Chapter 1
Otariid Ethology: One Researcher's Historical Perspective

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Abstract This chapter summarizes methods used to study otariids from the late 1700s to the early 1960s, when a scientific publication claimed that the California sea lion (*Zalophus californianus*) used echolocation. That paper triggered the first-ever conference on all diving mammals which, over time, became the Society for Marine Mammalogy. The chapter then briefly discusses otariid life cycles by sex, differences in otariid annual cycles by latitude, and nature of social behavior and social organization on land. It describes manipulative experiments used to test females for the duration of estrus, and the possible existence of female mate choice. Finally, it discusses the first deployments of multiple dive time-depth recorders to reveal diving behavior at sea, and the first deployments of those recorders that were coupled with isotope injections to explore diving physiology in marine mammals.

Keywords Social organization · Life cycle · Annual cycle · Estrus · Mate choice · Diving behavior · Diving physiology

1.1 Introduction

Field studies on otariid seals began in the 1700s and 1800s in different parts of the world. Researchers back then asked very basic questions because it was not known how many species existed, where they were found, population sizes, seasons for pupping and mating, and basic information about social behavior. Species studied in the earliest years included the Galapagos (*Arctocephalus galapagoensis*), northern (*Callorhinus ursinus*), subantarctic (*Arctocephalus tropicalis*), South African (*Arctocephalus pusillus pusillus*) and South American (*Arctocephalus australis*) fur seals; and the Steller (*Eumetopias jubatus*), California (*Zalophus californianus*), Galapagos (*Zalophus c. wollebaeki*) and South American (*Otaria flavescens*) sea

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C. Campagna, R. Harcourt (eds.), *Ethology and Behavioral Ecology of Otariids and the Odobenid*, Ethology and Behavioral Ecology of Marine Mammals,
https://doi.org/10.1007/978-3-030-59184-7_1

lions. Early researchers differed somewhat in their research interests, and they usually published their results in the languages they spoke, usually French, English, Spanish, or German. The use of different languages somewhat limited the sharing of information among field researchers. Some researchers possibly knew of a few others that had similar research interests, but no regional or international communities of researchers had yet formed. Furthermore, this early research was conducted by established, working scientists. No college courses were available on marine mammal biology at that time, few graduate students were looking for projects, and the public then had no concern about marine mammal welfare.

This chapter traces how our present international community of researchers developed out of this background. This is my personal view of the field, based on my research, meetings I attended, and the literature published between 1963 and 1998. For another assessment of this field, see LeBoeuf and Würsig (1985).

1.2 Otariid Study Methods Over Time

The earliest research methods used to study pinnipeds were voyages of discovery to lands unknown or little known to westerners, and laboratory dissections of cadavers brought back from those voyages. Little was known in the 1700s about which species of mammals existed where, so voyages of discovery were made to see and collect specimens for anatomical and taxonomic purposes. Vitus Bering made two voyages into the North Pacific Ocean in that century. Georg W. Steller (1749) was the naturalist on the second trip, and he published the first scientific descriptions of the northern fur seal and Steller's sea lion. Karl Wilhelm Illiger (1811) first identified pinnipeds as a separate taxonomic group of mammals, based on anatomy. Elliott (1882) and later Scammon (1884) conducted voyages of discovery that involved new marine mammal sightings. These journeys continued into the mid 1960s with little change in methods. On one such voyage to Guadalupe Island, Mexico, Carl L. Hubbs (1956) discovered that the Guadalupe fur seal (*Arctocephalus townsendi*) had survived the era of fur sealing in the eastern Pacific islands.

The first modern otariid researcher specifically trained in animal behavior, and who used modern methods to study otariid social behavior in the field was Richard S. Peterson. He collected quantitative data on the social behavior of tagged northern fur seals on St. Paul Island, Alaska from 1961–1964 (Peterson 1965). His data collection methods were not described in his dissertation, in his book on the California sea lion (Peterson and Bartholomew 1967), nor to me when I was his graduate student. He started an elephant seal research project at Año Nuevo Island which Burney J. Le Boeuf and students later turned into a world-class program. Peterson died before any of his other otariid work was published, a scientific loss.

