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ACTIVITY PATTERNS AND TIME BUDGETS OF THE DECLINING SEA OTTER POPULATION AT AMCHITKA ISLAND, ALASKA

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Abstract: Time budgets of predators may reflect population status if time spent foraging varies with local prey abundance. We assumed that the sea otter (*Enhydra lutris*) population at Amchitka Island, Alaska, USA, had been at equilibrium since the early 1960s and collected time budgets of otters to be used to represent future conditions of currently expanding sea otter populations. We used radiotelemetry to monitor activity–time budgets of otters from August 1992 to March 1994. Sea otter activity was directly linked to sex, age, weather condition, season, and time of day. Sea otters differed in percent time foraging among cohorts but not within cohorts. Percent time foraging ranged from 21% for females with very young (≤ 3 weeks of age) dependent pups to 52% for females with old (≥ 10 weeks of age) pups. Otters foraged more and hauled out more as local sea conditions worsened. Adult males spent less time foraging during winter and spring, consistent with seasonal changes in prey selection. Time spent foraging was similar to that reported for otters in California and an established population in Prince William Sound, Alaska, but greater than that of otters in recently established populations in Oregon and Alaska. Despite current evidence indicating that the population was in decline during our study, we were unable to recognize this change using time budgets. Our results illustrate the importance of stratifying analyses of activity patterns by age and sex cohorts and the complexity inherent in comparisons of behavioral data between different populations relying on distinct prey bases.

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The use of an indicator for assessing the population status of an apex predator has broad relevance in wildlife management. Predators, especially marine carnivores, are typically cryptic and logistically difficult to survey. More than 20 years ago, Eberhardt (1977) proposed using activity–time budgets to assess status of marine mammal populations. The rationale behind his proposal had 3 essential assumptions: (1) food is an important limiting resource to many marine mammal species (Estes 1977); (2) predation by marine mammals reduces the abundance and quality of their prey (Bowen 1997); and (3) percent time foraging (especially the search and pursuit of prey) increases as the abundance and quality of prey declines (Krebs 1978). Under this scenario, Eberhardt's conceptual model predicts that percent time foraging should increase as populations approach equilibrium density and competition for food increases, and should remain high relative to expanding populations that are not food-limited. Eberhardt (1977) further suggested that contrasts

between equilibrium populations and populations known to be below equilibrium density could be used to identify and categorize indicators of population status, such as time spent foraging.

The sea otter provides a useful model to evaluate Eberhardt's hypothesis. Unlike other marine mammals, sea otters do not store the excess benefits of foraging as blubber. Instead, they must have constant access to food to fuel growth, reproduction, homeostasis, and a high metabolic rate (Morrison et al. 1974, Costa and Kooyman 1982). Given this constraint, the effort invested in feeding by sea otters should reflect their immediate needs and the overall availability of prey.

History provided an opportunity to evaluate Eberhardt's hypothesis for sea otters. Overexploitation during the Pacific maritime fur trade reduced once-abundant sea otter populations to a small number of remnant colonies. These colonies began to recover following protection early in the 20th century, but in a temporally discordant manner (Kenyon 1969). By the mid-20th century, some of these populations had achieved equilibrium levels whereas others were only recently reestablished and growing rapidly (Rotterman and Simon-Jackson 1988, Estes 1990, Riedman and Estes 1990).

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The earliest indication that sea otter activity–time budgets varied with population status was based on data obtained during the 1970s from Oregon and from 2 locations in Alaska’s Aleutian archipelago: Amchitka and Attu (Estes et al. 1982; Table 1). This contrast was made because, at the time, the sea otter population at Amchitka was well studied (Kenyon 1969, Estes 1977) and assumed to have been at equilibrium density for several decades, whereas the populations at Attu and Oregon were recently reestablished (Attu naturally, Oregon by relocation from Amchitka [Jameson et al. 1982]) and far below equilibrium density. Activity–time budgets were assessed at all 3 locations by visual scan sampling at half-hour intervals from dawn to dusk. These data indicated that otters at Attu and Oregon both spent about 18% of the daylight hours foraging, spread evenly throughout the day, whereas otters at Amchitka spent about 55% of the daylight hours foraging, with distinct crepuscular peaks in foraging activity.

This earlier work indicated a strong relationship between activity–time budget and population status in sea otters, but left a number of important questions unanswered. Foremost among these was the degree to which otters feed at night, and whether individual time budgets varied among and within age–sex cohorts. Resolving these questions requires individual identification and the ability to observe, at least indirectly, nocturnal activity. This was accomplished using radiotelemetry in a series of studies

in California and Prince William Sound, Alaska (Loughlin 1979, Ribic 1982, Garshelis 1983, Payne and Jameson 1984, Ralls and Siniff 1990). The capture of animals for instrumentation permitted reliable cohort assessment, and the data from field observations indicated that approximately 45% of all feeding occurred at night. Furthermore, these previous studies found that activity–time budgets differed among cohorts from day to day, and across seasons. Other early studies demonstrated strong sexual segregation within sea otter populations (Lensink 1962, Kenyon 1969, Schneider 1971, Garshelis et al. 1986, Jameson 1989). It was thus apparent that activity–time budgets based on scan samples could be inconsistently biased, depending on the precise spatial distribution of age and sex groupings and the exact location along a shoreline where the samples were obtained.

Although these findings resulted from telemetry studies, they focused on expanding sea otter populations in Alaska (Garshelis 1983, Monson and DeGange 1995) and California (Estes et al. 1986, Jameson 1989, Ralls and Siniff 1990). No parallel research had been conducted on an equilibrium population that, according to theory, should characterize the future conditions of the expanding populations.

Our objective was to contrast data from Amchitka Island with similar data from prior studies in central California (Ralls and Siniff 1990) and Prince William Sound, Alaska (Garshelis 1983),

Table 1. Results from studies of sea otter time budgets.

