NOCTURNAL FORAGING ECOLOGY AND ACTIVITY BUDGET

OF THE SEA OTTER (*ENHYDRA LUTRIS*)

IN ELKHORN SLOUGH, CALIFORNIA

A thesis submitted to the faculty of
San Francisco State University
In partial fulfillment of
The requirements for
The degree

Master of Science
In
Marine Science

by

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San Francisco, California

May, 2003

CERTIFICATION OF APPROVAL

I certify that I have read *Nocturnal foraging ecology and activity budget of the sea otter (Enhydra lutris) in Elkhorn Slough, CA* by Sarah Margaret Wilkin, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requirements for the degree: Master of Science in Marine Science at San Francisco State University.

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NOCTURNAL FORAGING ECOLOGY AND ACTIVITY BUDGET OF THE SEA OTTER (*ENHYDRA LUTRIS*) IN ELKHORN SLOUGH, CALIFORNIA

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2003

Sea otter (*Enhydra lutris*) foraging behavior has been well studied in a variety of habitats during the daytime. Improved night vision equipment has made observation of nocturnal behavior possible for the first time. In this study, I quantified the nocturnal foraging behavior of sea otters in Elkhorn Slough by direct observation using night vision goggles. Duration of successful nocturnal dives (those resulting in prey capture) were not different from diurnal dive durations (reported by Jolly, 1997; nocturnal $\bar{x}$ = 44.64 sec, diurnal $\bar{x}$ = 45.46 sec, t = 0.628, p > 0.05). Foraging success was greater at night, as fewer dives were required to obtain prey items (1.41 dives/prey item; diurnal success rate = 1.63 dives/prey item). Prey species composition differed, with significantly more crabs (*Cancer* sp.) consumed at night than during daytime.   I also constructed a nocturnal energy budget using scan sampling methodology. Sea otters spent 22% of the time foraging, which was greater than the 16% estimated from diurnal scan samples (T. R. Kieckhefer, Pacific Cetacean Group, unpub. data). Night vision technology is an important new tool for studying sea otter biology and constructing unbiased 24-hour estimates of energy consumption and activity budgets.

I certify that the Abstract is a correct representation of the content of this thesis.

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ACKNOWLEDGEMENTS

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Introduction

The sea otter (*Enhydra lutris*) is an aquatic carnivore found in the coastal waters of the eastern North Pacific Ocean. There is considerable interest in the southern sea otter (*E. lutris nereis*), a subspecies comprised of the population of sea otters residing off California, because it is listed as threatened under the federal Endangered Species Act (ESA; Reidman and Estes 1990), and is protected under the Marine Mammal Protection Act. Historically, 16,000 to18,000 sea otters inhabited the coastal waters of California before the fur trade of the 18th and 19th centuries. By 1911, when the population gained legal protection, it contained only 50 to 100 individuals (USFWS 1982). Recovery has been slow, generally around 5-7% a year, despite the closure of nearshore net fisheries that entangled sea otters (Estes 1990). The California population was most recently estimated to be approximately 2,100 individuals (USGS 2002). This contrasts with the Alaskan sea otter population, which recovered quickly to pre-exploitation levels, especially in the Aleutian Islands (Kenyon 1969).

The slow recovery rate of the California population is a matter of concern, but determining the cause(s) is a difficult matter. Fecundity and pup survival rates are relatively the same in California and Alaskan populations (Garshelis et al. 1990, Reidman and Estes 1990), so differences in mortality rates is implicated, with an expected higher mortality rate in California. Fisheries bycatch initially resulted in greater mortality rates but was essentially eliminated with the closure of the set-net fishery in central California in 1985 (Estes 1990). Although the population increased significantly after this action, it

again plateaued around 1990 (USFWS 1995). Other potential causes of mortality include disease, parasites, or food limitation (Estes 1986, USFWS 1995). This paper will focus on food limitations.

Foraging primarily on benthic macroinvertebrates, sea otters require large amounts of energy. They must consume up to 25% of their body weight per day to maintain their metabolic rate, which is 2.5 times that of other mammals of comparable size (Costa and Kooyman 1984, Reidman and Estes 1990). Unlike other marine mammals, sea otters lack a thick insulative blubber layer, and depend on their thick pelt and high metabolic rate to maintain their body temperature in the cold marine environment (Costa and Kooyman 1984). Although an adequate amount of prey could be obtained in a relatively short time period (Shimek and Monk 1977), the high metabolic rate could not be maintained for the full 24-hour period with only one large meal. The specific dynamic action, or the increase in metabolic rate caused by food digestion, must be spread throughout the day and night (Loughlin 1979, Costa and Kooyman 1984). Sea otters, therefore, should forage both diurnally and nocturnally, contradicting early reports that they only foraged during the daytime (Kenyon 1969).

Using radiotelemetry and diurnal visual observations, researchers have concluded that sea otters are highly efficient, active predators. An average foraging bout is 2.5 to 3.3 hours duration, with otters completing approximately three bouts per day (Loughlin 1979, Ribic 1982). Individual variability results in temporal spacing of bouts; no more than 50% of otters are generally observed foraging at any one time (Shimek and Monk

1977). Diurnally, there is a population-wide maximum of foraging activity in the morning and afternoon with a mid-afternoon lull (Estes et al. 1986).

The exact mechanisms sea otters use in searching for and detecting prey remain unknown. Based on observations by human divers, sea otters may forage primarily using tactile senses in kelp-forest environments, where the prey is mostly epifaunal (Shimek 1977). Vision apparently plays a small role, and smell or chemosensory cues might be used (Kvitek et al. 1988). The soft-bottom environment presents more of a challenge, as the prey is infaunal and theoretically more difficult to detect below the substrate's surface (Jolly 1997). Average success rates (dives resulting in capture of prey/total dives) in soft-bottom environments, however, are great, ranging from 53% to 80%, with mean duration of successful dives between 37.2 and 75 seconds depending on prey species (Kvitek et al. 1988, Jolly 1997).

Activity budgets are a measure of the amount of time an individual spends in each of several activity categories during a period of time, generally 24 hours. Several authors (Eberhardt 1977; Shimek and Monk 1977; Estes et al. 1986) have proposed that sea otter activity budgets, particularly the amount of time spent foraging, might be used as indicators of population status. This argument assumes that food is an important limiting resource in equilibrium populations and that prey availability varies with the length of occupancy by sea otters. In the initial occupation of a location, sea otters would first consume large prey with high caloric content and spend a relatively short amount of time foraging because of high prey abundance. As the availability of prey decreases, the

predator diet diversifies to include smaller, cryptic, and/or more mobile prey, and consequently foraging times (or relative amount of time spent foraging in an energy budget) would increase (Eberhardt 1977).

Activity budgets of California sea otters have been calculated and compared with other sea otter populations by several authors (Shimek and Monk 1977, Estes et al. 1986). Two main methodologies have been used to obtain energy budgets for sea otters: radiotelemetry and scan sampling. Each has its advantages and disadvantages. Scan sampling is a visual "snapshot" of a population, in which instantaneous behaviors are recorded for each visible animal (Altman 1974). The main advantages are a large sample size (all visible animals are included) and the ability to determine exact behavior states, because each animal is directly observed. There also is a low monetary cost associated with this method. Shimek and Monk (1977) and Estes et al. (1986) used energy budgets obtained from scan samples to argue that sea otters in California were not food limited, because the amount of time allocated to foraging (21-28%) was less than sea otters in Alaska (50-62% time foraging), where the population was at carrying capacity.

Visual scans are limited to accessible areas and can be restricted because of weather and time of day. Garshelis et al. (1990) criticized the use of scan sampling to estimate the percentage of time sea otters spent foraging, because nighttime activities could not be observed. They argued that diurnal visual observations may not create a time budget representative of 24-hour activity patterns. Some observations were available to substantiate this claim. In 1974, Shimek and Monk (1977) conducted the

first nighttime observations of sea otters by using shore-based floodlights to illuminate a group of sea otters southeast of Point Cabrillo, CA. By slowly turning on the lights every hour, they determined the number of sea otters resting throughout the night. They proposed greater foraging activity occurred at 2400 h based on low numbers of resting otters at that time. However, this work was limited to the extreme near-shore area and was severely limited by nighttime fog (S. Shimek, pers. comm.).

Using radio telemetry, individual energy budgets can be obtained throughout a 24-hour period because constant monitoring is possible. Monitoring can be conducted in poor weather, and at all times of day and night. Individual animals can be followed for long periods of time (days, weeks, or even months). The disadvantages include a limited sample size (only those animals with radio tags are monitored) and the monetary cost of radio telemetry equipment (transmitters, receivers, and data loggers), which can be prohibitive. In addition, fewer behavioral categories can be distinguished using only radio signals (either logged by a machine or being recorded by observers). These are: resting at the surface, characterized by an uninterrupted signal; foraging, characterized by long (>30 sec) interruptions in the signal, followed by continuous signals for 15 to 120 secs; and other/unknown activities (such as grooming, swimming, and social interactions), indicated by intermediate signals not fitting either of the other two patterns.

