

Foraging patterns of California sea otters as indicated by telemetry

Katherine Ralls, Brian B. Hatfield, and Donald B. Siniff

Abstract: Foraging behavior was studied in 38 sea otters (*Enhydra lutris*) implanted with radio transmitters. The observed foraging behavior of instrumented individuals was similar to that of uninstrumented otters observed in previous studies: dive duration varied with prey type but not with prey size, dive success was highest for small prey, and the length of surface intervals increased with prey size. However, telemetry revealed that some otters foraged farther offshore and made longer dives than was indicated by visual observations. Individuals within age–sex classes varied in several aspects of foraging behavior, including the duration of dives and length of surface intervals. There were no overall differences between the dive durations or surface intervals during the day and during the night, though some individuals had longer dives or surface intervals during either the day or the night. There were differences in the foraging behavior of the various age–sex classes, the most striking being those between juvenile males and females. Juvenile males foraged much farther offshore ($\bar{x} = 1280$ m) in deeper water ($\bar{x} = 30.1$ m) than other otters and made long dives during both the day ($\bar{x} = 104.4$ s) and the night ($\bar{x} = 122.7$ s). Juvenile females fed for longer periods than other otters.

Résumé : Le comportement de quête de nourriture a été suivi chez 38 Loutres de mer (*Enhydra lutris*) porteuses d'un émetteur-radio greffé. Le comportement alimentaire de ces animaux était semblable à celui de loutres sans émetteur observées au cours d'études antérieures : la durée des plongées variait en fonction des types de proies et non en fonction de leur taille, le succès des plongées était supérieur lorsque les proies étaient petites et la durée des intervalles en surface entre les plongées augmentait en fonction de la taille des proies. Cependant, la télémétrie a permis de constater que certaines loutres recherchaient leur nourriture plus au large et faisaient des plongées de plus longue durée qu'il n'apparaissait après de simples observations visuelles. Le comportement de quête de nourriture variait chez les divers individus d'une même classe d'âge–sexe, et cela sous plusieurs aspects, notamment la durée des plongées et la durée des intervalles en surface. Il n'y avait pas de différence systématique entre la durée des plongées ou des intervalles en surface la nuit et le jour, mais les plongées et les intervalles en surface duraient plus longtemps chez certains animaux, la nuit comme le jour. Il y avait des différences de comportement alimentaire entre les diverses classes d'âge–sexe, notamment entre les mâles et les femelles immatures. Les mâles juvéniles cherchaient leur nourriture beaucoup plus au large ($\bar{x} = 1280$ m) et en eau plus profonde ($\bar{x} = 30,1$ m) que les autres loutres et faisaient des plongées de plus longue durée, aussi bien le jour ($\bar{x} = 104,4$ s) que la nuit ($\bar{x} = 122,7$ s). Les femelles juvéniles se nourrissaient pendant de plus longues périodes que les autres loutres.

[Traduit par la Rédaction]

Introduction

Sea otters forage in rocky substrate and soft-bottom communities, diving to search for prey and returning to the surface to breathe and consume their catch. Foraging sea otters are relatively easy to observe from shore, hence the foraging behavior and diet of this species have been studied in many parts of its range, including Russia, Alaska, and California. Most published data on sea otter foraging patterns were

obtained by visual observations made during the day on unidentified individuals; these data are reviewed by Riedman and Estes (1990).

Observations of unidentified foraging individuals in California suggested that there is a great deal of individual variation in diet and foraging patterns (Estes et al. 1981). Ongoing studies of individually recognizable (flipper-tagged) adult females are documenting that each female typically specializes on only one to three of the much larger range of prey species utilized by the population (Riedman and Estes 1990). However, there is still comparatively little published information on individual and possible age–sex class variation in sea otter foraging patterns.

Possible diel differences in the foraging patterns of individuals and age–sex classes are largely unexplored, although it is known that sea otters forage during the night as well as the day (Loughlin 1979; Ribic 1982; Garshelis et al. 1986). Information on the distances offshore and water depths at which otters forage along the California coast is not available.

Received October 13, 1994. Accepted October 27, 1994.

K. Ralls. Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, DC 20008, U.S.A.

B.B. Hatfield. National Biological Survey, P.O. Box 70, San Simeon, CA 93452, U.S.A.

D.B. Siniff. Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, U.S.A.

We compare data from radio-tagged otters with those collected by visual observations of uninstrumented otters in previous studies and present new information on several aspects of otter foraging behavior: individual, age–sex class, and diel variation in the length of dives and surface intervals; distance offshore and water depth at foraging locations; and the length of foraging bouts and the intervals between them.

