

## Sea Otters and Oil: Ecologic Perspectives

---

---

---

---

### **Katherine Ralls**

Department of Zoological Research  
National Zoological Park  
Smithsonian Institution  
Washington D.C. 20008

### **Donald B. Siniff**

Department of Ecology, Evolution,  
and Behavior  
University of Minnesota  
Minneapolis, Minnesota 55455

### **Introduction**

---

Otters comprise the subfamily Lutrinae of the family Mustelidae, order Carnivora. Most are associated with fresh water; only two species are associated with the marine environment. The marine otter, or chungungo, *Lutra felina*, which ranges along the west coast of South America, is somewhat smaller than its more extensively studied counterpart in the North Pacific, the sea otter, *Enhydra lutris* (Mason and MacDonald, 1986). The ensuing discussion will focus on the latter species.

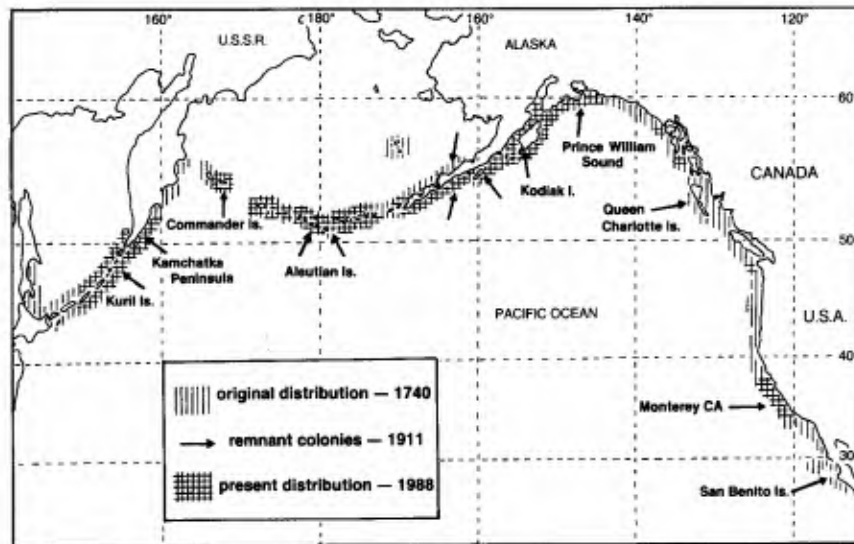
The sea otter exploited the marine environment more recently in geologic time than did other mammals, and is consequently less specialized for life in the ocean. Its dense fur, streamlined shape, and amphibious habits are shared with its more terrestrial relative, the river otter. However, it possesses many aquatic adaptations (Estes, 1980), such as hindflippers, loss of the clavicle (which allows great flexibility of the pectoral girdle), and large kidneys. As a predator of marine invertebrates in the nearshore community, the sea otter possesses a modified dentition having strong, flattened premolars and molars well suited to crushing hard-shelled prey (Kenyon, 1969; Reidman and Estes, 1988).

The sea otter is the largest lutrinid (Mason and MacDonald, 1986) and the smallest marine mammal. An adult male can weigh up to 45 kg; females are considerably smaller (Estes, 1980).

## Distribution and Abundance

The sea otter originally inhabited a large area in the North Pacific, ranging from the northern islands of Japan northward along the eastern coast of Kamchatka, through the Commander, Aleutian, and Pribilof islands to the Alaskan peninsula, and south along North America as far as central Baja California (Kenyon, 1969; Estes, 1980) (Fig. 7-1). However, the species was heavily exploited for its fur and was reduced to scattered, remnant populations by the beginning of the twentieth century. Some of these populations subsequently became extinct, but others increased when sea otters won legal protection under a number of statutes, beginning with the Treaty for the Preservation and Protection of Fur Seals in 1911 (Kenyon, 1969; Estes, 1980).

Sea otters now reoccupy most of their historic range across the North Pacific, from the southern end of the Kuril Islands eastward to Prince William Sound in the northeastern Gulf of Alaska (Reidman and Estes, 1988). In the 1960s and 1970s, Alaskan sea otters were translocated to southeast Alaska, British Columbia, Washington, and Oregon (Jameson



**Figure 7-1** Distribution of the sea otter (Kenyon, 1969).

*et al.*, 1982). The Oregon population died out, but the others became established and appear to be increasing. In the late 1970s, the total population was estimated to number at least 100,000 individuals, and perhaps as high as 150,000 (Kenyon, 1981).

