Sea Otter Foraging and Feeding Behaviors: A Review

Sea otters, *Enhydra lutris*, are unique in the range of their foraging and feeding behaviors and their ability to adapt to different local ecologies. Investigations have been made into otter behaviors such as feeding specialization, hierarchical prey selection, use of search images, dive lengths and surface intervals. Numerous observations have been made of otters exhibiting the use of tools. The possibility that tactile and oral sensory systems may play a part in foraging and feeding has been investigated. Observations have been made of the opportunistic capture of seabirds and of foraging in intertidal areas. This paper summarizes several important papers which have been published in the field over the past forty years.

Key words: diving, *Enhydra lutris*, feeding, foraging, sea otter, tool use

Sea otters in United States waters are classified into three subspecies. *Enhydra lutris nereis* is found along the California coast and is commonly called the southern sea otter. *E. l. lutris* from the western Alaskan archipelago and *E. l. kenyoni* from Prince William Sound, Alaska, the eastern Alaskan islands and northern Oregon are known collectively as the northern sea otter. A fourth classification has been proposed by Cronin et al. (1996) for otters from the Kuril islands (*E. l. gracilis*) but this is not officially recognized (Anderson et al. 1996).

Otters are unique among marine mammals in their foraging and feeding behaviors. These include the consumption of a large variety of prey species, the ability to learn new foraging techniques and the use of tools. This paper summarizes a selection of articles published over the past 40 years addressing three questions: what otters eat, how they forage, and how they consume their prey.

Adult male otters in Alaska can grow up to 148 cm in length and can weigh 45 kg or slightly more (Rotterman and Simon-Jackson 1988). Otters are the only marine mammals that have no blubber. To compensate for this, they must consume 20-37% of their body weight daily (Kenyon 1981; Rotterman and Simon-Jackson 1988). Limbaugh (1961), Vandevere (1969) and others made detailed studies of the variety otter prey sources in different habitats to better understand the range of species affected. Riedman and Estes (1990) developed comprehensive lists of known prey items for both northern and southern sea otters.

Studies by Estes et al. (1982) and Kvitek et al. (1993) were designed to explore the interaction between otters and invertebrate populations. Most investigators used non-invasive shore-based surveying techniques in their observations. Otters were found to change their environments significantly, depleting sea urchin and abalone populations in particular. Antonelis et al. (1981) and Ostfeld (1982) performed studies of hierarchical prey selectivity in captive and wild otters. They found evidence to confirm the hypothesis that otters choose prey with the highest ratios of caloric-value obtained to energy-expended in foraging.

Several studies of otter activity patterns have investigated diving behaviors. Feeding usually takes place in shallow waters of 3-9 m when prey is abundant, but otters are capable of reaching great depths. In one extreme case, an individual was recorded at a depth of 97 m where it was found drowned, apparently after having attempted to take bait from a crab pot (Kenyon 1978). In shallow water, the otter's hind-paws may be seen protruding from the water while it removes prey from the substrate (Limbaugh 1961).

Ralls et al. (1988, 1995), Estes and others (Estes 1977; Estes et al. 1982) performed detailed observations of foraging behaviors. Studies were designed to gather information on how the various qualities of the prey species influence otter's foraging tactics (e.g., dive times and surface intervals). As with surveys of prey species, observations in these studies were most often performed visually.

Hines and Loughlin (1980) made underwater observations in the wild, and Houk and Geibel (1991) performed experiments on captive otters to test their ability to detect paralytic shellfish poisoning in butterclams. In each case, investigators found evidence that otters rely primarily on tactile and other non-visual sensory systems in foraging. Several interesting anecdotal reports of tool use and other consumption-related behaviors by observers such as McCleneghan and Ames (1976), Kenyon (1978, 1981), Van Wagenen et al. (1981) conclude the paper.

DISCUSSION

Sea otters, *Enhydra lutris*, subsist in the wild on a diet comprised primarily of macroinvertebrates and some fish. They spend varying proportions of their daily time budgets in foraging, depending on prey availability. Otters use hierarchical prey selection and often specialize in prey types. They routinely use tools in foraging and feeding behaviors and are highly adaptive in learning new techniques.

