi^2 = 16.71$, $p = 0.001$, respectively).

Table 2. Percentage of prey consumed by adult sea otters by location (unknown items excluded)

	Clam	Crab	Octopus	Sea star	Sea cucumber	Mussel	Snail	Unknown bivalve	Red sea urchin
Duk Point	14.7	27.7	1.7	34.5	0.6	10.7	0.0	10.2	0.0
Cape Alava	23.7	64.4	1.7	6.8	0.0	0.0	0.0	1.7	1.7
Sand Point	12.8	63.4	2.4	0.6	0.0	6.1	1.2	13.4	0.0
Norwegian Memorial	64.5	30.3	0.0	0.0	0.0	0.0	1.3	4.0	0.0
Total	23.1*	45.0*	1.7	13.9*	0.2	6.1*	0.6	9.2	0.2

* Indicates significant differences in prey consumed among locations ($p \leq 0.001$)

Overall, females consumed significantly more clams than males ($\chi^2 = 106.71$, $p < 0.001$). Males consumed more crabs ($\chi^2 = 4.05$, $p = 0.044$), mussels ($\chi^2 = 14.24$, $p < 0.001$), and unknown prey items ($\chi^2 = 20.22$, $p < 0.001$) than females. All other prey items were consumed similarly by both sexes.

Dive Durations

The mean foraging dive duration (\pm SD) was 35.6 ± 19.9 s ($n = 202$). The shortest dive recorded (5.3 s) was by an adult male at Sand Point who consumed an unknown prey item, and the longest (122 s) was an unsuccessful dive recorded for an adult female at Norwegian Memorial. The longest dive in which a prey item was captured was 93.9 s by a female at Sand Point.

Longer dives occurred when sea otters captured clams (mean 45.8 ± 17.7 s, $n = 49$) and sea stars (mean 42.5 ± 17.9 s, $n = 17$). The shortest dives were for small, unknown prey items (mean 22.4 ± 15.7 s, $n = 25$). During 80.1% of observed successful foraging dives, one prey item was captured; two prey items were observed 18.0% of the time, and three prey items were captured on 1.9% of the foraging dives.

Dive durations differed significantly among locations (ANOVA: $F_{(3,197)} = 21.5$, $p < 0.001$), with location and tide explaining 22.0% of the variation in dive length. The greatest mean dive duration was at Norwegian Memorial (mean 55.4 ± 23.6 s, $n = 30$) and was longer than that at Sand Point (mean 27.4 ± 15.4 s, $n = 68$, $p < 0.001$) and Duk Point (mean 35.1 ± 17.8 s, $n = 100$, $p < 0.001$). Sea otters at Duk Point dove longer than the otters at Sand Point ($p = 0.035$). Mean dive durations were not significantly different for males, females, or females with pups (ANOVA: $F_{(2,143)} = 1.72$, $p = 0.183$).

Successful vs Unsuccessful Dives

Of the 833 foraging dives recorded, 81.4% were successful, but this percentage varied with location (Wald statistic = 10.79, $p = 0.001$). Duk Point and Cape Alava had the lowest proportion of successful dives with a mean percent of 76.0% and 78.3%, respectively. Dives were more successful at Sand Point and Norwegian Memorial (85.0% and 87.7%, respectively). No relationship was found between the number of unsuccessful dives and the gender of the sea otters (Wald statistic = 0.493, $p = 0.483$), nor between the number of unsuccessful dives and independent females vs females with pups (Wald statistic = 0.590, $p = 0.442$).

Discussion

At the time the translocated sea otter population in Washington was studied in 1986 and 1987

(Bowlby et al., 1988), feeding frequencies were 9.5 and 11.2%, respectively. The overall diurnal feeding activity reported in this study for 2003 and 2004 (7.6%) was also low and suggests that there is still high food abundance in the Washington sea otter population range. These data corroborate the observed steady annual growth rate in this population (Jameson & Jeffries, 2005), the difference between the estimated carrying capacity of 2,734 sea otters for this area (Laidre et al., 2002), and the 2005 abundance total of 814 sea otters. Taken together, these independent lines of evidence support the hypothesis that the Washington population is still below equilibrium density.