The remnant population in California, which is classified as threatened by the U.S. Fish and Wildlife Service (Ladd, 1986a), also increased in size. It currently ranges along the coast between approximately Point Año Nuevo in the north and the Santa Maria River in the south, although some individuals wander beyond these limits (Leatherwood *et al.*, 1978). The central part of the California range is inhabited primarily by adult females and pups, along with juveniles and some territorial males; the most northern and southern areas are inhabited largely by males (Estes and Jameson, 1983). In 1987, the U.S. Fish and Wildlife Service translocated sea otters to another part of their historic range, San Nicolas Island off southern California (Ladd, 1986a,b; Brownell, 1988). The California population contains 1800 to 2000 individuals (Kenyon, 1981).

### Preferred Habitat

---

Sea otters are primarily a coastal species. However, in areas where the water is shallow, large numbers of individuals sometimes occur far from shore. They are frequently found over 8 km from shore off the Copper River Delta in the Gulf of Alaska (Monnett, 1987) and over 30 km from shore around Unimak Island in the Bering Sea (Kenyon, 1969). Sea otters prefer to rest in kelp, as it helps keep them from drifting and perhaps affords some protection from white sharks (*Carcharodon carcharias*). In California, sea otters are most commonly observed inshore of the outer limit of the giant kelp (*Macrocystis pyrifera*) canopy (Reidman and Estes, 1988). However, juvenile males spend much of their time in open water beyond the limits of the kelp (Siniff and Ralls, 1988), and otters are abundant in many areas, such as Prince William Sound, Alaska, where there is very little kelp.

Sea otters occur over a variety of substrate types and nearshore communities. In California, areas with rocky bottoms support higher densities of otters (approximately 5 individuals/km<sup>2</sup>) than those with sandy bottoms (0.8 individuals/km<sup>2</sup>) (California Department of Fish and Game, 1976). This difference indicates that rocky bottoms are more productive communities and support a greater variety of invertebrate prey species taken by sea otters (Reidman and Estes, 1988).

## Site Fidelity and Movement Patterns

---

Individual sea otters typically remain within a small area from day to day. In California, the average distance between successive daily locations, determined by radiotracking, ranged from 0.7 km for adult males to 2.4 km for juvenile males (Siniff and Ralls, 1988). Movements of over 10 km per day are infrequent, but in both California and Alaska, otters sometimes move over distances of 100 km or more within a few days. Thus, home ranges consist of heavily used areas connected by travel corridors. Individuals can also range over extended areas (Ribic, 1982a; Garshelis and Garshelis, 1984; Monnett and Rotterman, 1987; Siniff and Ralls, 1988). During a 2-year study period in California adult females visited an average of 24 km of coastline, juvenile females 47 km, adult males 98 km, and juvenile males 128 km (Siniff and Ralls, 1988).

In Alaska, sea otters often make long-distance seasonal movements between breeding and wintering areas (Garshelis and Garshelis, 1984; Monnett and Rotterman, 1987). In California, males may (Estes and Jameson, 1983; Jameson, 1989) or may not (Loughlin, 1980; Siniff and Ralls, 1988) show similar behavior; females in California do not move seasonally.

An otter's movements appear to be governed by its preference for specific kelp beds and feeding areas (Loughlin, 1977). Otters of all ages and both sexes, including territorial males, sometimes travel for long distances and then return to the same area (Loughlin, 1977; Estes and Jameson, 1983; Garshelis and Garshelis, 1984; Garshelis *et al.*, 1984; Siniff and Ralls, 1988). At least 5 of 17 male California sea otters that were tagged and moved a distance of 72 km returned to the vicinity of their capture location within 9 months (Odemar and Wilson, 1969; Wild and Ames, 1974). We observed two males in California that were moved approximately 150 km. One returned within a week and the other in about 1 month.

## Reproduction

---

Sea otters can mate and pup throughout the year; reproductive activities are more seasonal in Alaska than in California. In Prince William Sound, mating generally occurs in fall and most pups are born in May (Garshelis *et al.*, 1984). The same pattern probably exists throughout Alaska, although the pupping peak may extend into summer in some areas, with mating activity common as late as December (Kenyon, 1969; Schneider, 1973). In

the western Pacific, there may be two reproductive peaks, one in June–July and the other in September–October (Barabash-Nikiforov *et al.*, 1968). In California, there is a pupping peak in spring and a smaller, secondary one in fall (Siniff and Ralls, 1988).