Food sources.-The major food sources for otters are benthic invertebrates and epi-benthic sluggish bottom fish (Kenyon 1981; Rotterman and Simon-Jackson 1988; Kvitek et al. 1993). Otters eat a wide variety of prey from more than seven phyla including clams, snails, chitons, limpets, octopi, crustaceans, starfish, sea urchins, sand dollars, anemones, polychaete worms, echiuriods, tunicates, sea cucumbers, fish and kelp (Kvitek et al. 1991). A few otters have been observed feeding on birds, although debate continues as to whether the flesh passes through the system undigested (Van Wagenen et al. 1981) or is of some caloric value (Riedman and Estes 1988). Kvitek et al. (1991) reported that otters in captivity consume without hesitation virtually anything offered to them including bread, marshmallows and peanuts.

Variation by region.-Prey selection by otters varies from region to region. Macroinvertibrates are relatively more abundant in the range of the southern otter than the northern otter. Several studies have shown that more fish is eaten by northern otters than by southern otters, probably due to differences in availability (Estes et al. 1982; Van Wagenen et al. 1981; Ralls et al. 1988; Riedman and Estes 1990). Estes (1977) reported that otters in Alaska appeared to take fish opportunistically and were not observed feeding exclusively on either fish or invertebrates.

Differences exist in prey selection between habitats in close proximity to each other as well. Sea urchins were the most selected prey of otters from Amchitka and Attu islands in Alaska in a study by Estes et al. (1982) using surface scanning. The greatest difference between the areas was in consumption of fish. Otters caught fish 60 times more frequently at Amchitka where it composed 60% of stomach contents by volume than at Attu. No other single prey item composed more than 3.5% of the total stomach contents by volume at either Amchitka or Attu. Otters consumed macroinvertebrates (mussels, crabs, clams and *Octopus*) more frequently at Attu than Amchitka, while otters at Amchitka were more likely than those at Attu to consume invertebrate fauna associated with algal holdfasts and coralline algae. In a prior study, Estes (1977) observed otters at Attu eating false jingle shells (*Pododesmus* spp.) and sea urchins (*Strongylocentrotus polyacanthus*) while those at Amchitka did not.

Estes et al. (1982) hypothesized that the differences in diet at Amchitka and Attu reflect structural differences between the communities. Prey was scarcer at Amchitka where the otter population was denser. This may have led to increased fish consumption as invertebrate populations decreased through predation.

In another study undertaken in Alaska, Garshelis et al. (1986) observed otters in Prince William Sound consuming diets almost entirely different from the diet at Amchitka and Attu. Items eaten by otters in Prince William Sound included crabs, cockles (*Clinocardium nuttalli*), various clam species, mussels and fat innkeepers (*Echiurus echiurus*). Kvitek et al. (1993) observed further prey differentiation in other areas of Alaska.

Specialization.-Although they consume a large variety of prey species, otters are energy and not nutrient limited. There is no evidence to suggest that they require more than one type of prey for survival (Ostfeld 1982). This may contribute to the tendency of many individual otters to engage in prey specialization (Riedman and Estes 1988, 1990). Lyons (as cited in Ralls et al. 1988) observed otters specializing in three or more types of prey in flipper tag studies and found that specialization choices may be maintained for up to three years. Ralls et al. attributed differences in nocturnal and diurnal foraging patterns between individuals to prey specialization, especially as certain crabs such as Cancer spp. and octopus are nocturnal.

Selection and availability.-Prey selection in different regions also reflects availability over time. Limbaugh (1961) recorded otters from the Monterey Bay area of the California coast in 1953 eating, in order of preference, red abalones (*Haliotis rufescens*), sea urchins (*Strongylocentrotus franciscanus*), purple-hinged scallops (*Hinnites gigantean*), California mussels (*Mytilus californianus*), various species of snails and possibly sea cradles or gumshoe chitons (*Cryptochiton stelleri*).