Studies of sea otters using radiotelemetry have been conducted since the 1970s and are ongoing in California (Loughlin 1977, 1979; Ribic 1982, Garshelis et al. 1986, Ralls and Siniff 1990, Ralls et al. 1995, Tinker pers. comm.). Telemetry has provided a

good insight into the nocturnal activities of sea otters, when visual observations have been impossible. Sea otters show no apparent diel behavior pattern (diurnal, nocturnal, crepuscular, etc.) but instead can be characterized as arrhythmic, with an alternating pattern of periods of activity (foraging, travel, grooming) and inactivity (rest) that continues for the entire 24-hour period (Ribic 1982). Arrhythmic behavior is relatively uncommon among the higher vertebrates (Cloudsley-Thompson 1961). Telemetry studies allow a detailed examination of the behavior of a few individuals (those animals with radio tags). However, for population-wide studies, the monetary cost of radio telemetry equipment to sample an adequate percentage of the population can be prohibitive. This is especially true given the variability in activity within and among individual sea otters in most telemetry studies (Ribic 1982, Garshelis 1983, Ralls et al. 1995). In one study, the percentage time spent foraging at night varied between two locations (Garshelis 1983). Differences in time spent foraging at night between age/sex classes also have been reported (Ralls and Siniff 1990). Given this variability, it is difficult to justify extrapolating diurnal behavior data (such as activity budgets) to a full 24-hour period. However, the advantages of using scan samples to construct energy budgets are obvious.

The specifics of nocturnal foraging (including rates of consumption and prey species composition), have been impossible to quantify using visual observations. Nocturnal prey consumption has been hypothesized by at least two authors. Loughlin (1977) reported hearing frequent tool use at night, which was common in diurnal consumption of mollusks, and theorized that nocturnal consumption of mollusks was

occurring. In an effort to explain their low estimate of diurnal energy consumption, Garshelis et al. (1986) theorized that nocturnal prey consumption rates or energy obtained during nocturnal foraging may have been greater than observed during diurnal foraging. Greater periods of time spent at the surface for consumption of prey at night (in the telemetry record) indicated that predation on crabs was greater at night (Garshelis et al. 1986). Both authors stressed that their hypotheses were necessarily speculative, given their inability to make visual observations at night. Feinholz (1988) observed one sea otter foraging nocturnally using a spotlight; several others were heard pounding rocks against their chests and foraging was inferred.

The recent commercial availability of Generation III night vision equipment has made direct visual observations feasible in total darkness (ambient light levels as low as 0.0001 lux, or the equivalent of an overcast sky at night with no moon). The sea otter is an ideal subject for one of the first studies of nocturnal behavior of a marine mamml because of its use of nearshore habitats, nocturnal activity, and frequent periods of time spent at the water's surface when handling and consuming prey items.

My objective was to examine differences between nocturnal and diurnal foraging of sea otters in Elkhorn Slough, California. Foraging success rates and prey species composition were of particular interest because of the inability to obtain these measures using telemetry. The foraging mechanism used by sea otters to detect and capture prey also can be examined using nighttime observations. If vision plays a role, nocturnal foraging dives would be expected to be of longer duration and have a lesser success rate

than diurnal foraging due to the absence of light. I expected consumption of the same prey species, in the same relative proportions as diurnal foraging. I also was interested in using this new technology to obtain an unbiased nocturnal energy budget of sea otters by conducting visual scan samples. The many advantages of scan sampling could be obtained while overcoming the main constraint of needing artificial light sources, which can potentially disrupt animal behavior.

Methods

The study area was the ocean outlet of Elkhorn Slough, Monterey County, CA, from Seal Bend to the Highway One bridge (Fig. 1). These limits were chosen because they encompass the primary foraging region in the Slough (Feinholz 1998), and other areas (the Upper Slough, Moss Landing Jetty) were deemed navigational challenges at night. Elkhorn Slough is a soft-bottom tidal embayment that has been seasonally occupied by a maximum of 50 sea otters since March 1984 (Kvitek et al. 1988) and year-round since 1995 (Jolly 1997). The population was male-dominated, because it was first colonized by a juvenile male invasion front. However, adult females have been observed, and at least two females with pups have been observed since 2000 (Y. Gideon, pers. comm). The exact age/sex structure of the population was unknown. The primary prey species consumed by sea otters in Elkhorn Slough were clams (especially the Washington

clam, *Saxidomus nuttalli*, and the gaper clam, *Tresus nuttalli*), crabs, primarily *Cancer sp.*, and the fat inkeeper worm, *Urechis caupo* (Kvitek et al. 1998).

Boat-based surveys were conducted, weather permitting, in October and November 2000, June and July 2001, and September 2001 to March 2002. Months were stratified into four approximately seven-day periods based on moon phase. After preliminary surveys, I determined most sea otter foraging occurred before midnight. For the focal animal study, two surveys were randomly allocated to each stratum, one beginning one hour post-sunset and the other four hours post-sunset. Using Generation III night vision goggles (ITT Industries Model 5001P/Omni IV), one scan sample was conducted for most surveys (n=38). A high-powered spotlight (MBS-410 Maxa-Beam Searchlight) was used on some of the surveys to illuminate subjects. An infrared filter (MBA-1850), fitted to the lens, minimized disturbance because sea otters cannot see infrared wavelengths, but the night vision goggles amplified this light into the visual spectrum.

For each animal, a focal follow (Altman 1974) observation period of 30-60 minutes duration was conducted. Dive duration and duration at water's surface was recorded to the nearest second, and prey items were noted and identified when possible. One to three focal animals were sampled per survey. This survey methodology was consistent with that used by Jolly (1997), permitting direct comparisons between the data sets.

For a random sampling of individuals, duration of successive dives was tested for independence using the successive mean difference test (Zar 1996). If successive dives were found to be independent, then all dives for each animal could be used in statistical tests, thus increasing the sample size. Nocturnal foraging efficiency (number of dives required to obtain a prey item) and time expenditures (duration of successful [resulting in prey capture] and unsuccessful dives, and prey handling time) were compared with diurnal data obtained for the same population by Jolly (1997) using two-sample one-tailed t tests and Mann-Whitney U tests when the assumptions of parametric statistics were violated. To assess the potential importance of vision to sea otter foraging, I tested whether nocturnal dives were of greater duration and more often unsuccessful than diurnal dives. Success rate was calculated as the average cumulative number of dives required to obtain prey. A value of 1.0 would indicate that 100% of dives were successful; a 2.0 would indicate a 50% success rate, as two dives were required for each prey item (one unsuccessful dive followed by one successful dive).

Prey species composition was analyzed for all samples of focal animals, although prey identification was possible with a greater degree of accuracy when the spotlight was used. Proportions of prey species consumed at night were compared with those obtained via diurnal sampling in the same area with a similar methodology (Jolly 1997) using a Pearson X^2 test. Differences in prey handling times for different prey types also were analyzed using a Mann-Whitney U test.

Differences in foraging with respect to moon phase were analyzed by calculating mean duration of dives for each day of moon phase on which sampling was conducted and plotting the relationship. A polynomial regression model was fit to the data and assessed for statistical significance.

One scan sample was recorded per survey night. During each scan sample, each animal present in the study area was counted and behavior was classified into one of six categories: rest, forage, groom, travel, social/sexual (interaction with another sea otter), or hauled out on land.

Behavior data were used to create an average activity budget for nocturnal behavior of sea otters in Elkhorn Slough. Using a Chi-squared test, this nocturnal activity budget was compared to a daytime activity budget calculated using data collected by the Pacific Cetacean Group (PCG; Thomas R. Kieckhefer, unpublished data). Surveys by PCG also were conducted in a small boat a maximum of 4 times per month from 1999-2000. Surveys were always performed between 1000 h and 1400 h. The data were subdivided to include only those observations within the same study area. Data from two behavior groups (travel and groom/travel) were combined to approximate the nighttime travel category.

On three surveys conducted from dusk until dawn, scan samples were conducted once per hour. Two observers and one boat driver/data recorder were used for these surveys, with each observer responsible for all animals on their side of the boat. These surveys were conducted from May to July 2002 to determine sea otter abundance and

behavior throughout the entire nighttime. A paired *t*-test was used to assess the difference in overall sea otter abundance between the first half of the night (2000 h-0100 h) and the second half of the night (0100 h-0600 h). Differences in the two main behavior states (foraging and resting) also were examined using a paired *t*-test. The detection ability of the night vision goggles was assessed by comparing animals seen at dusk (ambient light, observations made using naked eye) and the first survey after full dark (observations made using night vision) and the last survey in full dark and the first survey after dawn (paired *t*-test).