Methods

Field procedures

We implanted intraperitoneal radio transmitters in 40 sea otters captured off the central California coast between 7 March 1984 and 30 December 1985. Implantation of the transmitters had no adverse effects on reproduction and survival of the otters (Ralls et al. 1989). Capture methods and locations, anesthesia, and implantation procedures are given in Ralls and Siniff (1990). Captured otters were weighed and a vestigial premolar was extracted from the majority of individuals so that age could be estimated from cementum annuli (Garshelis 1984). Individuals were classified as juveniles (<3 years) or adults (5–15 years) based on their mass, estimated age, and, for females, reproductive history during the monitoring period (Siniff and Ralls 1991).

Radio signals from the instrumented otters were detected with a directional four-element Yagi antenna mounted on the roof of a van, and with a Cedar Creek Bioelectronics Laboratory (Bethel, Minn.) radio receiver. Because radio signals are not transmitted through seawater, we were able to determine whether an individual was foraging or resting (Ralls and Siniff 1990), and collect data on the duration of dives and length of surface intervals, foraging bouts, and the intervals between foraging bouts, solely by listening to the radio signal from an individual otter.

We sampled foraging behavior in two ways. Method 1: we monitored individual otters over 24-h periods (Ralls and Siniff 1990). Most of these data were recorded between San Simeon and Point Sur; the distribution of 24-h watches along the coast by age–sex class is shown in Fig. 1 of Ralls and Siniff (1990). A team of two to four people, each taking a 6- to 10-h shift, followed individuals continuously for one or more 24-h periods and, based on the radio signal, recorded the duration of dives and subsequent surface intervals, foraging bouts, and the intervals between foraging bouts. When a foraging otter was visible from the shore, we also recorded information on the size, type, and number of prey captured. Size was categorized, on the basis of the estimated length, as small (<5 cm), medium (5–10 cm), large (10–15 cm), or extra large (>15 cm). We did not obtain estimates of an otter's location during individual dives, surface intervals, and foraging bouts because it was impossible for a single observer to simultaneously collect continuous temporal data and drive to a new location to triangulate on the radio signal. Because visual observations indicated that the occasional dives shorter than 10 s were rarely feeding dives and that surface intervals shorter than 5 s were almost always the result of interruption by another otter, these were excluded from analyses. We defined the day as the period from half an hour before sunrise to half an hour after sunset (Pacific Standard Time).

Lengths of foraging bouts and the intervals between bouts were measured to the nearest minute. If more than 30 min elapsed between two feeding dives, these two dives were taken as the end of one foraging bout and the beginning of a second foraging bout, respectively. Records with a large amount of activity recorded as “unknown” (Ralls and Siniff 1990) and those where there was any ambiguity as to the end of a foraging bout were not used for determining bout and interbout-interval length. Only complete foraging bouts were used for calculating foraging bout length, but intervals between bouts were measured as long as the end of the first bout and the beginning of the next were known. Method 2: we searched for each otter daily during daylight. When an otter was found, we recorded its activity, based on the characteristics of the radio signal, as “resting,” “foraging,” or “other” (Ralls and Siniff 1990). We then estimated the otter's location off the coast, if possible, by triangulating on its radio signal (White and Garrott 1990). For locations within about 800 m from shore, precision was estimated at 0.03–0.06 ha and accuracy at 41–110 m (Mercure 1988). The triangulated locations were used to estimate two characteristics of the locations where otters foraged and rested: distance offshore and water depth.

Estimates of distance offshore and water depth

To estimate distance offshore, the coastline of the study area was digitized in UTM coordinates and a BASIC program was written to calculate the distance from each otter-location to the nearest point on the shore. Estimates of water depth along the coast were based on the appropriate subset of the National Ocean Service hydrographic data base (Barlow 1988). Water depth was contoured in 10-m intervals and the position of each otter-location in relation to these contours was used to estimate depth to the nearest 10 m.

Statistical procedures

To compare the foraging behavior of our instrumented otters with earlier data on the foraging behavior of uninstrumented otters in California (Estes et al. 1981), which consisted of observations made during the day on unidentified individuals, we pooled all observed dive and surface times irrespective of the individual otter. One-way analysis of variance was used to compare the length of dives and surface intervals in relation to prey size and type. All ANOVA was performed with the computer program SAS (SAS Institute Inc. 1985). Other statistical procedures were calculated by hand or with the computer program SYSTAT (Wilkinson 1989).

To determine if there were differences in the length of observed and unobserved dives and surface intervals made during the day, we used a sign test on the mean lengths of observed and unobserved dives and surface intervals made by individual otters.