By the end of the 1960s, populations of sea urchins in Monterey Bay had decreased considerably and no longer made up any appreciable proportion of otter diets in the area. Vandevere (1969) observed otters along the same area of the California coast consuming a different set of prey species 15 years after Limbaugh's observations. Items recorded by Vandevere include turban snails (*Tegula montereyi* and *T. brunnea*), red abalones (*H. rufescens*), black abalones (*Haliotis cracherodii*), opalescent squids (*Loligo opalescena*), kelp crabs (*Pugettia* spp.), ocher sea stars (*Pisaster* spp.), sunflower stars (*Pycnopodia* spp.), bat stars (*Patiria* spp.), plumed sabellid worms (*Eudistylia* spp.), ascidians (*Chordata* spp.), *Styela montereyensis*, seaweed in small quantities, algae (*Macrocystis angustifolia* and *M. pyrifera*), crabs (*Cancer antennarius, Pugettia producta* and *Loxorhynchus crispatus*), large purple urchins (*Strongylocentrotus purpuratus*), chitons (*Ischnochiton* spp.), California mussels (*M. californianus*), purple-hinged scallops (*Hinites multieugosus*), gaper clams (*Tresus nuttalli*) and sun stars (*Helianthoides* spp.).

Other prey items consumed by otters in the Monterey Bay area include pink short-spined starfishes (*Pisaster brevispinus*), common Washington clams *(Saxidomus nuttalli*), abalone jingles *(Pododesmus cepio*), octopus (*Octopus* spp.) and snails in seen 1975 (McCleneghan and Ames 1976).

Scat studies.-Few studies of otter scats have been undertaken because of the difficulty in gathering samples. Faurot et al. (1986) undertook a study of 67 scats collected in 1976 and 1982 at Cypress Point, California. Analysis revealed consumption of sea urchins (*S. purpuratus*), mussels (*M. californianus*), leaf or goose barnacles (*Pollicipes polymerus*), crabs *(Cancer* and *Pugettia* spp.), isopods (*Idotea* spp.), and chitons (*Lepidozona* spp., *Mopalia lignosa* and *Tonicella lineate*). Barnacles passed through the gut largely undigested. Faurot et al. found chiton species only in the 1982 samples and not in those from 1976. They speculated that as the chitons in the 1982 scats were cryptic, only lucky or experienced otters were likely to find them.

Green and Brueggeman (1991) obtained 50 samples at a haulout site on the north side of the Alaska Peninsula in 1986. As expected, these scats were different by composition to those used by Faurot. Mussels (*M. edulis*), clams (*Siliqua* spp., *Spisula polynyma*, *Tellina lutea*), sand dollars (*Echinarachnius parma*), and helmet crabs

(*Telmessus cheiragonus*) were the dominant species by analysis in Green and Brueggeman's study.

Hydration.-Otters maintain hydration through drinking seawater taken in during prey consumption and from prey itself. Invertebrates have higher electrolyte levels than fish and may require wild otters to drink seawater directly to maintain a balance. (Tuomi 2001).

Foraging patterns.-Otters forage by diving to retrieve prey and returning to the surface to feed and breathe. An otter's pelage is loose and can be pulled about to create "pouches" in the axilla of the foreleg in which to carry prey (Vandevere 1969; Kenyon 1978; Rotterman and Simon-Jackson 1988). These pouches can hold up to 25 sea urchins depending on size. Forepaws are adapted for digging, gathering and holding prey, and are often used to hold and manipulate tools. Claws may be extended to assist in grasping. Prey is selected by touch from a mixture of prey, other species and pebbles (Kenyon 1981). Vandevere (1969) and Kenyon (1978) speculated that otters are right handed since they always use the right forepaw to store food in the left pouch. Forepaws are not used in swimming (Kenyon 1981).

Kenyon (1981) noted that although they are social animals at rest, otters scatter individually during foraging. Mother otters leave their pups floating on the surface while they dive for prey.

Hierarchal prey selection.-Antonelis et al. (1981) obtained results showing hierarchical prey preferences in a marathon study of three captive otters observed over a 17-hour period in 1974. Otters in the study were supplied with a mixture of live arthropods, bivalves, urchins and gastropods. Prey selection was mixed for the first four hours. Otters then concentrated feeding on single food types in turn until each was depleted. After the 5th hour they had consumed all live arthropods and switched to arthropod parts and urchins. When these were depleted, otters concentrated on bivalves and gastropods in turn. This sequence of consumption is consistent with the theory that prey with higher ratios of caloric-intake to foraging-effort are preferred.

