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The American Naturalist, Vol. 120, No. 2 (Aug., 1982), 242-258.

Vol. 120, No. 2 The American Naturalist August 1982

ACTIVITY AND PREY ELECTION IN THE SEA OTTER: INFLUENCE OF POPULATION STATUS ON COMMUNITY STRUCTURE

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Submitted August 24, 1981; Accepted February 20, 1982

Most work concerning interactions among species at different trophic levels can be divided into two categories. One of these is essentially a view of the system from the top down. From this perspective the question of interest is, How do consumers influence populations within the prey guild? More generally, In what ways is the influence of consumers transmitted down the food web (e.g., Brooks and Dodson 1965; Paine 1966; Harper 1969; Janzen 1970; Laws et al. 1975; Virnstein 1977; Brown et al. 1979)? The other is a perspective of the system from the bottom up. From this latter perspective the question of interest is, How do various qualities of the prey guild influence the foraging tactics of consumers (e.g., Emlen 1966; Schoener 1971; Freeland and Janzen 1974; Pulliam 1974; Werner and Hall 1974; Charnov 1976)? Although both of these perspectives ultimately concern the interaction between consumers and their prey, heretofore they have been dealt with separately, both in theory and in practice. This division is understandable since the two perspectives are clearly separable by the human intellect. Yet it is easy to imagine consumer-prey interactions as viewed from one perspective influencing those as viewed from the other. For example, in many natural communities it is well known that the influences of consumers go far beyond a simple depression of their preferred prey. Such influences should be expected to have feedback effects on the foraging behavior of the consumers. Consequently, the amalgamation of these two perspectives in the study of at least some consumer-prey systems would seem to be in order.

Such an amalgamation of perspectives would seem to be especially important to the study of natural communities in which (1) the consumers are capable of varying their diets; and (2) consumer-prey interactions constitute important structuring processes, thereby influencing the availability of prey. In rocky littoral and sublittoral marine communities, these two conditions often hold for interactions involving both herbivores (Paine and Vadas 1969; Lawrence 1975; Vadas 1977; Lubchenco 1978) and carnivores (Dayton 1971; Connell 1972; Paine 1974; Menge 1976; and others).

Sea otters (*Enhydra lutris*) and the rocky sublittoral communities in which they feed, are especially well suited for examining the relations between prey selection

Am. Nat. 1982. Vol. 120, pp. 242–258.

and the predator-mediated influences on community organization for a number of reasons. First, sea otter predation has a profound influence on community structure (Lowry and Pearse 1973; Estes and Palmisano 1974; Dayton 1975; Estes et al. 1978; Duggins 1980; Breen et al. 1982). Second, at equilibrium density, populations of sea otters appear to be food limited (Kenyon 1969). Consequently, changes in prey availability are likely to exert strong influences on their foraging tactics. Third, food consumption by sea otters is easy to observe. This situation is unusual among carnivores and extremely rare among wild populations of predatory vertebrates. Lastly, human activities in the North Pacific region have provided situations in which populations of sea otters, and their associated communities, can be examined at various stages of recovery from overexploitation.

In the present paper, we compare diets and time budgets among three populations of sea otters at different stages of recovery from overexploitation. This information is interpreted in view of the effects of sea otter predation on community organization.

STUDY AREAS AND DESIGN

Sea otters were eliminated from most of the northeastern Pacific Ocean during the fur-hunting era of the eighteenth and nineteenth centuries. By the early twentieth century, they had been reduced to a few isolated populations scattered from the Kuril Islands to Baja California (Kenyon 1969; Ogden 1941). All of these populations were small, and some subsequently became extinct. Others recovered and grew, and several populations in the western and central Aleutian Islands reached what is thought to be pre-exploitation abundance, at equilibrium density, by about the mid-1900s (Kenyon 1969; "equilibrium density" henceforth indicates a population that appears to be resource limited). Because of their low reproductive rate and weak dispersal capability, sea otters remain absent from a few isolated island groups in the Aleutian archipelago, and along most of the coast of North America from southeast Alaska to Baja California (Estes 1980).

Sea otters dramatically influence the structure and organization of nearshore communities in the northeast Pacific region by preying on and thereby limiting herbivorous invertebrates, primarily sea urchins (Estes and Palmisano 1974; Estes et al. 1978; Duggins 1980; Breen et al. 1982). The result is a well-developed macroalgal flora and associated fish fauna where otters are abundant (Simenstad et al. 1977). At locations where sea otters are scarce or absent, sea urchins are large and abundant and kelp is absent or heavily grazed.

Our study locations were Amchitka and Attu islands in the western Aleutian archipelago, and Blanco Reef, Oregon. Amchitka supports an abundant sea otter population which probably has been at or near equilibrium density for at least 30 yr. This judgment is based on a sharp increase in mortality rate and an overall constancy in population size, following the period of recovery from exploitation that occurred during the first half of this century (Kenyon 1969; Abegglen 1977; Estes 1977). The rocky sublittoral community at Amchitka is characterized by small and sparse invertebrates, dense kelp beds, and an abundant nearshore fish fauna (Estes et al. 1978).