Over the years, there has been a notable shift in diet at Sand Point and Duk Point suggesting a change in the availability of prey items. Prey consumption at Duk Point in 1987 consisted primarily of clams, then octopus (Bowlby et al., 1988). In the authors' 2003 and 2004 study, the main prey items were sea stars and crabs, followed by clams, mussels, unknown bivalves, octopus, and sea cucumbers. In 1986 and 1987, Bowlby et al. found that sea otters at Cape Alava consumed crabs and clams as well as sea cucumbers, while at Sand Point, the prey items consumed were primarily octopus, then sea urchins. Prey consumed at both Cape Alava and Sand Point in 2003 and 2004 consisted primarily of crabs, then clams. While prey consumption has remained similar at Cape Alava, the prey consumed at Sand Point has shifted notably. Bowlby et al. did not include Norwegian Memorial in their 1986-1987 study. Since the Bowlby et al. study, there has been a notable shift in sea urchin consumption along the outer Washington coast. The current study and the Laidre & Jameson (2006) study found the number of sea urchins in the diet of sea otters along the outer Washington coast to be negligible ($< 1.0\%$).

Based on the relationship between the amount of time sea otters spent foraging and food availability, Garshelis et al. (1986) hypothesized that time budget data may be used to assess the availability vs limitation of prey in different parts of a population's range. This has been supported by studies on diurnal patterns of activity for sea otters at Amchitka Island, Alaska, a population hypothesized to be at or near equilibrium density compared with a population at Attu Island, Alaska, considered to be below equilibrium density (Estes et al., 1982; Estes, 1990). The time sea otters invested in foraging at Amchitka Island was reported at 51.0 to 58.0%, while Attu Island sea otters invested only 16.0 to 18.0% of their time feeding. Differences in time that sea otters dedicate to foraging and their foraging tactics are closely linked to their influence on the structure of the community in which they forage (Estes

et al., 1982). Prey abundance, accessibility, and prey preference, as well as the length of time sea otters have occupied an area, may all influence time spent foraging. Estes et al. (1982) concluded that sea otters at Amchitka Island adjusted their foraging activities to exploit fish (60.0% of their diet), which also resulted in changes in their diurnal feeding activities. Similarly, a small translocated population of sea otters at Blanco Reef in Oregon (below equilibrium) spent 17.0% of the day feeding (Estes et al., 1982) compared to a California population (hypothesized to be approaching equilibrium density) where Estes et al. (1986) found the index of sea otter feeding activity was 21.0 to 28.0%.

This study concentrated on four rocky coastal and subtidal substrate locations in Washington. The highest frequency of resting behavior was observed at Cape Alava and Duk Point, which also had the lowest frequencies of feeding activities of all locations. Daily movements and seasonal distribution shifts throughout the sea otters' known range in Washington have been observed (Jeffries, 2004; Lance et al., 2004). Cape Alava is thought to be a protected area that sea otters occupy in the winter due to winter storm waves or currents (Lance et al., 2004), and it also may be utilized as a protected area in the spring and summer months. These results suggest that sea otters in the present study may have used the sites differently, with Cape Alava and Duk Point used more as resting sites, while Sand Point and Norwegian Memorial are used more as feeding sites.

Sea otters are thought to select prey items that maximize their energy intake, presumably to meet their high metabolic requirements (Ostfeld, 1982; Garshelis, 1983). As preferred prey items become less abundant, sea otters may spend more time foraging in search of the prey items and/or they may switch to other prey items (Ostfeld, 1982; Garshelis, 1983). For example, red abalones have a very high caloric content (994 kcal) compared with kelp crabs (43 kcal) (Ostfeld, 1982). Although more time is spent harvesting the red abalone (Ostfeld, 1982), the overall net energy gain may make it beneficial for sea otters to consume such prey items when available. Prey items thought to be of high preference to sea otters include sea urchins, abalone, cancer crabs, and large clams (Kenyon, 1969; Garshelis, 1983). Less preferred prey (also of lower caloric content) are thought to include snails, kelp crabs, sea stars, mussels, sea cucumbers, and chitons (Ostfeld, 1982; Garshelis, 1983; Lance et al., 2004).

Sea otters in Washington consumed primarily crabs, clams, and sea stars. The remaining prey items (in declining numbers) consisted of unidentified bivalves, mussels, octopus, snails, sea

cucumbers, and a sea urchin. Similar to Laidre & Jameson (2006), no predation on fish or abalone was reported. At each location, the main prey type was different. Almost half of the prey consumed at Duk Point in this study were sea stars and mussels, which, based on the caloric classification by Ostfeld (1982) and Garshelis (1983), are of lower caloric content. This suggests that prey of higher preference in terms of caloric content are less abundant or depleted at Duk Point, which fits with the suggestion that this area may be used more as a resting site than a feeding site.