Ostfeld (1982) obtained similar results in a study he conducted of foraging strategies and prey switching by otters that had been relocated to Santa Cruz, California after an absence from the area of over 100 years. He noted a strong hierarchical preference among otters as prey availability changed over the course of the first two years after relocation. Otters predated on sea urchins to depletion before switching to kelp crabs and clams. As seen in the earlier study by Antonelis et al., otters choose foods with higher caloric-intake to foraging-effort ratios before turning to less desirable prey items in sequence.

Use of search images and other mechanisms.-Ostfeld suggested this behavior shows that otters use patch selection and tactile search image formation to choose the most desirable prey available at any given time. In addition, he found that otters tended to repeat captures of the same prey species during successful dive sequences and to switch following recurrent failure. He theorized that two mechanisms could be proposed to explain this behavior, and that both mechanisms may work simultaneously. First, otters may use a search image until the frequency of encounters drops and the image is lost. Second, otters may select specific patches for foraging, and therefore be more likely to encounter a single prey type until that patch is depleted.

Time budgets.-Several studies of otter foraging patterns and time budgets have been made. Estes and others (Estes 1977; Estes et al. 1982) measured activity patterns at Amchitka and Attu islands using shore-based surface scanning. A consistent relationship was found between population density and the proportion of time devoted to foraging. Otters at Amchitka foraged for 50-55 percent of the time while those at Attu foraged for only 15-17 percent daily. Contrary to expectations, females with pups at Amchitka spent 30 percent less time than single animals in foraging. Estes et al. hypothesized that this may reflect a compromise between the need for adequate nutrition and the need to avoid separation from pups while diving. On the contrary, there were no differences in time devoted to foraging between mothers with pups and singles foraging at Attu. Garshelis et al. (1986) reported similar results in a study undertaken in Prince William Sound, Alaska in 1979-1982.

Another difference observed between Amchitka and Attu involved foraging patterns. Otters at Amchitka increased their foraging efforts at dawn reaching a maximum at around 0800 h, and exhibited a second peak in the evening between 1800-1900 h. Otters at Attu foraged throughout the day with no discernable peaks in activity. Unsuccessful dives were twice as frequent at Amchitka as at Attu.

Estes et al. attributed differences in time budgets and foraging patterns at Amchitka and Attu to the importance of fish at Amchitka where benthic invertebrates are scarce relative to those available at Attu. Catching fish requires visual clues and a relatively large investment of time and energy in search and pursuit as compared to the capture of sessile prey.

Dive lengths.-Ralls et al. (1988) used radio-telemetry studies to gather data on dive lengths and depths and nocturnal as well as diurnal foraging patterns. They compared data obtained from individually instrumented animals in the wild to results obtained using visual shore-based surveys undertaken at about the same time. The mean length of dives observed visually for instrumented and uninstrumented otters was 52.14 s (n=712) while that for instrumented otters as measured by radio-telemetry was longer at 73.56 s (n= 8254). Dive length correlated directly to water depth. Ralls et al. hypothesized that the differences noted between visually and radio-telemetry observed dive lengths may be attributed to the difference between the depth of water at the maximum distance from shore which a land-based observer can see and water depth beyond that point. Juvenile males were observed spending much of their time far offshore in deep water beyond kelp beds. Riedman and Estes (1990) also observed juvenile males foraging in deeper water and further from shore than other classes.

Visual observation data collected by Ralls et al. were used to compare dive lengths, surface intervals, and success rates for prey capture between age/sex classes. Dive length was shown to vary with prey type, but not with prey size. Dives resulting in the catch of mussels were shortest, while those for octopus were longest. The longest mean dive time of any of the otters in the study by Ralls et al. was 116 s for an adult male. In general adult males exhibited the longest dive lengths, followed in order by adult females, juveniles females and females with pups, and juvenile males.

Nocturnal v. diurnal foraging.-Ralls et al. compared nocturnal and diurnal foraging patterns for several activities. Individual otters differed widely in length and number of nocturnal versus diurnal dives, and in surface intervals. No discernable overall pattern was observed – some otters were more active nocturnally, some diurnally and some were equally active at both times. The main difference observed was that mean intervals between feeding bouts were longer nocturnally (209.80 min, n=25) than diurnally (187.70 min, n=288).