Attu was devoid of sea otters until the early to mid-1960s (Jones 1965) although it clearly supported an abundant population before the fur-hunting era (Kenyon 1969). Attu supported about 400 otters in 1977 (J. A. Estes, unpubl. data) all of which occurred along its eastern shores. Judging by estimates of sea otter density at Amchitka (Estes 1977) and the amount of habitat available on Attu (Kenyon 1969), this number is roughly one tenth to one twentieth the potential population size at equilibrium density. Outside the otter's range on Attu, the rocky sublittoral community is characterized by abundant and large herbivorous macroinvertebrates, sparse kelp beds, and comparatively few nearshore fishes (Estes et al. 1978; J. A. Estes and C. A. Simenstad, in prep.). Sea otter predation has reduced the size of sea urchins and other epibenthic prey within the otter's present range at Attu (Simenstad et al. 1978); however to date this has not visibly enhanced the algal guild.

Oregon was devoid of sea otters until June 1970, when the State Fish and Game Departments of Alaska and Oregon translocated 29 animals from Amchitka Island to a point near Port Orford. In 1971, more otters were translocated from Amchitka to sites near Port Orford and Cape Arago (24 and 40, respectively). Originally sea otters probably were most abundant along Oregon's south coast (including Cape Blanco), and smaller numbers inhabited areas to the north (Jameson 1975). Many of the recently translocated animals died or dispersed to other areas shortly after release. The number of sea otters at Blanco Reef, however, remained between about 20 and 25 from 1972 through 1974, when our data were gathered. It is not possible to reliably estimate the maximum population density of sea otters that the area near Cape Blanco is capable of sustaining, although the population we studied certainly was far below that level. Dense populations of sea urchins are a typical feature of the rocky sublittoral community in this area (Jameson 1975).

METHODS

We determined sea otter activity by scanning the ocean's surface, through 10× binoculars or a 50 to 80× telescope, from coastal points or prominences that afforded largely unobstructed view of the adjoining coastlines and their adjacent waters. Each otter observed was classified as foraging, resting, grooming, traveling, or interacting (see Estes [1977] for definitions of these activities). Activity scans were carried out at various times during daylight hours between dawn and dusk, and the data later pooled into 1-h intervals. Scans were made by sweeping the field of view slowly through an arc from a point on the coast at one side of the observer to a point on the other. In these sweeps we noted only otters whose activity could be categorized quickly and easily.

The main drawback in estimating activity budgets from scan samples, as we have done, is that estimates may be biased if there is spatial segregation of different activities. We attempted to eliminate or reduce possible effects of small-scale spatial heterogeneity in activity by observing at several different locations, all of which encompassed large areas and provided unobstructed views. After watching the otters in each of these locations, we became familiar with specific locations where the animals traditionally rested and with the larger areas in which they fed. Essentially, the entire sea otter population in Oregon was observable from one location. Consequently we are confident that our samples, when taken together, represent the activity of sea otters from each population that we studied. A small bias against foraging activity probably is inherent in our scanning technique because otters below the surface were not seen (virtually all dives are to obtain food). We attempted to reduce this bias by scanning the ocean's surface at a rate slow enough so that any point within the observed area was watched for a period at least equal to the duration of an average dive (about 1 min). These difficulties theoretically could have been avoided by monitoring the activity of individuals over time and constructing patterns of population activity based on a sufficiently large sample. We decided against this method chiefly because adequate marking or tracking techniques for sea otters has not been developed.

Though the sea otter is a benthic and epibenthic predator, it must return to the surface of the ocean to consume its food, at which time one can identify the prey. We identified the prey items during each surface period. When possible, each otter was classified as a male (by the presence of a penile bulge), female (abdominal teats), or female with pup.

Scans of activity and observations of foraging were made at Amchitka from June through August 1971 and 1972; August and September 1977; and on a more limited basis in January and February 1971 (fig. 1). Comparable data were gathered from Attu in June through August 1976–1977, from Khlebnikof Point, Chichagof Point, and the Holtz Bay-Golstov Point area (fig. 1). At that time those areas contained 55%–60% of the population at Attu (J. A. Estes, unpubl. data). Activity and foraging of otters at Blanco Reef were observed during July and August 1974, 4 yr after their translocation from Amchitka Island.

RESULTS

Time Budget

There was a consistent relation between sea otter population density (i.e., numbers relative to equilibrium density) and the proportion of time (≅ percentage of animals) devoted to various activities (table 1). The most conspicuous difference was in the respective percentages of time invested in foraging, 50% to 55% at Amchitka compared to 15% to 17% at Attu and Blanco Reef. Sea otters at Amchitka, compared with those at Attu and Blanco Reef, spent only half as much time resting, and half to a third as much time in other activities. This pattern generally was consistent among locations and over years (1971–1972 and 1977) at Amchitka. It also was consistent among locations (Chichagof Point and Holtz Bay) at Attu.