Results

During the 18 (non-continuous) months of this study, 50 focal animal surveys were conducted, with 58 focal animal follows and 38 scan surveys completed. Many scheduled surveys were canceled due to inclement weather, as the night vision equipment cannot be used in fog or rain. Additional problems were found on very windy nights when whitecap waves were present on the Slough. Between 2.5 and 46 minutes of observation were obtained per animal, with a total of 880 foraging dives observed. Observations were terminated if the animal moved out of the study area, stopped foraging, or was lost for more than 15 minutes by the observers.

The feasibility of using the current night vision technology (Generation III) was verified. The goggles allowed the easy location, identification, and relocation of individual otters. Observations of foraging activity were easy to accomplish using the

goggles alone, although the use of the infrared spotlight greatly augmented the night

vision, especially for prey species identification. The detection ability using the night

vision goggles was the same as using the naked eye; no difference was seen between

numbers of animals observed using ambient light (dusk/dawn) and after full dark (the

period after dusk/before dawn; paired t-test; $t = 0.83$, n=6, p $= 0.444$).

There was no correlation between successive dive duration, duration of

unsuccessful dives, or duration at the surface for the randomly selected animals (n=10),

with no deviation from what would be expected if dive duration was random. All dive

durations for each animal, therefore, were treated as independent samples.

Duration of successful dives at night was not significantly different than during

daytime (Table 1; daytime data from Jolly 1997). Duration of prey handling and

unsuccessful dives during nighttime were significantly less than during the day. Success

rate (cumulative number of dives needed for prey capture) during nighttime was

significantly less than daytime, indicating that foraging otters were more successful at

night. Sample size was judged to be sufficient, given the relatively high power (greater

than 41%) for successful dive duration, the only non-significant result.

The identification of prey species was more difficult at night than during the

daytime, particularly on the nights when the spotlight was not used; therefore, the

proportion of unidentified prey items (i.e. "unknown") was high (427 of 604 dives or

70%) compared with diurnal sampling (only 8% of prey items were unidentified in Jolly

1997). Therefore, the "unknown" category was not included in the comparison between

nocturnal and diurnal prey composition. Nocturnally, prey were consumed in significantly different proportions than during the day (X^2 = 71.4, df = 3, p < 0.001; Fig. 2). Fat innkeeper worms, *Urechis caupo*, were consumed significantly less frequently and crabs (generally *Cancer* sp.) more frequently at night than during the daytime; the other categories were not statistically different (subdivided X^2 analysis).

Duration of prey handling did differ significantly among crabs and clams, the categories with the most observations (U = 1880.5, p = 0.02). Prey handling duration for crabs was the longest and also most variable ($\bar{x}$ = 62.4 sec, SE = 10.3 sec, Fig. 3). Fat innkeeper worms required little prey handling; this duration was shortest and least variable, but based on a low sample size ($\bar{x}$ = 19.4 sec, SE = 0.7, n = 10). Prey handling of clams was intermediate in both duration and variability ($\bar{x}$ = 34.8 sec, SE = 1.8, n = 131).

Foraging behavior was not statistically related to moon phase. Dive duration for neither successful nor unsuccessful dives indicated a significant relationship, using a second-order polynomial regression equation (successful dives: polynomial r^2 = 0.048; unsuccessful dives: polynomial r^2 = 0.071; Fig. 4).

A generalized nocturnal energy budget was calculated based on 38 surveys (Fig. 5); 245 total animals were observed, the behavioral state of only one animal was unknown. Sea otter abundance was variable, ranging from 0 to 21 animals per survey ($\bar{x}$ = 6.6, SE = 0.76, n = 38). The three all-night surveys also displayed variability in number of animals, although general behavioral trends were observed.

Sea otter abundance and behavior changed during the course of the nighttime. There were fewer animals present in the study area during the first half of the night ($\bar{x}$ = 9.3 sea otters) than the second half ($\bar{x}$ = 19.3 sea otters), although the difference was not statistically significant (Fig. 6, paired t-test, t = 1.890, p = 0.19). The greatest number of animals was observed during the 0100 h to 0200 h surveys, but variability in counts also was greatest during this time period (Fig. 6). Several differences were observed in behavior during the nighttime (Fig. 7). The most dramatic differences were observed in the categories of foraging and resting. Significantly more foraging was conducted in the first half of the night, and more resting occurred in the early morning hours (Fig. 8; paired t-test, t = -10.62, p < 0.01). A slight increase in the proportion of animals foraging, and corresponding decline in the proportion of animals observed resting, occurred in the last observation period (0500 h to 0600 h).

The nocturnal energy budget was significantly different than the diurnal energy budget (Fig. 9, χ^2 = 21.43, p < 0.001). Significantly more foraging (22% of time) occurred at night than during the daytime (16% of time). A greater percentage of time spent socializing also was observed at night (11%) than during the day (7%). More sea otters were observed resting and traveling during the day (55% and 14%, respectively) than at night (44% and 11%, respectively). A small number (< 1%) of sea otters were observed hauled out on land during day and night.

Discussion

Night vision has been used in other studies, but rarely in research on mammals, particularly marine mammals. Only one other researcher of marine mammals has employed the newest night vision technology (pinniped foraging; M. Weise, UCSC, pers. comm.). Generation III night vision offers extreme sensitivity, and creates an entirely new field of research, with a few limitations. Because the observer's field of vision is limited to approximately 40 degrees, scanning must be modified accordingly, and animals may still be missed. The low magnification available (the maximum is a 3x lens, which significantly reduces light levels and image quality) requires the observer to be relatively close to the animal, which required boat-based observations for this study instead of shore-based (where a 15-45x spotting scope can be employed during the daytime). Also, some error in classifying otters into behavioral states would be expected because the observer classified behaviors based primarily on characteristic movement patterns (i.e. rolling for vigorous grooming, porpoising or quickly swimming for travel, etc.) that were distinguishable from a distance. A bias also existed in the identification of animals and behavior classifications used in scan sampling. However, the ability to detect animals using night vision did not differ from using the naked eye, so the methods were directly comparable.

The possibility of correlation between successive dives of an animal is generally not addressed in the literature (Swihart and Slade 1985). The mean successive difference analysis indicated that, for this study, successive dives were not correlated and could be

treated as independent samples. This greatly increased the sample size without violating

the assumptions of statistics. This statistical test was easy to perform, and should be used

in other analyses involving multiple measurements on the same animal (i.e. telemetry

studies).

Whereas most of the foraging parameters did differ significantly between

nocturnally and diurnally foraging sea otters, the difference was in the opposite direction

than expected. Duration of prey handling and unsuccessful dives were both significantly

less at night than during the day. Prey handling at the surface should be primarily tactile,

so the amount of light should not affect the duration of prey handling. There also is a low

level of ambient light, mostly anthropogenic, in Elkhorn Slough even on overcast or

moonless nights. Given the sensitivity of sea otter vision (Mass and Supin 2000), there

could be adequate light for vision at the surface. The shorter duration of unsuccessful

dives indicated that perhaps there was a quicker decision made by the sea otters to

abandon dives if no prey items were quickly found. Because sea otters forage primarily

in prey patches such as bivalve beds, the primary cost expenditure to a foraging sea otter

should be in locating a patch to exploit (Kvitek et al. 1988, Jolly 1997). By terminating

unsuccessful dives more quickly, sea otters could move to a different area in search of a

prey patch. Although location data was not recorded, I do feel that this was observed

occasionally, when more of the time spent at the surface between unsuccessful dives was

spent in directional swimming, and surfacings were farther apart than observed for an

animal successfully foraging.

Prey species composition also differed significantly between nighttime and daytime foraging, with the difference statistically attributed to more crabs and fewer fat innkeeper worms eaten at night than during the day. However, the prey was unidentified for the majority of successful dives (70%). If a prey was recorded as unidentified, the sea otter was observed performing characteristic prey consumption behavior, such as pounding or obvious prey manipulation, during its duration at the water's surface, but the specific item was not seen due to poor light, orientation of the animal, or the boat's distance from the animal. If the animal surfaced at a distance from the observers, the boat was driven closer. Therefore, there was a bias in the ability to identify prey items requiring more time or effort for sea otter handling and consumption. Fat innkeeper worms require almost no manipulation and can be consumed quickly. Many were likely consumed whole before we could approach the animal, and some (potentially large) proportion of the "unknown" prey items were likely fat innkeeper worms. Therefore, no real conclusions about the relative proportions for this prey item should be drawn. Conversely, consumption of crabs is extremely conspicuous, requiring a great deal of manipulation and a long duration at the surface. The number of crabs observed as prey items is very reliable, and I believe that the data reflects a real difference in the proportions of crabs consumed during the nighttime and daytime. This is probably due to the greater levels of nocturnal activity by *Cancer* crabs, which would make them more conspicuous to foraging sea otters (McDonald et al. 2001).

Duration of successful dives was not significantly different between nocturnal and diurnal periods. This is consistent with the only other comparison of nocturnal and diurnal foraging behavior, analyzed through the dive durations of nine radio telemetered sea otters, for which dives were of the same duration day and night (Loughlin 1979). I calculated a mean difference of only 0.8 seconds per dive between mean duration of successful dives during day and night. Even if the results were statistically different, such a small difference is probably not biologically significant.

