Activity-Time Budgets of Sea Otters in California

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BROUGHTON. 1985. Use of yohimbine to reverse immobilization of polar bears by ketamine hydrochloride and xylazine hydrochloride. J. Wildl. Dis. 21:390–394.

REYNOLDS, H. V., J. A. CURATOLO, AND R. QUIMBY. 1976. Denning ecology of grizzly bears in northeastern Alaska. Int. Conf. Bear Res. and Manage. 3:403–409.

ROGERS, L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Trans. North Am. Wildl. and Nat. Resour. Conf. 41:431–438.

SEAL, U. S., A. W. ERICKSON, AND J. G. MAYO. 1970. Drug immobilization of the Carnivora. Int. Zoo Yearb. 10:157–170.

SEBER, G. A. F. 1973. The estimation of animal abundance and related parameters. Charles Griffin and Co., London, U.K. 506pp.

SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods. 7th ed. Iowa State Univ. Press, Ames. 507pp.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman and Co., San Francisco, Calif. 859pp.

STIRLING, I., E. BROUGHTON, L. Ø. KNUTSEN, M. A. RAMSAY, AND D. S. ANDRIASHEK. 1985. Immobilization of polar bears with Telazol on the western coast of Hudson Bay during summer 1984. Can. Wildl. Serv. Prog. Note 157. 7pp.

———, W. CALVERT, AND D. ANDRIASHEK. 1980. Population ecology studies of the polar bear in the area of southeastern Baffin Island. Can. Wildl. Serv. Occas. Pap. 44. 31pp.

———, C. JONKEL, P. SMITH, R. ROBERTSON, AND D. CROSS. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. Can. Wildl. Serv. Occas. Pap. 33. 62pp.

TIETJE, W. D., AND R. L. RUFF. 1980. Denning behavior of black bears in boreal forest of Alberta. J. Wildl. Manage. 44:858–870.

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ACTIVITY-TIME BUDGETS OF SEA OTTERS IN CALIFORNIA

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Abstract: Daily time budgets and activity patterns of sea otters (*Enhydra lutris*) were determined by scan sampling at 4 study areas in central California. Diet was determined by direct observation of foraging animals. Average time invested in foraging ranged from 11 to 71% among viewing areas (1–2 km of coastline) and from 21 to 28% among study areas (8–10 km of coastline). Foraging time budgets were unrelated to season or the length of time that an area had been inhabited by otters. The diet of sea otters in California consisted almost entirely of marine invertebrates. These patterns were consistent with our review of other information on sea otter activity and diet in California. Diurnal foraging patterns were distinctly crepuscular at all sites and times sampled but one. Afternoon peaks in foraging activity were greater than morning peaks. Time budgets and diets were similar to those of sea otter populations in Alaska and the Soviet Union that were known to be below equilibrium density, thus suggesting that the presently curtailed growth of the California sea otter population is not due to food limitation.

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An estimated 16,000–18,000 sea otters inhabited coastal waters of California prior to the fur trade of the 18th and 19th Centuries. By 1911, when they became legally protected, the California population contained only 50–100 animals (U.S. Fish and Wildl. Serv. 1982). The remnant population increased thereafter and by 1976 had grown to an estimated 1,800–2,000 animals, occupying a linear coastal range of about 280 km in central California (Calif. Dep. Fish and Game, unpubl. rep., Sacramento, Calif., 1976). Further increases in abundance and range were expected because large expanses of unoccupied habitat occurred at each end of the population's range. Available census and survey data, however, indicate that the population has not changed measurably in abundance since about 1970 (Estes and Jameson 1983).

There are 2 possible explanations for the ob-

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served lack of growth. One is that the population, having increased during most of this century, is now limited by density dependent factors, such as competition for food or other requisite resources. The other possibility is that the population is below equilibrium density, but with further growth limited by density independent factors, such as human-caused disturbances. Documented sources of mortality that are likely density independent include white shark (*Carcharodon carcharias*) attacks (Ames and Morejohn 1980), illegal shooting, and incidental entanglement in fishing nets (Ames et al. 1984; F. E. Wendell et al., unpubl. rep., Calif. Dep. Fish and Game, Morro Bay, Calif., 1984). Both possibilities have been argued (Miller 1980, Estes 1981) but with little direct, supporting data.

Eberhardt (1977) proposed several approaches for assessing the status of marine mammal populations. One approach, time budget analysis, derives from an assumption of foraging theory—that net energy yield from feeding increases concomitantly with an increase in time spent feeding (Schoener 1971). Thus, if a consumer's net energy requirement is roughly fixed, then a reduction in abundance, size, or quality of available prey would lower the yield-time curve so as to increase the time invested in feeding.

This study was founded on this assumption. First, we describe diurnal activities and time budgets of the California sea otter population and compare variation between seasons, among areas, and over time. Second, we compare our results with time budgets from Alaska populations of known status. On the basis of these and other data, we discuss likely causes for the present lack of growth in the California sea otter population.