Surface intervals.-Surface intervals between dives were directly related to prey size. The unweighted mean of surface intervals for all otters observed in the study was 64.50 s (n=7944). In general, adult females with pups had the longest surface intervals, but there was considerable variance in intervals by individuals of all age/sex classes. Larger prey such as crabs, abalones and octopi often took up to several minutes to consume, causing longer intervals for all classes.

Success rates.-Otters in this study had the highest instances of foraging success with small, hard-bodied prey, but the lowest success with calorically rich items such as clams, abalone and crabs. Success was measured by the presence or absence of prey seen when the otter surfaced. Success rates ranged from 28 percent for an adult male preying principally on clams to 96 percent for an adult female with a pup preying primarily on mussels. Juvenile females showed the lowest success rates by class and spent longer periods of time in foraging.

Stealing.-In addition, juvenile females were most in danger of having their prey stolen by another otter, especially when the prey was desirable such as *Cancer* spp. crabs. Riedman and Estes (1990) described cases of prey stealing by females and territorial males in the Monterey area. In addition, they note instances of “hostage behavior” wherein an adult male will grab a pup while the mother is absent foraging and relinquishes it only when the mother gives up her catch.

Feeding bouts.-Mean average time of feeding bouts in this study ranged from 77 to 373 min and was shortest for an adult male feeding on clams and longest for a juvenile female feeding on small, hard-bodied prey. The mean interval between feeding bouts was 187.7 min (n=288) which correlates closely with the estimated 180 min for food to pass through an otter's digestive system.

Predation on birds.-Observers (e.g., Van Wagenen et al. 1981; Riedman and Estes 1988) have noted a small number of otters predating on birds both in California and in Alaska. In California otters have predated on several species including western grebes (*Aechmophorous occidentalis)*, cormorants (*Phalacrocorax* spp.), surf scooters (*Mellanita perspecillata*), common loons (*Garvia immer*), and gulls (*Larus* spp.). In Alaska, otters have been observed catching and consuming common teals (*Anas crecca*), pelagic cormorants *(Phalacrocorax pelagicus*) and either a fulmar (*Fulmarus* spp.) or a shearwater (*Puffinus* spp.). Individuals seen hunting birds were observed approaching the animals from below as they rested on the water surface, then dragging the target underwater while wrestling with and biting it.

Van Wagenen and others (Van Wagenen et al 1981, Riedman and Estes 1988) observed attacks on birds lasting up to 10-15 min. Van Wagenen et al. speculated that certain atypical individuals (males in all observations where identifiable) may have learned this behavior since it is most often seen in two specific areas in California although observations may be biased since those areas are easily accessible by observers. Kenyon (1969) theorized that otters predating on birds in Alaska might do so in response to being nutritionally stressed.

Tactile sensory systems.-Riedman and Estes (1988) concluded that this behavior shows otters can learn new and innovative foraging strategies since they presumably use visual cues to capture birds from below the surface in contrast to their heavy reliance on tactile sensitivity to locate and capture sessile invertebrates (Riedman and Estes 1988). Rotterman and Simon-Jackson (1988) also consider otters to be primarily dependent on tactile sensory systems through the forepaws and mystacial vibrissae. Shimek (1977) observed similar behavior by otters patting the surface of rocks, feeling into cracks and digging through silt and cobble substrate when foraging for snails, echiuroid worms and other prey.

Riedman and Estes (1988) have reported instances of a non-predatory bird-related behavior. They observed two instances of a female (possibly the same individual each time) carrying the carcass of a bird (red phalarope *Phalaropus fulicaria*) on its chest as if it were a pup for at least one hour without attempting to consume it. This behavior may be related to the fact that mothers sometimes carry the carcasses of their dead pups for several days before releasing them.

Underwater tool use.-Houk and Geibel (1974) recorded the underwater foraging behavior of an otter in the wild in California. During a dive, the otter located a rock and used it underwater to pound at a prey which was deeply recessed (about 0.60 m) in a rock crevice. The otter surfaced after 15-20 s with the rock. It then dove again, hammering at the prey for an additional 88 s with three breaks of 5 s each, during which it would drop the rock and attempt to pull the prey free. Each time it failed, the otter picked the same rock up and tried again.