Successful dives were lowest at Duk Point and highest at Norwegian Memorial. However, variability in the success of foraging dives could reflect both the difficulty in capturing different types of prey and the overall abundance of prey available at these geographic locations. Similar to Laidre & Jameson (2006), the present study found no relationship between the number of successful dives and the sex of the sea otter or the presence of a pup. In this study, the average success rate (81.4%) was similar to the 77.0% success rate reported by Laidre & Jameson (2006) in Washington. In California, an average success rate of 70.0% was reported (Loughlin, 1977). In Prince William Sound, Alaska, the success rate was 80.0 to 96.0% (Garshelis, 1983), while at Amchitka Island and Attu Island, Alaska, success rates were 92.9% and 96.6%, respectively (Estes et al., 1982).

In this study, dive durations within the 20-m contour depth ranged from 5.3 s to 122.0 s, with a mean dive duration of 35.6 s. Although dive durations are correlated with the depths to which sea otters are diving, variation among locations and between sexes have also been recorded (Garshelis, 1983). Foraging dives have been found to have a mean duration ranging from 85.0 s in southeast Alaska (Bodkin et al., 2004), to 61.0 s in Prince William Sound (Garshelis, 1983), to 56.4 s in California (Loughlin, 1977). Laidre & Jameson (2006) report an average dive duration of 55.0 s, which likely reflects the differences in bathymetry in the areas of the coast sampled. Dive duration in Washington has been found to be inversely correlated with prey size. In the present study, there were differences in dive duration between locations, and these locale differences may relate to differences in prey availability. Sand Point had a high dive success rate, the highest feeding activity, and the least amount of time spent foraging. Of the four locations, prey availability would be predicted to be highest at this location.

In conclusion, the sea otter population in Washington is increasing and does not appear to be expanding outside its current range (with the exception of a few sightings of single sea otters

outside of the population range, south near Cape Arago and Cape Disappointment, Oregon, and north in Makah Bay, Washington; Jameson & Jeffries, 2004). Throughout the years, there has been a noticeable shift in the prey consumed in local areas. These areas are being utilized differently by sea otters in Washington—some as resting sites and others as feeding sites. However, based on the relatively low observed time invested in feeding, food availability in the current range does not appear to be limited. This supports the prediction that the Washington population is below equilibrium density and has the potential to continue to grow within this area. There is debate, however, as to the extent and degree to which the Washington sea otter population will expand (Laidre et al., 2002; Laidre & Jameson, 2006). Continued monitoring of sea otter health, prey consumption and availability, activity and movement, population growth, and habitat suitability will assist in future management policies and recovery plans.