In California, the period from copulation to birth is about 6 months (Estes and Jameson, 1983), and is thought to include a variable period of delayed implantation (Kenyon, 1981). Kenyon (1969) estimated the gestation period in Alaska to be about 120 days. Birth may occur on land (Jameson, 1983) but aquatic births—at least in California—are thought to be more common. Although twins are reported, they are apparently never successfully raised (Jameson and Bodkin, 1986). Most pups are weaned within 5–8 months (Garshelis *et al.*, 1984; Payne and Jameson, 1984; Wendell *et al.*, 1984; Monnett, 1987). After about 4 months of age, the pup's diet consists mostly of prey captured by its mother, although the pup continues to suckle until they separate (Payne and Jameson, 1984).

Female sea otters reach sexual maturity at 3–5 years of age in Alaska (Kenyon, 1969; Garshelis *et al.*, 1984). There are no comparable data for California, except for the single observation of a pup produced by a 4-year-old female (Wendell *et al.*, 1984). Males are thought to reach sexual maturity at 5 or 6 years of age (Green, 1978; Schneider, 1978) but generally begin breeding at a somewhat older age. Garshelis (1984) found that none of the breeding males sampled from Prince William Sound was younger than 6 years.

Early studies of reproductive tracts from animals collected in the Soviet Union and Alaska suggested that sea otters generally give birth only once every 2 years (Barabash-Nikiforov *et al.*, 1968; Kenyon, 1969; Schneider, 1973). However, subsequent observations of tagged individuals showed that most females pup annually (Jameson and Johnson, 1979; Loughlin *et al.*, 1981; Estes and Jameson, 1983; Garshelis *et al.*, 1984; Wendell *et al.*, 1984; Siniff and Ralls, 1988).

Some sea otter populations in Alaska have increased at rates as high as 16% per year (Kenyon, 1969; Estes 1982). Annual increment of the California population is currently above 5% (Jameson and Estes, 1988), a rate which characterized the population for many decades (Ralls *et al.*, 1983; Brody, 1987) except for a 10–15 year period beginning in the early 1970s when there was no apparent increase (Estes and Jameson, 1983; Wendell *et al.*, 1986; Brody, 1987). The population dynamics of sea otters are not well understood. A recently developed computer model may provide some insights (Brody, 1987). The relevance of modeling to predicting recovery rates after oil spills is addressed in Chapter 12 in this volume.

## Social Organization and Reproductive Behavior

---

Sea otters are polygynous. Breeding males defend territories seasonally or year round in "female areas" occupied by reproductive females and their young (Kenyon, 1969; Calkins and Lent, 1975; Loughlin, 1980; Estes and Jameson, 1983; Garshelis *et al.*, 1984; Jameson, 1989). A male usually forms a temporary consortship, lasting 1–4 days, with an estrous female (Kenyon, 1969; Vandever, 1970; Garshelis *et al.*, 1984). The two remain close together during this period. Males may attend females with large pups, or even some with small pups, although copulation is rarely successful until after the nursing period is over (Kenyon, 1969; Calkins and Lent, 1975; Garshelis *et al.*, 1984). Adult females do not always remain in the territory of a single male.

Large numbers of males congregate in "male areas" where few reproductive females are present. The groups include individuals too young to breed and older males when these are not maintaining seasonal territories. Male otters are usually the first to colonize new habitat, so male areas tend to be located at the edge of the range, where food is more abundant (Benech, 1981; Estes and Jameson, 1983; Garshelis *et al.*, 1984, 1986). Otters often rest in groups called "rafts," their composition fluid. Groups consisting primarily of females are usually small in California and Prince William Sound, although aggregations of more than 100 females have been observed in parts of Alaska (Monnett and Rotterman, 1987). Throughout this range, males may rest in very large rafts consisting of hundreds of individuals (Kenyon, 1969; Garshelis *et al.*, 1984). Otters sometimes emerge from the water to rest on ice or land; they do this more frequently, and in larger groups, in Alaska and the U.S.S.R. than in California (Kenyon, 1969; Faurot, 1985), perhaps because of the more severe climate and less human disturbance in northern waters.