While gathering activity data at Attu and Amchitka in 1977, we distinguished females with dependent pups from single animals (table 2). This distinction was most easily made during the first 1 or 2 mo following birth when pups were still small, helpless, and in their natal pelage. Larger juveniles, although still dependent on their mothers, had taken on the adult pelage and in general appeared more like adults than did small pups. For this reason, and because each animal usually was observed for no more than a few seconds during each activity scan,

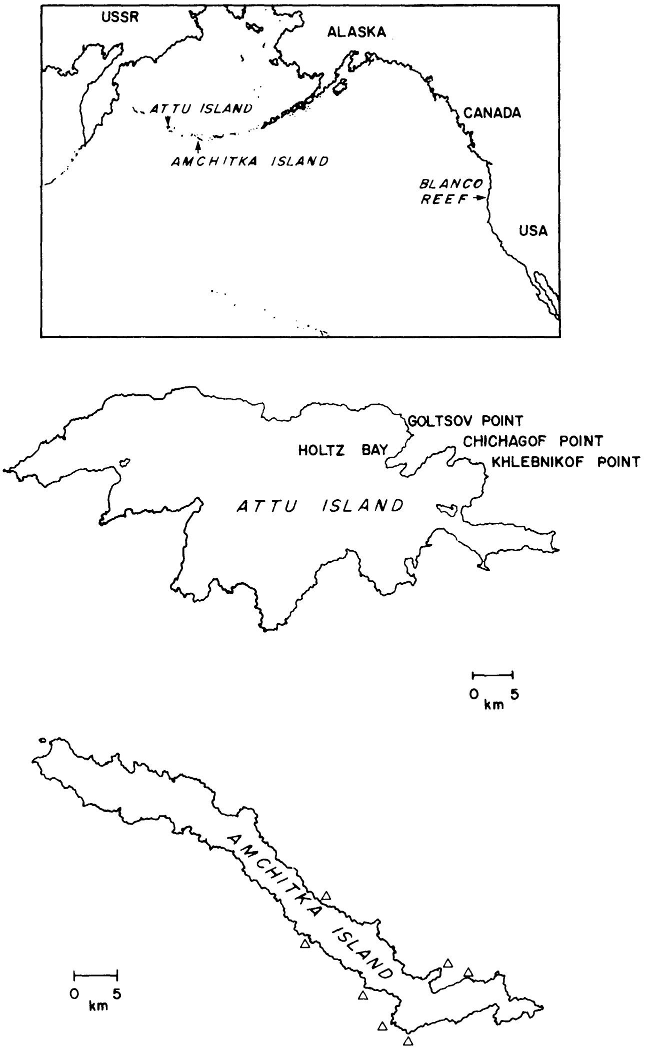

FIG. 1.—Locations of the study areas. Arrows show locations at Amchitka Island where activities and feeding were observed.

our data are mainly indicative of the behavior of females with small, recently born pups. When analyzed as 2 × 5 contingency tables by chi-square approximations, the overall percentage activity of single animals versus females with pups did not differ significantly at Attu (Chichagof Point, $\chi^2_4 = 3.51$; $P > .40$), Holtz Bay, $\chi^2_4 = 5.03$; $P > .20$), or at Amchitka Island ($\chi^2_4 = 9.09$; $.10 > P > .05$). We anticipated that females with pups would invest more time than single animals in both grooming and foraging. A small but consistent increase was seen in females with pups in percentage of time spent grooming at both Attu and Amchitka (table 2). However, there were no apparent differences in time spent foraging between

TABLE 1

PERCENTAGES OF TIME SPENT BY SEA OTTERS IN THE FIVE CATEGORIES OF ACTIVITY AT ATTU ISLAND; BLANCO REEF, OREGON; AND AMCHITKA ISLAND (Averages taken over all daylight hours and give equal weight to each hour.)

LOCATION AND TIME	NO. OF ANIMALS OBSERVED	ACTIVITY				
		Foraging	Resting	Grooming	Traveling	Other
Chichagof Point, Attu, summer 1976 and 1977	2,463	17.8	47.4	18.2	11.5	4.9
Holtz Bay, Attu, summer 1977	4,206	15.5	57.1	13.0	11.5	3.0
Blanco Reef, Oregon, summer 1974	3,762	16.8	59.3	16.7	9.3	1.0
Amchitka Island, winter 1970–1971	1,758	55.0	30.2	7.8	ND*	7.0
Amchitka Island, summer 1972	2,918	57.6	32.1	2.7	ND*	7.6
Amchitka Island summer 1977	3,709	50.7	34.4	7.6	5.4	1.9

* ND = no data. At Amchitka in 1970–1972, traveling sea otters were lumped into the "other" category.

females with pups and single animals at Attu. Females with pups at Amchitka spent 20% less time foraging than did single animals. These results are contrary to our initial expectations that females with pups would forage more than single animals because of the added nutritional requirements of the pup. As a tentative explanation, we suggest that the decrease in percentage of time spent foraging by females with pups at Amchitka reflects a compromise on the mother's part between maintaining adequate nutrition and avoiding separation from her pup.

TABLE 2

PERCENTAGES OF TIME SPENT IN THE FIVE ACTIVITY CATEGORIES BY SINGLE SEA OTTERS VERSUS FEMALES WITH PUPS AT AMCHITKA AND ATTU ISLANDS DURING SUMMER, 1977 (Averages taken over all daylight hours and give equal weight to each hour.)