To examine individual effects on the duration of dives and surface intervals, we performed a series of one-way ANOVAs on the data for each class. We then examined class and day/night effects using the mean lengths of the day and night dives and surface intervals for each otter in an analysis of variance. This ANOVA used a repeated-measures design because we included only otters for which we had data for both day and night. Planned comparisons of class means

Table 1. The average durations of dives made by sea otters prior to the capture of various prey types and sizes and the average durations of the subsequent surface intervals.

	Duration of dive (s)			Surface interval (s)		
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
Prey type						
Mussel	38.3	1.16	161	68.4	2.81	158
Tunicate	42.0	15.14	5	48.0	16.32	5
Sea star	42.6	6.19	11	59.0	7.47	11
Clam	57.9	1.73	181	99.3	5.03	182
Crab						
<i>Pugettia</i> spp.	61.0	6.40	40	119.7	14.52	37
<i>Cancer</i> spp.	68.7	5.10	40	293.1	29.30	47
Abalone	68.7	15.45	3	431.0	111.29	4
Small prey*	79.1	2.94	189	99.9	4.54	188
Octopus	126.9	14.55	15	160.5	50.97	13
Prey size						
None	64.5	0.94	897	32.5	1.36	860
Small	61.9	1.65	336	63.0	2.67	335
Medium	65.9	2.61	123	80.2	5.10	123
Large	69.0	2.59	150	151.3	11.38	150
Extra large	61.4	2.83	99	190.4	16.35	98

Note: Otters often dived repeatedly in the same location prior to the capture of large prey such as clams or abalones. Prey types are arranged in order of increasing dive length. Otters often captured more than one mussel or small prey item that was pounded with a rock during a single dive.

*Small, hard-bodied prey that the otter pounded with a rock before eating.

were made using orthogonal contrasts (Sokal and Rohlf 1981). Simultaneous testing for age–sex class, individual (differences among otters within classes), and day–night effects on the duration of dives and surface intervals could not be conducted because of the unbalanced nature of the data resulting from unequal numbers of observations per otter and unequal numbers of otters within classes.

Our data on distance offshore and water depth were unbalanced in the same ways as our data on the length of dives and surface intervals. We therefore used a similar sequence of two ANOVAs, testing first for individual differences among otters within classes and then for class and activity (foraging or resting) effects.

Mann–Whitney *U* tests were used to compare diurnal and nocturnal dive durations and surface interval lengths for individual otters. Kruskal–Wallis tests were used to compare the length of foraging bouts, and the intervals between them, that occurred at different times of day. χ^2 tests were used to test for differences among classes in the length of feeding bouts and the intervals between them. Examination of standardized residuals (Haberman 1973) was used to identify the categories responsible for a significant χ^2 value.

Results

The 40 instrumented otters consisted of 9 adult males, 5 juvenile males, 16 adult females, and 10 juvenile females. The adult females gave birth to 19 pups during the study (Siniff and Ralls 1991). We monitored individual otters for varying periods of time; not all of them were equally accessible for data collection. Therefore, we were not able to col-

lect all types of data for every otter and sample sizes varied among analyses. No feeding data were collected on one adult male and one adult female.

Length of dives and surface intervals

The unweighted mean length of all dives was 74 s ($n = 8,254$). Means for individual otters ranged from 41 to 149 s. Five individuals had mean dives lengths over 125 s. Twelve otters made at least one dive longer than 200 s and the longest dive timed lasted 246 s. The unweighted mean of all surface intervals was 66 s ($n = 6,662$). Mean surface intervals for individual otters ranged from 26 to 155 s.

Is the observed foraging behavior of instrumented otters different from that of uninstrumented otters?

Examination of the pooled data on observed dives and surface intervals indicated that when the instrumented otters could be observed, their foraging behavior, in terms of the relationship between the lengths of dives and surface intervals and the size and type of prey captured, was similar to that of the uninstrumented otters observed by Estes et al. (1981). Dive lengths varied when individual types of prey could be distinguished (Table 1; $F_{[8]} = 29.2$, $P < 0.000$), but were similar when prey were classified only by size (Table 1). Individuals foraging primarily on large prey such as clams, abalone, or rock crabs tended to have the lowest percentage of successful dives, whereas those foraging on mussels and small, hard-bodied prey that they pounded with a rock had the highest success rates (Table 2). Surface intervals varied with both prey type (Table 1; $F_{[8]} = 42.3$, $P <$

Table 2. Percentage of successful dives by individual otters in relation to the principal type(s) of prey they were capturing.