Time foraging by cohort (%) ^a						Study year(s)	Method ^b	Area	Population status	Reference
Mean	AF	AM	JF	JM	FWP					
	43	38	50	44	21–52	1992–1994	T	Amchitka	Decreasing	This study
53				34		1977	D	Amchitka	Stable	Estes et al. 1982
58						1972	D	Amchitka	Stable	Estes et al. 1982
15–18				16–19		1977	D	Attu, AK	Increasing	Estes et al. 1982
37	37	37				1980–1981	T	Nelson Bay, AK	Increasing	Garshelis et al. 1986
47	47	47			53	1980–1981	T	Green Island, AK	Stable	Garshelis et al. 1986
11						1986–1987	D	Washington	Increasing	Bowlby et al. 1988
17						1977	D	Oregon	Increasing	Estes et al. 1982
	40	40	50	35	40	1984–1987	T	California	Increasing	Ralls and Siniff 1990
21–28						1981–1982	D	California	Increasing	Estes et al. 1986
34	36	33				<1978	T	California	Stable	Loughlin 1980
24						1974	D	California	Stable	Shimek and Monk 1977
					2–26	1969	D	California	Increasing	Sandegren et al. 1973

^a AF = single adult females, AM = adult males, FWP = females with dependent pups of any age, JF = juvenile females, JM = juvenile males.

^b Method: D = Diurnal scan sample, T = Radiotelemetry and includes nocturnal foraging.

to determine how activity patterns change as populations approach equilibrium density. Based on repeated scan surveys of Amchitka conducted during the 1970s and 1980s (Estes 1977, Estes et al. 1982) indicating that otters spent a similar amount of time foraging during both periods, our general hypothesis assumed that the Amchitka population was at equilibrium density. Furthermore, we predicted that strong intraspecific competition for food would be reflected by Amchitka sea otters spending more time foraging than otters in increasing populations. Using the published literature on sea otter activity-time budgets, we further predicted that the increased competition and limited prey base at Amchitka would require juveniles to spend more time foraging than adults, and that intraspecific competition would cause juvenile females to spend more time foraging than juvenile males (Ralls and Siniff 1990). Likewise, we expected that competition for food combined with the energetic demands of a dependent pup would force females with pups of any age to spend more time foraging than nonreproductive females, as was found in an established population in Prince William Sound, Alaska (Garshelis et al. 1986).

Several years after completion of our field studies at Amchitka, an examination of sea otter demographics throughout the Aleutian chain indicated that the population had been in rapid decline prior to and during the time of our work, presumably because of increased predation by killer whales (Estes et al. 1998). This knowledge complicated the interpretation of our results and nullified our original objectives, i.e., the Amchitka population was not at equilibrium during our study. However, retrospectively, this study represented the ideal test of whether activity-time budgets can represent population status because only after the study was finished did we recognize the status of the population.

METHODS

Study Area

Amchitka Island (51.5°N, 179°E), in the Rat Island group of the Aleutian archipelago, is located at the boundary between the North Pacific Ocean and Bering Sea, 2,160 km WSW of Anchorage, Alaska (Merritt 1977). Amchitka harbored a remnant sea otter population at the end of the fur trade estimated to contain roughly 100 animals during the early 1900s (Kenyon 1969). This population increased to an estimate of 4,500

during 1943, then declined to about 1,500 by 1950 due to increased mortality caused by food limitation. The population was estimated at >6,000 by at least the early 1970s based on estimates derived from shore-based counts and whole-island aerial surveys (Estes 1977). The sea otter population at Amchitka Island was not surveyed again until June 1993, when 3,377 independent otters were counted by shore-based observers under near-perfect viewing conditions. In hindsight, this count provided the first indication of a possible population decline.

Capture and Instrumentation

We captured 115 sea otters during the summers of 1992 ($n = 96$) and 1993 ($n = 19$), using floating tangle nets or diver-operated Wilson traps (Ames et al. 1986). Each otter >9 kg was tagged in both rear flippers with color-coded plastic ear tags (Temple Tags, Temple, Texas, USA) in a unique color and placement combination to permit visual identification (Ames et al. 1983). An additional 22 female otters, including all palpably pregnant females, were marked with flipper tags only.

We anesthetized all otters >9 kg with a combination of fentanyl/droperidol (RBI, Natick, Maine, USA) at 0.25–0.55 mg/kg and diazepam (Valium®; Steris Laboratories, Inc., Phoenix, Arizona, USA) at 0.07–0.2 mg/kg intramuscularly as soon as possible following capture (D. H. Monson, U.S. Geological Survey, unpublished data). Radiotransmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA) were surgically implanted (Williams and Siniff 1983, Ralls et al. 1989) in 80 otters in 5 distinguishable cohorts: adult males (AM), juvenile males (JM), adult females (AF), juvenile females (JF), and dependent pups (DP; Table 2). We further divided parous females into 3 groups based on the age of their pup: females with very young pups (FVYP), pup age ≤ 3 weeks postpartum; females with young pups (FYP), pup age >3 weeks to ≤ 10 weeks postpartum; and females with old pups (FOP), pup age >10 weeks postpartum.

We estimated age of captured pups from body mass by using the regression of Monnett et al. (1991). We calculated the age of pups born during the study from their estimated birthdays, determined as the midpoint between the last sighting of its mother without the pup and the first sighting of her with a new pup. Births that occurred during the study period were recognized within a few days postpartum. A premolar was extracted for age determination from all non-pups (Schneider 1973, Garshelis 1984, Bodkin et

Table 2. Sample sizes for sea otters at Amchitka Island, Alaska, August 1992–March 1994. A total of 62 otters were sampled for a minimum of 24 hr. Changes in otter age during the study resulted in some individuals being sampled in more than 1 cohort.

Cohort ^a	Instrumented <i>n</i>	Sampled <i>n</i>	Activity bouts	Hours sampled	Complete activity bouts
AF	13	26	70	1,348	46
JF	8	11	26	563	20
FVYP	3	7	13	260	9
FYP	9	5	12	252	10
FOP	10	10	22	436	16
AM	21	17	69	1,272	43
JM	5	5	12	269	11
DP	11	4	9	174	6
Total	80	85	233	4,574	161

^a AF = adult females, AM = adult males, DP = dependent pups, FVYP = females with very young pups (≤ 3 weeks), FYP = females with young pups (> 3 and ≤ 10 weeks), JF = juvenile females, JM = juvenile males.

al. 1997). All independent otters ≤ 3 years of age were classified as juveniles to reflect the typical minimum age of sexual reproduction (Riedman and Estes 1990, Jameson and Johnson 1993).