The modern field of pinniped research began to coalesce as a result of some research by Thomas C. Poulter (Fig. 1.1), a polymath and former munitions designer. While looking for a remote site from which to launch small rockets in

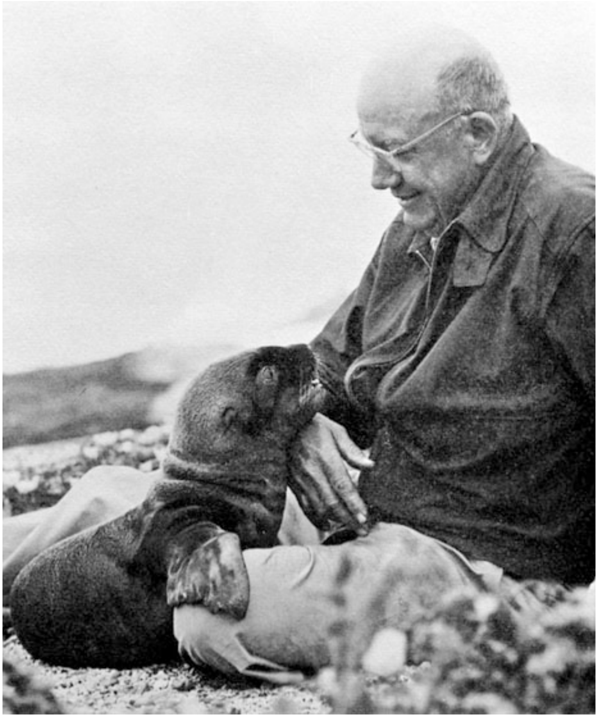

Fig. 1.1 Dr. Thomas C. Poulter, early 1960s (Photo by Richard Jennings)

1961, he landed on Año Nuevo Island in central California. The island was inhabited by four species of pinnipeds; harbor (*Phoca vitulina*) and northern elephant seals (*Mirounga angustirostris*), and Steller and California sea lions (Fig. 1.2). Poulter recognized the island and the animals thereon as valuable research resources. He contacted Robert T. Orr of the California Academy of Science, a pinniped specialist, to help him survey the island and publish papers describing the populations there.

Poulter established a pinniped research laboratory in an abandoned Nuclear missile base at the southern end of San Francisco Bay, near Fremont, California (Fig. 1.3). He built pens and water pools for keeping and feeding pinnipeds, and populated the facility with representatives of each of the species found on the island. He built an anechoic water tank in one of the buildings for making high quality underwater recordings of the sounds these animals made. He located the anatomical source of those sounds by recording from three directions. Based on his recordings of California sea lions (but not the other species) he published a paper in the journal *Science* claiming that this species uses echolocation (Poulter 1963). He somehow acquired a totally blind but robust northern fur seal female which he used as (apparent) evidence that other otariids used echolocation as well. He named this facility the Biological Sonar Laboratory.

While searching the literature for a topic to present in a 1963 graduate seminar, I first read Donald Griffin's recent book on bat echolocation *Listening in the Dark* (Griffin 1959), and was surprised to also find Poulter's paper claiming pinniped

Fig. 1.2 Año Nuevo Island, California in summer 1968. All animals shown are non-breeding *Zalophus* males

Fig. 1.3 The Biological Sonar Laboratory, Fremont California in the late 1960s. It is now Coyote Hills Regional Park, Fremont (Photo by Roger L. Gentry)

echolocation. I called him to ask for an interview, and we met a week later. He began the interview by describing how his idea of pinniped echolocation had originated. When he was in the Antarctic with Admiral Byrd in the 1930s, the long, eerie-sounding calls of Weddell seals often came up through the ice on which he stood and he wondered what function they served. Griffin's book suggested to him that they may have been used in echolocation.

Poulter showed me two other projects that were then under way in his laboratory. Charles E. Rice was studying the echolocation abilities of blind humans in an anechoic room, and Ronald J. Schusterman was studying perception, cognition, learning, and problem-solving in California sea lions in his own compound and test tank. He used that species because they are highly food-motivated and easily trainable. Schusterman was a comparative psychologist and used all the data collection methods common to others in his field: event recording, time-ruled check sheets, the longitudinal histories of known individuals, and others (Schusterman 1981). When the interview ended, Poulter invited me to join the laboratory and measure underwater auditory localization in California sea lions for my master's thesis (Gentry 1966). The ability to locate the source of a sound was critical to his claim of echolocation. I conducted the hearing study after learning from Schusterman how to train research animals and how to make the required measurements.