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STUDY AREAS AND METHODS

Study areas were located at: (1) the north shore of the Monterey Peninsula, (2) the south shore of the Monterey Peninsula, (3) Big Creek, and (4) Piedras Blancas (Fig. 1). Although occupied by otters for differing lengths of time, they were common at each location. Following near extinction from overhunting during earlier years, Big Creek was 1st reinhabited in the mid-1940's, Piedras Blancas and the southern Monterey Peninsula both in the late 1950's, and the northern Monterey Peninsula in the late 1960's (Calif. Dep. Fish and Game, unpubl. rep., Sacramento, Calif., 1976). On the basis of rangewide population surveys done in spring and autumn 1982, from 39 to 82 sea otters inhabited each study area (Table 1). All areas contained females with pups. Together, the areas contained 15–18% of the population in California, currently estimated at 1,350–1,400 individuals (R. J. Jameson and J. A. Estes, unpubl. data). All study areas contained extensive rocky reef and kelp forest habitat, with giant kelp (*Macrocystis pyrifera*) or bull kelp (*Nereocystis leutkeana*) the principal surface canopy-forming species.

Each study area was divided into contiguous subsegments (hereinafter called "viewing areas," Fig. 1), of such sizes and locations that, using binoculars and a spotting scope, all sea otters within each viewing area could be seen and their activities identified from a single observation post. Viewing area boundaries were determined by natural landmarks, such as breaks in the kelp canopy, islets, and rocky promontories.

We observed otter activity at the 2 Monterey Peninsula study areas from January through October 1981, and at Big Creek and Piedras Blancas from April through July 1982. Each study area was sampled 4 times. The Monterey Peninsula study areas were sampled in alternate months, and the Big Creek and Piedras Blancas study areas were sampled each month during the respective study periods. One day (dawn to dusk) was spent in every viewing area during each sample period. The order in which viewing areas were observed was randomly se-

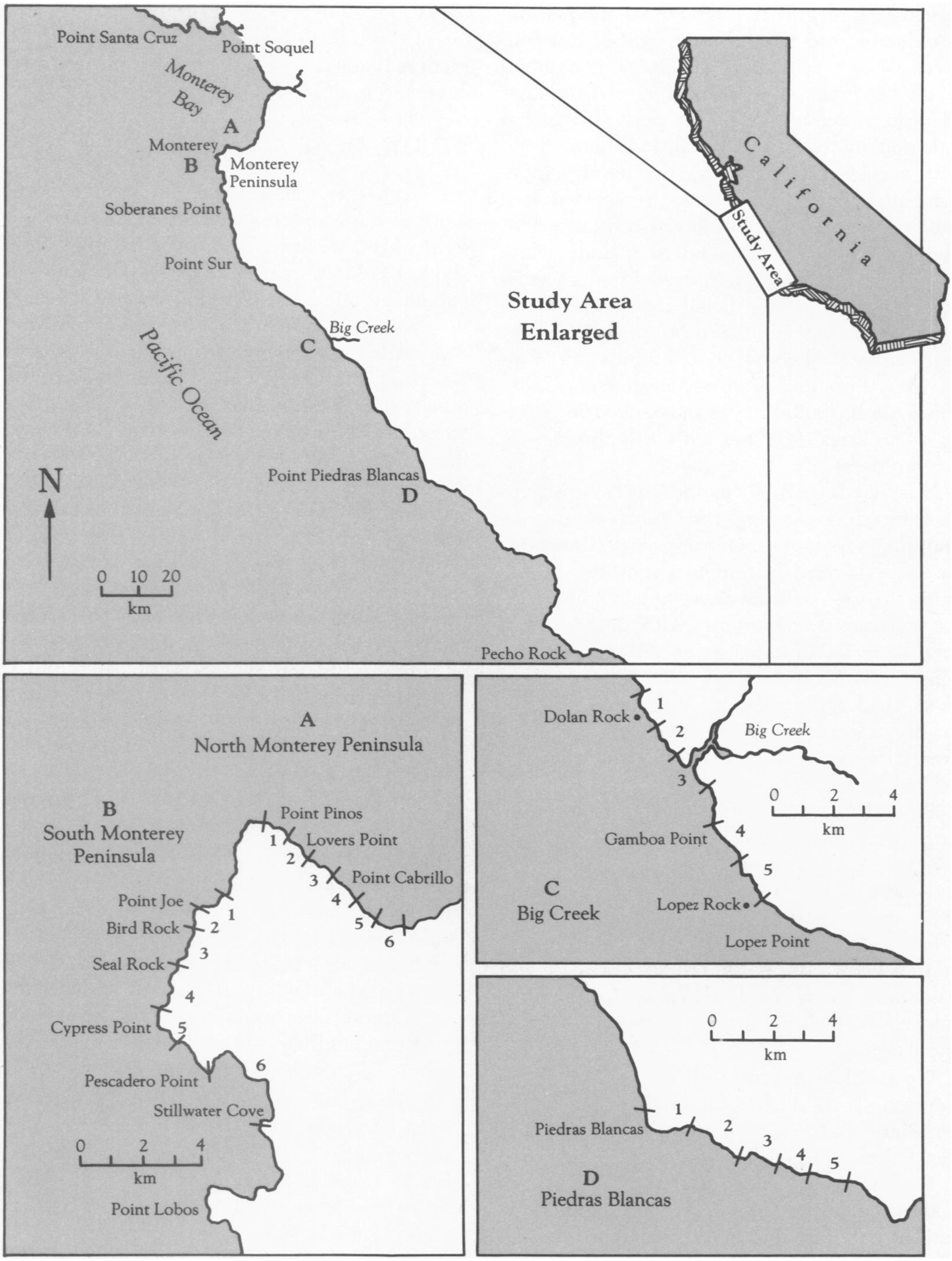

Fig. 1. Boundaries of viewing areas on the 4 study areas in central California.