Successful dives (%)	Principal prey type(s) captured	Age–sex class of individual otter	No. of dives observed
28	Clams	Adult male 1	860
34	Clams	Adult male 2	96
47	Crabs (<i>Cancer</i> spp.)	Juvenile female 1	71
47	Abalone*; all other prey	Adult female 1	217
51	Crabs (unidentified)	Juvenile female 2	49
52	Crabs (unidentified)	Adult female 2	66
62	Crabs (unidentified)	Juvenile female 3	71
67	Crabs (<i>Cancer</i>)	Juvenile female 4	46
75	Crabs (unidentified)	Adult female 3	232
80	Clams	Adult male 3	59
85	Crabs (<i>Pugettia</i> spp.); small prey	Adult male 4	97
90	Mussels	Adult male 5	180
95	Small prey†	Juvenile female 5	150
95	Small prey†	Adult female 4	43
96	Mussels	Adult female 5	114

Note: Individuals with two prey types (e.g., crabs; small prey) listed captured approximately equal numbers of each type.

*Repeated dives were required to capture a single abalone.

†See Table 1.

0.000) and prey size (Table 1; $F_{[5]} = 122.5$, $P < 0.000$). They were shortest after unsuccessful dives and longest after the capture of large prey such as rock crabs, abalone, and octopus that often took an otter several minutes to eat.

Are there differences between observed and unobserved dives or surface intervals?

There were no consistent differences in the mean durations of observed and unobserved dives and surface intervals made by individual otters during the day (Table 3, sign test, $P > 0.5$ for both dives and surface intervals), therefore we combined observed and unobserved dives and surface intervals in subsequent analyses.

Are there individual, age–sex class, and day–night effects?

Our first data set included 24 otters with data on dives and surface intervals collected during both day and night. As only two were adult males, we excluded this class from the analysis. One-way ANOVAs for each of the remaining classes indicated that there were significant differences among the durations of dives made by individuals within each class, with $P < 0.0001$ for all classes. There were also significant differences among the lengths of surface intervals for individuals within all classes ($P < 0.0001$ in all cases) except the juvenile males.

We tested for age–sex class and day–night effects using a repeated-measures ANOVA on the mean durations of dives and surface intervals for 22 individual otters (Table 4). Overall, there was no difference between the durations of day and night dives and no interaction between class and day–night. There were significant differences among the classes in the duration of dives made during the night ($F_{[3,18]} = 3.8$, $P < 0.03$) but not during the day. During the night, juvenile

males (jm) and adult females (afp) with pups made longer dives than juvenile and adult females (af) (jm vs. jf: $F_{[1]} = 4.6$, $P < 0.04$; jm vs. af: $F_{[1]} = 10.3$, $P < 0.005$; af vs. afp: $F_{[1]} = 4.2$, $P < 0.04$). During the day, juvenile males made longer dives than juvenile females ($F_{[1]} = 4.4$, $P < 0.05$). A more detailed examination of the data revealed much individual variation: some individuals made longer dives at night, some made longer dives during the day, and some made dives of about the same length during both periods (Mann–Whitney U test; $P < 0.05$; Table 5).

Overall, there was no difference between the lengths of day and night surface intervals and no interaction between class and day/night (Table 4). There were significant differences between classes in the length of surface intervals during the day ($F_{[3,18]} = 3.6$, $P = 0.04$) but not during the night. During both day and night, juvenile males and females with pups had longer surface intervals than juvenile and adult females (day: jm vs. jf: $F_{[1]} = 5.8$, $P < 0.03$; jm vs. af: $F_{[1]} = 7.1$, $P < 0.02$; af vs. afp: $F_{[1]} = 4.8$, $P < 0.04$; night: jf vs. afp: $F_{[1]} = 4.9$, $P < 0.04$; af vs. afp: $F_{[1]} = 4.6$, $P < 0.05$).

The surface interval data were similar to the dive duration data in that some otters had longer surface intervals at night, some during the day, and others had surface intervals of about the same length during both periods (Mann–Whitney U test, $P < 0.05$; Table 5). However, fewer individuals (9) had significant differences between the length of day and night surface intervals than between day and night dive durations (15 individuals) and values of the test statistic, U , tended to be smaller for surface intervals than for dive lengths.

Distance offshore and water depth

Our second data set included 38 otters for which we could estimate distance offshore and water depth. One-way ANOVAs

Table 3. Comparison of the mean lengths of observed and unobserved dives and surface intervals made by individual otters during the day.