Forty-seven percent of known births to study animals occurred from May through July (Monson 1995). Because otters were captured during June of each year, we assumed that adult and juvenile birthdays were 1 June, and any otter passing from juvenile to adult during the study was assigned to a new cohort on that date. We further classified adult males as territorial and nonterritorial, based on the degree of site fidelity and other characteristic aspects of behavior (Calkins and Lent 1975, Loughlin 1980, Garshelis 1983, Jameson 1989).

Following surgery, each otter was given an intravenous injection of 0.2–0.4 mg/kg naloxone (Narcan[®]; Wildlife Pharmaceuticals, Inc., Fort Collins, Colorado, USA) to reverse anesthesia and released into an observation pen for about 2 hours. Before release, each otter was given an intramuscular booster of naloxone at similar dosage. All instrumented otters were relocated within a few days of surgery and no noticeable side effects were observed. We located and monitored radiotagged otters with programmable scanning receivers and 3–4-element Yagi antennae. Radios were designed to transmit continuously for ≥ 2 years. Dependent pups < 9 kg were neither tagged nor instrumented.

Activity Monitoring

Shore-based observers collected activity data. Visual contact was maintained whenever possible using binoculars or high-power spotting scopes (Questar Corporation, New Hope, Pennsylvania,

USA). We monitored radiotagged sea otters for bouts of 3 to 24 hours, approximately twice per week, between 7 August 1992 and 11 March 1994. Each complete 24-hr bout consisted of 144 10-min observations during which the activity occurring at the conclusion of each 10-min period was recorded (Altmann 1974). The location of the focal otter in UTM coordinates and weather data were recorded hourly. The radio frequencies we used did not transmit through salt water, and thus provided a distinct indication of active versus inactive activity and foraging behavior (via lost signals) without visual observations (e.g., at night and during inclement weather).

We recognized 9 separate categories of activity: (1) foraging; (2) resting; (3) grooming; (4) swimming (if swimming and grooming simultaneously, grooming was noted); (5) consorting (2 or more otters fighting, copulating, or playing); (6) mooching (pups or adults taking food from another otter); (7) hauled out; (8) active-unknown (telemetry signals indicated the otter was active but the signals did not follow the characteristic pattern of foraging or swimming); and (9) unknown (faint, brief, or lost signal). Activity bouts that included > 50 min of continuous unknown activity were discontinued and not used in the 24-hr analyses. Four activities—foraging, swimming, resting, and hauled-out—could be determined without visual confirmation by distinct radio signal patterns. Swimming otters do not have noticeable silent periods characteristic of foraging otters during a dive, and hauled-out otters have a noticeably louder signal compared with otters resting in the water. This is easily noted during the transition between water and land.

Because we were primarily interested in foraging and resting activity, we used 3 categories for analysis: (1) foraging, (2) resting (includes the sum of resting and hauled out), and (3) other. Intervals classified as active unknown or unknown were also included in the other category to avoid overestimating percent times foraging and resting-hauled out (Ralls and Siniff 1990).

Seasons and Weather

We divided the calendar year into 4 seasons: winter (Jan-Mar), spring (Apr-Jun), summer (Jul-Sep), and fall (Oct-Dec) to coincide with a concurrent dietary analysis of sea otters at Amchitka (Watt et al. 2000). Three aspects of weather (rain, local sea condition, open sea condition) were quantified and included as covariates to test for the affect of weather on activity. Rain was classified as none, light, medium, or heavy. We classified sea condition on a modified Beaufort scale: (1) calm (light ruffle), (2) chop (no white caps), (3) light (white caps but seas light), and (4) heavy (white caps with seas heavy in the immediate vicinity of the focal otter [local sea condition] and the adjacent unprotected ocean [open sea condition]). A hauled-out otter was assigned a local sea condition of 0.

Statistical Analyses

We grouped individuals by cohort and used nested analysis of variance (ANOVA; MacAnova, Oehlert and Bingham 1993) with the weather covariates to compare percent time foraging among cohorts. The nesting allowed us to account for any individual variation or variation within cohort and the analysis of covariance adjusted the mean percent times for the effects of weather. Mean percent time in each of the 3 activities was calculated using the model $\hat{Y} = u + l + o + r + \hat{s}$ where u is the constant for all cohorts and l , o , and r are the covariates local sea condition, open sea condition and rain, respectively, and \hat{s} is the overall mean for the cohort being estimated. We used crossed (2-factor) ANOVA to examine percent foraging by season with cohort and season as the factors. Females with pups were included but kept in separate groups based on pup age to distinguish pup age-related differences. Dependent pups were not included in statistical tests comparing cohorts because their activity was dependent on their mothers. If an individual otter was sampled >1 time in a particular cohort, we weighted the means of repeat samples by the number of samples for the 2-stage

nested design. We calculated variance components for corrected mean square denominator values and degrees of freedom in the F -test to account for unbalanced nested designs (Montgomery 1993), and we used the Bonferroni procedure to test differences among means.

We used the Wilcoxon signed rank test across individuals within each cohort to compare percent time foraging during diurnal versus nocturnal periods. We assigned diurnal and nocturnal periods by using U.S. Naval charts of daily sunrise and sunset for nearby Adak Island, Alaska. This method eliminated observer subjectivity in assigning light and dark periods during the fieldwork. In all tests, P -values of <0.05 were considered statistically significant. We used simple linear regression to display the relationship between activity and sea conditions but relied on the nested ANOVA for the test of significance. Area graphs were plotted to display the distribution of activity across a 24-hr period for each cohort.

RESULTS

Time Budgets

We monitored 69 sea otters for 27,444 10-min observations (Table 2). Approximately 32% of the 233 activity bouts were terminated at <24 hr. These data were not used in population-wide sta-

Table 3. Time budgets for all cohorts of sea otters sampled during a radiotelemetry study at Amchitka Island, Alaska, August 1992–March 1994. The mean percent time spent in each activity category represents the weighted mean for all otters per cohort. Percentages were corrected for covariates.