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Literature Cited

- Bodkin, J. L., Esslinger, G. G., & Monson, D. H. (2004). Foraging depths of sea otters and implications to coastal marine communities. *Marine Mammal Science*, 20, 305–321.
- Bodkin, J. L., Ballachey, B. E., Cronin, M. A., & Scribner, K. T. (1999). Population demographics and genetic diversity in remnant and translocated populations of sea otters. *Conservation Biology*, 13, 1378–1385.
- Bowlby, C. E., Troutman, B. L., & Jeffries, S. J. (1988). Sea otters in Washington: Distribution, abundance, and activity patterns. *Final report prepared for National Coastal Resources Research and Development Institute*. Newport, OR: Hatfield Marine Science Center.
- Brancato, M. S., Davis, J. W., Jameson, R. J., Bowlby, C. E., & Milona, L. (2008). *Chemical contaminants, pathogen exposure and general health status of live and beach-cast Washington sea otters* (*Enhydra lutris kenyoni*) (Final report). Lacey: U.S. Fish and Wildlife Service–Western Washington Fish and Wildlife Office.
- Estes, J. A. (1990). Growth and equilibrium in sea otter populations. *Journal of Animal Ecology*, 59, 385–401.
- Estes, J. A., Jameson, R. J., & Rhode, E. B. (1982). Activity and prey election in the sea otter: Influence of population status on community structure. *The American Naturalist*, 120, 242–258.
- Estes, J. A., Smith, N. S., & Palmisano, J. F. (1978). Sea otter predation and community organization in the Western Aleutian Islands, Alaska. *Ecology*, 59, 822–833.
- Estes, J. A., Underwood, K. E., & Karmann, M. J. (1986). Activity-time budgets of sea otters in California. *Journal of Wildlife Management*, 50, 626–636.
- Garshelis, D. L. (1983). *Ecology of sea otters in Prince William Sound, Alaska*. Ph.D. dissertation, University of Minnesota, Minneapolis. 321 pp.
- Garshelis, D. L., Garshelis, J. A., & Kimker, A. L. (1986). Sea otter time budgets and prey relationships in Alaska. *Journal of Wildlife Management*, 50, 637–647.
- Gelatt, T. S., Siniiff, D. B., & Estes, J. A. (2002). Activity patterns and time budgets of the declining sea otter population at Amchitka Island, Alaska. *Journal of Wildlife Management*, 66, 29–39.
- Jameson, R. J. (1998). Translocated sea otter populations off the Oregon and Washington coasts. In M. J. Mac, P. A. Opler, C. E. Puckett Haecker, & P. D. Doran (Eds.), *Status and trends of the nation's biological resources* (pp. 684–686). Washington, DC: U.S. Geological Survey.
- Jameson, R. J., & Jeffries, S. J. (2004). *Results of the 2004 survey of the reintroduced sea otter population in Washington State*. Olympia: Washington Department of Fish and Wildlife.
- Jameson, R. J., & Jeffries, S. J. (2005). *Results of the 2005 survey of the reintroduced sea otter population in Washington State*. Olympia: Washington Department of Fish and Wildlife.
- Jameson, R. J., Kenyon, K. W., Johnson, A. M., & Wight, H. M. (1982). History and status of translocated sea otter populations in North America. *Wildlife Society Bulletin*, 10, 100–107.
- Jeffries, S. (2004). Appendix 1a. Report on tracking radio-tagged sea otters along the Washington coast from 2001 to 2003. In M. S. Brancato, L. Milonas, C. E. Bowlby, R. Jameson, & J. W. Davis (Eds.), *Chemical contaminants, pathogen exposure and general health status of live and beach-cast Washington sea otters* (*Enhydra lutris kenyoni*) (Fish and Wildlife Report FFS #1N59) (pp. 83–129). Washington, DC: Department of the Interior.
- Kannan, K., Kajiwarra, N., Watanabe, M., Nakata, H., Thomas, N. J., Stephenson, M., et al. (2004). Profiles

- of polychlorinated biphenyl congeners, organochlorine pesticides, and butyltins in southern sea otters and their prey. *Environmental Toxicology and Chemistry*, 23, 49-56.
- Kenyon, K. W. (1969). The sea otter in the eastern Pacific Ocean. *North American Fauna*, 68, 1-352.
- Krebs, J. R. (1978). Optimal foraging: Decision rules for predators. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 23-63). Oxford, UK: Blackwell Scientific. 494 pp.
- Kvitek, R., Giampietro, P. T., & Bowlby, C. E. (1998). Sea otters and benthic prey communities: A direct test of the sea otter as keystone predator in Washington State. *Marine Mammal Science*, 14, 895-902.
- Laidre, K. L., & Jameson, R. J. (2006). Foraging patterns and prey selection in an increasing and expanding sea otter population. *Journal of Mammalogy*, 87, 799-807.
- Laidre, K. L., Jameson, R. J., Jeffries, S. J., Hobbs, R. C., Bowlby, C. E., & VanBlaricom, G. R. (2002). Estimates of carrying capacity for sea otters in Washington State. *Wildlife Society Bulletin*, 30, 1172-1181.
- Lance, M. M., Richardson, S. A., & Allen, H. L. (2004). *Washington state recovery plan for the sea otter*. Olympia: Washington Department of Fish and Wildlife.
- Loughlin, T. R. (1977). *Activity patterns, habitat partitioning, and grooming behavior of the sea otter, Enhydra lutris, in California*. Ph.D. dissertation, University of California, Los Angeles.
- Ostfeld, R. S. (1982). Foraging strategies and prey switching in the California sea otter. *Oecologia*, 53, 170-178.
- Packard, J. M., & Ribic, C. A. (1982). Classification of behavior of sea otters (*Enhydra lutris*). *Canadian Journal of Zoology*, 60, 1362-1373.
- Riedman, M. L., & Estes, J. A. (1990). The sea otter (*Enhydra lutris*): Behavior, ecology, and natural history. *United States Fish and Wildlife Service Biological Report*, 90(14), 1-126.
- Scheffer, V. B. (1940). The sea otter on the Washington coast. *Pacific Northwest Quarterly*, 10, 370-388.