LOCATION	NO. OF ANIMALS OBSERVED	ACTIVITY				
		Foraging	Resting	Grooming	Traveling	Other
Chichagof Point, Attu						
single animals	1,349	17.6	49.1	16.2	11.7	5.5
females/pups	534	18.5	42.7	25.3	10.9	2.6
Holtz Bay, Attu						
single animals	3,912	15.4	57.8	12.9	11.5	2.5
females/pups	294	16.3	48.0	15.0	11.2	9.5
Amchitka Island						
single animals	3,207	53.4	33.3	6.7	4.8	1.8
females/pups	502	33.5	41.6	13.3	9.2	2.4

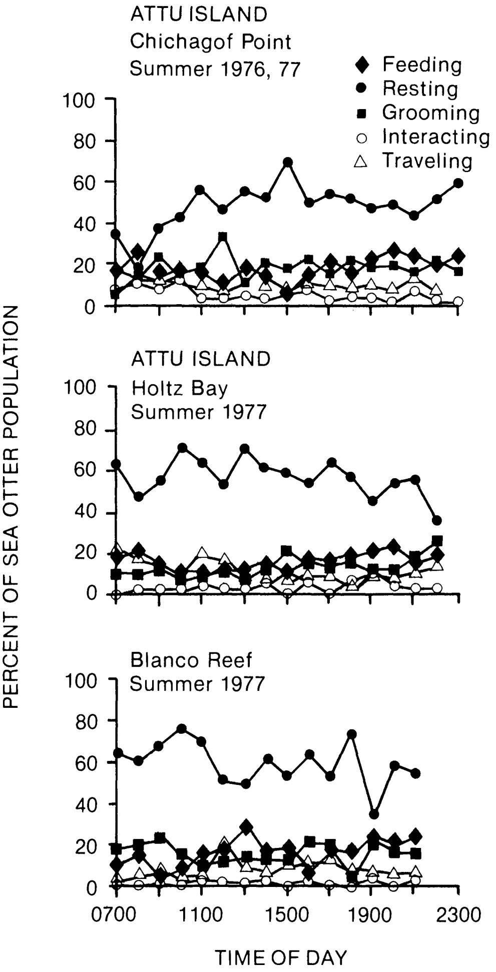

FIG. 2.—Sea otter activity as a function of time of day at Attu Island and Blanco Reef, Oregon.

Activity Patterns

Diurnal activity patterns of otters were remarkably different among locations (figs. 2, 3). Most conspicuous was the distinct bimodal peak in foraging at Amchitka, with concurrent declines in resting. The hypothesis that diurnal foraging and resting patterns were not significantly different from random variation about a uniform distribution is rejected (Run test, $P < .05$). Increased foraging began near dawn and reached a maximum at about 0800 h (Bering Standard Time, subtract one hour for local sun time). The second increase in foraging began in mid to late afternoon, reached a maximum at 1800 to 1900 h, then declined toward dusk. In contrast to the rather sharply defined foraging pattern at Amchitka, foraging and resting at Attu remained nearly constant throughout the day ($P > .05$).

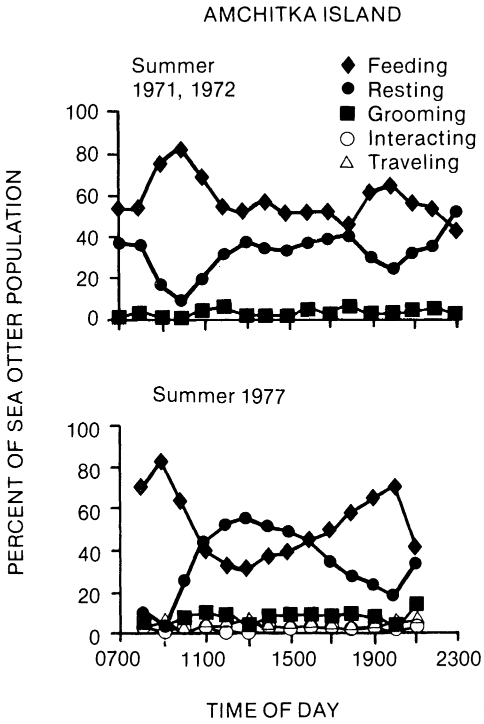

FIG. 3.—Sea otter activity as a function of time of day at Amchitka Island.

There were no apparent diurnal cycles or patterns in any of the remaining categories of activity at either Attu or Amchitka ($P > .05$). The diurnal activity of sea otters at Blanco Reef was similar to that at Attu ($P > .05$) in lacking any well-defined peaks.

The bimodal distribution in foraging and resting activity in the population at Amchitka as a whole (fig. 3) was contributed by single animals rather than by females with pups (fig. 4).

We tested the hypothesis (Wilcoxon signed-rank test) that pairs of diurnal activity patterns (percent activity vs. time of day from figs. 2 and 3) within a particular category of activity (i.e., foraging, resting, grooming, and traveling, but not "other") were not significantly different ($P > .05$) for all possible pair-wise combinations of the following data sets: Holtz Bay, Chichagof Point, Blanco Reef, Amchitka (summer 1972), Amchitka (summer 1977), Amchitka (summer 1977, females with pups only). There are 15 possible combinations (C^{6}_{2}) for each activity except traveling, for which there are 10 possible combinations ([C^{5}_{2}]; the activity categories of "traveling" and "other" were not separated in observations made during 1970–1972 [fig. 5]).