After finishing my research, I assisted Schusterman in testing California sea lion females for visual acuity, learning, cognition, and problem solving. We also studied social behavior between his females and a half-grown male. He later published a paper stating that this species could not use echolocation (Schusterman 1967). This was probably a correct assertion because the visual acuity of this species is sufficient to find food without using sound. However, the paper forever severed the working relations between him and Poulter. The Bio-Sonar Laboratory remained active until Poulter's death at the laboratory in 1978.

During the summer of 1965 the laboratory's photographer, Richard Jennings, asked me to help transport photographic equipment to Año Nuevo Island, where he was filming the social behavior of Steller sea lions. He worked from a blind on the edge of a breeding group, at times within arm's reach of the animals. He had a close view of all aspects of Steller sea lion behavior, including male territorial behavior, births, mating, pup-rearing, female aggression, movements to sea and back by females, and pup play. Some aspects of social behavior changed with time of day, wind speed, and tide height. This trip made it clear to me that the behavior of animals in the wild was much closer to my own interests than was underwater directional hearing.

After finishing the laboratory work, I studied social behavior of Steller sea lions at the island for my doctorate (Gentry 1970). The field work covered three breeding seasons and raised questions about the effect that climate and physical factors, like wind and tide, had on otariid social behavior. To answer those questions I then studied several other species of otariids. The first was social behavior of the New Zealand fur seal (*Arctocephalus forsteri*) on the South Neptune Islands of Australia. Following that I studied social behavior and diving in the northern fur seal in Alaska and Russia (from 1974 to 1998), then social and diving behavior of the

New Zealand sea lion (*Phocarctos hookeri*), and finally diving behavior of the South African fur seal. The results of all these studies were presented at marine mammal conferences but not all the data reached publication due to time constraints between projects. This background, as well as the published literature, contribute to the remainder of this chapter.

1.3 Otariid Life Cycles

The family Otariidae consists of six species of sea lions and nine of fur seals. Male and female otariids have very different life cycles. Juvenile males gather on traditional non-breeding sites where they develop fighting skills in play matches, alternating with feeding bouts at sea. After a number of years, which varies among species, males grow large enough to compete for territories on sites where females traditionally land and give birth. If successful in establishing a territory, they spend one or more breeding seasons defending the territory from other males, and mating when possible. Males risk losing their territory if they leave land to feed during the breeding season. Therefore, all otariid males fast while holding territory. They prepare for this fast by laying down extra fat (termed the "fatted male effect") before the breeding season. This effect even occurs in captive California sea lion males and is accompanied by an increase in male-male aggression (Schusterman and Gentry 1971). The breakdown of stored fat during fasting substitutes for both food and water for approximately 4 weeks. Territorial males drink seawater if it is available in their territory (Gentry 1980). When older males lose their territories to younger males, they usually move to landing areas[1] where juvenile males gather. They may return yearly until they become senescent. The rigors of territorial life limit the male's lifespan to about three quarters that of females.

Females first arrive on breeding areas[2] at about age 4 or 5 at the start or end of a breeding season, depending on species. They mate with an established male and undergo a delayed implantation of the blastocyst that results in birth about 12 months later. Females come into estrus and mate a few days after giving birth. In contrast to the territorial behavior of males, adult females of all species have some freedom to move about the breeding area, both before and after parturition. Females can live for 20 to 25 years.

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[1]The places where non-breeding males landed were referred to as "Hauling Grounds" by early sealers. The term "Landing Area" avoids jargon and more clearly describes what animals do there.

[2]Similarly, early sealers called the places where mating occurred, "Rookeries," in reference to rooks, a bird species. The term "Breeding area" more clearly describes what animals do there.

1.4 Otariid Annual Cycles

Three types of annual cycles exist among otariids. The Galapagos fur seal and sea lion breed and feed in tropical waters and do not undergo an annual migration. Their reproductive behavior tends to be asynchronous without the formation of dense breeding colonies. Two species, the northern fur seal and Antarctic fur seal (*Arctocephalus gazella*), breed at high latitudes in a brief season (4 to 6 weeks) after which males depart while females remain nearby, foraging for 4 to 5 months until their offspring reach weaning age. Thereafter, females migrate alone to more temperate waters where they forage until the next breeding season begins. All other otariids breed and feed in temperate waters. Females and young may remain at the breeding site until the young are able to swim to more distant landing sites. These mothers often support their young until they are 1 year old, and a few females suckle both a newborn and the unweaned pup from the previous season. The sexes usually separate after a breeding season that lasts 4 to 6 weeks.