Cohort ^a	<i>n</i>	Time foraging (%)		Time resting (%)		Other (%)	
		Mean	SE	Mean	SE	Mean	SE
AF	26	42.5 BCD ^b	2.44	44.1	2.23	13.4	1.77
JF	11	49.9 CD	3.16	38.6	5.36	11.5	2.50
FVYP	7	21.0 A	3.95	60.8	6.78	18.1	1.77
FYP	5	39.1 CD	3.95	50.2	5.36	10.6	1.58
FOP	10	51.8 D	3.48	40.0	3.49	8.20	1.19
AM	17	37.5 B	3.00	45.5	2.23	16.9	2.14
JM	5	44.3 BCD	3.89	41.3	5.00	14.4	5.10
DP ^c	4	30.6	8.34	52.6	6.30	16.8	3.64

^a AF = adult females, AM = adult males, DP = dependent pups, FOP = Females with old pups (>10 weeks), FVYP = females with very young pups (<3 weeks of age), FYP = females with young pups (>3 and ≤10 weeks of age), JM = juvenile males, JF = juvenile females.

^b Mean percent foraging times with the same letters are not different at $P < 0.05$ (Bonferroni comparison of means).

^c Dependent pup activity was not independent from their mothers and was not tested against other cohorts. Percent times are listed for reference only.

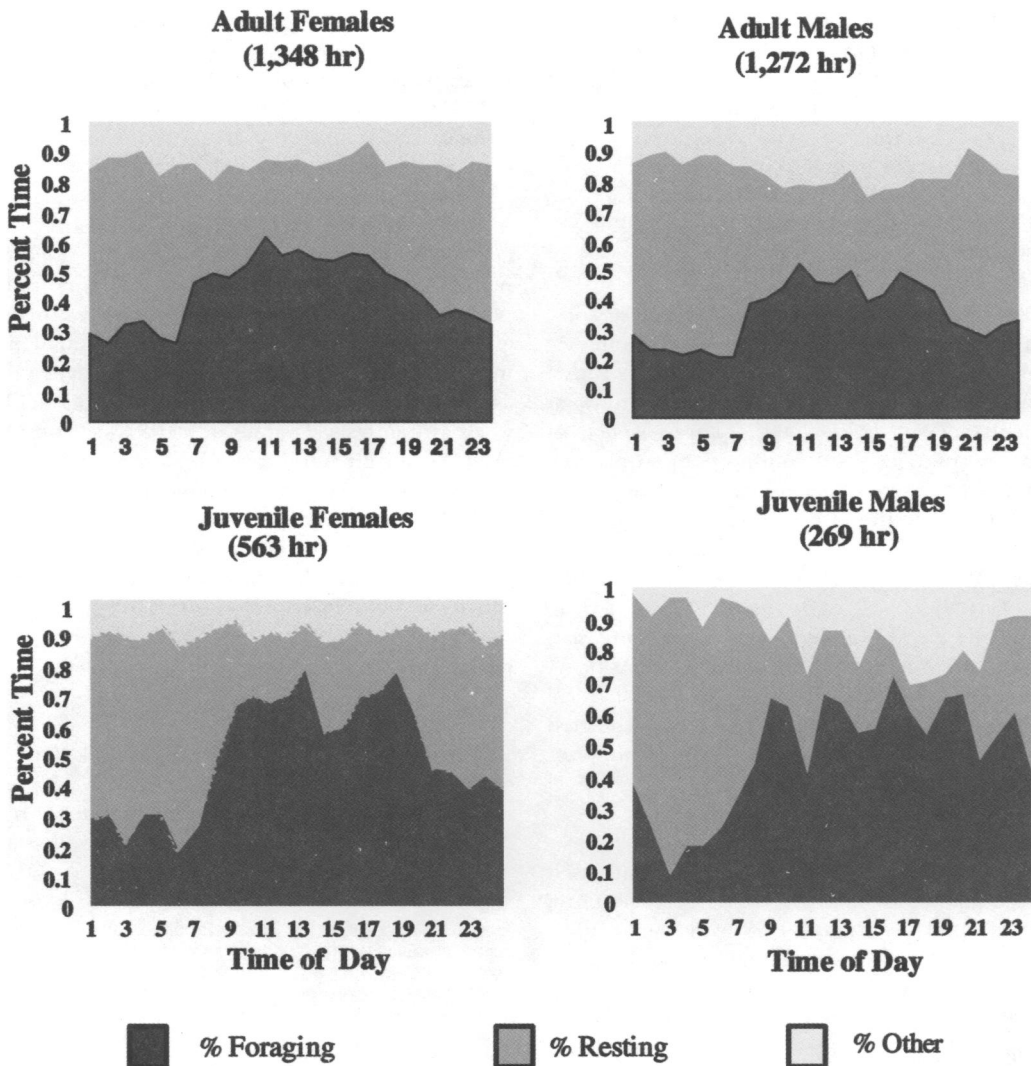


Fig. 1. Daily activity of sea otter age-sex cohorts at Amchitka Island, Alaska, USA, during August 1992–March 1994. Each hour represents the grand mean for all samples of each individual sampled. Sample numbers indicate the hours of observation.

tistical analysis because of inconsistencies in the time of day the observations were made.

Testing all 24-hr observation bouts together indicated a difference in foraging time among cohorts ($F_{6, 50.8} = 12.44$, $P < 0.001$) but not among individuals in the same cohort ($P > 0.07$ for all cohorts; Table 3). Among the various cohorts, FVYP spent the least time foraging whereas FOP and juveniles spent the most time foraging (Table 3). Adults and juveniles did not differ within their respective sex ($P > 0.05$ for each). Females with young pups were similar to AM ($P > 0.05$). No difference occurred in percent time foraging

between territorial and nonterritorial AM ($P = 0.45$).