Table 1. Number of sea otters counted in the study areas in central California during population surveys conducted in 1982 (see Estes and Jameson [1983] for survey methods).

	Season					
	Spring[a] 1982			Fall 1982		
Study area	Independents[b]	Pups	Total	Independents	Pups	Total
North Monterey Peninsula (A)	55	13	68	35	3	38
South Monterey Peninsula (B)	55	16	71	70	12	82
Big Creek (C)	48	10	58	49	11	60
Piedras Blancas (D)	40	8	48	33	6	39
Totals			245			219

[a] Spring = Mar–May and fall = Oct–Dec.
[b] All sea otters except dependent pups.

lected. In total, the study was based on 1,150 hours of observation time.

Activity was estimated by scan sampling (Altmann 1974) the viewing areas at 0.5-hour intervals with 7 or 10X binoculars. This was found to be the minimum time interval required to carefully observe each animal in a viewing area. Scans were done at such a rate as to virtually eliminate the chance that an animal submerged on a foraging dive would be missed.

The activity of each sighted otter was categorized as foraging, resting, or other. Procedures were similar to those described by Estes and Smith (1973) and Estes et al. (1982). Normally, all viewing areas at 1 study area were sampled before work at another area was begun. Periods of inclement weather or poor viewing, which occurred infrequently during the course of this study, were avoided.

The sampling procedure was used to describe diurnal activity patterns and time budgets for sea otters. We further analyzed these data for the following sources of variation: (1) among viewing areas within study areas (time budgets only), (2) among study areas, and (3) over time within study areas. Percent activity data were transformed to arcsin square roots for statistical analyses.

Diet was determined by observation of foraging animals through a 50–80X telescope, at distances between about 50–250 m, while they were on the ocean's surface consuming their prey. Prey were identified to the lowest possible taxa. Data from Big Creek were gathered concurrently with the activity study. Data from Piedras Blancas (Estes et al. 1981) and the Monterey Peninsula (K. J. Lyons and J. A. Estes, unpubl. data) were gathered before and after activity studies at the respective areas.

RESULTS

Time Budgets

The proportion of time devoted to the 3 categories of activity was highly variable among viewing areas (Table 2). For example, time spent foraging ranged from 22 to 60% at the northern Monterey Peninsula area and from 11 to 71% on the southern Monterey Peninsula. Variation among contiguous viewing areas was lower at the Big Creek and Piedras Blancas areas.

Sea otter abundance was not uniform among viewing areas (Table 2). Foraging intensity among viewing areas was negatively correlated with sea otter abundance. Correlations between transformed percent foraging and percent sea otter abundance were significant for the 2 sites on the Monterey Peninsula ($t_{10} = 3.84$, $P < 0.005$), Big Creek and Piedras Blancas ($t_8 = 2.47$, $P < 0.025$) and for data gathered by Shimek and Monk (1977) in 1974 ($t_5 = 16.86$, $P < 0.005$). This pattern might be explained by an aggregated distribution of resting animals in several viewing areas, superimposed on a uniform spatial distribution of foraging activity. However, we reject this explanation because the total number of sightings of foraging animals over viewing areas was significantly different from uniform (χ^2 tests, $P < 0.001$) at all 4 study areas. However, the correlation between abundance of foraging animals (as indicated by numbers of sightings) and percent foraging activity was not significant (t-tests, $P > 0.05$) in all cases.

Despite the variation in activity among viewing areas, activity time budgets were similar among study areas. Mean foraging time across viewing areas within each study area ranged between 21 and 28% (Table 2). No seasonal ef-

Table 2. Percent activity of sea otters by viewing area at North Monterey Peninsula (A), South Monterey Peninsula (B), Big Creek (C), and Piedras Blancas (D), in central California, 1981–82. (Standard deviations are given in parentheses.)

Study area	Viewing area[a]	*N* observations	% time spent		
			Foraging	Resting	Other
A	1	1,149	22 (1.2)	59 (1.5)	19 (1.2)
	2	831	25 (1.5)	54 (1.7)	20 (1.4)
	3	570	34 (2.0)	50 (2.1)	16 (1.5)
	4	411	29 (2.2)	43 (2.4)	29 (2.2)
	5	593	22 (1.7)	53 (2.0)	25 (1.8)
	6	59	60 (6.4)	9 (3.7)	32 (6.1)
	Total	3,613	26 ± 0.7	53 ± 0.8	22 ± 0.7
B	1	1,062	11 (1.0)	68 (1.4)	21 (1.2)
	2	91	71 (4.8)	14 (3.6)	15 (3.7)
	3	308	18 (2.2)	50 (2.8)	32 (2.7)
	4	284	35 (2.8)	51 (3.0)	14 (2.1)
	5	843	26 (1.5)	56 (1.7)	18 (1.3)
	6	1,529	19 (1.0)	56 (1.3)	25 (1.1)
	Total	4,117	21 ± 0.6	57 ± 0.8	22 ± 0.6
C	1	219	43 (3.3)	50 (3.4)	7 (1.7)
	2	442	37 (2.3)	56 (2.4)	8 (1.3)
	3	684	15 (1.4)	74 (1.7)	10 (1.1)
	4	276	24 (2.6)	66 (2.9)	10 (1.8)
	5	380	30 (2.4)	57 (2.5)	13 (1.7)
	Total	2,001	28 ± 1.0	63 ± 0.9	9 ± 0.6
D	1	226	25 (2.9)	59 (3.3)	17 (2.5)
	2	266	29 (2.8)	56 (3.0)	14 (2.1)
	3	667	21 (1.6)	65 (1.8)	14 (1.3)
	4	772	19 (1.5)	65 (1.8)	18 (1.4)
	5	327	32 (2.6)	52 (2.8)	13 (1.9)
	Total	2,208	23 ± 0.9	62 ± 1.0	15 ± 0.8