The movements that male otariids use in fighting, threat displays, and mating appear to be instinctual, not learned by young males that observe and mimic the behavior of adult males. Two sets of observations support that statement. Poulter raised orphaned Steller sea lion pups in his laboratory in the early 1960s, and I kept northern fur seal mothers and pups in the laboratory in the late 1970s. Pups in both cases used recognizable components of adult male fights and threat displays, and sexually mounted each other correctly, without ever having witnessed such behavior in adult males.

I helped Gerald (Gerry) L. Kooyman record diving behavior of South African fur seals in 1978 at Kleinzee, South Africa (Fig. 1.4). We did not observe their breeding behavior and social organization because the season had ended before we arrived. However, whenever we approached, captured, or physically restrained females for instrument attachment, they acted more like California sea lions than like other fur seals. During the approach phase of a capture if one female fled, then all others near her would also flee, and ultimately the beach would be cleared of animals. California sea lions flee in that way but northern fur seals do not. Also, when we caught these females with a noose pole they vigorously rolled sideways like noosed California sea lions do, and resisted being restrained for instrument attachment much more vigorously than did northern fur seals. Interestingly, Berta and Churchill (2012) consider the South African fur seal to be taxonomically closer to sea lions than to other fur seals. Our observations of female behavior at capture tend to support that statement.

1.5 Social Behavior and Organization

All otariids have similarities in their general form of social organization (McCann 1980). Adult males are larger than females and establish seasonal breeding territories. Females are gregarious, but do not appear to form stable social bonds except

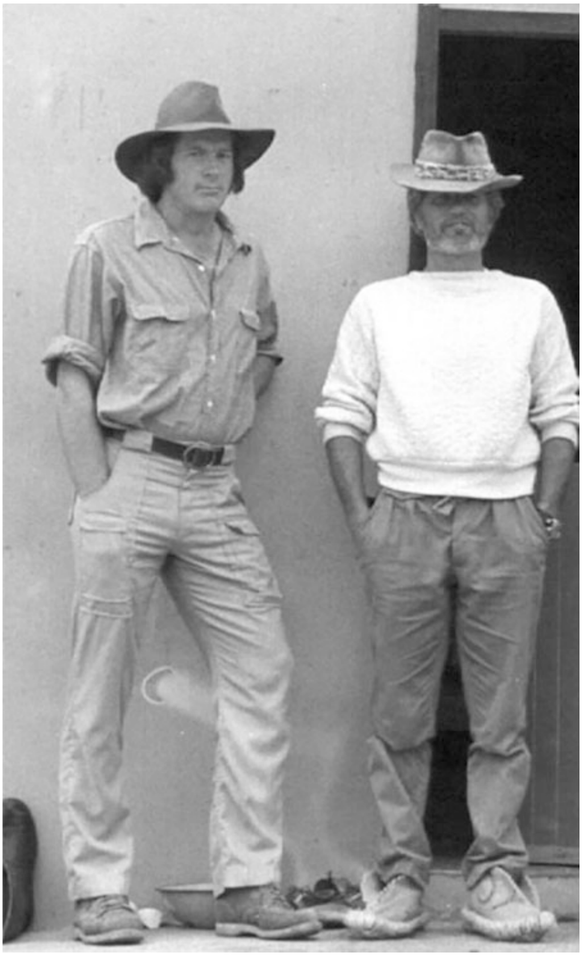

Fig. 1.4 Gerry Kooyman (right) and the author in Africa

with their young. Breeding occurs seasonally at specific locations and times of year when individuals congregate in shoreline breeding colonies (with the exception of the Australian sea lion, *Neophoca cinerea,* McIntosh and Pitcher, Chap. 26). Social organization among otariids, as a rule, involves male territoriality during the breeding season. Otariids have not developed the alternative forms of social organization that occur in group-living terrestrial mammals, such as social dominance hierarchies, or group territorial defense (Schein 1975). One factor that may explain this difference is that otariids tend to feed individually at sea and only form groups seasonally and briefly on land.

Male otariids usually establish territories before the first females arrive for the breeding season. The males' body conditions deteriorate during an extended fasting interval, and many begin to abandon their territories before all females have mated. Most species mate and females rear their young on sand or cobble beaches, or on rock substrate at the sea's edge. A few species have been seen climbing nearly vertical rock surfaces.