Mothers and pups have strong social bonds, remaining together until the pup is weaned (Payne and Jameson, 1984); however, mothers that are ill or in poor condition may abandon pups (Garshelis and Garshelis, 1987). Weaning appears to be abrupt. In Prince William Sound, most male weanlings move long distances soon after they separate from their mothers. They establish new home ranges in male areas; females tend not to travel as far and remain within the natal female area (Monnett and Rotterman, 1987). Adult females sometimes reassociate with weaned pups (Garshelis and Garshelis, 1987); nothing is known about the frequency of this behavior or the extent to which female otters might associate with older related individuals.

Behaviors associated with reproduction can be injurious and even

fatal (Garshelis *et al.*, 1984). While copulating, or attempting to, the male secures a bite-hold on the female's nose or face (Kenyon, 1969; Vandever, 1970), sometimes leaving her with bloody lesions (Brosseau *et al.*, 1975) and lasting scars (Foott 1971). Although territorial males occasionally fight (Fisher, 1939; Vandever, 1970; Loughlin, 1977), the frequency and extent of resulting injuries are unknown.

### **Trophic Levels and Feeding Habits**

---

Feeding otters alternately dive to obtain prey and float at the surface to consume it. Pups less than about 6 weeks old are unable to dive and must remain on the surface while their mothers search for food (Payne and Jameson, 1984). The use of rocks as tools to dislodge or break open hard-shelled prey is more common in California (Hall and Schaller, 1964) than in Alaska (Kenyon, 1969).

Most sea otters feed almost entirely on macroinvertebrates, although in some areas they also consume epibenthic fish (Estes *et al.*, 1981; Maminov and Shitkov, 1970). At the population level, the diet becomes more varied after sea otters have occupied an area for several years (Estes *et al.*, 1981; Garshelis *et al.*, 1986; Reidman and Estes, 1988). Typically, after colonizing a new area, most of the otters consume large, calorically rich prey items. As these become scarcer, the diet begins to include smaller items and less preferred species. Individual otters show marked variation in food preference; one individual may feed largely on clams and another on mussels and turban snails (Estes *et al.*, 1981; Lyons and Estes, 1985; Siniff and Ralls, 1988). These differences persist over long periods of time (Lyons, 1987). Individuals also differ with respect to average dive length, time at the surface, feeding-bout length, and the interval between feeding bouts (Siniff and Ralls, 1988).

In the wild, otters can feed as much as 12 hours each day (Garshelis *et al.*, 1986; Siniff and Ralls, 1988). In California, juvenile females seem to spend more time feeding than males or females of other age classes, and often feed during the day, when other otters are resting (Siniff and Ralls, 1988). As a group, otters show no particular preference for day or night feeding, though they are most active during late afternoon, early evening, and early morning. Individuals differ in their diurnal feeding patterns, perhaps in association with the accessibility of their prey. The interval between feeding bouts is about 3 hours, which is the time it takes for food to be digested and cleared from the gut (Stulken and Kirkpatrick, 1955; Costa, 1978; Ribic, 1982b; Siniff and Ralls, 1988).

## Metabolism and Thermoregulation

---

The otter's rapt attention to feeding directly reflects its need to fuel a metabolic rate which is over twice that of a terrestrial mammal of comparable size (Morrison *et al.*, 1974; Costa and Kooyman, 1982; Davis *et al.*, 1988). Captive animals consume 190–250 kcal/kg/day (Estes, 1980). There are no comparable values for wild otters, but Costa (1978) estimated that they must consume the equivalent of 23–33% of their body weight per day. Sea otters are locked into a feeding mode which cannot be interrupted.

Unlike all other marine mammals, the sea otter has little subcutaneous fat to aid in reducing heat loss; it must depend on its dense pelage for insulation. The pelage consists of an outer layer of guard hairs and an extremely dense underfur with over 100,000 hairs per square cm (Kenyon, 1969). The hairs are arranged in bundles, each containing approximately one guard hair and 70 underfur hairs. Bundle density varies over the body, ranging from about 2400 per square cm on the forearm to 851 on the dorsal surface. Air is trapped within the fur, adding to its insulative value (Kenyon, 1969; Costa and Kooyman, 1982; Davis *et al.*, 1988).

The pelage must be continually groomed to be effective. Loughlin (1977) described a somewhat stereotyped sequence of grooming. After an initial period of vigorous rolling and somersaulting, the otter rubs various parts of its body with the forepaws. It then licks and rubs its tail, hindquarters, chest, and forepaws. Sea otters typically groom themselves rather than each other. However, young pups are unable to groom themselves, and a female may spend up to 20% of the daylight hours grooming her pup (Sandegren *et al.*, 1973).