Daily Activity

Foraging activity occurred throughout the diurnal period in all cohorts except FVYP and increased during early morning in all cohorts except FYP and FVYP (Figs. 1, 2). All cohorts except FYP and FVYP spent more time foraging diurnally than nocturnally ($P \leq 0.05$ for each; Table 4). A pup-age-related trend was apparent among parous females with a proportionally decreasing amount of nocturnal foraging as the

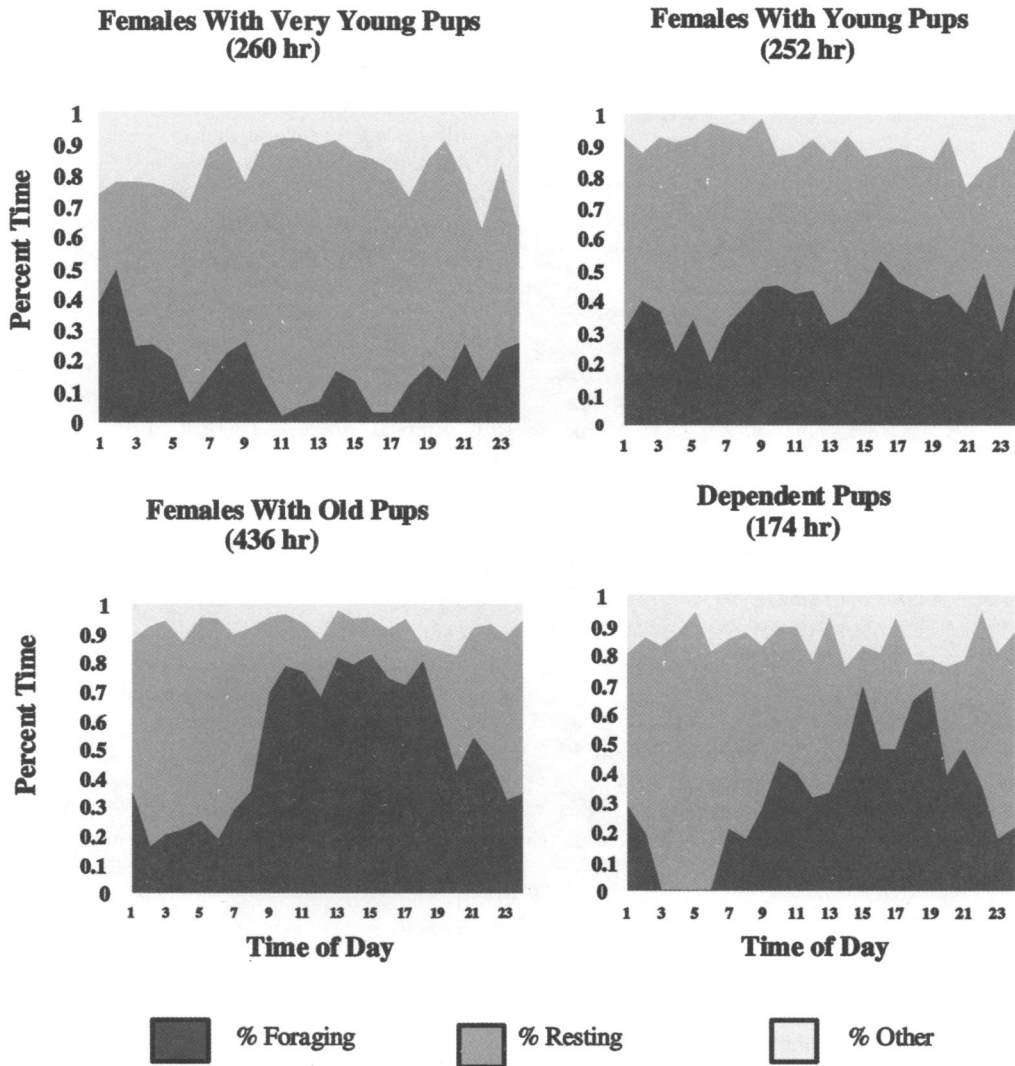


Fig. 2. Daily activity of female sea otters with pups of various ages (very young <3 weeks; young >3 weeks and <10 weeks; old >10 weeks), and dependent pups at Amchitka Island, Alaska, USA, August 1992–March 1994. Each hour represents the grand mean for all samples of each individual sampled. Sample numbers indicate the hours of observation.

pup aged. Females with very young pups spent the least amount of time foraging, and foraged equally by night and day (Table 4). Because more pup births occurred during the summer (Monson 1995), the proportion of nocturnal foraging for FVYP was even more striking. Females with pups shifted to predominately diurnal foraging when the pups were >10 weeks of age possibly due to decreased predation risk from bald eagles (*Haliaeetus leucocephalus*; Gelatt 1996). All cohorts except DP foraged throughout the 24-hr period (Figs. 1, 2).

Weather-Related Activity

Each cohort increased percent time foraging with worsening local sea conditions. The effect was strongest for AF, who increased foraging time by 10% with each categorical increase in local sea condition ($P = 0.0004$). This relationship was highly significant when averaged across all cohorts ($F_{1, 72} = 9.8, P = 0.003$; Fig. 3). However, it should be noted that we were limited for samples of sea otters foraging in a local sea condition > 2. Adult females were the only cohort in which rain was correlated with activity ($P = 0.03$). For each

Table 4. Percent time spent foraging by sea otters during diurnal and nocturnal periods at Amchitka Island, Alaska, August 1992–March 1994. Percentages in each category represent the average of the weighted-means of each individual otter for the sex–age cohort corrected for weather covariates. Sex–age cohorts are listed in the same order as Table 3. Mean is across all individuals and SE are mean standard errors.

Cohort ^a	Diurnal		Nocturnal		<i>P</i> ^b
	Mean	SE	Mean	SE	
AF	25.5	2.2	17.0	1.9	0.05
JF	31.0	1.3	18.9	1.7	0.01
FVYP	10.9	2.0	10.7	3.1	0.93
FYP	23.7	2.6	15.4	4.1	0.22
FOP	35.5	2.0	15.5	3.1	0.005
AM	23.0	1.8	14.5	1.9	0.01
JM	28.1	1.2	16.2	2.2	0.04
Mean	25.8		15.9		

^a AF = adult females, AM = adult males, DP = dependent pups, FOP = females with old pups (>10 weeks of age), FVYP = females with very young pups (≤3 weeks of age), FYP = females with young pups (>3 and ≤10 weeks of age), JF = juvenile females, JM = juvenile males.