Behavioral differences are known among otariids. The New Zealand sea lion, for example, may breed on dirt or grass under shade trees instead of on beaches (The Snares Island, Crawley and Cameron 1972; Figure of Eight Island, New Zealand, Gentry, pers. obs.). Females that breed on Enderby Island mate on beaches as do the females of other otariids. But after mating, they move uphill and inland where they raise their young under dense brush (Gentry, unpublished data) unlike the other species I studied. Male Galapagos fur seals tend to hold territories where shade exists, and about 16% of male Juan Fernandez fur seals (*Arctocephalus philippii*) establish fully aquatic territories (Boness and Francis 1991). These are only minor deviations from the typical otariid pattern.

Otariid breeding sites can be quite stable over time. Northern fur seals have bred on Bering Island, Russia for 275 years. This stability results either from natal philopatry (females giving birth at the site of their own births), or site fidelity (repeat birthing at the same location when the mother's birth site is unknown). The best evidence for breeding near the natal site comes from tagging studies of northern fur seals. From 1956 to 1968, the U.S. government intentionally killed 315,000 females on terrestrial breeding colonies to reduce herd size and stimulate the population growth rate. Some 7940 of these animals had been tagged at birth, and about 78% of them were later killed on the breeding area of their own births. A few were killed within meters of the exact birth sites recorded during tagging (reported in Gentry 1998). The females in my study that had been marked as adults gave birth within about 8.3 m of the exact location in successive years. The dates of their arrival at the colony depended on whether the individual female was pregnant; those that were pregnant in successive years arrived within about 3 days of the same date each year. Those that missed a yearly pregnancy arrived about 7 days later than their usual date, but returned to their typical date the following year if they were again pregnant (Gentry 1998) This predictability implies that the female population is not the mass of anonymous animals it appears to be from casual observation. It is a collection of individuals, each having tendencies to use a specific birthing site at a specific time of season. While such fine-scale patterns of social organization are not well-known for other species, it is possible that long-term detailed behavioral observations of known individuals, and/or genetic studies, will reveal even more subtle aspects of social structure in otariid colonies.

Female otariids arriving at the start of a breeding season typically join existing female groups rather than resting alone among males. They are gregarious but not social; at least there is no evidence of female-female social bonds beyond kin. Such evidence might be found by observing known individuals repeatedly resting together, moving among female groups together, or leaving for and returning from foraging trips together. Females on shore typically move from one female resting group to another in unpredictable pattern, and in the absence of male interference. If female social bonds occur in any species, they would most likely develop in those that do not make an annual migration (see Wolf and Trillmich 2007, 2008; Wolf et al. 2007).

The unhindered movement of females from one resting group to another during the breeding season shows that female groups are not “harems” that are under the control of males. The opposite seems to be true. Female northern fur seals form groups on highly predictable breeding areas irrespective of the individual males that have established territories there in any given year. Females may give birth and mate at a given site for 15 or more seasons, whereas males hold a territory for from one to three seasons. This means that females choose birthing and mating sites, not the individual males that are present.

The tendency of male otariids to herd females is not uniform among species. Male New Zealand sea lions on territory never herded females during my study. Some half-grown males attempted to herd females that were arriving from sea, briefly and unsuccessfully. Steller sea lion males in California occasionally blocked the movements of females, but only briefly and early in the season, especially when females were on their way to sea. Northern fur seal males herded females only at the start of the season when the female group was small. Later in the season, when female group size had increased, some females escaped the group whenever the male left to capture a newly-arriving female. That is, male herding of females in the northern fur seal became counter-productive at some group size and most males eventually stopped all attempts to herd.

The male reproductive strategy in northern fur seals is not to increase their reproductive success by forcibly herding females into groups. It is to establish a well-defined territory on ground where females predictably gather, and to take advantage of female gregariousness to increase their reproductive success. The large size and aggressive demeanor of adult male otariids did not evolve in the context of dominating females, but as essential components of male-male competition for access to female gathering sites. The term “harem,” used to describe collections of females associated with a single male, is misleading when applied to otariids, and should be abandoned.

The social behavior of New Zealand sea lions seems to differ from that of the other otariids I studied in terms of male territorial behavior, male-female interactions, and stability of the female population. In two seasons, breeding males established territorial sites only after the females had arrived, not before as in other temperate breeding otariids. Females at the east end of the breeding beach formed a single group, and thereafter moved westward. Every few days a group of 10 or more females that lacked pups would gather at the west end of the female group, huddle tightly, then rush about 10 m west and stop where there were no other females. A few days later all remaining females would join them and abandon the area they had formerly occupied. The males holding these just-abandoned territories would then swim west of the female group and establish a new territory into which the females would move later in the season. Some males defended three different territorial sites along the beach, apparently trying to keep in contact with the moving female group. The breeding aggregation moved on average about 3 m/day throughout the season.