## Summarizing the Risk

---

Many features of the life history of otters predispose them to exposure to spilled oil. They are coastal animals with strong site fidelity; they feed on benthic organisms that accumulate and store hydrocarbon residues from contaminated sediments (Neff, this volume, Chapter 1); and they spend a great deal of time at the surface moored to kelp beds that capture oil. The risk is amplified by circumstances that bring otters together to form loose associations, or rafts, sometimes numbering a hundred or more individuals. Under those circumstances, large groups of animals can be exposed simultaneously.

Isolated populations, such as the one along the coast of California,



are most endangered. As we have learned from the 1989 *Exxon Valdez* accident in Prince William Sound, a regional disaster can kill many animals. The prognosis is not necessarily bleak, however, because "seed" or "pioneer" populations from remote areas can spread and recolonize, as they did after the near-extinction of sea otters at the turn of the century. And we now know that it is sometimes feasible to translocate otters to unoccupied areas where they once thrived.

For the individual otter, contamination by oil spells an almost certain fate. An otter's normal preoccupation with grooming becomes obsessive, displacing other behaviors, including feeding, resting, and caring for young. Despite its efforts, the otter may not be able to restore the insulative value of its coat.

## References

- Barabash-Nikiforov, I. I., Marakov, S. V., and Nikolaev, A. M. (1968). "Otters." *Izd. Nauka, Leningrad.*
- Benech, S. V. (1981). "Observations of the Sea Otter *Enhydra lutris* Population Between Point Buchon and Rattlesnake Creek, San Luis Obispo, California, January through December 1980," VIII-6-81 Ecomar, Inc., Santa Barbara, California.
- Brody, A. (1987). A spatially explicit simulation model of the California sea otter population. In "Population Status of California Sea Otters" (D. B. Siniff and K. Ralls, eds.), Final Rep. Contract No. 14-12-001-3003. Minerals Manage. Serv., Los Angeles, California.
- Brosseau, C., Johnson, M. L., Johnson, A. M., and Kenyon, K. W. (1975). Breeding the sea otter at Tacoma Aquarium. *Int. Zoo Yearb.* 15, 144-147.
- Brownell, R. L., Jr. (1988). California sea otter translocation. *Mar. Mammal. Sci.* 4, 85.
- California Department of Fish and Game (1976). "A Proposal for Sea Otter Protection and Research, and Request for Return of Management to the State of California," 2 vols. (unpublished report).
- Calkins, D. G., and Lent, P. C. (1975). Territoriality and mating behavior in Prince William Sound sea otters. *J. Mammal.* 56, 528-529.
- Costa, D. P. (1978). The ecological energetics, water, and electrolyte balance of the California sea otter, *Enhydra lutris*. Ph.D. Thesis, University of California, Santa Cruz.
- Costa, D. P., and Kooyman, G. L. (1982). Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Can. J. Zool.* 60, 2761-2767.
- Davis, R. W., Williams, T. M., Thomas, J. A., Kastelein, R. A., and Cornell, L. H. (1988). The effects of oil contamination and cleaning on sea otters (*Enhydra lutris*). II. Metabolism, thermoregulation, and behavior. *Can. J. Zool.* 66, 2782-2790.
- Estes, J. A. (1980). *Enhydra lutris*. *Mammal. Species* 133, 1-8.
- Estes, J. A. (1982). The case of the sea otter. In "Problems in Management of Locally Abundant Wild Mammals" (P. A. Jewell, S. Holt, and D. Hart, eds.), pp. 167-180. Academic Press, New York.
- Estes, J. A., and Jameson, R. J. (1983). "Summary of Available Population Information on California Sea Otters," POCS Tech. Pap. No. 83-11, Interagency Agreement No. 14-12-001 Minerals Manage. Serv. Washington, D.C.