[a] Location of areas in Fig. 1.

fect on activity budget was detectable at either area on the Monterey Peninsula ($\chi^2_4 = 0.8$, $P = 0.93$; $\chi^2_4 = 0.6$, $P = 0.96$ for winter–spring vs. summer–fall samples at the north and south study areas, respectively). There also was no significant change in foraging activity between 1974 and 1981 at the north Monterey Peninsula Study Area ($\chi^2_1 = 0.1$, $P = 0.74$).

Activity Patterns

The diurnal pattern of activity consisted of morning and afternoon peaks in foraging, separated by a mid-day lull (Fig. 2). The number of resting animals was inversely related to the number foraging so that their combined percentage was uniform over time. The activity category "other" appeared to be of similar magnitude at all study areas and times. Foraging activity began to intensify near dawn, peaked at about 0600 hours (PST), and declined to minimum levels by about 0900 hours. The afternoon foraging peak began about 1300 hours, reached a maximum at 1600–1800 hours, and continued until dusk. The afternoon peak in foraging was higher than the morning peak. Morning peaks in foraging activity ranged between 32 and 37%, afternoon peaks between 48 and 63%. A single departure from this general pattern occurred during winter at the north Monterey Peninsula Study Area (Fig. 2), where no changes in activity through the day were evident. However, data were not collected in winter at this site before 0600 or after 1700 hours because of the shortened daylength.

Diet

Otters fed almost exclusively on invertebrates at each of the study areas although in somewhat different proportions. At the respective study areas of the Monterey Peninsula, Big Creek, and Piedras Blancas (18,577; 303; and 820 foraging dives observed), diet consisted of about 24, 9, and 31% crustaceans (mostly crabs); 32, 56, and 25% molluscs (mostly gastropods); 18, 5, and 3% echinoderms; and 22, 24, and 38% unidentified. Unidentified prey probably