^b Wilcoxon signed rank 2-tailed probability.

categorical increase in rain intensity, AF decreased foraging time approximately 17% and increased percent time hauled out by 19%. We did not observe any influence of the weather covariates in the remaining cohorts.

Seasonal Activity

Because time budgets within each cohort were similar ($F_{1, 82} = 0.36$, $P = 0.55$) between sampling years, we pooled the data to compare seasons. Adult females and AM were the only classes with sample sizes adequate to allow seasonal comparisons. We did not detect any seasonal difference activity in AF, the group with the largest sample ($P > 0.1$ for each). Adult males, in contrast, spent less time foraging ($F_{3, 23} = 7.56$, $P = 0.001$) during winter (32%) and spring (31%) than summer (43%) or fall (42%). Likewise, AM spent more time swimming ($F_{3, 23} = 3.95$, $P < 0.03$) during winter (3.2%) than during spring, summer, or fall (<1% for each) and resulting in a seasonal difference in the other category for AM ($F_{3, 23} = 4.36$, $P = 0.01$). These seasonal patterns did not differ between territorial and nonterritorial AM (2-tailed Mann-Whitney, $P > 0.9$). We separated hauled-out and resting behavior for all age classes and found that otters were hauled-out about 25% and 18% of the time during winter and spring, compared with 3% and 6% during summer and fall, respectively.

DISCUSSION

Time Budgets

Variability in behavior among sea otter cohorts was influenced by several factors, including the differing effects of weather, season, time of day, and in females with pups, by the age of the pup. Foraging times for adult otters at Amchitka were similar to those reported for an expanding population of otters in California (Ralls and Siniff 1990). However, male and female juveniles did not differ in time spent foraging in contrast to Ralls and Siniff (1990) who documented JF spending 16% more time foraging than JM. Adult otters at Amchitka spent slightly more time foraging than otters at recently reoccupied Nelson Bay, Alaska, and less than otters in the long-established population at Green Island, Alaska (Garshelis et al. 1986). Juvenile Amchitka otters also foraged for slightly less time than juveniles at Green Island.

Percent time foraging for females with pups appeared to be dependent on pup age. As pups age and become more independent, they require greater caloric intake, consume more solid food (Hanson et al. 1993), and can presumably withstand longer periods between feedings. This is reflected by an increase in the duration of forage bouts, dive times, and time spent foraging by the mother, as well as more diurnal foraging (Gelatt 1996). The large difference in foraging time for females with pups of various ages at Amchitka are not directly comparable with California or Alaska data because previous researchers did not separate females with pups into like age groups (Garshelis et al. 1986, Ralls and Siniff 1990).

Daily Activity

We did not observe distinct crepuscular peaks in foraging as reported in California (Ralls and Siniff 1990) and Amchitka (Estes et al. 1982). During the 1970s, when kelp forest fishes composed more than half of the estimated prey biomass consumed by otters at Amchitka, foraging activity peaked sharply around crepuscular periods when these fishes were captured in the largest numbers (Estes et al. 1982). During our study, kelp forest fishes were a much smaller proportion of the diet (Watt et al. 2000) and crepuscular peaks in foraging activity were not apparent.

Weather

Previous studies have recognized a relationship between increased activity in sea otters and wors-

ening weather conditions (Fisher 1939, Lensink 1962, Sandegren et al. 1973, Garshelis 1983, Estes et al. 1986). We found similar results, as otters at Amchitka tended to forage more and haul out more during rough seas. Garshelis (1983) suggested that Alaskan otters spent more time foraging due to persistent rainy weather. Collectively, these findings indicate that otters in otherwise similar populations might differ in activity simply due to differing climatic conditions.

Seasonal Differences

The seasonal patterns in time budgets of otters at Amchitka were unique. Winter–spring usually is a period of starvation and increased mortality in sea otters (Kenyon 1969), yet we observed reduced foraging and little mortality during winter–spring. Garshelis (1983) reported an increase in activity, specifically foraging activity, during winter at Green Island, Prince William Sound, Alaska. This suggests a thermoregulatory response, in which otters in an area of consistent prey resources spent a relatively greater amount of time foraging during the cooler months of winter and spring to maintain homeostasis.

The seasonal difference we observed was strongest for AM, and may be related to their dietary preferences for smooth lumpstickers (*Aptocyclus ventricosus*; Watt et al. 2000). Lumpstickers undergo episodic spawning migrations during the winter and early spring from the epipelagic zone to coastal waters (Il'inskii and Radchenko 1991), where they occasionally become available as prey for sea otters and have been recorded in Amchitka sea otter diets (Kenyon 1969). Lumpstickers were present in high densities during 1993–1994, but they were absent or rare at Amchitka during the 1970s (Estes 1977, Estes et al. 1982). The availability of spawning lumpstickers at Amchitka during our study appears to have mitigated the usual winter–spring starvation-induced mortality and provided a high-energy food source during a time of typical food stress. However, juvenile sea otters rarely ate lumpstickers and adult males ate more than adult females (Watt et al. 2000), thereby reducing their percent time foraging. These findings illustrate the complexities of extrapolating time budgets across cohorts and seasons.