The relationship between dive duration and moon phase also was not significant. Thus, the increase and decrease in ambient light during the cycle of the month due to moon phase does not appear to play a significant role in sea otter foraging behavior.

Sea otters are relatively unique in exhibiting an arrhythmic foraging pattern; most animals have sensory adaptations to one light level, and these adaptations reduce efficiency at other light levels. Diurnal species have increased spatial and temporal acuity and sensitivity to color, whereas nocturnal species foster other adaptations to enhance their visual sensitivity at low light levels (Fraser and Metcalfe 1997). Juvenile salmon forage visually both nocturnally and diurnally, but foraging at low light intensity (0.03 lux, equivalent to a full moon) is less efficient than foraging at light intensities equivalent to sunrise (Fraser and Metcalfe 1997). In contrast, I found nocturnal foraging by sea otters was more efficient than diurnal foraging.

These results (no difference in dive duration but differences in foraging efficiency) help answer the question: are they visual predators? Sea otters do have

relatively good vision. Anatomical studies have indicated that sea otters are emmetopic (able to focus clearly) in both air and water (Murphy 1990). They have an accommodative distance (a measure of how far they can physically change the shape of the eye to maintain the focal point on the retina) of 60D, which is three times greater than any terrestrial animal but similar to a diving bird, the cormorant (*Phalacrocorax sp.*; Murphy 1990). Like the cormorant, the sea otter probably accomplishes this accommodation using an extensive array of muscles attached to the iris that contract and expand to change the curvature of the lens (Murphy 1990). Sea otters have a visual acuity of 7 degrees (equivalent to human vision of 20/140) in air and water, comparable with other marine mammals and superior to terrestrial mustelids (Mass and Supin 2000). Behavioral tests also indicated that sea otters have good underwater visual acuity. Sixty percent of the time, test animals were able to distinguish between two objects with an area ratio of 1:1.06, and performance was improved with larger size differentials. The California sea lion, *Zalophus californianus*, performed slightly better at the same test (Gentry and Peterson 1967).

Marine mammals also must have adaptations allowing them to see at low light levels, due to the attenuation of light through the water column. Sea otters possess a well-developed *tapetum lucidum*, a specialized reflective layer behind the retina that enhances the light-gathering capacity of the eye and is often found in nocturnal animals (Reidman and Estes 1990). However, some other specializations for low light levels are not found in sea otters, such as orbital enlargement, found in most pinnipeds, which

possibly increases visual sensitivity underwater (Reidman and Estes 1990). Also, the iridial musculature discussed earlier may actually inhibit the sea otter's ability to focus at lower light levels, when the pupil is fully dilated. A related species, the Asian "clawless" otter (*Amblonyx cineria cineria*) had poorer underwater visual acuity at lower light levels than at greater light levels (Schusterman and Barrett 1973).

Some of the earliest reports of underwater observations of sea otter foraging indicated some visual component. Houk and Geibel (1974) reported a sea otter locating an abalone recessed 0.61 m in a rock crevice, and using a rock as a tool to break it off. The sea otter dropped the rock and appeared to locate it visually before surfacing. Upon its next descent, the same rock was picked up and used (Houk and Geibel 1974). However, Shimek (1977) observed a sea otter patting boulders with its forepaws – presumably searching tactually for prey. He surmised that otters may use vision to locate a suitable area (patch) but use tactile senses to locate individual prey items (Shimek 1977).

Relative to epifaunal prey in a kelp forest environment, the soft-bottom infaunal prey of an estuary like Elkhorn Slough should be more difficult for sea otters to detect visually. Sea otters foraging on clams in another local soft-bottom habitat did not seem to spend time visually searching for prey items, because sediment clouds obscured the bottom as soon as the substrate was disturbed on one foraging dive (Hines and Loughlin 1980). The data from my study confirm the hypothesis that sea otters do not require vision for the detection and capture of prey items, particularly infaunal bivalves and fat

innkeeper worms. Crabs (*Cancer* sp.) were observed more frequently as prey items at night, which also was suggested in a study of Alaskan sea otters in Nelson Bay (Garshelis et al. 1986). Crabs are epifaunal and more active at night (Mc Donald et al. 2001), and likely easier to detect tactically by foraging sea otters (Garshelis 1983).

One potential source of error for this study was the different time frames during which foraging was studied by focal animal follows. Jolly's 1997 study was conducted shortly after sea otters permanently colonized Elkhorn Slough in 1995-1996. This results in a minimum of four years (1996-2000) temporal difference between the two studies. There is a possibility that the prey base has changed since that time, and differences observed in foraging behavior are related to this change. I do not believe that to be true for several reasons. First, other studies in soft-bottom environments have documented major differences in benthic prey communities only after 25 years of sea otter occupation (Kvitek et al. 1992). The study presented here was conducted only 5 to 7 years post-colonization. Two years after colonization, Jolly (1997) found an increased bivalve density in the Slough, although a decrease in biomass was documented. Finally, if the sea otter population had caused a dramatic decline in available prey during the three intervening years, I would expect sea otter foraging to be less successful and dives to be greater in duration, as otters were required to increase search time to locate prey items. Instead, the opposite was observed – foraging sea otters had a greater success rate, and dives were less or the same duration.

Elkhorn Slough also could have changed physically in the intervening five years. Malzone (1999) found significant erosion occurred in intertidal areas, but the subtidal environment gained 8.7×10^4 ($\pm 4.4 \times 10^4$) m^3/yr of sediment in the five-year period from 1988 to 1993. Similar erosion rates were predicted into the near future (Malzone 1999), so the five-year period of 1995 to 2000 probably had a similar increase in sediment volume. In addition, the Slough morphology has evolved into a wide-bottomed channel, with an extensive subtidal area and a gentle bathymetric gradient (Malzone 1999). This could have increased potential bivalve habitat, and resulted in increased prey availability. The current speed in the channel is also believed to have increased (B. Watson, pers. comm.), which would potentially increase food supplies for suspension and detritus feeding invertebrates, including clams, crabs, and fat innkeeper worms, and therefore increase the potential prey base for sea otters in Elkhorn Slough (S. Kim, pers. comm.). These alternative explanation also could be why foraging success did not decrease in the five-year time difference between studies.

Regarding activity budgets, both diurnal and nocturnal observations were conducted during the same time frame (1999-2002) and were boat-based, which should allow for the same advantages (the ability to more closely approach an animal for better observations if needed) and disadvantages (the likelihood of bypassing an animal that is submerged). As boat speed and other methodologies were the same, activity budgets obtained from both studies should reflect similar observations of the same population.

The differences between nocturnal and diurnal foraging observed in this study

(Fig. 5) help substantiate the criticism of Garshelis et al. (1990) that extrapolating diurnal

scan samples to construct a 24-hour activity budget was flawed because of the implicit

assumption that the percentage time spent in diurnal and nocturnal foraging are identical.

Assuming that foraging effort at night was the same as daytime effort would overestimate

the amount of time spent resting and underestimate the amount of time spent foraging

during the 24-hour period, which is especially critical if used as a measure of population

status. Based solely on diurnal scan samples, sea otters in Elkhorn Slough would spend

only 16% of their time foraging, indicating their population status was considerably

below equilibrium density. Time spent foraging at night (22%) was greater than day but

still substantially less than the 50% time spent foraging by populations at equilibrium

density (Estes et al. 1986). The estimate of nocturnal foraging was more comparable

with two other diurnal studies based on scan samples from nearby rocky bottom habitats:

24% reported in Shimek and Monk (1977) and 26% reported in Estes et al. (1986).

Although no estimates of nocturnal activity budgets have been made for rocky bottom

environments, it would be interesting to test whether sea otters in those areas also

demonstrated an increase in the percentage of time spent foraging at night.

Although the reported results from scan sampling were fairly consistent, all are

less than the percentage of time spent foraging reported by studies using radiotelemetry

in California. Loughlin (1979) reported radio tagged sea otters foraged 34.9% of the time;

Ribic (1986) reported 53% of time spent "active," which included foraging, travel, and

grooming; and Ralls and Siniff (1990) found 35 to 50% percentage of time sea otters were foraging, with differences dependent on sex/age class. The differences between estimates obtained from scan sampling and radio telemetry are usually attributed to the visual bias against reporting foraging, because these sea otters are submerged for long periods of time and are more likely missed by observers than stationary sea otters resting at the surface. However, most scan samples (including my study) are designed so that the likelihood of missing submerged sea otters is low. In this study, I found the mean foraging dive duration at night was less than one minute ($\bar{x}$ = 44.6 sec for successful dives, $\bar{x}$ = 55.03 sec for unsuccessful dives), and a mean prey handling time at the surface of around 30 seconds. At the boat speed used, no area was covered in less than a minute, so that observers should have had the opportunity to see the foraging animal during the interval when the animal was at the surface. In addition, actively foraging otters are usually conspicuous at night, when auditory cues are important for observers. Pounding of prey items and sea otter breath sounds before and after diving are both obvious cues in the detection of animals. I do not believe that a significant proportion of foraging animals were "missed" during observations in this study.