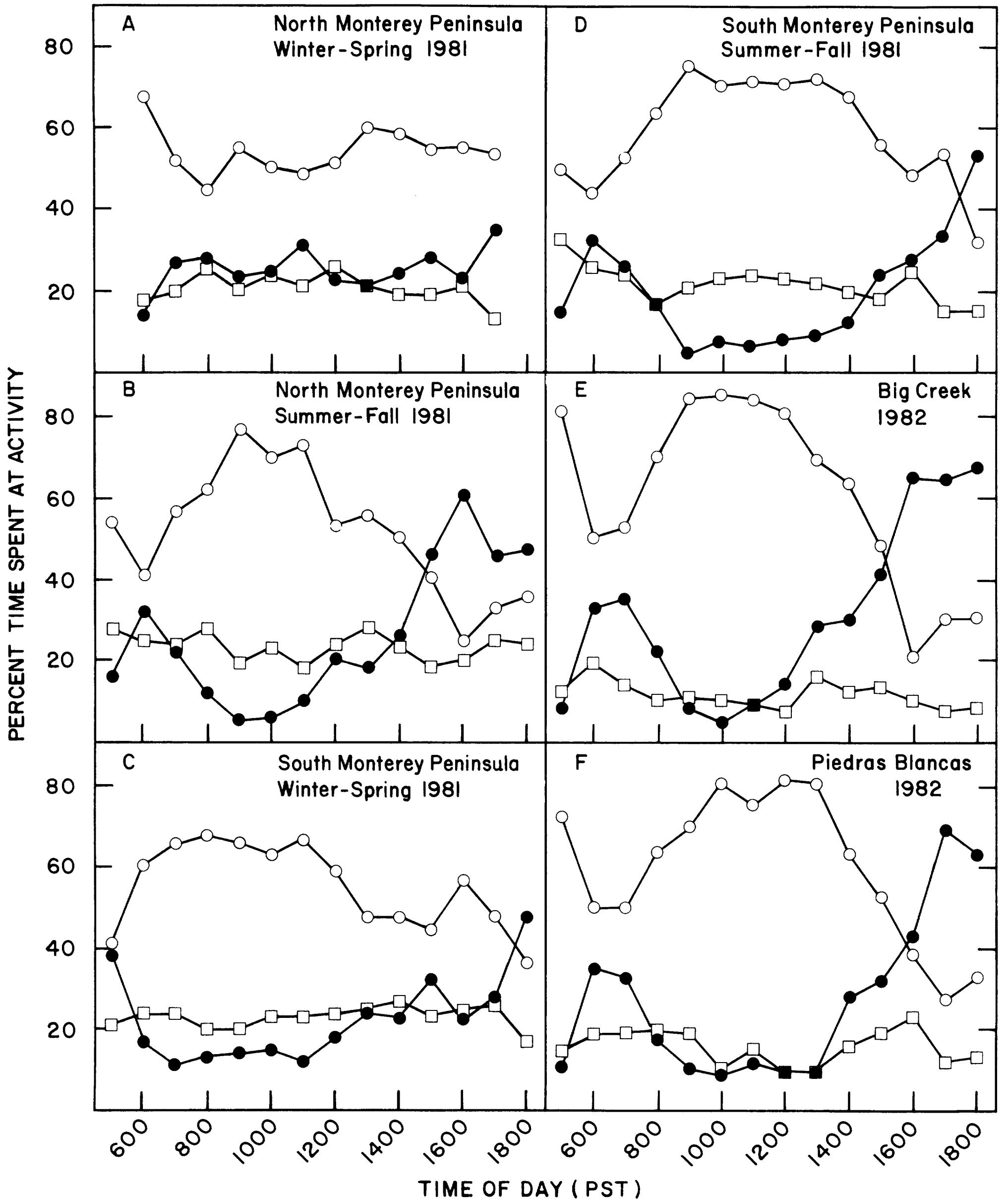

Fig. 2. Temporal patterns of sea otter activity at each of the 4 study areas in central California. Open circles = resting, closed circles = foraging, squares = other. (Dates were as follows: NMP winter–spring = Jan, Mar, and May; NMP summer–fall = Jul and Sep; SMP winter–spring = Feb and Apr; SMP summer–fall = Jun, Aug, and Oct; and BC and PB = Apr–Jul).

were mostly invertebrates that could not be seen clearly because of their small size or the orientation of the otters.

DISCUSSION

Sea Otter Population Assessment

Activity time budgets should be helpful in determining the factor or factors presently limiting population growth of sea otters in California. Available evidence supports this assertion:

1. The size and abundance of many invertebrate prey species are limited by sea otter predation (Estes and Palmisano 1974, Duggins 1980, Breen et al. 1982, Hardy et al. 1982, Estes and VanBlaricom 1985).

2. Food appears to be the main resource ultimately limiting the growth of undisturbed sea otter populations in Alaska (Kenyon 1969; A. M. Johnson, pers. commun.) and the Soviet Union (M. K. Maminov, pers. commun.).

3. Sea otters in undisturbed populations at or near equilibrium density spend substantially more time foraging than do animals from populations below equilibrium density (Estes et al. 1982, Garshelis 1983). This information indicates that time spent foraging can be variable and that individuals in growing populations, when eventually faced with depleted food resources, will increase the time allocated to foraging before they starve.

Together these ideas and findings provide a conceptual format and standard of comparison for judging whether the California population of sea otters is at or below equilibrium density. If time allotted to foraging was uniformly high (by Alaskan standards) throughout the sea otter population in California, we would surmise that further growth probably was limited by food availability. Alternatively, uniformly low foraging time allotments would suggest that some other factor was limiting the population, whereas variable allotments might indicate that the extent to which food was limiting differed between the center and ends of the population's range.

Activity-Time Budgets

The magnitude of spatial variation in activity-time budgets by sea otters in California depends largely on the units of measurement. Among viewing areas (i.e., about 1–2-km segments of coastline) variation in activity is high. Causes for such small-scale variation in activity are unknown, although they likely relate to some aspect of habitat quality, such as food availability or the suitability of resting sites. Consistently small standard deviations of percent activity within viewing areas (Table 2) indicate that the high variation among viewing areas is not a result of sampling error.

At the level of study areas (i.e., about 8–10-km segments of coastline) variation in activity-time budgets was much less than among viewing areas, indicating that patterns on this scale adequately characterized local segments of the population. Given that assumption, the data reported herein, together with those obtained by other investigators (Table 3), demonstrate a general consistency in activity-time budgets by sea otters in California. There is no indication that sea otters spend more time foraging in areas where their population has been established the longest (i.e., where competition for food thus should be most intense). Available data span a variety of situations, from Big Creek and Soberanes Point near the center of the population's present range, to the area north of Santa Cruz at the northern periphery of the range. This finding is especially interesting in view of the broad range in time allocations reported from sea otter populations in Alaska (Estes et al. 1982, Garshelis 1983). Data gathered (by the same techniques employed in this study) from the Aleutian Islands, Alaska, and from Oregon indicate that otter populations below equilibrium density allocate 15–20% of their time to foraging, whereas those at equilibrium density forage 50–55% of the time.

Results from radio telemetry studies of sea otters in California by Loughlin (1980), Ribic (1982), and Siniff and Ralls (unpubl. data) have been excluded from this summary, although Ribic's (1982) analysis indicates that visual observations and the interpretation of radio signals provide similar results (see fig. 2 in Ribic [1982]). However, Ribic's data do not discriminate foraging from several other categories of activity; and Loughlin's (1980) data, which indicate 34% foraging, are based on a small sample (6 animals with only several days data from each animal). Preliminary data from D. B. Siniff and K. Rall's ongoing study are consistent with those from the visual studies.

The coastline at Santa Cruz was actually beyond the permanent range of sea otters (defined at its ends by large concentrations of males) at the time King's (1976), Yellin et al.'s (1977) and Pearse's (unpubl.) data were gathered (Table 3). The animals they observed should be considered extralimital wanderers. Data from King (1976) and Yellin et al. (1977) were obtained prior to the establishment of a large congregation of resting males at Soquel Point in 1977, whereas Pearse's data were gathered after the group became established. However, Pearse did not sample the Soquel Point area (pers. commun.) so his data may be biased against resting otters.