Our findings show that activity patterns and time budgets in sea otters are influenced by complex factors that cannot be detected by visual scan sampling. Perhaps the most important of these are the individual effects of age, sex, and

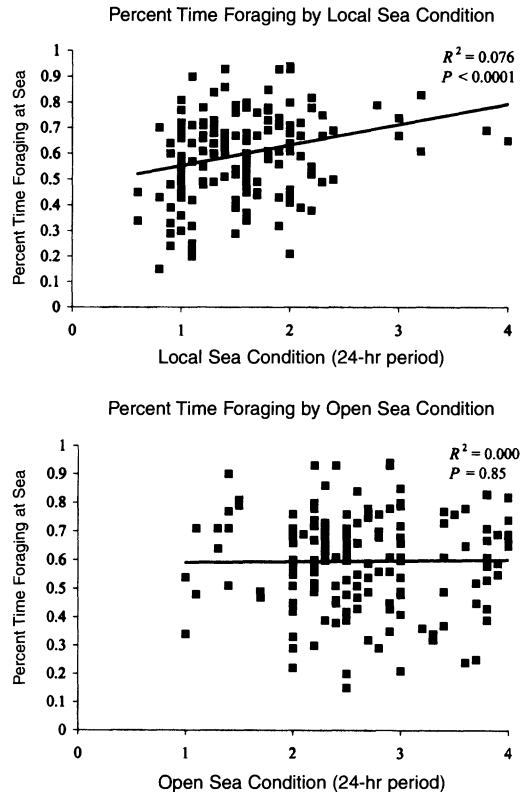


Fig. 3. Percent time foraging for sea otters at Amchitka Island, Alaska, USA, with sea conditions. Local sea condition was defined as the condition in the close vicinity of the focal otter: (1) calm (light ruffle), (2) chop (no white caps), (3) light (white caps but seas light), and (4) heavy (white caps with seas heavy). Open sea condition was the open unprotected ocean during the same time.

reproductive condition. The overall percent time foraging ranged from 21 to 52% across cohorts. This variation reflects the importance of accurate cohort identification of the focal animal and cautions against using diurnal scan sampling to estimate time budgets. Because sea otters segregate sexually, scan samples of any particular area will reflect the cohort that happens to occupy that area, potentially misrepresenting the local population.

Our results indicate that time spent foraging by sea otters at Amchitka during the early 1990s was similar to that estimated from scan samples during the 1980s. However, the combination of factors acting on time budgets of sea otters makes any comparison between areas or time periods untenable. The best approach for interpopulation contrasts based on telemetry data probably is to use the vector of values from the various

age–sex classes rather than 1 population-level measurement.

MANAGEMENT IMPLICATIONS

Recent work has documented a substantial decrease in sea otter populations throughout the Aleutian Islands (Estes et al. 1998) and indicates that the population has declined to approximately 10% of the 1965 level (A. Doroff, U.S. Fish and Wildlife Service, unpublished data). The extent of this decline at Amchitka was indicated by our 1993 count of 3,377 otters, about 52% of the estimated population size derived from surveys conducted during the early 1970s (Estes 1990). In retrospect, we clearly were not studying a stationary population.

The lack of similar data from a time when the population was at maximum density makes a rigorous assessment of change impossible. Our findings emphasize that a suite of independent and cumulative factors affects the variation in activity–time budgets between populations. We still do not know how activity varies with changes in population density. Is this a linear response or does the shift occur abruptly as resources become limiting? The available data from all telemetry and scan sampling studies suggest a rather broad range of percent time foraging. Thus, a simple step function at the point of resource limitation seems unlikely. Measurements of activity also must account for other important variables, including season, weather, and the exact nature of the prey.

We make 2 general conclusions from this work. First, activity–time budgets are not reliable indicators of the population status of sea otters. Second and perhaps of greater general importance in wildlife research, by focusing so strongly on hypotheses structured by preconceptions from our previous work, we became hampered by the inertia of past knowledge (D. L. Garshelis, Minnesota Department of Natural Resources, personal communication). Consequently, we were reluctant to accept that a population decline had occurred despite our survey results indicating such an event. This second point underscores the first and indicates that activity–time budgets may be a useful tool for understanding the ecology of sea otters, but are not a reliable metric of population status.

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LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.
- AMES, J. A., R. A. HARDY, AND F. E. WENDELL. 1983. Tagging materials and methods for sea otters, *Enhydra lutris*. *California Fish and Game* 69:243–252.
- , ———, AND ———. 1986. A simulated translocation of sea otters, *Enhydra lutris*, with a review of capture, transport, and holding techniques. California Department of Fish and Game Marine Research Technical Report Number 52.
- BODKIN, J. L., J. A. AMES, R. J. JAMESON, A. M. JOHNSON, AND G. M. MATSON. 1997. Estimating age of sea otters with cementum layers in the first premolar. *Journal of Wildlife Management* 61:967–973.
- BOWEN, W. D. 1997. Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series* 158:267–274.
- BOWLBY, C. E., B. L. TROUTMAN, AND S. J. JEFFRIES. 1988. Sea otters in Washington: distribution, abundance, and activity patterns. Unpublished final report prepared for National Coastal Resources Research and Development Institute, Newport, Oregon, USA. Washington State Department of Wildlife, Olympia, USA.
- CALKINS, D., AND P. C. LENT. 1975. Territoriality and mating behavior in Prince William Sound sea otters. *Journal of Mammalogy* 56:528–529.
- COSTA, D. P., AND G. L. KOOYMAN. 1982. Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Canadian Journal of Zoology* 60:2761–2767.
- EBERHARDT, L. L. 1977. "Optimal" management policies for marine mammals. *Wildlife Society Bulletin* 5:162–169.
- ESTES, J. A. 1977. Population estimates and feeding behavior of sea otters. Pages 511–526 in M. C. Merritt and R. G. Fuller, editors. *The environment of Amchitka Island, Alaska*. Energy Research and Development Administration, National Technical Information Service, U.S. Department of Commerce, Springfield, Virginia, USA.
- . 1990. Indices used to assess status of sea otter populations: a reply. *Journal of Wildlife Management* 54:270–272.