I believe that the differences in estimates between methodologies (scan sampling and telemetry) may be attributable to differences between population-level patterns and individual animals. Ribic (1982) described an apparent contradiction: populations of sea otters demonstrated crepuscular foraging, whereas individual animals indicated no activity rhythms (as reported by Loughlin 1979). However, she and other authors

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(Garshelis 1983, Ralls and Siniff 1990) have reported extreme variability among individual telemetered animals. It is possible that an adequate sample size cannot be obtained using radiotelemetry (due to monetary cost) to correctly measure population parameters.

An alternative explanation is that scan sampling is biased towards areas in which more resting (and conversely, less foraging) occurs. I believe that, whereas many sea otters forage within Elkhorn Slough, some individuals may use other areas for foraging, including Moss Landing Harbor, the Moss Landing Jetty area, or the nearshore waters of Monterey Bay, and then return to the protected waters in Elkhorn Slough for resting. This also may help explain the increase in relative abundance of animals during the early morning hours, as sea otters foraging elsewhere moved into Elkhorn Slough to rest.

Although still useful in understanding sea otter ecology, the need to have precise calculations of activity budgets to assess population status may be less important today. Gelatt et al. (2002) recently concluded that activity-time budgets were not reliable indicators of sea otter population status. They determined that a host of independent and cumulative factors accounted for variability in activity budgets between populations, and the number of animals (or level of the population relative to carrying capacity) could not be simply extracted (Gelatt et al. 2002).

An increase in the amount of time spent foraging at night was not expected based on other accounts of sea otter biology. Daylong radiotelemetry studies have indicated that sea otters have approximately three foraging bouts per day, usually two during the

daylight hours and one at nighttime (Ribic 1986). Whereas Gelatt et al. (2002) did not report crepuscular peaks in foraging activity, they reported that adult male sea otters, juvenile males, and females without pups spent more time foraging diurnally than nocturnally. Therefore, percentage of time spent foraging during the day would be more than that spent in nocturnal foraging; if the generalized model of three foraging bouts were true, twice as much time should be spent foraging during the day than during the nighttime. One explanation for the result of this study is a potential bias in both studies - the time period during which data were collected. The diurnal activity budgets were obtained solely during the mid-day (1000 h to1400 h) period; this may not be representative of energy budgets for the entire daytime. Unfortunately, I did not have control over this methodology, because the data were collected by another group. Estes et al. (1986) reported a mid-day lull in activity that separated morning and afternoon foraging peaks. A similar result was seen in individual telemetered sea otters by Ribic (1986), and in female sea otters by Loughlin (1979). Therefore, the reported diurnal activity budget may be underestimating the percentage time spent foraging and overestimating the time spent resting. Whereas nocturnal scans were obtained for the entire nighttime, a disproportionate number are from the early night (2100 h to 2400 h), which may result in some categories (particularly foraging) being overestimated.

However, other results do contradict the generalized behavior pattern. Loughlin (1979) observed that male sea otters in Monterey conducted approximately 50% of their foraging at night. Because the sea otter group in Elkhorn Slough was predominately

males (Feinholz 1998), the findings of this study may be accurate – slightly more foraging by sea otters occurs during night than during day in Elkhorn Slough, but the percentages are not that different from expected, if an equal amount of time is spent foraging during the day and night by male sea otters.

My study also indicated that sea otter behavior was not constant during the night. Throughout the study area, the number of foraging individuals decreased during the night. These sea otters apparently shifted their behavior to resting, as there was a concurrent increase in that behavior category. Overall abundance of sea otters also increased from dusk to a peak around 0100 h (Fig. 6), indicating that sea otters moved into the study area throughout the first half of the night to rest.

Haulout behavior (sea otters resting on land) is not usually observed in California sea otters, although it is frequently reported among animals in Alaskan populations (Reidman and Estes 1990). It has been reported in California (Faurot 1985), but never before in Elkhorn Slough. We observed few animals ashore at night (3 individuals or 1%), but observing animals ashore is extremely difficult using night vision goggles, when sea otters can easily be confused with rocks or debris or not seen at all, especially against the dark background of mudflats common in Elkhorn Slough. It is certainly possible that greater numbers of sea otters were ashore at night and not detected. However, relatively few animals were observed ashore during the daytime (also around 1%), when observation should be more straightforward (T. Keikheifer, PCG, unpub. data), so it appears that sea otters rarely come ashore in Elkhorn Slough.

In conclusion, I demonstrated one potential application of night vision technology to help answer difficult questions regarding sea otters. Presented here are the first data quantifying nocturnal foraging and the first nocturnal energy budget for sea otters calculated using visual scan samples. The differences observed in this study between diurnal and nocturnal foraging and activity patterns should serve as a caution that measures of foraging ecology cannot simply be extrapolated from daytime to nighttime, especially in making quantitative estimates. Energy consumption and net gain is dictated by prey species composition and success rate (number of prey per time), both of which differ nocturnally. In this study, the identified prey composition of nocturnal foraging of sea otters included more energy-rich crabs and fewer fat inkeeper worms, which are much less energetically valuable (Jolly 1997). In addition, the nocturnal foraging success rate was significantly greater and the time spent in unsuccessful dives less. The combination of these three factors indicated that sea otters foraging nocturnally in Elkhorn Slough gained significantly more energy per effort than during diurnal foraging. This may be important for estimating sea otter impacts on prey populations, evaluating the status of sea otter populations, and determining diel energy budgets of sea otters.

Visual observations at night overcome some limitations of telemetry, and are especially useful in answering population-level, site-specific, and long-term questions. Data can be gathered on a large cross-section of the population, including all age and sex classes, increasing potential sample size. There is no potential for capture bias. This is especially important in population-wide studies of sea otters due to the large degree of

individual variability reported in telemetry studies (Ribic 1982, Garshelis 1983, Ralls et al. 1995). For site-specific questions, all data will be obtained from the study area. In a telemetry study, there is always the potential for a telemetered animal to move out of the desired study area, decreasing the sample size; in a scan-sampling study, this is never a concern, because your research is not focused on individuals, but rather on one (or several) locations. Night vision also is useful for long-term studies, as there also is no worry about tag loss or failure. A visual study using night-vision could be conducted indefinitely, covering years or decades, as the only cost (other than the initial equipment purchase and vehicle operation costs) is in observer time.

Soft-bottom and rocky sub-tidal environments have long been recognized to have different implications on sea otter foraging behavior (Kvitek and Oliver 1998). The obvious next application of night vision technology in the study of sea otters would be to do a similar study to this one in a rocky bottom, kelp forest habitat. Also of interest would be examining individual otters (such as telemetered animals) to determine if individual differences exist in prey consumption or success rates between night and day.

Although this study was not properly designed to construct an unbiased 24-hour sea otter activity budget, a sampling design to answer that question is feasible. Night vision also could be used to conduct scan samples in other environments (rocky bottom substrates, other locales in California or Alaska) to compare these results with diurnal observations and to help provide a more complete understanding of sea otter behavior and biology.

Visual observations of nocturnal behavior in sea otters and other animals in a variety of habitats are now practical and highly recommended. Night vision gives scientists a powerful new tool to answer important questions, and the applications are only increased when combined with existing technologies such as radiotelemetry.

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Table 1. Foraging time expenditure (sec) and efficiency for nocturnal and diurnal observations of sea otters.   Values are mean (standard deviation). Comparison of duration of successful dives was made using a two-sample, one-tailed t-test. Other comparisons were made using Mann-Whitney U tests.