Age–sex class and otter No.	Mean dive duration (s)			Mean surface interval (s)		
	Observed	Unobserved	Observed longer?	Observed	Unobserved	Observed longer?
Adult males						
1	57.3	48.9	+	49.6	66.3	–
2	73.8	78.0	–	53.1	54.2	+
3	41.3	56.0	–	60.0	–	na
4	62.4	97.7	–	37.7	73.5	–
5	80.9	43.8	+	94.8	48.0	–
6	61.5	63.6	–	–	91.7	na
Adult females						
1	64.8	75.7	–	53.0	54.7	–
2	57.7	45.0	+	57.3	43.1	+
3	70.8	59.7	+	60.5	37.5	+
4	94.3	63.2	+	87.5	96.2	–
5	71.6	74.3	–	70.3	34.1	+
6	138.5	144.9	–	163.4	157.0	+
7	88.7	64.1	+	93.0	122.6	–
Adult females with pups						
1	152.5	145.1	+	160.9	110.6	+
2	74.0	52.6	+	89.5	69.3	+
3	41.1	59.6	–	64.1	67.7	–
4	91.1	98.1	–	93.8	67.0	+
Juvenile male						
1	134.5	128.8	+	67.3	96.4	–
Juvenile females						
1	138.4	129.4	+	105.1	106.7	–
2	56.2	60.7	–	31.7	14.6	+
3	94.8	105.8	–	105.8	69.2	+
4	78.2	86.7	–	122.6	51.1	+
5	75.8	72.4	+	79.0	44.0	+
6	47.7	36.3	+	59.2	23.3	+
7	122.2	90.7	+	143.2	73.9	+

Table 4. Dive durations and surface intervals for otters in different age/sex classes.

	n	Dive duration (s)				Surface interval (s)			
		Day		Night		Day		Night	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Juvenile males	5	104.4	16.6	122.7	13.2	101.5	9.3	78.2	11.6
Juvenile females	8	86.5	9.1	86.5	11.5	69.8	7.2	68.7	11.5
Adult females	4	61.7	5.7	59.1	8.3	60.4	11.9	62.9	13.2
Adult females with pups	5	84.8	17.2	102.6	14.0	93.2	12.8	108.0	16.6

for each class indicated that there were significant differences among individuals in distance offshore for all classes except juvenile males (adult males: $F_{[2]} = 8.1$, $P < 0.0005$; juvenile females: $F_{[9]} = 7.2$, $P < 0.0001$; adult females: $F_{[11]} = 44.8$, $P < 0.0001$; adult females with pups: $F_{[4]} = 2.9$, $P < 0.03$) and for water depth for the adult males, juvenile females, and adult females (adult males: $F_{[2]} = 5.5$,

$P < 0.005$; juvenile females: $F_{[9]} = 29.0$, $P < 0.0001$; adult females: $F_{[11]} = 27.3$, $P < 0.0001$).

We tested for class and activity (foraging–resting) effects using repeated-measures ANOVAs on the mean estimates of distance offshore and water depth for individual otters for which we had at least 10 foraging and 10 resting locations (Table 6). Because only one adult male and no adult females

Table 5. Average durations of dives and surface intervals during the day and night for individual sea otters belonging to five age–sex classes.

Dive duration (s)				Surface interval (s)			
Day		Night		Day		Night	
Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>
Adult females							
62.8	433	47.8	285 ^D	48.6	406	52.9	273 ^N
45.1	736	56.4	36 ^N	43.3	709	46.6	35
71.3	538	83.3	468 ^N	54.0	522	50.1	463
141.2	62	139.5	91	160.9	62	151.3	86
66.9	52	95.9	67 ^N	119.4	46	155.2	59
Adult females with pups							
53.9	334	95.3	153 ^N	66.6	312	64.7	141
63.1	286	59.1	87	86.2	273	89.6	85
94.9	75	104.6	104 ^N	78.6	67	104.0	96 ^N
147.7	80	151.8	56	130.6	73	134.0	46
Juvenile females							
72.9	272	68.7	134 ^D	49.2	266	53.3	130
71.7	97	72.8	141	49.4	96	40.7	146 ^D
102.3	206	73.8	102 ^D	78.5	206	75.9	95
49.9	217	38.9	210 ^D	47.4	213	30.0	211 ^D
84.6	266	78.8	60 ^D	69.6	271	55.4	53
90.2	124	94.2	147	77.8	127	62.2	149 ^D
94.0	116	133.9	44 ^N	80.6	114	123.3	44
Adult males							
62.5	161	138.2	49	71.5	147	145.7	43 ^N
Juvenile males							
105.7	72	75.8	35 ^D	142.0	70	51.4	33 ^D
114.7	68	116.9	51	81.4	66	111.9	49 ^N
40.6	7	128.7	15 ^N	112.8	6	98.1	15
131.7	105	137.9	22	87.2	102	71.1	23
129.3	91	154.3	32 ^N	93.9	83	53.8	30 ^D

Note: Each row presents data for an individual otter. D, dives or intervals were significantly longer during the day; N, dives or intervals were significantly longer during the night (Mann–Whitney *U* test, $P < 0.05$).