Differences among foraging and resting patterns were highly significant ($P < .01$) for all possible contrasts of high versus low population densities (i.e., all 15 comparisons), and generally marginally significant ($.05 > P > .01$) or not significant ($P > .05$) for contrasts of similar population density (i.e., high vs. high

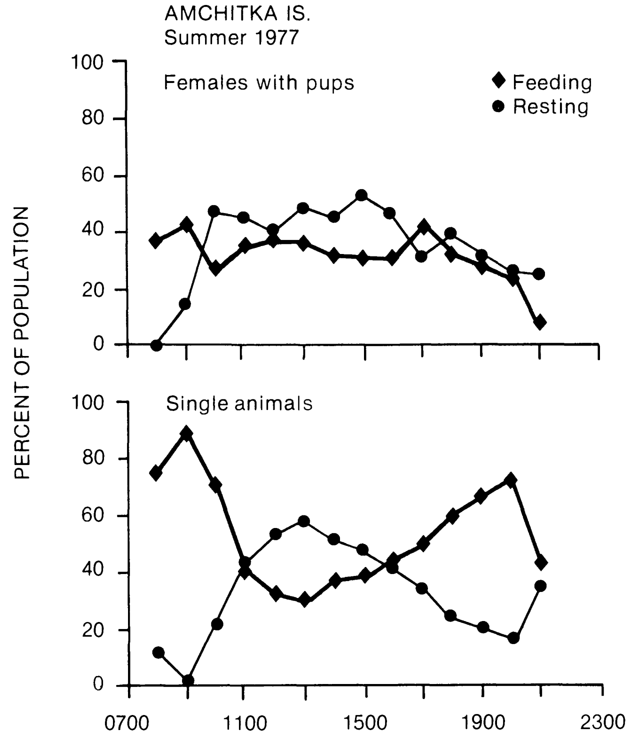

FIG. 4.—Diurnal foraging and resting activities of single sea otters and females with pups at Amchitka Island, summer 1977.

or low vs. low). The three comparisons of contrasts of similar population densities between which differences were highly significant involved foraging activity patterns of females with pups at Amchitka. This finding supports our earlier observation that females with pups at Amchitka foraged less during the day than did single animals. Grooming and traveling conform less well to the expected array (fig. 5), although differences between areas of high versus low density populations generally occurred. In these activities, females with pups are again exceptions to the expected pattern for contrasts between both similar and different population densities.

Food Selection

Sea urchins were the most frequently occurring food item in the diet of otters at Amchitka, Attu, and Oregon (table 3). Unknown food items ranked second at all three locations. Most "unknown items" were organisms too small to be seen clearly. We suspect that most of these were small sea urchins.

The greatest difference observed in diets at Amchitka and Attu was in occurrence of fish; this item was captured about 60 times more frequently at Amchitka