Group movements of New Zealand sea lions suggest that adults have no apparent attachment to specific land sites as do other otariids. Perhaps breeding on featureless sand makes one site as good as any other for parturition and mating. However, just breeding on sand does not explain why females constantly moved along the beach. These movements seem to explain why males did not try to establish territories before the females arrived.

In my experience, New Zealand sea lion males do not herd females, even those that are obviously ready to mate. Several males showed no response when fully receptive females left their territories and entered the territory of an adjacent male. However, small juvenile males frequently herded pups into small groups, blocked their movements, and tried to mount them sexually just as males of some other species act toward females. This herding behavior by small juvenile males wanes with age and apparently does not serve as practice for some future adult need, as it seems to in other species.

1.6 Otariids and the Society for Marine Mammalogy

Otariid seals, especially the California sea lion, played a central role in focusing scientific attention on marine mammal biology, and on bringing marine mammal welfare to the public's attention. These trends started with a series of marine mammal conferences that Poulter held at his laboratory. He had spent decades in research and understood the importance to researchers of having contact with peers. He announced that a first-ever conference would be held on biological sonar and all diving mammals at his laboratory in the summer of 1964. The response was very positive. The 25 active marine mammal researchers at that time attended. The group included academics but also some researchers from a U.S. Navy laboratory who were using California sea lions in their research. The dolphin biologist John C. Lilly attended, as did Winthrop Kellogg and Victor B. Scheffer, whose book on pinnipeds (Scheffer 1958) had recently become available. Gerry Kooyman and I were the only two graduate students there.

From the formal way conference attendees first met and conversed it was clear that they did not know each other personally. By conference's end, however, they had clearly found common ground and were sharing research ideas and addresses, just as modern researchers do, and were looking forward to another conference. Poulter complied and held a few more conferences at the laboratory but moved it across the bay to the Stanford Research Institute in Palo Alto when the audience outgrew his laboratory space. Thereafter, the audience grew steadily until Poulter, when quite old, turned over future conferences to Kenneth S. Norris, then at the University of California in Santa Cruz. Norris expanded the meetings to include all marine mammal species, and all research topics that were of interest to the attendees. A vote held in 1981 formally created the Society for Marine Mammalogy with its first meeting in San Francisco. Today, over 50 years after Poulter's first meeting, few of the Society's well over 2000 international members know that the Society's original birthplace was an abandoned missile base in rural California, or that a paper wrongly claiming echolocation in the California sea lion was the catalyst that brought society members together. However, most members realize that marine

Fig. 1.5 Attendees of the Fur Seal Symposium, Cambridge, England 23–27 April 1984. Front row, left to right, G.I.H. Kerley, L.A. Fleischer, D. Torres. Second row: R.L. Gentry, R.L. DeLong, P.D. Shaughnessy, G.L. Shaughnessy, M.E. Goebel, A.E. York, A. Trites, P. Majluf, T. S. McCann, A. Ponce-de-Leon. Third row: B. Tollu, C.W. Fowler, D.F. Costa, M.N. Bester G.L. Kooyman, I. Stirling, R.W. Davis, D.W. Doidge, J.L. Bengtson, F. Trillmich, R. Vaz-Ferreira. Back row: P. Jouventin, J.-P. Roux, J.P. Croxall, T.G. Smith, D.M. Lavigne, R.H. Mattlin, J.H.M. David, R.M. Laws, W.N. Bonner, and M.O. Pierson (Photographer unknown)

mammal research questions being asked today are far more complex than attendees of the 1964 conference could have imagined.

The two best-known otariid species in the 1960s were the northern fur seal and California sea lion. Research on northern fur seals was funded by the U.S. government due to its treaty obligation to three other nations[3] to kill northern fur seals for pelts for the fashion industry. Most of the funded research was on population dynamics, but one study involved social behavior of known individuals (Peterson 1965). Peterson later worked with George Bartholomew and published a major work on the California sea lion (Peterson and Bartholomew 1967). These were two of the earliest papers on otariids that focused on social behavior.