Table 6. Distance offshore and water depth for foraging and resting otters in different age–sex classes.

	Distance (m)						Depth (m)					
	Foraging			Resting			Foraging			Resting		
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
Juvenile males	1280.0	91.4	4	1025.1	40.6	3	30.1	0.8	4	28.0	2.0	3
Juvenile females	470.9	34.4	9	671.9	52.2	7	17.9	1.7	9	22.5	1.9	7
Adult females	346.9	76.2	12	376.0	48.4	12	22.0	1.7	12	22.2	1.4	12

with pups met these criteria, these classes were not included in this analysis.

Overall, there was no effect of activity state on distance offshore but a significant interaction between class and activity state ($F_{[2,19]} = 11.0$, $P < 0.0007$). There were significant differences among classes with respect to distance

offshore whether otters were foraging ($F_{[2,19]} = 20.3$, $P < 0.0001$) or resting ($F_{[2,19]} = 25.0$, $P < 0.0001$). Juvenile males foraged farther offshore than juvenile and adult females, but there was no difference between the two female classes (jm vs. jf: $F_{[1]} = 26.9$, $P < 0.0001$; jm vs. af: $F_{[1]} = 40.2$, $P < 0.0001$). Juvenile males rested farther offshore than

Table 7. Numbers of feeding bouts and intervals between feeding bouts of various lengths of otters in different age–sex classes.

	Feeding bout length (min)			Interval length (min)					
	<150	150–250	>250	<150	150–249	250–349	350–449	450–549	>550
Adult males	19	6	2 (–)	7	6	9	0	1	0
Juvenile males	41	14	2 (–)	30	7	4	5	2	1
Adult females	40	23	10	19	16	8	7	8	3
Adult females with pups	30	13	2 (–)	25	10	3	0	0	3
Juvenile females	29 (–)	14	17 (+)	35	7	1	4	3	0

Note: Categories significantly ($P < 0.05$) larger or smaller than expected are indicated by plus and minus signs, respectively.

juvenile and adult females, and juvenile females rested farther offshore than adult females (jm vs. jf: $F_{[1]} = 11.5$, $P < 0.003$; jm vs. af: $F_{[1]} = 44.3$, $P < 0.0001$; jf vs. af: $F_{[1]} = 17.0$, $P < 0.0006$).

Similarly, there was no overall effect of activity state on water depth but a significant interaction between class and activity state ($F_{[2,19]} = 3.7$, $P < 0.04$). There were significant differences among classes with respect to water depth when otters were foraging ($F_{[2,19]} = 4.0$, $P < 0.04$) but not when they were resting. Juvenile males foraged in deeper water than juvenile and adult females but there was no difference between the two female classes (jm vs. jf: $F_{[1]} = 8.0$, $P < 0.01$; jm vs. af: $F_{[1]} = 5.1$, $P < 0.03$).

Length of feeding bouts and the intervals between them

The mean length of 294 foraging bouts was 140 min. The entirely nocturnal foraging bouts (119 min; $n = 43$) were similar in length to those that occurred entirely during daylight hours (121 min; $n = 62$), but the mean length of bouts that spanned the transition period from day to night or night to day was greater (210 min; $n = 25$) (Kruskal–Wallis test, $P < 0.05$). Mean foraging bout lengths for individual otters ranged from 77 min (an adult male foraging primarily on clams in Morro Bay) to 373 min (a juvenile female foraging on small, hard-bodied prey items in the San Simeon area).

The distribution of the number of bouts of various lengths differed significantly among classes (Table 7; $\chi^2 = 23.24$, $P < 0.01$). Examination of standardized residuals indicated that adult and juvenile males and adult females with pups had fewer long feeding bouts (greater than 250 min) than expected, while juvenile females had fewer short bouts (less than 150 min) and more long bouts (greater than 250 min) than expected (Table 7).

The mean interval between foraging bouts was 188 min ($n = 228$). Mean values for individuals ranged from 81 to 301 min. The distribution of lengths of time between foraging bouts did not differ significantly among classes (Table 7).

Discussion

The observed foraging behavior of instrumented individuals was similar to that of uninstrumented otters observed in previous studies (Estes et al. 1981; Ostfeld 1982; Garshelis 1983; Riedman and Estes 1990), suggesting that the implanted transmitters had little effect on otter foraging behavior. The telemetry data also confirmed the extensive variation in the

foraging patterns of individual otters predicted by Estes et al. (1981): individuals varied with respect to dive duration and success rate, surface interval length, size and species of prey consumed, foraging bout length, and the degree of difference between diurnal and nocturnal foraging patterns.