Collectively, these data suggest that population growth of sea otters in California presently is not limited by food availability, and further, that this nonequilibrium status occurs through-

Table 3. Comparative findings from sea otter time budget studies in California, Alaska, and Oregon.

Location and year (source)	*N* observations	% time spent		
		Foraging	Resting	Other
Piedras Blancas, 1982 (this study)	2,208	23	62	15
Big Creek, 1982 (this study)	2,201	28	63	9
Southern Monterey Peninsula, 1981 (this study)	4,112	21	57	22
Northern Monterey Peninsula, 1981 (this study)	3,558	26	53	21
Soberanes Point, 1983 (Riedman 1984)		22	68	11
Northern Monterey Peninsula, 1974 (Shimek and Monk 1977)	3,621	24	62	14
Northern Monterey Peninsula, 1977 (Harris 1977)	495	17	61	22
Santa Cruz, 1974–75 (Yellin et al. 1977)	397	28	51	22
Santa Cruz, 1981–83 (J. S. Pearse, unpubl. data)	430	38	50	12
Santa Cruz, 1975 (King 1976)	244	23	59	11
Blanco Reef, Oregon, 1974 (Estes et al. 1982)	3,762	17	59	27
Attu Island, Alaska (Estes et al. 1982)	4,206	16	57	27
Amchitka Island, Alaska, 1977 (Estes et al. 1982)	3,709	51	34	15
Amchitka Island, Alaska, 1972 (Estes et al. 1982)	2,918	58	32	11

out the population. If the sea otter population in California is food limited, this situation must be reconciled with the comparatively small amount of time spent foraging because information from food limited populations in the Aleutian Islands indicates a foraging effort about 2× that presently being expended anywhere in California.

It is unlikely that different thermal environments between Alaska and California affect metabolism so as to constrain sea otters to be less active in California because summer sea-surface temperatures are similar between the western Aleutian Islands (8–11 C, J. A. Estes, unpubl. data) and central California (10–14 C, G. R. VanBlaricom, unpubl. data from Piedras Blancas; Calif. Dep. Fish and Game, unpubl. data from Granite Canyon). Furthermore, sea otters have a broad thermal-neutral zone that extends in both directions well beyond the coastal temperature extremes of California and the Aleutian Islands (Morrison et al. 1974). There may be other factors that hold foraging times in California to the observed level although it is presently unknown what these might be or how they differ between Alaska and California.

Diurnal Activity Patterns

Diurnal fluctuation in foraging and resting activity patterns is a general feature of sea otter behavior in California, but exceptions occur at some areas and times; e.g., winter–spring 1981 at our northern Monterey Peninsula study area (Fig. 2). This observation suggests that activity fluctuations vary in response to environmental factors, rather than being endogenous rhythms. Diel variation in activity among Alaskan populations has been interpreted similarly (Estes et al. 1982, Garshelis 1983); the responsible variable was food availability.

Diurnal activity patterns also may be influenced by factors other than food availability. We have observed that short-period wind waves disrupt resting animals, and Garshelis (1983) has shown that windy conditions tend to inhibit the formation of resting groups in Prince William

Sound, Alaska. Strong northwesterly winds typically blow along the west coast of North America during most of the year. This condition is especially prevalent in central California. Winds usually abate at night and begin to build again by mid- to late morning, reaching maximum intensity by mid- to late afternoon. Wind intensity patterns, therefore, are consistent with the afternoon increase in foraging activity, possibly being responsible for the fact that foraging is typically more intense in the afternoon than in the morning. This hypothesis remains untested however. One prediction of this hypothesis is that the intensity of afternoon foraging should be greater on windy than on calm days.

We recognize 3 potential difficulties in constructing activity time budgets from data obtained by scan sampling. First, one would expect a bias against foraging animals in such data because foraging animals are submerged part of the time. Since we adjusted scanning rate to account for the normal range of dive times (Estes et al. 1981), bias against foraging animals probably was negligible. Second, the activities of individuals may be influenced by the area they happen to be in at the time they are observed. Garshelis (1983) found that food selection varied markedly among small, contiguous patches of habitat in Prince William Sound, and we have shown here that activities often varied substantially among viewing areas. However, we sampled large expanses of coastline at each study area, and as discussed earlier, the overall consistency in results among study areas indicates that the data adequately portray patterns of activity in local populations. Third, and potentially more serious, we did not observe activity during the hours of darkness. Because sea otters feed day and night in California (Loughlin 1980, Ribic 1982), time budgets ideally should be based on the full 24-hour day, rather than just the hours of daylight. Although we were unable to make observations at night, 2 studies employing radio telemetry (Loughlin 1980, Ribic 1982) found no differences in sea otter activity between day and night. These findings were consistent with Shimek and Monk's (1977) limited data on nocturnal activity based on direct observation with floodlights, and collectively, they indicate that 24-hour time budgets of sea otters in California are similar to those we have calculated for daylight hours only. The most important comparison, however, is with Amchitka Island where there is no information on nocturnal activities. If we assume an extreme-case scenario, in which there is no nocturnal foraging, the sea otter population at Amchitka Island would spend about 35–41% of the 24-hour day foraging. This minimal estimate is still substantially greater than the time allocated to foraging by sea otters in California.