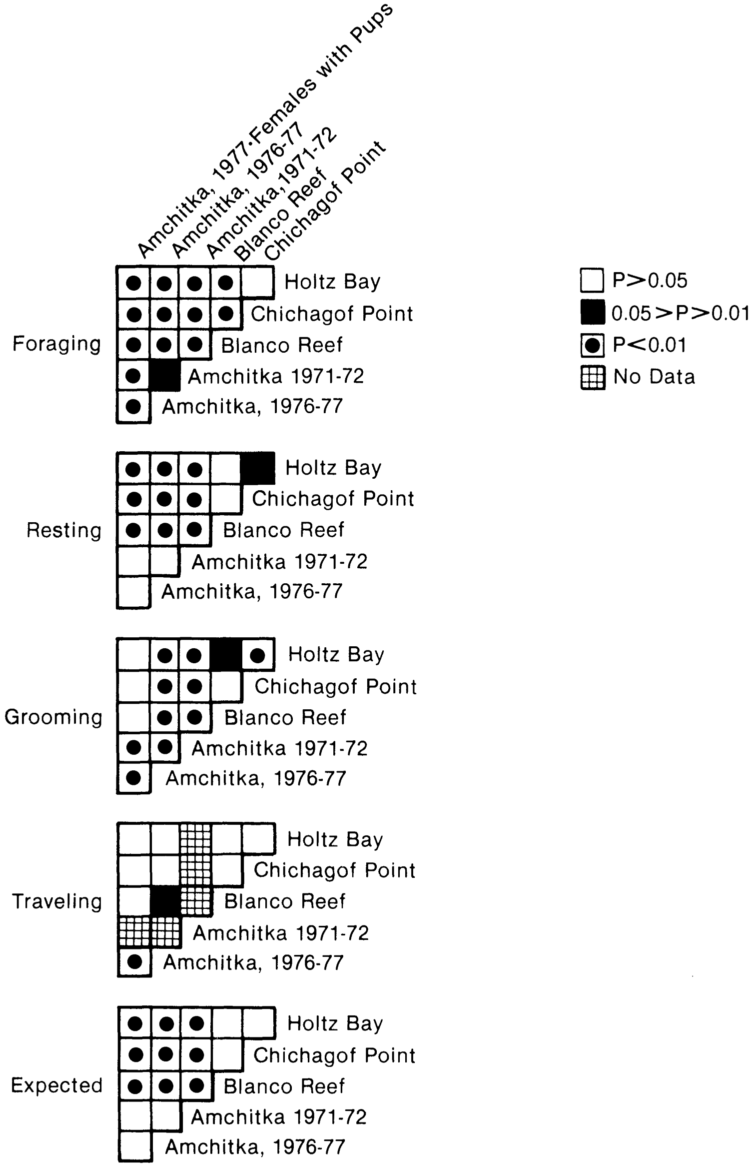

FIG. 5.—Wilcoxon signed-rank tests of the hypotheses that two diurnal activity patterns are not significantly different. The array of possible contrasts is presented as a matrix for each activity category, the elements of which correspond to specified row vs. column comparisons. The expected array (bottom) shows these positions in the matrix corresponding to contrasts between areas of similar and different sea otter population densities (high-high or low-low; or high vs. low). In the expected array, contrasts in behavior between areas of different population density are significantly different whereas contrasts between areas of similar population density are not.

TABLE 3

PERCENTAGE OF TOTAL DIVES BY SEA OTTERS THAT RESULTED IN THE CAPTURE OF DIFFERENT KINDS OF PREY, AMCHITKA AND ATTU ISLANDS AND OREGON

	LOCATION; NO. OF DIVES (in parentheses)		
PREY	Amchitka (584)	Attu (567)	Oregon (425)
Sea urchins	47.8	70.2	63.8
Mussels	.4	2.5	3.1
Sea stars	.8	.5	.5
Crabs	1.4	3.2	5.2
Clams	.4	1.8	1.6
Octopus	.0	.2	.9
Anemone	.0	.2	.0
Algal holdfasts	2.6	.0	.0
Fish	12.3	.2	.0
Fish eggs	.0	.9	.0
Chitons	.8	.7	.2
Coralline algae	.2	.0	.0
Unknown	26.7	16.2	14.6
Unsuccessful	7.1	3.4	. . .*

* Percentage not determined, but known to be small.

than at Attu. In sea otter stomachs from Amchitka examined during recent years, fish made up over 60% of the contents by volume (Burgner and Nakatani 1972, as summarized in Estes et al. 1978). The disparity between percent volume of fish and capture frequency probably resulted from the large size of fish compared with sea urchins and other invertebrates. For example, a 35-mm test diameter urchin (the maximum size at Amchitka) weighs about 15 g, whereas adult rock greenling are roughly one to two orders of magnitude heavier. None of the remaining 11 categories of food composed more than 3.5% of the total at either Amchitka or Attu. Unsuccessful dives were twice as frequent at Amchitka as at Attu. Generally, macroinvertebrates other than sea urchins (i.e., mussels, crabs, clams, and *Octopus*) were more frequent in the diet at Attu, whereas algal holdfasts and coralline algae were more common at Amchitka. (Although algal holdfasts and coralline algae [principally *Clathromorphum* spp.] are not themselves directly consumed by sea otters, the otters break them apart and feed on the associated invertebrate fauna [O'Claire 1977; J. A. Estes, unpubl. observations].) Although sample sizes for these species were small, diets at Attu and Oregon were similar and contrasted with that at Amchitka.

The composition of diets at Attu and Amchitka was significantly different ($\chi^2_{13} = 28.38; P < .01$). In general, these differences reflect structural differences between the two communities (Estes and Palmisano 1974; Palmisano and Estes 1977; Simenstad et al. 1978; Estes et al. 1978). Since fish biomass per individual is much greater than that of sea urchins, fish probably are the single most important food of otters at Amchitka and there can be no doubt that nearshore fish are instrumental in maintaining the high density otter population (Estes 1977) that occurs there. On the other hand, fish made up only an insignificant portion of the diet of sea otters at Attu.

TABLE 4

Composition of Sea Otter Diet at Amchitka Island by Time of Day

Time of Day	No. of Dives Observed	Percent Fish	Percent Other	Percent Unsuccessful
Morning and evening foraging peaks (1100 h and before and 1700 h and after)	311	19.9	71.7	8.4
Mid-day resting peak (1200 to 1600 h)	273	0	94.9	5.1

At Amchitka the proportion of fish in the otter's diet during morning and evening differed significantly ($\chi^2_2 = 23.94$; $P < .005$) from that of the mid-day period (table 4). In fact, all fish captures (72 of 584 observations of foraging made at Amchitka) occurred during morning and evening.

DISCUSSION

The explanation for differences among locations in foraging behavior by sea otters (i.e., a view of the food web from the bottom up) quite clearly must include consideration of the ecological processes whereby sea otter populations at high and low densities influence the composition and abundance of their prey (i.e., a view of the food web from the top down). Of particular interest is the biological mechanism producing morning and evening peaks in foraging activity of sea otters at Amchitka Island. One immediately can dismiss the unlikely hypothesis that this behavior has a direct genetic basis on the grounds that sea otters translocated from Amchitka to the coast of Oregon assumed uniform diurnal activity patterns. Therefore, we conclude that uniform foraging (and resting) activity is most advantageous to otters at Attu and along the coast of Oregon, whereas crepuscular foraging activity is advantageous to sea otters at Amchitka. What then are the possible explanations for this difference? By themselves, the situations at Attu and Oregon are uninteresting and uninformative because foraging activity would be expected to be distributed uniformly throughout the day in the absence of selective forces to the contrary. However, the contrast between those situations and the one at Amchitka is interesting because it provides the opportunity to examine differences in activity patterns in light of known or suspected similarities and differences between the habitats of these areas. The weakness in this method is that we cannot establish cause and effect with certainty, although we can limit the reasonable alternatives to several manageable hypotheses.