However, telemetry revealed that otters often made longer dives than indicated by previous visual observations. The mean duration of all dives timed by telemetry was 74 s, compared with an average of 50–60 s in previous studies based on visual observations (Estes et al. 1981). Although Loughlin (1977) obtained a mean dive duration of 57 s using telemetry, the few individuals he studied were foraging close to shore near Monterey. Visual observations suggested that “dives longer than 125 s almost never occurred” in California (Estes et al. 1981). In contrast, we found that 5 of 32 otters had mean dive durations exceeding 125 s. However, the duration of the longest dive we timed, 246 s, was similar to previous reports of maximum dive duration of 200 and 275 s in California (Estes et al. 1981; and Loughlin 1979; respectively) and 205 s in Alaska (Garshelis 1983). Foraging data collected by visual observations appear to be biased towards individuals feeding near shore where they can be easily seen.

There was no general tendency for dives or surface intervals to be longer during the day or the night, although many individuals had significantly longer dives or surface intervals during either the day or the night. This diel variation in dive duration may reflect a tendency for some individuals to specialize on different prey species, occurring at different mean depths, by day and night. Some of the many prey items available to the California sea otter population may be more vulnerable at night. For example, crabs belonging to the genus *Cancer* and octopuses are generally thought to be nocturnal and are presumably more easily found by otters during this active period (Estes and VanBlaricom 1985; Ricketts and Calvin 1986; Barr and Barr 1983). However, because the mean lengths of diurnal and nocturnal foraging bouts were similar, length of surface intervals was related to the size of the prey consumed, and differences in the distributions of diurnal and nocturnal surface interval lengths were less frequent than those for dive durations, many individuals may have similar diurnal and nocturnal rates of caloric intake.

Differences between the foraging patterns of juvenile males and juvenile females were particularly striking. Juvenile males often foraged farther offshore over deeper water than otters in other age–sex classes and tended to make long

dives. Because the juvenile males were not visible from shore while foraging, we were unable to tell what type of prey they were capturing. Although juvenile males had long surface times, when measured by telemetry these may not be a completely reliable indication of the consumption of large prey. Visual observations of uninstrumented juvenile males and the instrumented females with pups suggested that some of the long surface intervals measured in these classes were due to brief social interactions (with other juvenile males and the female's pup, respectively) during the time the otter was consuming its catch. However, juvenile males also had fewer long feeding bouts than expected, again suggesting that they were consuming prey of reasonably high caloric value.

In contrast, juvenile females foraged closer to shore and made shorter dives. They tended to have longer foraging bouts than otters in the other age-sex classes and many of them had short mean surface intervals, suggesting that they were capturing small prey of low caloric value. Observations indicated that they often fed on kelp crabs and small items such as turban snails and mussels. Our foraging data on juvenile females are consistent with time-budget data indicating that juvenile females devote a great deal of time and energy to obtaining sufficient food (Ralls and Siniff 1990).

The discovery that some otters forage in deeper water than previously suspected contributed significantly to the protection of the threatened California sea otter population. Based on our data, gill nets, formerly a major source of mortality to this population (Wendell et al. 1986), were prohibited in depths less than 30 fathoms (54 m) over most of the otter's range in California (Fulton 1989; C. Benz, U.S. Fish and Wildlife Service, personal communication). Since this additional protection was provided, the sea otter population in California, formerly stable or declining, has been increasing at 5–7% per year (J. Estes, Biological Survey, U.S. Department of the Interior, personal communication).

Acknowledgements

We thank the Minerals Management Service for providing major funding for this study (Contract No. 14-12-001-30033), the U.S. Fish and Wildlife Service (Permits PRT-2-9246, PRT-14752, and PRT-699234), and the California Fish and Game Commission for granting the permits required for the work. The Friends of the National Zoo, the Research Opportunities Fund of the Smithsonian Institution, and the National Science Foundation also provided partial financial support. We are grateful to the many people who contributed to the study, especially J.A. Ames, J.L. Bodkin, R.A. Hardy, B.B. Hatfield, and F.E. Wendell, who captured the sea otters, T.D. Williams, who implanted the transmitters, and L.M. Ferm, A. Mercure, S.D. Osmeck, P.J. Pietz, and M. Skupski, who collected data for extended periods. A. Mercure estimated the precision and accuracy of the triangulated locations, K. Forney contoured water depths along the coast and provided estimates of water depth for the otter locations, R.A. Garrott calculated distance offshore, J. Ballou assisted with analysis of variance, and L. Hayek provided statistical advice.