As scientific interest in pinnipeds grew, a major symposium on all pinniped species was held in 1977 at Guelph University, Canada, that attracted more than 100 attendees. By 1981 some data were available on most of the otariid species, especially on fur seals, that were more numerous and widespread than sea lions. Researchers were still working in isolation from each other. To further improve communication, a symposium on fur seals was held in 1984 at the British Antarctic Survey in Cambridge, England (Croxall and Gentry 1984). Papers were presented by

[3]Japan, Russia, and England (acting through Canada).

27 first authors representing 13 nations, reporting on 11 species of fur seals (Fig. 1.5).

Most studies in the 1980s focused on observing social behavior and describing it in print. Field conditions and the individual interests of the researchers probably determined the data being collected. Some of the topics of interest were means by which males won and defended territories, duration of territorial tenure, and males' mating success. The topics of interest for females were their arrival dates, dates and locations of parturition and mating, and timing and duration of feeding trips to sea. Together, these seemed to be the key factors that affected the next generation of adults.

1.7 Manipulative Behavioral Experiments

U.S. managers that were responsible for northern fur seal populations were concerned that killing young males for pelts had reduced the overall pregnancy rate, resulting in fewer pups. When too few males were available for mating, the critical factor in the overall pregnancy rate was the duration of estrus. To measure it, we fitted females with a harness that prevented coitus and paired them with a captive adult male for 15 minute test sessions several times daily while scoring the fine details of their behavioral interactions (Gentry 1998). The females had ready access to tanks of fresh seawater where they were fed fish and squid for the duration of their tests, about 30 days. Test females not in estrus were consistently aggressive toward the male. When estrus began, their threats toward the male stopped and then resumed when estrus ended, as indicated by their recorded behavior toward the test male. All females in our tests followed this pattern. These tests may have been the first use of behavioral indicators to estimate the duration of a physiological process in otariids.

We used the same methods to test whether the concept of female mate choice applied to northern fur seals. Females that our tests had shown to be in estrus were fitted with the harness mentioned above and transported to a landing area where males of varying ages, from juvenile to senescent, were available. We selected a male, drove it close to the female, and took notes on the fine components of their behavioral interactions. Results showed that estrous females were sexually receptive to any male, irrespective of age, size, or social status if access to them was provided (Gentry 1998).[4] Females usually mate with prime adult males, not because they prefer them but because prime males actively exclude non-prime males from the land sites that females predictably use for pupping. Similar manipulative experiments could be conducted on other otariid species.

Philopatry begins within the first 30 days of life, and may be based on where the pup suckled, not on where it was born. Northern fur seal pups that had been born on

[4]Estrus females that are physically restrained will sexually present lordosis to humans if they are touched near the pelvic area.

breeding areas were taken with their mothers to our holding facility and held for 30 days while the mothers were tested for the duration of estrus. Thereafter, the pups and their mothers were returned to their original birth site and released. The mothers immediately left on foraging trips but the pups did not remain there. They walked overland (pups of that age do not swim) about 2 km to the holding facility where they had last suckled. They called for their mothers near the compound and, not finding her, walked through the village still calling. We returned these pups to their birth sites as many as nine times but they persisted in returning to the holding facility. This was not a planned experiment but an accidental finding. It could be systematically tested with other otariid species if the basis of philopatry is of interest.

1.8 Research on Diving Behavior

The development and first use of dive recorders is fully reviewed in the book *Diverse Divers* (Kooyman 1989). Kooyman's goal was to study the relationship between diving behavior and diving physiology. He was not getting that information from his first Time-Depth Recorder (TDR) because it ran for only 1 h and, when deployed on Weddell seals, recorded only a single dive during that interval. After seeing my 1974 data on the predictable land-sea movements of female northern fur seals, he decided that an instrument that ran for a week would record all dives the females made on a trip to sea. He obtained a grant, found an instrument maker, built units having that capability, and we deployed them in 1975 (Kooyman et al. 1976) using handling methods developed for that purpose (Gentry and Holt 1982).

By 1983, Kooyman had used the instrument to measure diving in northern, Antarctic, South African, South American, and Galapagos fur seals, and the Galapagos sea lion. The colleagues with whom he worked on these projects gathered to present and discuss their collective data, and to decide on the concepts to be published. Chapter writing followed and the book appeared in 1986 (Gentry and Kooyman 1986).

The first low voltage electronic components needed to measure diving became available in 1984. Kooyman used them to build a completely different kind of dive instrument from the more physical one used before. It weighed a few ounces instead of 1 kg, and it stored the data in digital format. These features made it possible to record many aspects of diving other than time and depth. The first new parameter he measured was swim speed; a small paddle-wheel on the nose of the instrument provided that information, and the data were stored in memory chips.