Activity	N	Nighttime (mean ± SE) sec	Daytime[†] (mean ± SE) sec	Stat	p[‡]	power
Prey handling (s)	614	33.30 (± 1.21)	40.50 (± 1.39)	171851 U	0.008*	
Successful dive (s)	603	44.64 (± 0.97)	45.46 (± 0.87)	0.628 t	0.530 NS	~41
Unsuccessful dive (s)	110	55.03 (± 2.64)	63.96 (± 1.62)	4693.5 U	0.004*	
Foraging success rate	565	1.42 (± 0.04)	1.63 (± 0.05)	139435.5 U	0.000**	

[†]Daytime data obtained from Jolly (1997). [‡] **:$p<0.001$; *: $p<0.05$; NS : not significant, with α = 0.05
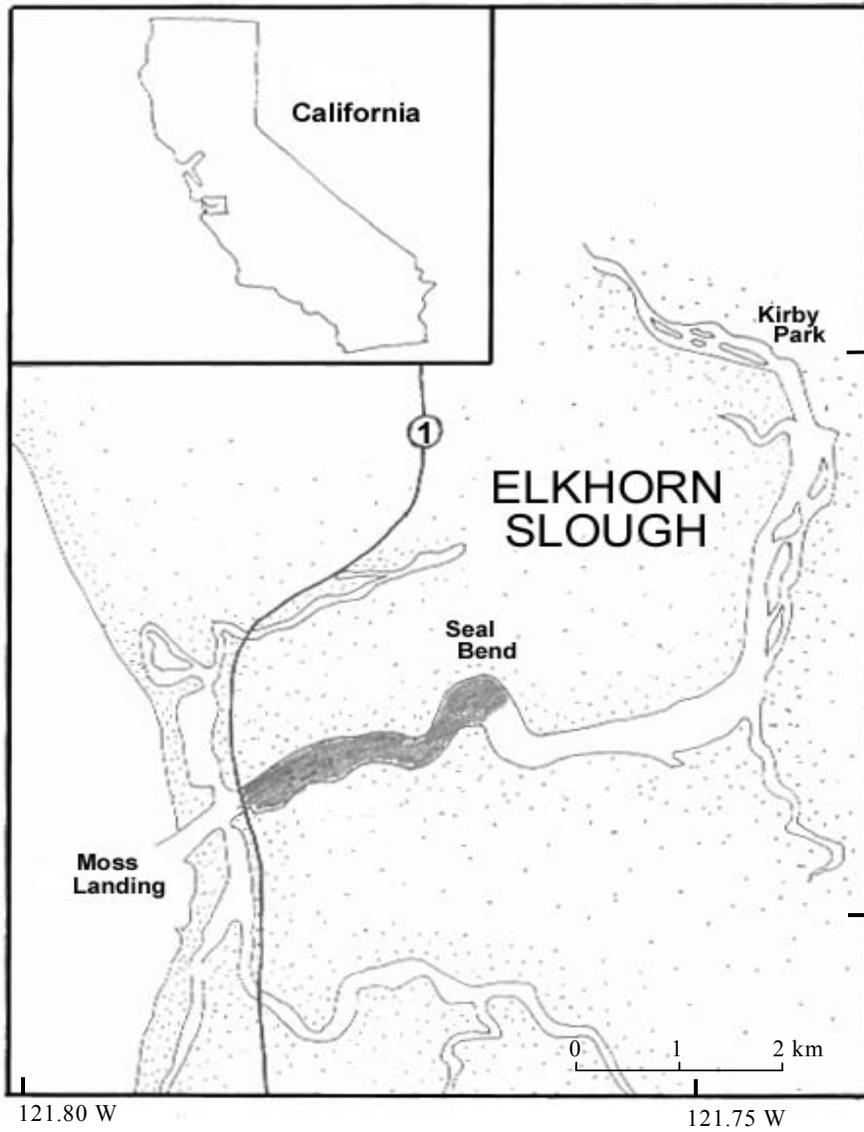
Figure 1. The study area in Elkhorn Slough, Monterey County, California. Observations of sea otters were conducted nocturnally in the shaded area from the Highway 1 bridge to Seal Bend.
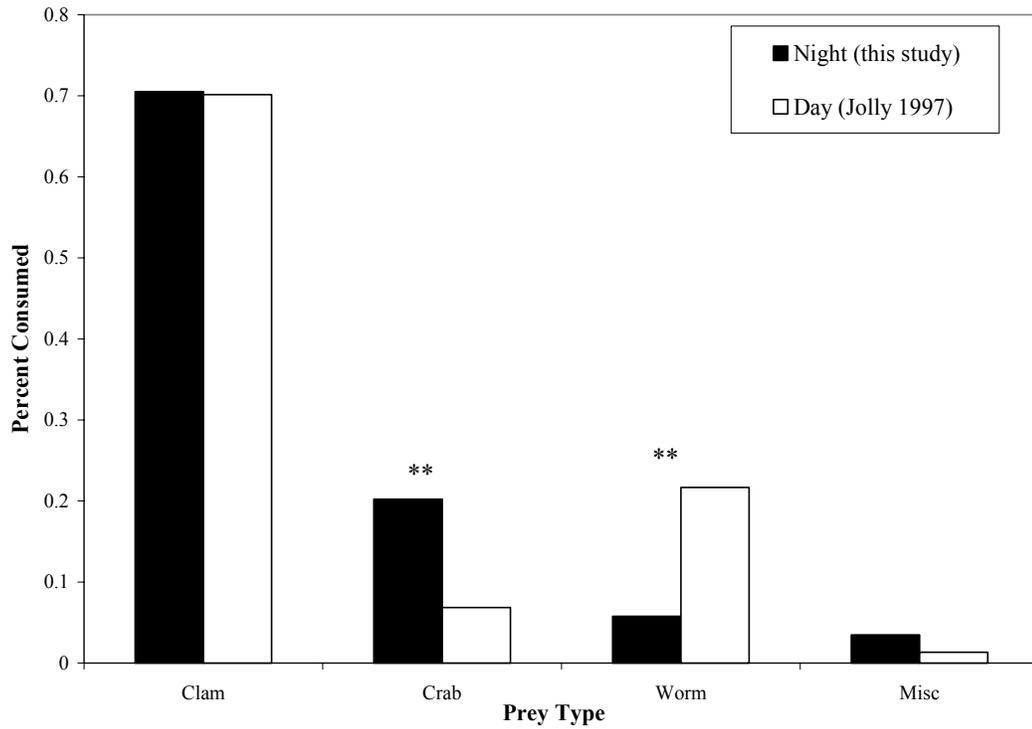
Figure 2. Percent prey consumed by foraging sea otters in Elkhorn Slough, CA. Asterisks indicate categories of significant difference between nocturnal and diurnal prey consumption (assessed via subdivided Chi-squared analysis). Clam = gaper or Washington clam, crab = *Cancer* sp., worm = fat innkeeper worm.
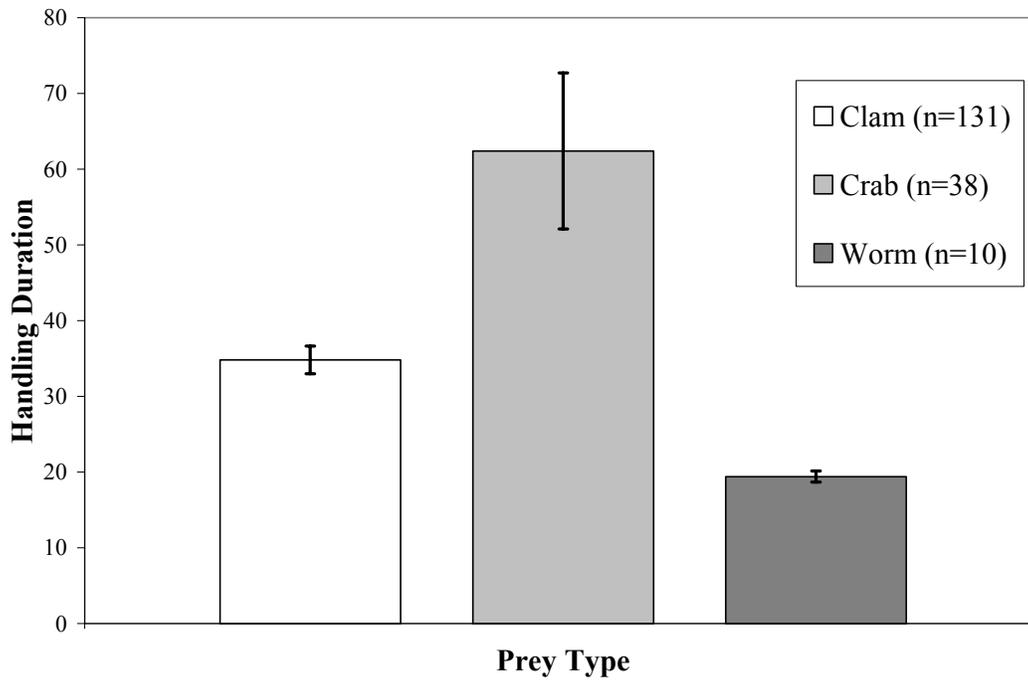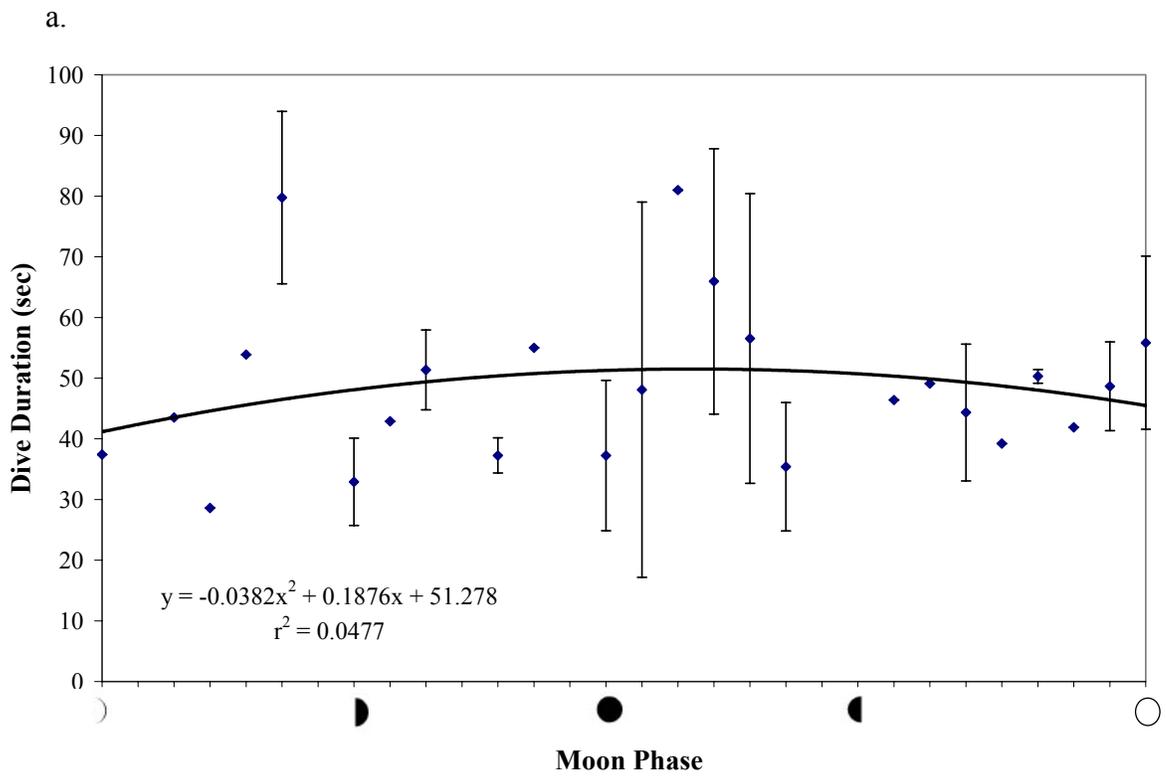
Fig. 3. Mean prey handling duration by prey type. Sample size varied by prey type and is listed in the legend. Key to prey types: clam is gaper or Washington clams; crab is *Cancer* sp.; worm is fat innkeeper worm. Error bars are standard error.