In the space of 15 s the otter pounded the prey 45 times at a rate of about three hits/s, changing between two positions several times during the retrieval. It began pounding while lying on its stomach with its head bent upwards, then rolled onto its back with its head turned sideways and pounded over its right shoulder. At the end of the second dive, the otter ascended without the rock but was seen to visually locate it before ascending. Upon descending for a third time, the otter relocated and used the same rock. It was able to loosen the prey after 30 s pounding on the third dive. The otter then dropped the rock, surfaced and consumed the prey. The rock weighed about 879 grams upon examination after the otter had finished using it.

Other underwater observations.-Hines and Loughlin (1980) performed an underwater study in 1976-1977 in Monterey Harbor. The average number of otters seen in the area during observations was one animal, while the maximum was four. Otters used tactile sensitivity of the forelimbs as the primary sense to locate and capture prey. Dive times averaged 45-80 s and were mostly unsuccessful. Foraging dives covered about 50 m in a circuitous searching pattern except in areas where clams were abundant and dives covered an area of 10 m or less. When collecting clams, otters retrieved an average of 6 clams at any one time with a maximum of 19 clams collected in one dive. Hines and Loughlin experienced difficulty in underwater observations because otters foraging in soft substrate usually stir up large clouds of sediment making observations difficult or impossible.

Digging holes.-Otters searching for prey under the substrate dug holes up to 1.0-1.5 m across and 0.5 m deep. The entire body of the otter was sometimes below the substrate surface before it moved away. Otters returned to the surface and resumed digging in the same holes on subsequent dives several times. Holes were enlarged laterally using a rolling motion while digging. Enlargement laterally has the advantage of saving energy as compared to digging straight down. Digging otters had a "dog-like" appearance and faced into the current. Hines and Loughlin also observed otters in Alaska removing clams from the substrate in a similar manner using the forepaws to dig while maintaining a head downward position.

Otters had increased success rates on subsequent dives to clam patches where they had previously been digging. Hines and Loughlin speculated that this may be an example of learning since the entire patch is usually covered in disturbed sediment on subsequent dives, precluding the use of visual clues. They cited a proposal by Gentry and Peterson (1967) that otter vision may be better adapted to predator detection than for underwater prey detection.

Use of non-visual cues.-Kvitek et al. (1993) made similar observations of otters digging holes larger than or equal to 0.12 m square in a study on diet and foraging behavior of otters in southeast Alaska. They noted in particular the ability of otters to consistently locate large clams in areas where clam siphons were retracted below the sediment surface or obscured by overlaying debris and were therefore not visible or immediately apparent through tactile sensing. Kvitek et al speculated that otters may rely on other sensory modalities in locating this type of hidden prey, suggesting electroreception or chemoreception warrant further investigation.

Oral detection of paralytic shellfish poisoning.-Kvitek and Geibel (1991) performed experiments on wild otters in connection with paralytic shellfish poisoning in butter clams (*Saxidomus giganteus*), the primary food source for otters in the Kodiak archipelago and Montague Strait, Alaska. Six otters (1-6) were held captive in netted pens in their regular habitat for the duration of the experiment. They were fed low toxicity clams in pretreatment, highly toxic clams in treatment and low toxicity clams in post-treatment. Otters 1-3 reduced their consumption rates by up to 80 percent when the diet was switched from low to high toxicity clams. Otters 4-5 adapted to the increased toxicity by rejecting clam siphons and gills with attached tissues (31 to 63%). All five of these otters responded to the new diet within one hour of the beginning of treatment. The last otter (6) exhibited the only actual case of paralytic shellfish poisoning. Its diet was immediately switched back to uncontaminated clams and it recovered quickly before being released in a healthy condition.

When the diet for otters 1-5 was switched back to low toxicity clams in post-treatment feeding returned to pretreatment levels, but discards of siphons remained high. Pretreatment levels of discards for otters 1-5 averaged 5.2 percent, treatment levels averaged 25.1 percent, and post-treatment levels averaged 19.6 percent. Kvitek and Geibel considered this behavior to be a highly adaptive response given the chronic toxicity of butter clams where toxic dinoflagellate blooms occur and the importance of butter clams in the diets of otters in those areas. The results of the study strongly suggest that otters can detect paralytic shellfish poisoning orally since their rapid response in behavioral shifts came too quickly for toxicity to take effect digestively. Kvitek and Geibel suggested that increased levels of siphon rejection at the post-treatment stage may be due to conditioning learned during treatment or may be in response to the remaining low levels of toxicity which otters ingested even though the most poisonous parts of those clams consumed in the treatment phase had been removed. Continued rejection of highly toxic clams would reduce the chance of gradual toxic build up. Kvitek and Geibel theorized that prior experience may have contributed to minor differences in response times in otters 1-5 and to the lack of response in otter 6.