- Estes, J. A., Jameson, R. J., and Johnson, A. M. (1981). Food selections and some foraging tactics of sea otters. In "Proceedings of the Worldwide Furbearer Conference, 1980" (J. A. Chapman and D. Pursley, eds.), pp. 606-641. Frostburg, Maryland.
- Faurot, E. (1985). Haulout behavior of California sea otters, *Enhydra lutris*. *Mar. Mammal. Sci.* **1**, 337-340.
- Fisher, E. M. (1939). Habits of the southern sea otter. *J. Mammal.* **20**, 21-36.
- Foott, J. O. (1971). Nose scars in female sea otters. *J. Mammal.* **51**, 621-622.
- Garshelis, D. L. (1984). Age estimation of living sea otters. *J. Wildl. Manage.* **48**(2), 456-463.
- Garshelis, D. L., and Garshelis, J. A. (1984). Movements and management of sea otters in Alaska. *J. Wildl. Manage.* **48**, 665-678.
- Garshelis, D. L., and Garshelis, J. A. (1987). Atypical pup rearing strategies by sea otters. *Mar. Mammal. Sci.* **3**(3), 263-270.
- Garshelis, D. L., Johnson, A. M., and Garshelis, J. A. (1984). Social organization of sea otters in Prince William Sound, Alaska. *Can. J. Zool.* **62**, 2648-2658.
- Garshelis, D. L., Garshelis, J. A., and Kimker, A. T. (1986). Sea otter time budgets and prey relationships in Alaska. *J. Wildl. Manage.* **50**, 637-647.
- Green, B. (1978). Sexual maturity and senescence of the male California sea otter (*Enhydra lutris*). M.Sc. Thesis, San Jose State University, San Jose, California.
- Hall, E. R., and Schaller, G. B. (1964). Tool-using behavior of the California sea otter. *J. Mammal.* **45**, 287-298.
- Jameson, R. J. (1983). Evidence of birth of sea otter on land in central California. *Calif. Fish Game* **69**, 122-123.
- Jameson, R. J. (1989). Movements, home range, and territories of male sea otters off central California. *Mar. Mammal. Sci.* **5**, 159-172.
- Jameson, R. J., and Estes, J. A. (1988). Status of the California sea otter population. Abstr., *Am. Soc. Mammal. Annual Meetings*, Clemson, South Carolina.
- Jameson, R. J., and Bodkin, J. L. (1986). An incidence of twinning in the sea otter (*Enhydra lutris*). *Mar. Mammal. Sci.* **2**, 305-309.
- Jameson, R. J., and Johnson, A. M. (1979). Evidence of annual reproduction among sea otters. *Abstr., 3rd Bienn. Conf. Biol. Mar. Mammal.*, Seattle, Washington.
- Jameson, R. J., Kenyon, K. W., Johnson, A. M., and Wight, H. M. (1982). History and status of translocated sea otter populations in North America. *Wildl. Soc. Bull.* **10**, 100-107.
- Kenyon, K. W. (1969). The sea otter in the eastern Pacific Ocean. *North Am. Fauna* **68**, 1-352.
- Kenyon, K. W. (1981). Sea otter, *Enhydra lutris*. In "Handbook of Marine Mammals" (S. H. Ridgway and R. J. Harrison, eds.), vol. 1, pp. 209-223. Academic Press, New York.
- Ladd, W. (1986a). New hope for the Southern sea otter. Part 1. *End. Spec. Tech. Bull.* **11**(8 & 9), 12-14.
- Ladd, W. (1986b). New hope for the Southern sea otter. Part 2. *End. Spec. Tech. Bull.* **11**(10 & 11), 5-7.
- Leatherwood, S., Harrington-Coulombe, L. J., and Hubbs, C. L. (1978). Relict survival of the sea otter in central California and evidence of its recent redispersal south of Point Conception. *Bull. South. Calif. Acad. Sci.* **77**, 109-115.
- Loughlin, T. R. (1977). Activity patterns, habitat partitioning, and grooming behavior of the sea otter, *Enhydra lutris*, in California. Ph.D. Thesis, University of California, Los Angeles.
- Loughlin, T. R. (1980). Radio telemetric determination of the 24-hour feeding activities of sea otters, *Enhydra lutris*. In "A Handbook on Biotelemetry and Radio Tracking" (C. J. Amlaner, Jr. and D. W. MacDonald, eds.), pp. 717-724. Pergamon, Oxford.