a.

$$y = -0.0382x^2 + 0.1876x + 51.278$$
$$r^2 = 0.0477$$

b.
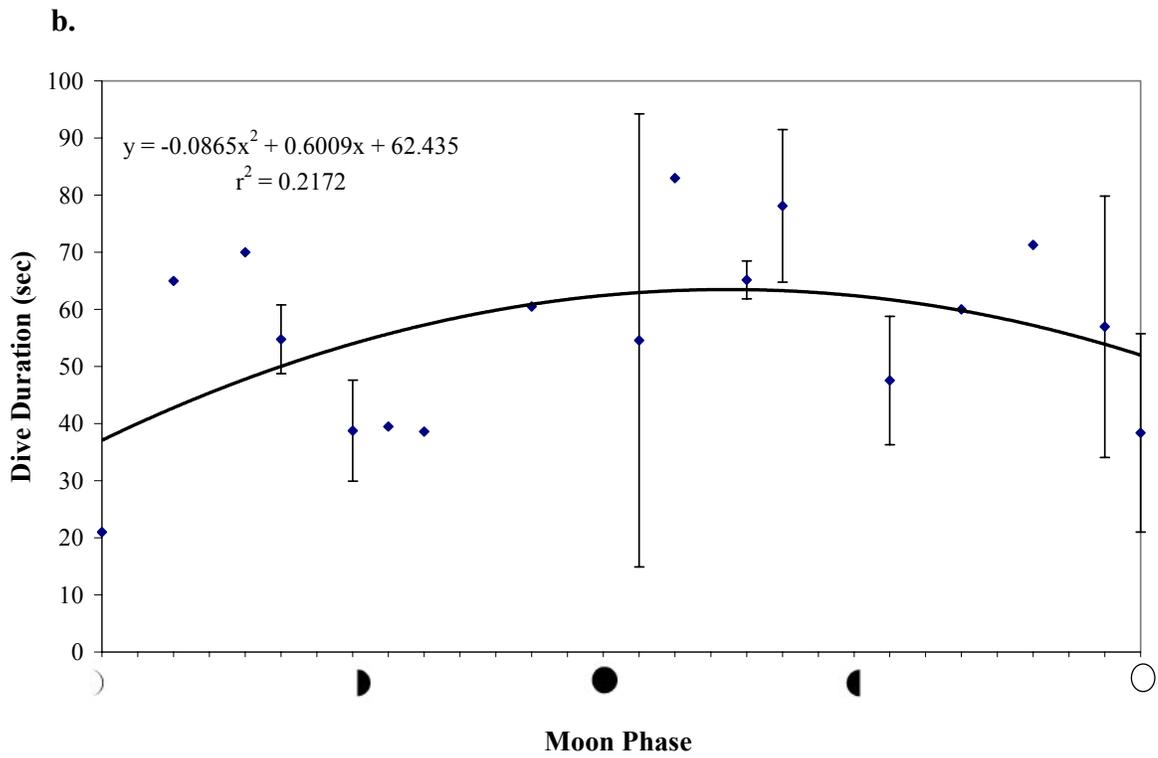
Figure 4. Duration of successful (a) and unsuccessful (b) dives averaged and plotted against day of moon phase. Second order polynomial equations (shown) were fitted but were not statistically significant. Each point is the mean dive duration for all sea otters observed on days with the same moon phase. Error bars are standard deviation.
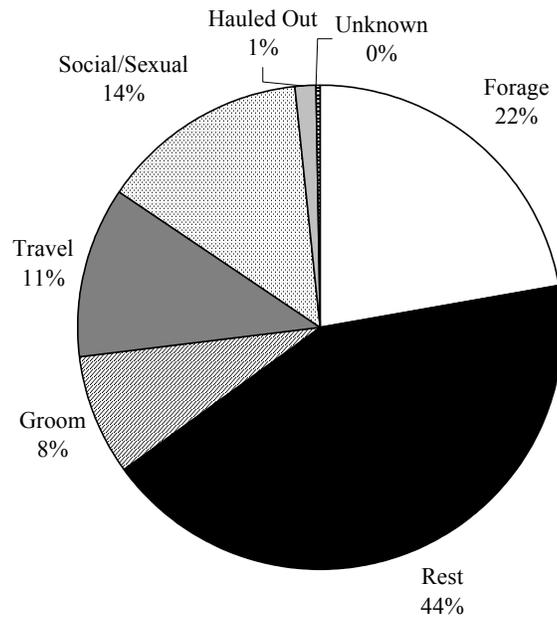
Fig. 5. A generalized nocturnal energy budget for sea otters in Elkhorn Slough, CA, based on 38 surveys conducted using night vision equipment. Sea otters were observed and approached, if necessary, from a boat to classify their behavior into one of the six listed categories. Only 0.004% (1 of 245 observed animals) were unable to be classified ("unknown").
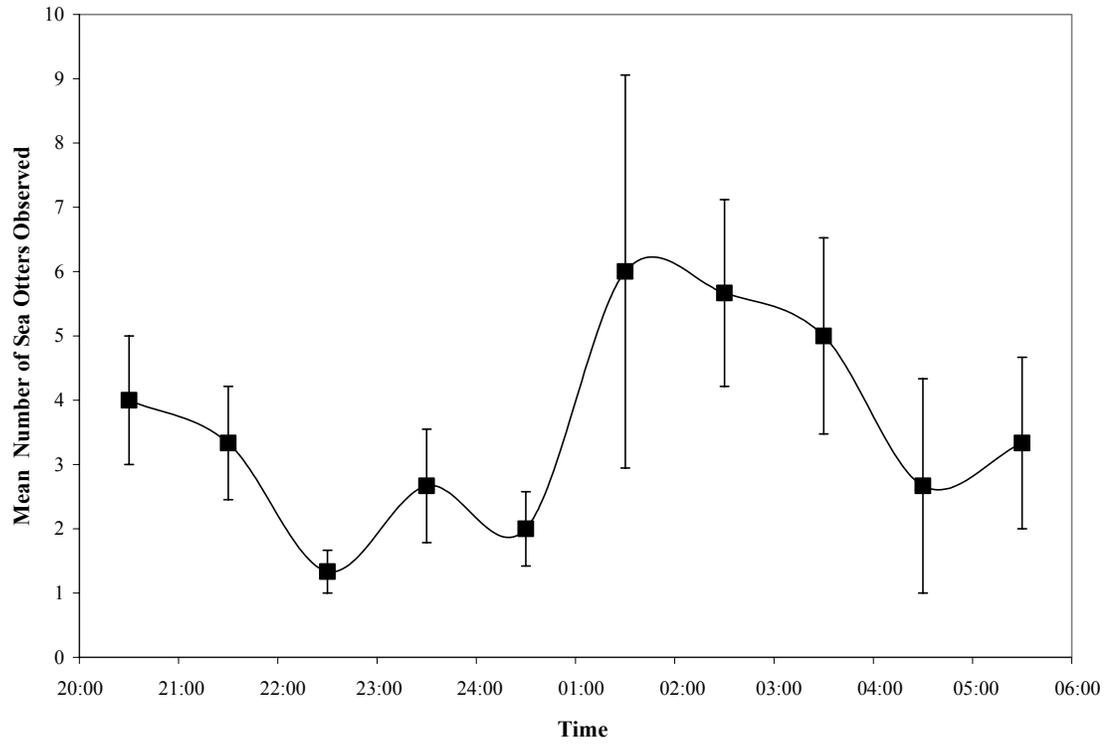
Fig. 6. Mean number of sea otters observed during the nighttime, from three all-night surveys with scan samples conducted once per hour from sunset until dawn. Error bars are standard error.
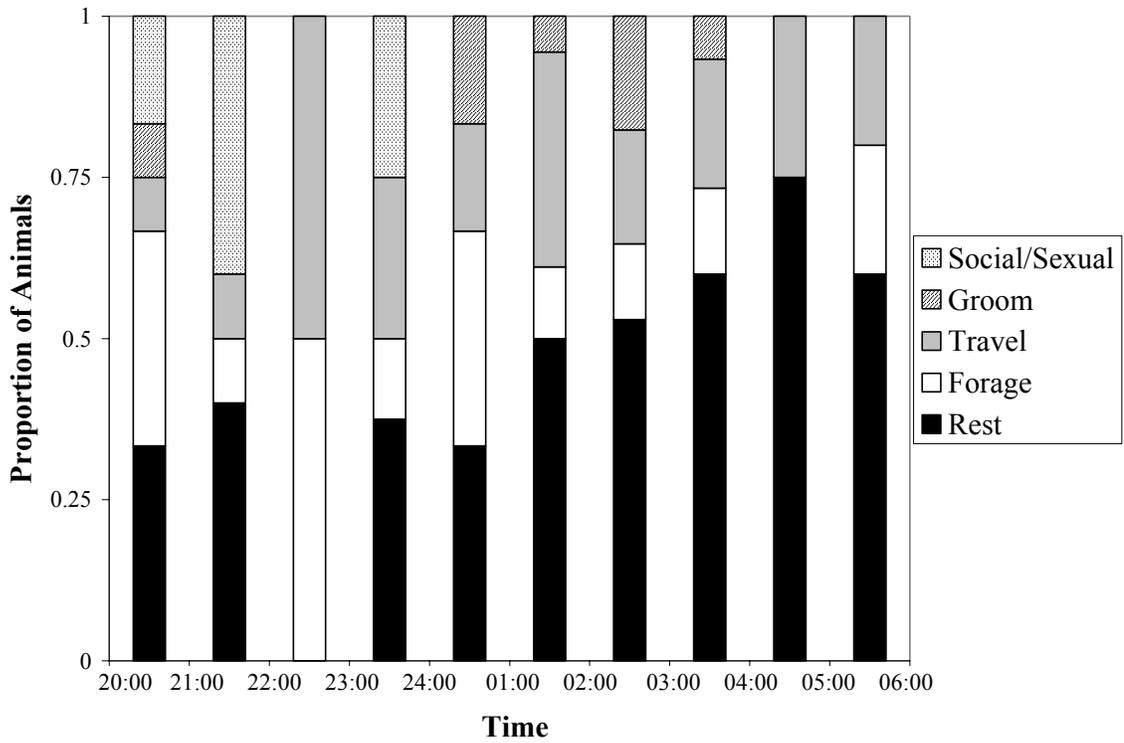