Intertidal foraging.-Vandevere (1969) observed otters feeding in intertidal areas during high tide along the California coast in 1968 and 1969. Otters predated on black abalones and turned over rocks to obtain *Ischnochiton* species in sandy areas. Otters gathered turban snails at a rate of up to 10 per min from the kelp canopy without diving.

Consumption behavior and tool use.-Limbaugh (1961) was one of the first investigators to give detailed descriptions of sea otter feeding behavior. She described otters using the chest and abdomen as a table for all feeding which is done while floating on the back. Adult otters continually wash their pelages by rolling with food clasped tightly to the chest. Rocks 1.0 to 1.5 cm in diameter on average and up to 2.5 cm for flat rocks are used to fracture the hard parts of prey. The same rock may be used repeatedly in a single feeding bout. Females share food with their pups and possibly with males. Feeding takes place in a "leisurely fashion". Finished shells are discarded by dropping them to one side or in rolling over.

Kenyon (1978, 1981) observed otters in California in the late 1970s and early 1980s. He described the otter as unique among carnivores in having no sharp cutting edges in their teeth. Even the canines are blunt and rounded, adapted to crushing shells and chitonous coverings. Otters have only two pairs of lower incisors while all other carnivores have three pairs. The incisors protrude from the mouth and assist in scraping food from shells. At the surface, otters use their forepaws to pass food to the mouth. Sea urchin shells are cracked by the teeth and internal egg masses are scooped from the broken shells. Soft-shelled mollusks are crushed and swallowed whole. Otters may retrieve rocks which are either balanced on the chest as an anvil or used as a hammer for opening hard-shelled mollusks. Hard-shelled mollusks may also be pounded against each other, or a piece of the mollusk's own shell may be used against it. When taken, fish are torn with difficulty into bite size chunks.

Learning by pups.-Vandevere (1972) made observations of pups, classified by size as small, medium and large, at Monterey Bay from December 1971 to July 1972. He described different interactions between mothers and pups in each of these stages. Mothers offered food to pups of all sizes. One small pup initially ignored a section of crab carapace offered by its mother, then manipulated and explored the surfaces of another carapace with its mouth. Medium pups appeared the most aggressive in taking food from mothers while large pups appeared to share. Only large pups were seen taking rocks offered by mothers and using tools in general. Six pups were observed pounding their bare chests with forepaws in what Vandevere assumed was a practicing mechanism, as this behavior is not seen in experienced adults.

Diving behavior was different for each of the three size classes. Small pups did not dive or attempt to follow mothers who dove. Medium pups submerged their heads and appeared to paddle along the surface following the movements of mothers below. Large pups dove with a mean average dive length of 50 s and a range from 7-94 s.

Kenyon (1981) described pups learning to forage as often bringing worthless food items to the surface such as pebbles, undersized sea urchins, and brightly colored starfish. He noted that pups receive solid food from mothers before and after weaning.

Opportunistic feeding behavior.-Harrold and Hardin (1986) observed a single otter located about 7.2 km north of Point Piedro Blancas, California. The apparently healthy otter was seen removing mussels from rocks on the shore approximately 1.0 m above the water line and consuming them out of water. No previous observations had been recorded of sea otters foraging or consuming prey on land in the wild. Although it was out of the water, the otter laid on its back on the exposed rocks to consume the mussels. It picked up food by rolling over onto its side to retrieve the prey, then returned to its back to feed. Observations of the area after the otter departed showed two patches 8.5 and 6.5 cm in diameter had been cleared of mussels (*M. californianus*) and gooseneck barnacles (*P. polymerus*). Harrold and Hardin suggested that the isolated area of coast where the observation was made, calm weather conditions and the temptation of extensive shoreline mussel beds contributed to the behavior. Vandevere (1969) reported that "pet" otters given food to the mouth on land would tuck it under the left forearm and hobble back to the water on three legs before consuming it.