- , R. J. JAMESON, AND E. B. RHODE. 1982. Activity and prey selection in the sea otter: influence of population status on community structure. *American Naturalist* 120:242–258.
- , M. T. TINKER, T. M. WILLIAMS, AND D. F. DOAK. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- , K. E. UNDERWOOD, AND M. J. KARMANN. 1986. Activity-time budgets of sea otters in California. *Journal of Wildlife Management* 50:626–636.
- FISHER, E. M. 1939. Habits of the southern sea otter. *Journal of Mammalogy* 20:21–36.
- GARSHELIS, D. L. 1983. Ecology of sea otters in Prince William Sound, Alaska. Dissertation, University of Minnesota, St. Paul, USA.
- . 1984. Age estimation of living sea otters. *Journal of Wildlife Management* 48:456–463.
- , J. A. GARSHELIS, AND A. T. KIMKER. 1986. Sea otter time budgets and prey relationships in Alaska. *Journal of Wildlife Management* 50:637–647.
- GELATT, T. S. 1996. Activity patterns and time budgets of sea otters at Amchitka Island, Alaska. Thesis, University of Minnesota, St. Paul, USA.
- HANSON, M. B., L. J. BLEDSO, B. C. KIRKEVOLD, C. J. CASON, AND J. W. NIGHTINGALE. 1993. Behavioral budgets of captive sea otter mother-pup pairs during pup development. *Zoo Biology* 12:459–477.
- IL'INSKII, E. N., AND V. I. RADCHENKO. 1992. Distribution and migration of smooth lump sucker in the Bering Sea. *Russian Journal of Marine Biology* 3–4:19–25.
- JAMESON, R. J. 1989. Movements, home range, and territories of male sea otters off central California. *Marine Mammal Science* 5:159–172.
- , AND A. M. JOHNSON. 1993. Reproductive characteristics of female sea otters. *Marine Mammal Science* 9:156–167.
- , K. W. KENYON, A. M. JOHNSON, AND H. M. WIGHT. 1982. History and status of translocated sea otter populations in North America. *Wildlife Society Bulletin* 10:100–107.
- KENYON, K. W. 1969. The sea otter in the eastern Pacific Ocean. *North American Fauna* 68.
- KREBS, J. R. 1978. Optimal foraging: decision rules for predators. Pages 23–63 in J. R. Krebs and N. B. Davies, editors. *Behavioural ecology: an evolutionary approach*. Blackwell Scientific, Oxford, United Kingdom.
- LENSINK, C. J. 1962. The history and status of sea otters in Alaska. Dissertation, Purdue University, West Lafayette, Indiana, USA.
- LOUGHLIN, T. R. 1979. Radio telemetric determination of the 24-hour feeding activities of sea otters. *Enhydra lutris*. Pages 717–724 in C. J. Amlaner and D. W. Macdonald, editors. *A handbook on biotelemetry and radio tracking*. Pergamon Press, New York, USA.
- . 1980. Home range and territoriality of sea otters near Monterey, California. *Journal of Wildlife Management* 44:576–582.
- MERRITT, M. L. 1977. Geographic setting. Pages 1–11 in M. L. Merritt and R. G. Fuller, editors. *The environment of Amchitka Island, Alaska*. Energy Research and Development Administration, National Technical Information Service, U.S. Department of Commerce, Springfield, Virginia, USA.
- MONNETT, C., L. M. ROTTERMAN, AND D. B. SINIFF. 1991. Sex-related patterns of postnatal development of sea otters in Prince William Sound, Alaska. *Journal of Mammalogy* 72:37–41.
- MONSON, D. H. 1995. Reproductive strategies in sea otters at Amchitka Island, Alaska. Thesis, University of California, Santa Cruz, USA.
- , AND A. DEGANGE. 1995. Reproduction, preweaning survival, and survival of adult sea otters at Kodiak Island, Alaska. *Canadian Journal of Zoology* 73:1161–1169.
- MONTGOMERY, D. C. 1993. Design and analysis of experiments. Third edition. John Wiley & Sons, New York, USA.
- MORRISON, P., M. ROSENMAN, AND J. A. ESTES. 1974. Metabolism and thermoregulation in the sea otter. *Physiological Zoology* 47:218–229.
- OEHLERT, G. W., AND C. BINGHAM. 1993. MacAnova user's guide. University of Minnesota School of Statistics Technical Report Number 493.
- PAYNE, S. F., AND R. J. JAMESON. 1984. Early behavioral development of the sea otter, *Enhydra lutris*. *Journal of Mammalogy* 65:527–531.
- RALLS, K., AND D. B. SINIFF. 1990. Time budgets and activity patterns in California sea otters. *Journal of Wildlife Management* 54:251–259.
- , ———, T. D. WILLIAMS, AND V. B. KUECHLE. 1989. An intraperitoneal radio transmitter for sea otters. *Marine Mammal Science* 5:376–381.
- RIBIC, C. A. 1982. Autumn activity of sea otters in California. *Journal of Mammalogy* 63:702–706.
- RIEDMAN, M. L., AND J. A. ESTES. 1990. The sea otter (*Enhydra lutris*): behavior, ecology, and natural history. U.S. Fish and Wildlife Service Biological Report 90(14).
- ROTTERMAN, L. M., AND T. SIMON-JACKSON. 1988. Sea otter. Pages 237–275 in J. W. Lentfer, project leader and editor. *Selected marine mammals of Alaska: species accounts with research and management recommendations*. Marine Mammal Commission, Washington, D.C., USA, and National Technical Information Service, Springfield, Virginia, USA.
- SANDEGREN, F. E., E. W. CHU, AND J. E. VANDEVERE. 1973. Maternal behavior in the California sea otter. *Journal of Mammalogy* 54:668–679.
- SCHNEIDER, K. B. 1971. Reproduction in the female sea otter. Federal Aid in Wildlife Restoration Project W-17-4. Project progress report. Alaska Department of Fish and Game, Anchorage, USA.
- . 1973. Age determination of sea otters. Federal Aid in Wildlife Restoration Project W-17-4 & W-17-5. Alaska Department of Fish and Game, Anchorage, USA.
- SHIMEK, S. J., AND A. MONK. 1977. Daily activity of sea otters off the Monterey Peninsula, California. *Journal of Wildlife Management* 41:277–283.
- WATT, J. P., D. B. SINIFF, AND J. A. ESTES. 2000. Interdecadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. *Oecologia* 124:289–298.
- WILLIAMS, T. D., AND D. B. SINIFF. 1983. Surgical implantation of radiotelemetry devices in the sea otter. *Journal of the American Veterinary Medical Association* 183:1290–1291.

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