Of the environmental factors commonly thought to cause diel activity patterns in animals (Cloudsley-Thomas 1960), optimal foraging and predator avoidance would seem to be the most reasonable explanations for differences in sea otter activity patterns among locations. Predation can be discounted. Bald eagles (*Haliaeetus leucocephalus*) are the only predators known to take substantial numbers of sea otters in the western Aleutian Islands (Sherrod et al. 1975).

Although eagles are abundant at Amchitka and absent at Attu (Murie 1959; Sekora 1973), they prey only upon recently born pups (Sherrod et al. 1975), and females with pups did not contribute to the crepuscular foraging peaks (fig. 4).

The more likely explanation for different sea otter activity patterns among locations is that each maximizes foraging efficiency in two distinctly different community types. That is, the intensification of feeding during morning and evening at Amchitka Island must be caused directly by changes in availability or perceived availability of food. We suspected that diel changes in the availability of fish were of primary importance for the following reasons: (1) fishes are an important dietary component of otters in areas where benthic invertebrates are scarce (Amchitka vs. other areas); and (2) fishes probably are difficult for otters to capture, requiring visual cues and a relatively large investment of time and perhaps energy in search and pursuit. More sessile prey, on the other hand, probably can be located by tactile or visual cues (Kenyon 1969) and a modest investment of time and energy in search and pursuit. These two factors might cause the availability of fishes to exert a strong selective pressure on foraging behavior, especially where they are major prey. If this hypothesis is correct, variation in dietary composition or foraging efficiency should be correlated with peak periods in foraging activity by sea otters. Otherwise, one would expect dietary composition or foraging efficiency to remain constant throughout the day. We rejected the latter alternative because all observations of fish captures at Amchitka occurred during the morning and evening foraging peaks (table 4).

Daily foraging and movement patterns are well known in tropical and warm temperate nearshore fishes (Hobson 1965, 1968, 1973; Hobson and Chess 1976; and references therein). In those systems most smaller planktivorous and benthic foraging species have evolved distinct diurnal versus nocturnal disparities in active versus sedentary behavior as mechanisms whereby they optimize foraging or avoid predators. By contrast, the larger piscivorous fishes are mainly crepuscular foragers and are most effective at capturing prey during twilight periods (Hobson 1965, 1968, 1972; Starck and Davis 1966; Collette and Talbot 1972). Munz and McFarland (1973) explained these observations on the basis of visual perception in fishes, and the way in which it is influenced by changes in the intensity and quality of light penetrating the water column. They argued that, among fishes with duplex eyes (i.e., with both rods and cones), visual perception is poorest near twilight because of the rapid change in light intensity during that period, and the consequent need to shift between photopic (cone use under high light intensity) and scotopic (rod use under low light intensity) vision. They supported this argument with their finding that the spectral positions of scotopic visual pigments in tropical reef fishes match closely the spectral quality of twilight underwater. Munz and McFarland (1973) also pointed out that twilight changes in light characteristics occur both at low and high latitudes and under clear or cloudy skies. Consequently, even though the behavior of nearshore fishes at high latitudes is unstudied, one might also expect them to be most vulnerable to predation during the twilight period.

Based on these observations, analyses, and arguments, we propose the following model, which relates foraging activity and food selection to sea otter abun-