- Loughlin, T. R., Ames, J. A., and Vandevere, J. E. (1981). Annual reproduction, dependency period and apparent gestation period in two California U.S.A. sea otters *Enhydra lutris*. *Fish. Bull.* **79**, 347–349.
- Lyons, K. J., (1987). Individual variation in the diet and foraging strategy in the female California sea otter, *Enhydra lutris*. *Abstr., Anim. Behav. Soc., 1987*, Williamstown, Massachusetts.
- Lyons, K. J., and Estes, J. A. (1985). Individual variation in diet and foraging strategy in the female California sea otter, *Enhydra lutris*. *Abstr. West. Soc. Nat. 66th Annu. Meet.*, Monterey, California.
- Maminov, M. K., and Shitkov, A. M. (1970). On the food of the sea otter on Paramushir Island. *Proc. Pac. Res. Inst. Fish Ocean. (TINRO)* **70**, 176–179.
- Mason, C. F., and MacDonald, S. M. (1986). "Otters: Ecology and Conservation." Cambridge Univ. Press, London and New York.
- Monnett, C. (1987). Movement, developmental and mortality patterns of sea otters in Alaska. Ph.D. Thesis, University of Minnesota, Minneapolis.
- Monnett, C., and Rotterman, L. (1987.) Movement patterns of adult female and weanling sea otters in Prince William Sound, Alaska. In "Population Status of California Sea Otters" (D. B. Siniff and K. Ralls, eds.), Final Rep. Contract No. 14-12-001-3003, pp. 193–235. Minerals Manage. Serv., Los Angeles, California.
- Morrison, P. M., Rosenmann, M., and Estes, J. A. (1974). Metabolism and thermoregulation in the sea otter. *Physiol. Zool.* **47**, 218–229.
- Odemar, M. W., and Wilson, K. C. (1969). Results of sea otter capture, tagging and transporting operations by the California Department of Fish and Game. *Proc. 6th Annu. Conf. Biol. Sonar Diving Mammals*, Stanford Res. Inst., Menlo Park, California, pp. 73–79.
- Payne, S. F., and Jameson, R. J. (1984). Early behavioral development of the sea otter, *Enhydra lutris*. *J. Mammal.* **65**, 527–531.
- Ralls, K., Ballou, J., and Brownell, R. L., Jr. (1983). Genetic diversity in California sea otters: Theoretical considerations and management implications. *Biol. Conserv.* **25**, 209–232.
- Reidman, M., and Estes, J. (1988). A review of the history, distribution and foraging ecology of sea otters. In "The Community Ecology of Sea Otters" (G. R. Van Blaricom and J. A. Estes, eds.), pp. 4–21. Springer-Verlag, Berlin.
- Ribic, C. A. (1982a). Autumn movement and home range of sea otters in California. *J. Wildl. Manage.* **46**, 795–801.
- Ribic, C. A. (1982b). Autumn activity of sea otters in California. *J. Mammal.* **63**, 702–706.
- Sandegren, F. E., Chu, E. W., and Vandevere, J. E. (1973). Maternal behavior in the sea otter. *J. Mammal.* **54**, 668–679.
- Schneider, K. (1973). "Reproduction in the Female Sea Otter," Prog. Rep. Federal Aid in Wildl. Restoration Proj. W-17-4 and W-17-5. Alaska Dept. of Fish and Game, Anchorage.
- Schneider, K. (1978). "Reproduction in the Female Sea Otter in the Aleutian Islands" (unpublished rep.). Alaska Dept. of Fish and Game, Anchorage.
- Siniff, D. B., and Ralls, K., eds. (1988). "Population Status of California Sea Otters," Final Rep. Contract No. 14-12-0013003. Minerals Manage. Serv., Los Angeles, California.
- Stulken, D. E., and Kirkpatrick, C. M. (1955). Physiological investigation of captive mortality in the sea otter (*Enhydra lutris*). *Trans. North Am. Wildl. Conf.* **20**, 476–494.
- Vandevere, J. E. (1970). Reproduction in the southern sea otter. *Proc. 7th Annu. Conf. Biol. Sonar Diving Mammals*, Stanford Res. Inst., Menlo Park, California, pp. 221–227.
- Wendell, F. E., Ames, J. A., and Hardy, R. A. (1984). Pup dependency period and length of reproductive cycle: Estimates from observations of tagged sea otters, *Enhydra lutris*, in California. *Calif. Dep. Fish Game* **70**, 89–100.

- Wendell, F. E., Hardy, R. A., and Ames, J. A. (1986). "An Assessment of the Accidental Take of Sea Otters, *Enhydra lutris*, in Gill and Trammel Nets," Mar. Resour. Tech. Rep. No. 54. Calif. Dept. of Fish and Game, Sacramento.
- Wild, P. W., and Ames, J. A. (1974). "A Report on the Sea Otter, *Enhydra lutris* L., in California," Mar. Resour. Tech. Rep. No. 20. Calif. Dept. of Fish and Game, Sacramento.