Fig. 7. Proportion of sea otters observed in each of five behavior categories over the course of three all-night surveys using night vision goggles. One boat-based scan survey was performed over the entire study area during each hour.
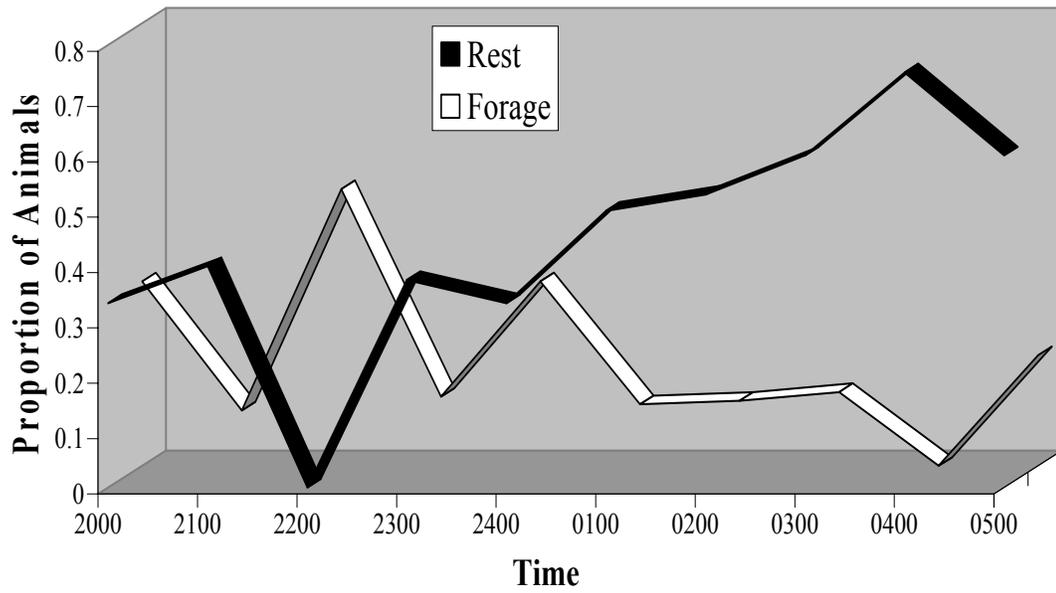
Fig. 8. Proportions of sea otters observed in two behavior states (foraging and resting) over the nocturnal period. A dramatic decrease in the proportion of foraging sea otters occurred during the second half of the night, while the number of resting animals increased.
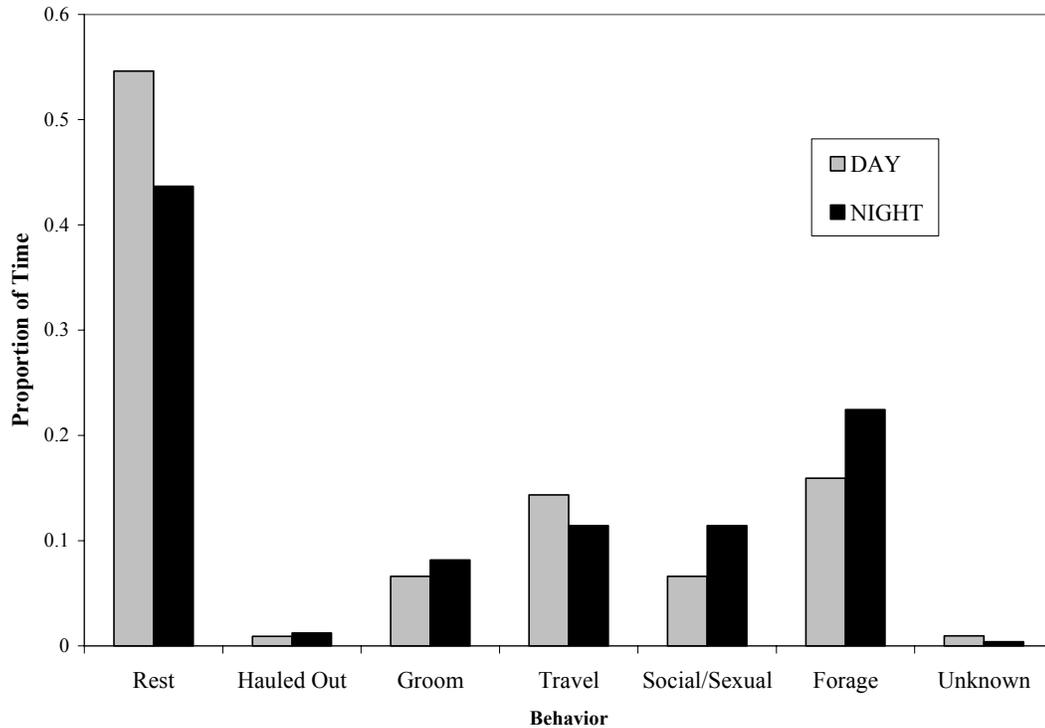
Fig. 9. Comparison of nocturnal ("NIGHT," black bars) and diurnal ("DAY," gray bars) activity budgets of sea otters in Elkhorn Slough, CA. Activity budgets were calculated by visual scan samples, using night vision goggles at night and naked eye or binoculars during the day. Sea otters were identified and their behavior was observed until it could be classified into one of the six possible categories: rest, hauled out (on land), grooming, traveling, socializing/sexual (interactions with another sea otter), and foraging. Fewer than 1% of observations were unable to be classified, and were recorded as unknown.