References

- Barlow, J. 1988. Harbor porpoise (*Phocena phocena*) abundance estimation for California, Oregon, and Washington: I. Ship surveys. *Fish. Bull.* **86**: 417–432.
- Barr, L., and Barr, N. 1983. Under Alaskan seas: the shallow water marine invertebrates of Alaska. Northwest Publishing Co., Anchorage, Alaska.
- Estes, J.A., Jameson, R.J., and Johnson, A.M. 1981. Food selection and some foraging tactics of sea otters. *In* Worldwide Furbearer Conference Proceedings, August 3–11, 1980, Frostberg, Md. *Edited by* J.A. Chapman and D. Pursley. University of Maryland Press, College Park. pp. 606–641.
- Estes, J.A., and VanBlaricom, G. 1985. Sea-otters and shellfisheries. *In* Marine mammals and fisheries. *Edited by* J.R. Beddington, R.J. Beverton, and D.M. Lavine. George Allen and Unwin, London. pp. 187–235.
- Fulton, C. 1989. Monterey Bay gill nets take tragic toll of sea otters and harbor porpoise. *Otter Raft* (Summer). p. 13.
- Garshelis, D.L. 1983. Ecology of sea otters in Prince William Sound, Alaska. Ph.D. thesis, University of Minnesota, Minneapolis.
- Garshelis, D.L. 1984. Age estimation of living sea otters. *J. Wildl. Manage.* **48**: 456–463.
- Garshelis, D.L., Garshelis, J.A., and Kimker, A.T. 1986. Sea otter time budgets and prey relationships in Alaska. *J. Wildl. Manage.* **50**: 637–647.
- Haberman, S.J. 1973. The analysis of residuals in cross-classified tables. *Biometrics*, **29**: 205–220.
- Loughlin, T.R. 1977. Activity patterns, habitat partitioning, and grooming behavior of the sea otter, *Enhydra lutris*, in California. Ph.D. thesis, University of California, Los Angeles.
- Loughlin, T.R. 1979. Radio telemetric determination of the 24-hour feeding activities of sea otters, *Enhydra lutris*. *In* Handbook on biotelemetry and radio tracking. *Edited by* C.J. Amlaner, Jr., and D.W. MacDonald. Pergamon Press, Oxford. pp. 717–724.
- Mercure, A. 1988. Analysis of the precision and accuracy of radiotelemetry equipment and procedures used in California. *In* Population status of California sea otters. *Edited by* D.B. Siniff and K. Ralls. U.S. Department of the Interior, Minerals Management Service, Pacific OCS Region, Los Angeles, Calif. pp. 116–132.
- Ostfeld, R.S. 1982. Foraging strategies and prey switching in the California sea otter. *Oecologia*, **53**: 170–178.
- Ralls, K., and Siniff, D.B. 1990. Time budgets and activity patterns in California sea otters. *J. Wildl. Manage.* **54**: 251–259.
- Ralls, K., Siniff, D.B., Williams, T.D., and Kuechle, L. 1989. An intraperitoneal radio transmitter for sea otters. *Mar. Mamm. Sci.* **5**: 376–381.
- Ribic, C.A. 1982. Autumn activity of sea otters in California. *J. Mammal.* **63**: 702–706.
- Ricketts, E.F., and Calvin, J. 1986. Between Pacific tides. 4th ed. *Revised by* J.W. Hedgpeth. Stanford University Press, Stanford, Calif.
- Riedman, M.L., and Estes, J.A. 1990. The sea otter (*Enhydra lutris*): behavior, ecology and natural history. Department of the Interior, U.S. Fish Wildl. Serv. Biol. Rep. No. 90.
- SAS Institute Inc. 1985. SAS user's guide: statistics, version 5 ed. SAS Institute Inc., Cary, N.C.
- Siniff, D.B., and Ralls, K. 1991. Reproduction, survival,

- and tag loss in California sea otters. *Mar. Mamm. Sci.* 7: 211–229.
- Sokal, R.R., and Rohlf, F.J. 1981. *Biometry*. 2nd ed. W.H. Freeman and Co., New York.
- Wendell, F., Hardy, R.A., and Ames, J.A. 1986. An assessment of the accidental take of sea otters, *Enhydra lutris*, in gill and trammel nets. Tech. Rep. No. 54, Marine Research Branch, California Department of Fish and Game, Long Beach.
- White, G.C., and Garrott, R.A. 1990. *Analysis of wildlife radiotracking data*. Academic Press, San Diego.
- Wilkinson, L. 1989. *SYSTAT: the system for statistics*. SYSTAT Inc., Evanston, Ill.