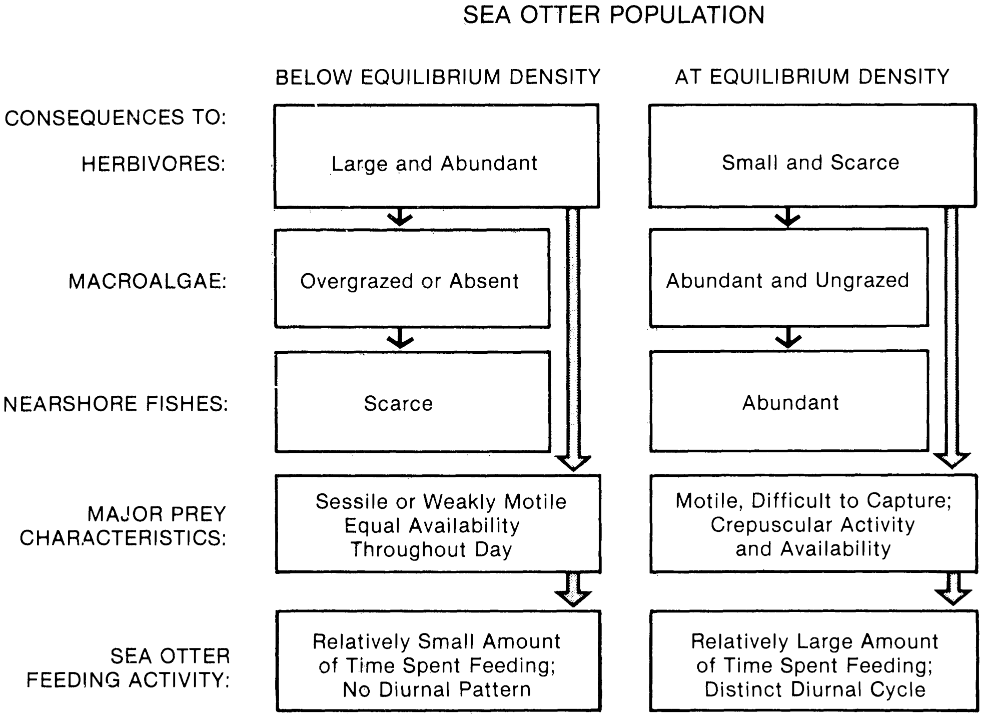

FIG. 6.—Ecological model for foraging activity patterns of sea otters.

dance and its consequent effect on sublittoral community structure (fig. 6). Sea otters at Attu exist far below equilibrium density. As a result, macroinvertebrates (primarily herbivorous sea urchins) are abundant, even in the center of the otters' present range. These invertebrates are the most conspicuous feature of the sublittoral community at Attu. Sea urchins and other sedentary macroinvertebrates are easily captured by sea otters and are equally available as prey throughout the day. Consequently, only a small amount of time is invested in foraging, and crepuscular peaks in foraging activity are absent. In contrast, Amchitka supports a dense population of otters that has been limited by food availability for 30 or more years. Sea otter predation has greatly reduced size and abundance of herbivorous sea urchins which, in turn, has facilitated the growth of kelp beds. This interaction has increased the abundance of nearshore fishes which, although preyed on by otters, are more elusive than sea urchins and probably most vulnerable to visual predators near twilight. Consequently, otters at Amchitka expend more time foraging than do those at Attu, not only because they are more nearly food limited, but also because available prey are more difficult to catch. In addition, to maximize foraging efficiency, they adjust foraging activity to correspond with periods of maximum availability or vulnerability of fishes.

In conclusion, the results of this study point up two issues that perhaps are of broader relevance to research and management in consumer-prey systems. The first is that time budgets and activity patterns may be useful measures of the status of other natural populations of consumers. Such measures could be implemented by resource managers without sacrificing the large numbers of animals required by many of the more traditional analyses of population structure. The second is that an understanding of the impact of consumers on the communities within which they forage may be fundamental to the development of predictive models of foraging behavior in many natural systems. Such a perspective might help community ecologists coalesce the related, but heretofore rather isolated subjects, of the determinants of community structure and optimal foraging theory.

SUMMARY

The population of sea otters (*Enhydra lutris*) at Amchitka Island has been at or near equilibrium density for at least 3 decades. At Amchitka, sea otters spent 55% of daylight hours foraging; there were distinct early morning and late afternoon peaks in foraging activity; and fish made up over 60% of their overall diet by volume. In contrast, the more recently established populations at Attu Island and off the coast of Oregon are far below equilibrium density. At both Attu and in Oregon, sea otters spent 17% of daylight hours foraging; there was no peak in foraging activity; and herbivorous macroinvertebrates made up their entire diet.

We interpret these observations in the following way. Subsequent to the overexploitation of sea otters, uncontrolled populations of herbivorous sea urchins greatly reduced or eliminated sublittoral kelp assemblages. In areas only recently reoccupied by otters, sea urchins are abundant and easily accessible as prey. Otters in these areas invest relatively little effort in foraging, and distribute that effort uniformly throughout the day. Where otters are abundant sea urchins are scarce, in turn promoting the growth of kelp beds and an associated fish fauna. Consequently otters at Amchitka invest more time in pursuit of more elusive prey (fish), and distribute that effort disproportionally toward morning and evening to correspond with availability of kelp bed fishes. These observations demonstrate that foraging tactics of a consumer are closely linked to its influence on the structure of the community.

ACKNOWLEDGMENTS

We thank Steven Brown, Nancy Coffey, Richard Glinski, David Irons, George Lee, J. Patrick McMahon, Robert Mayer, and Charles Simenstad for field assistance, cheerfully provided despite often dreary and unpleasant working conditions in the Aleutian Islands. The Aleutian Islands National Wildlife Refuge provided essential support; we are grateful to G. Vernon Byrd and John Martin, and in particular to George Putney and the crews of the R/V *Aleutian Tern*. Robert Anthony, Daryl Boness, Fred Bunnell, Ellen Chu, Douglas DeMaster, Roger Gentry, Gary Grossman, Christopher Harrold, Emmet Hooper, Ancel Johnson, Kenneth Norris, Donald Potts, Galen Rathbun, Charles Simenstad, Ian Stirling, and Bill Wright contributed stimulating discussion and/or reviewed various drafts of the manuscript. The U.S. Coast Guard and Air Force provided occasional transportation and access to their facilities in the Near Islands. Numerous individuals from these organizations contributed their time, energy, and expertise to assist us in repair of broken equipment, establishment of our field camps on Attu Island, transportation of food and heavy materials, and innumerable other ways. This work was supported by AEC contract AT(26–1)–520 and as a research project of the National Fish and Wildlife Laboratory, U.S. Fish and Wildlife Service.

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