Other Indicators of Population Status

Several other kinds of information relate to the question of status of the California sea otter population. First, if the population were food limited, fish might be expected to form a significant component of the diet. This is based on findings from the Aleutian (Kenyon 1969, Estes et al. 1981) and Kurile islands (Maminov and Shitikov 1970; M. K. Maminov, pers. commun.) that sea otter populations at carrying capacity feed extensively on fish, whereas those below carrying capacity feed exclusively on invertebrates. Although kelp forests in California support a diverse and abundant assemblage of fish (Quast 1971*a*,*b*; Burge and Schultz 1973; Miller and Geibel 1973; Bodkin 1986), including similar forms to those eaten in Alaskan and Soviet waters (e.g., hexagrammids, scorpaenids, and cottids), there were no observations of fish being eaten by sea otters at any of our study sites, nor have there been anywhere else in California (Ebert 1968, Wild and Ames 1974, Estes et al. 1981, Ostfeld 1982). Second, apparently suitable habitat with abundant food resources occurs at both ends of the present range. This situation, and the fact that prior to human exploitation California supported a population of 16,000–18,000 sea otters (U.S. Fish and Wildl. Serv. 1982), makes it difficult to understand why animals do not disperse into unoccupied habitats if food is a limiting resource. However, Ames et al. (Calif. Dep. Fish and Game, unpubl. rep., Sacramento, Calif., 1984) have diagnosed starvation as the cause of death in a number of sea otters from California in recent years. Although Ames et al. (Calif. Dep. Fish and Game, unpubl. rep., Sacramento, Calif., 1984) interpret this finding to mean that food is a limiting resource, related mortality appears to be less extensive in California than it is in Alaskan popluations that are known to be at carrying capacity.

CONCLUSIONS

Our data support the hypothesis that food resources are not limiting further growth in California's sea otter population. What then is limiting the population? A likely cause is entanglement in fishing nets. The average rate of population increase by sea otters in California was about 5%/year from the early 1900's to the late 1960's (Calif. Dep. Fish and Game, unpubl. rep., Sacramento, Calif., 1976; Ralls et al. 1983). Based on this growth rate, and the present population estimate of 1,400 individuals (U.S. Fish and Wildl. Serv. and Calif. Dep. Fish and Game, unpubl. data), a net gain of 70 individuals/year would be expected. This value is roughly equal to a recent estimate of annual entanglement mortality (F. E. Wendell et al., Calif. Dep. Fish and Game, unpubl. rep., Morro Bay, Calif., 1984) and consistent with Ames et al.'s (Calif. Dep. Fish and Game, unpubl. rep., Sacramento, Calif., 1984) finding that the number of beachcast otter carcasses for which cause of death was unknown, and set-net fishing effort, were closely correlated in time.

This conclusion has important implications to the consequences of translocating sea otters to establish new colonies in California, and to developing a strategy for achieving renewed growth in the existing population, both of which are objectives of the Southern Sea Otter Recovery Plan (U.S. Fish and Wildl. Serv. 1982). If, for example, the present lack of population growth is a density dependent effect, then the loss of translocated animals should produce compensatory changes in natural mortality or reproduction causing the population to return to equilibrium density. If however, as we argue, the lack of growth is largely a result of density independent influences, removal of animals should be additive to existing levels of mortality. Similarly, an increase in growth by the existing population, resulting from reduced entanglement mortality, should not be expected by the former (equilibrium) scenario, whereas it would be expected by the latter (nonequilibrium) one.

The following information would be helpful in further resolving the question of sea otter population status in California:

1. A more thorough assessment of the causes and magnitude of mortality by age and sex.
2. Time budgets and activity patterns from a sufficiently large number of known individuals. Such information might help to resolve a variety of important questions including: (1) individual variability in activity-time budgets, and (2) time budgets of sea otters at night and during periods of inclement weather.
3. Comparative data from a sea otter population that is known to be at equilibrium density, such as the one at Amchitka Island. We suspect that causes and magnitudes of mortality by age and sex will prove difficult to estimate with confidence. However, activity budgets of sea otters can be estimated by several techniques. Because food appears to be an important limiting resource to sea otter populations at equilibrium density, measurements of foraging activity probably will continue to be one of the best indicators of population status in this species.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

AMES, J. A., AND G. V. MOREJOHN. 1980. Evidence of white shark, *Carcharodon carcharias*, attacks on sea otters, *Enhydra lutris*. Calif. Fish and Game 66:196–209.

BODKIN, J. L. 1986. A comparison of fish assemblages in *Macrocystis* and *Nereocystis* kelp forests off central California. Fish. Bull. 84:In Press.

BREEN, P. A., T. A. CARSON, J. B. FOSTER, AND E. A. STEWART. 1982. Changes in subtidal community structure associated with British Columbia sea otter transplants. Mar. Ecol. Prog. Ser. 7: 13–20.

BURGE, R. T., AND S. A. SCHULTZ. 1973. The marine environment in the vicinity of Diablo Canyon with special reference to abalones and bony fishes. Calif. Dep. Fish and Game Mar. Res. Tech. Rep. 19. 433pp.

DUGGINS, D. O. 1980. Kelp beds and sea otters: an experimental approach. Ecology 61:447–453.