Consumption of birds.-Van Wagenen et al. (1981) described feeding behaviors associated with the consumption of birds. Otters which caught birds fed by stripping tissue from the breast, lower neck and legs, similar to the stripping behavior used for other large prey. Otters rolled in the water frequently to clear their pelages while birds were clasped in the forearms. Feathered pieces were discarded. Riedman and Estes (1988) observed similar behavior. In addition they noted the severing of the bird's head from its neck as an initial step in consumption, cranial contents being scooped out while the bird is held by the beak and the consumption of thigh meat by holding the webbed foot in a manner similar to that of a human consuming a turkey leg.

Tools.-Rocks and other items as large as softballs are used to dislodge prey items from the substrate (Ebert 1969). Riedman and Estes (1990) observed rocks, empty shells, driftwood, empty plastic or glass bottles, aluminum cans and other manmade objects being used as tools. Limbaugh (1961) witnessed an individual using seaweed to clean its pelage.

Vandevere (1969) observed otters along the California coast from October 1968 to June 1969. Otters were often seen using a rock as an anvil to break black turban snail shells (about 3 cm square) while holding the snail in their paws. Monterey and brown turban snails were secured in pelage pouches as many as 10 at a time, then individually broken by several blows from a rock at the surface. Each snail was consumed and its shell discarded in turn.

Innate knowledge of tool use.-Otters in the wild in Alaska do not generally use tools in predation, presumably because prey in Alaska is small enough to crush by the teeth (Vandevere 1969; Riedman and Estes 1990). However, otters transported to areas outside Alaska immediately begin using tools in the wild and in captivity (Vandevere 1969). Kenyon (1978) reported that a female otter from Amchitka Island transported to Woodland Park Zoo in Seattle, Washington used a stone to break the concrete edge of her pool until the stone was removed. She also used a stone to hammer at the cover of the pool drainpipe, apparently in an attempt to see what was underneath.

Other unique methods of prey capture.-Riedman and Estes (1990) observed a female otter at Monterey Bay using a glass bottle to pry rock oysters from rocks beneath the surface; an otter of unknown sex which had learned to reach into a bucket on the stern of a boat to obtain squid; and a juvenile female which regularly waited for handouts of anchovies from tourists and even occasionally threatened adult male California sea lions for their anchovies. Hines and Loughlin (1980) observed clams being pounded on rocks, twisted or pried open with the teeth.

Variation.-Riedman and Estes (1990) observed that tool use varied by prey species. Otters were seen rolling urchins between their forepaws to break the spines off. Live crabs were kept immobilized by wrapping them in kelp fronds draped over the otter's abdomen while the otter was consuming other prey. Riedman and Estes noted that wild otters rarely eat kelp but that captive otters at Monterey Bay Aquarium frequently consume it, preferring the stipes and bulbous gas floats.

Discarded aluminum cans.-Another example of the otter's ability to adopt innovative foraging techniques was seen by McCleneghan and Ames (1976) in February 1975 in Monterey Bay. They observed a single otter at the surface grasping a discarded aluminum soda-type can after a dive of 45 s in water 11 m deep. The otter bit the side of the can until it was torn open and removed an octopus. It then rolled to drop the can and consumed the octopus in the normal feeding position on its back.

Over the next 15 min the otter recovered 7 similar cans, 5 of which contained one octopus each. Each dive was timed at 40 to 90 s and it took a further 30 to 60 s to open and search each can. One can brought to the surface was apparently not made of aluminum and took the otter 3 min to open. This can also contained an octopus which the otter consumed. On at least two occasions, the otter thrust its forepaw into a can a retrieve an octopus but was unsuccessful in dislodging it. In these cases, the otter bit the can again to enlarge the hole and dumped the octopus out. Several abalone jingles were also retrieved from cans and consumed. No cuts or other injuries were observed to the otter's mouth. A human diver later investigated the area and found 22 cans, eight of which had been opened by the otter, 14 of which were intact and held octopi and two of which contained onespot fringeheads (*Neoclinus uninotatus*). Octopi with arm spreads as great as 35 cm were seen oozing into similar cans without damage.

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