The change from analog to digital format for recording diving behavior revolutionized the study of marine mammals. Dive instruments could now be built by anyone familiar with electronic components, and researcher demand for them created a new instrument industry. Instruments could now be made to measure many new aspects of foraging such as water temperature, prey capture attempts (via jaw movements), location at sea via satellite, prey finding using echolocation (in cetaceans) and, most recently, electrocardiograms on free-swimming whales

(Goldbogen et al. 2019). A scan of the recent literature suggests that these instruments have caused a major change in the questions that field workers are asking about marine mammals. The earlier research emphasis on social structure and behavior of otariids on land has been largely replaced by measuring behavior, ecology, and physiology of marine animals at sea.

1.9 Research Using Isotopes

Injecting animals with isotopes, especially animals that are carrying dive recorders, greatly increased the amount of physiological and environmental information obtainable for otariids. The first species studied using this combination was the northern fur seal in the early 1980s. The isotopes used were Oxygen 18, tritium, and deuterium-labeled water (Costa and Gentry 1986). Since that initial study, most of the world's otariid species have been studied using this combination of methods. The dive recorder gives information on at-sea behavior, and the isotopes reveal the physiological changes that accompany that behavior.

The details of how this combination of isotopes and dive recorders produces new physiological and environmental information is presented in Costa (1987). The biological factors that have been measured this way include milk production by mothers, milk intake by offspring, growth efficiency, body composition, energy expenditure, maternal investment in the young, metabolic fuel use, foraging energetics, foraging ecology, mass changes and metabolism during the perinatal fast, ontogeny of oxygen stores, physiological dive capabilities, activity-specific metabolic rates for diving, transit time and rest at sea, field metabolic rates, temporal patterns of milk production, parental attendance related to environmental fluctuations, and foraging energy expenditure in relation to environmental changes (specifically El Niño events). Some of these studies involved data from accelerometers contained in the dive instruments (see du Dot and Guinet, Chap. 4).

1.10 Concluding Remarks

Otariids are interesting from the standpoint of terrestrial social behavior as well as foraging behavior at sea. The way students can join in this area of research has changed greatly over the years. Decades ago, just learning about some topic and then finding a project where that information was needed was a viable way to find a research position. No counselor or teacher suggested that I read up on echolocation or pointed me toward Poulter's laboratory. Most of what I learned during those earliest research years came from working with other established researchers. A chance visit to an otariid breeding group steered me toward field research because it fit my interests better than did laboratory research. I spent three breeding seasons studying Steller sea lions, inventing data collection methods, and learning the vast difference between laboratory and field research. That study raised questions that could only be answered by comparing other otariid species that did not live in the climate of central California. I started by studying the New Zealand fur seal on a post-doctoral fellowship at the University of Adelaide, Australia. Afterward, because of my interest in otariids, a U.S. government agency hired me to study the northern fur seal in the Bering Sea, a project that was well-funded and lasted for 20 years. The position let me explore all topics that interested me, provided funds to help Gerry Kooyman develop his time depth recorder, and gave Dan Costa a chance to use dive recorders in combination with his isotope studies (Costa and Gentry 1986). This combination of dive recorders and isotopes seems to have completely changed the questions that modern researchers are asking.

My advice to students is as follows: do not try to enter science the way I did. Read broadly, then work with a counselor or a researcher who can steer you toward appropriate job opportunities. Simply blind-shopping for such an opportunity, as I did, will not work in today's world because of increased competition for jobs. No graduate students in the early 1960s were interested in marine mammals; today there are thousands. A good way to find openings in science is to attend professional conferences in your field of interest. Meet other students and make them your community; they could last throughout your entire career. Learn from working professionals how they fund their research, which funding agencies they use, and how to write proposals that will succeed. Publish only meaningful professional papers, and give conference talks only when you have solid results to report. Befriend older, more experienced researchers and learn from them how your career can mature. Vic Scheffer, my personal hero, worked on fur seals in midlife, retired, led seniors on an expedition to the Galapagos Islands at age 90, and at 103 gave philosophical lectures on the human condition in a series entitled, "Random Thoughts While Shaving." Never stop learning, teaching, or laughing. Discover whether you prefer pure science, i.e. deep, fundamental questions about evolution, ecology behavioral development etc., or applied science- applying scientific principles to management and/or conservation problems, but know that both require the same creative mental skills.

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