EBERHARDT, L. L. 1977. "Optimal" management policies for marine mammals. Wildl. Soc. Bull. 5:162–169.

EBERT, E. E. 1968. A food habits study of the southern sea otter *Enhydra lutris nereis*. Calif. Fish and Game 54:33–42.

ESTES, J. A. 1981. The case of the sea otter. Pages 167–180 *in* P. A. Jewell and S. Holt, eds. Problems in management of locally abundant wild mammals. Academic Press, New York, N.Y.

———, AND R. J. JAMESON. 1983. Summary of available population information on California sea otters. POCS Tech. Pap. 83-11 for Interagency Agreement 14-12-001. U.S. Fish and Wildl. Serv. and U.S. Minerals Manage. Serv. 29pp.

———, ———, AND A. M. JOHNSON. 1981. Food selection and some foraging tactics of sea otters. Pages 604–641 *in* J. A. Chapman and D. Pursley, eds. Proc. worldwide furbearer conference. Worldwide Furbearer Conf., Inc., Frostburg, Md.

———, ———, AND E. B. RHODE. 1982. Activity and prey selection in the sea otter: influence of population status on community structure. Am. Nat. 120:242–258.

———, AND J. F. PALMISANO. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

———, AND N. S. SMITH. 1973. Research on the sea otter, Amchitka Island, Alaska. Final Rep.

NVO-520-1, U.S. Atomic Energy Comm., Univ. Arizona, Tucson. 91pp.

———, and G. R. VanBlaricom. 1985. Sea otters and shellfisheries. Pages 187–235 *in* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne, eds. Marine mammals and fisheries. Allen and Unwin, London, U.K.

Garshelis, D. L. 1983. Ecology of sea otters in Prince William Sound, Alaska. Ph.D. Thesis, Univ. Minnesota, Minneapolis. 321pp.

Hardy, R. A., F. E. Wendell, and J. D. DeMartini. 1982. A status report on California shellfish fisheries. Pages 328–340 *in* B. Cicin-Sain, P. M. Grifman, and J. B. Richards, eds. Social science perspectives on managing conflicts between marine mammals and fisheries. Univ. California, Santa Barbara.

Harris, R. F. 1977. Feeding and other activities of the sea otter, *Enhydra lutris*, along Cannery Row, Monterey, California. B.A. Thesis, Univ. California, Santa Cruz. 16pp.

Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. North Am. Fauna 68. 352pp.

King, J. D., III. 1976. Sea otters and their habitat north of Santa Cruz, California. B.A. Thesis, Univ. California, Santa Cruz. 76pp.

Loughlin, T. R. 1980. Radio telemetric determination of the 24-hour feeding activities of sea otters, *Enhydra lutris*. Pages 717–724 *in* C. J. Amlaner, Jr. and D. W. MacDonald, eds. A handbook on biotelemetry and radio tracking. Pergamon Press, New York, N.Y.

Maminov, M. K., and A. M. Shitikov. 1970. On the food of the sea otter on Paramushir Island. Pac. Res. Inst. Fish. Ocean (TINRO) 70:176–179. [Trans. from Russian by M. O. Pierson.]

Miller, D. J. 1980. The sea otter in California. Calif. Coop. Oceanic Fish. Invest. Rep. 21:79–81.

———, and J. J. Geibel. 1973. Summary of blue rockfish and lingcod life histories: a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish and Game Fish Bull. 158. 137pp.

Morrison, P., M. Rosenmann, and J. A. Estes. 1974. Metabolism and thermoregulation in the sea otter. Physiol. Zool. 47:218–229.

Ostfeld, R. S. 1982. Foraging strategies and prey switching in the California sea otter. Oecologia 53:170–178.

Quast, J. C. 1971*a*. Estimates of the populations and standing crop of kelp bed fishes. Nova Hedwigia 32:509–540.

———. 1971*b*. Fish fauna of the rocky inshore zone. Nova Hedwigia 32:481–507.

Ralls, K., J. Ballou, and R. L. Brownell, Jr. 1983. Genetic diversity in California sea otters; theoretical considerations and management implications. Biol. Conserv. 25:209–232.

Ribic, C. A. 1982. Autumn activity of sea otters in California. J. Mammal. 63:702–706.

Riedman, M. L. 1984. Studies of the effects of experimentally produced noise associated with oil and gas exploration and development on sea otters in California. Final Rep. for Contract 14-16-009-78-937. U.S. Minerals Manage. Serv., Anchorage, Alaska. 51pp.

Schoener, T. W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369–404.

Shimek, S. J., and A. Monk. 1977. Daily activity of sea otter off the Monterey Peninsula, California. J. Wildl. Manage. 41:277–283.

U.S. Fish and Wildlife Service. 1982. Southern sea otter recovery plan. U.S. Fish and Wildl. Serv., Sacramento, Calif. 66pp.

Wild, P., and J. A. Ames. 1974. A report on the sea otter *Enhydra lutris* (L.) in California. Calif. Dep. Fish and Game Mar. Res. Tech. Rep. 20. 94pp.

Yellin, M. B., C. R. Agegian, and J. S. Pearse. 1977. Ecological benchmarks in the Santa Cruz County kelp forests before the reestablishment of sea otters. Final Rep. MMC-76-04. U.S. Mar. Mammal Comm., U.S. Dep. Commer. Natl. Tech. Inf. Serv. 125pp.

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