BEYOND BEAN COUNTING AND WHALE TALES

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ABSTRACT

Three developments have implications for the future study of marine mammal behavior: 1) The number and affiliation of researchers have increased from a few individuals representing the interests of government or industry to many people conducting studies from a variety of points of view; 2) The interpretation of natural selection's operation on social behavior and life history patterns has shifted from emphasizing group to individual benefits; and 3) The passage of the Marine Mammal Protection Act has committed the United States to manage, research and protect marine mammal populations. Despite negative aspects of each development, the overall effect on marine mammal research will be positive. The combination of these changes and the interaction and collaboration of researchers with diverse orientations will spur new and varied research efforts and lead to a deeper understanding of marine mammals.

To predict where a field is going one has to consider where it has been. During the past 15 years we have witnessed three developments that have implications for the future study of marine mammals. The first is a change in the number, affiliation and orientation of people doing marine mammal research, the second is a theoretical modification—a change in the interpretation of how natural selection operates—and the third results from U.S. legislation protecting marine mammals and making the management of them the responsibility of the federal government. On the whole, these developments signal a deeper understanding of marine mammals from many viewpoints.

MORE DIVERSE STUDIES

Much research on wild animals is determined, at least in its earliest stages, by anthropocentric interests. These interests reinforce certain studies and initiate trends that determine the information gained. Early investigations of sporting

game such as deer, ducks and fishes emphasized movements, distribution and feeding patterns—useful knowledge for hunters and fishermen. Much research on insects has focused on breeding biology and life cycles, important matters to know when the priority is pest and disease control. On the other hand, birds have been studied from a variety of viewpoints because much of the work was done by amateurs. Early attempts to understand marine mammals were aimed at increasing profits made by harvesting them for their furs, skins and oil. This meant obtaining practical knowledge useful in hunting the commercially valuable species such as the great whales, elephant seals, fur seals, harp seals and sea otters. Later attention focused on numbers, distribution, annual cycles and habits relating to management of populations. Until a few decades ago, relatively few people were doing research on cetaceans and pinnipeds. In the United States, these were employees of the federal or state governments or persons hired to represent the government. The single aim of their investigations was to manage the populations. Seeing to the welfare and abundance of populations meant increasing yield and profits. With few exceptions, these investigators did not have the luxury or time to pursue questions unrelated to management, such as the social behavior of individual animals, or to cast their findings in the general context of evolutionary theory. Similar priorities prevailed during the same period in Great Britain, Canada and the U.S.S.R. and determined the nature of marine mammal research.

For example, early investigations of northern fur seals (*Callorhinus ursinus*) in the United States reflected the economic interests of private industry and government. In the early 1800s, mercantile houses dealing in furs pressured the U.S. government to allow trade in Russian waters. Commerce in furs and other products of the north led to the purchase of Alaska and federal involvement in the management of the northern fur seal in the Pribilof Islands. At first, a branch of the Treasury Department, the "fur seal service," was given responsibility for counting and supervising the kill by Aleuts hired by the Alaska Commercial Company under an exclusive lease from the government. The earliest studies were conducted by federal or state government employees or independent researchers hired by the government. During the period from 1872 to 1913, Henry W. Elliott was sent to the islands by the Secretaries of the Smithsonian Institution and the Treasury Department—the first person sent especially to study the seals. He was followed by William Palmer and Frederick True, representing the National Museum, Barton W. Evermann commissioned by the State Department, Charles Townsend of the Smithsonian, Edwin W. Sims of the Department of Commerce and Labor, Elliott again and H. F. Gallagher as agents of the Department of Commerce and George Clark of the Bureau of Fisheries. The principal aim of these early investigators, as well as that of subsequent researchers with the Bureau of Commercial Fisheries and the National Marine Fisheries Service, was to obtain information bearing on the management, productivity and welfare of the fur seal population so that yield in pelts could be maximized. Reproduction, anatomy, food habits, migration, population dynamics, mortality and growth were investigated intensively.
A similar concentration on certain questions occurred at the state level. Along the west coast of the United States, state governments were charged with protecting marine resources. Fish and game departments counted populations of seals, sea lions and sea otters on a regular basis to assess their numbers and make determinations about protection or reduction of their numbers in relation to the welfare of related species, notably predators and prey. Thus, until about the 1950s, pinniped studies along the Pacific coast of the United States were conducted almost exclusively by a relatively few federal or state government employees charged with investigating questions relating to population welfare and abundance.

Early writings about cetaceans were of two kinds. The whaling captains and naturalists, Scoresby (1820), Scammon (1874) and Southwell (1899), made valuable contributions to our knowledge of cetacean natural history and behavior. However, the majority of early writings dealt with "stocks" and "populations" in the various ocean basins; the emphasis was on counting animals and determining how many could be harvested for profit. Because of the difficulty of studying whales in the open ocean, many investigators in the early part of this century concluded that the most useful studies were of dead animals at whaling stations. A great deal of effort was put into inspecting carcasses to determine food habits from stomach contents, reproductive status, age, parasitic infestations, disease and other biological parameters.

The picture of a few people doing primarily descriptive population research has changed greatly during the past two decades. Although the federal and state governments in the United States continue with active and in some cases expanded programs, and while their research pursuits often go beyond the requirements of management, the most obvious change is the preponderance of researchers from outside these agencies doing work on marine mammals. In the United States, this trend in pinniped research was gradual at first. It began accelerating during the 1950s with the field studies of G. A. Bartholomew from the University of California on northern fur seals and northern elephant seals (Mirounga angustirostris) (e.g., Bartholomew and Hubbs 1952; Bartholomew 1952, 1953, 1959; Bartholomew and Hoel 1953). R. J. Schusterman began studying sensory processes of pinnipeds in captivity in 1964 (Schusterman et al. 1965). Studies of the population sizes of large whales were initiated by the International Whaling Commission early in this century. William Schevill of Woods Hole Oceanographic Institution began studying cetaceans at sea in 1948 (e.g., see summary of right whale [Eubalaena glacialis] research in Watkins and Schevill 1982). Meanwhile, small toothed whales were virtually ignored. Not until an interest developed in keeping dolphins in captivity did behavioral research on these species commence (True 1890; Townsend 1914; McBride and Hebb 1948; Kellogg 1961; Tavolga 1966; Tavolga and Essapian 1957; Wood 1973; De Fran and Pryor 1980).

World War II and the launching of Sputnik on October 4, 1957, had a tremendous impact on increasing government support of scientific research in general and research on marine mammals in particular. For example, the first conference on the subject of marine mammals was sponsored by the Office of
Table 1. Research investigations reported at the Marine Mammal Meetings in San Francisco, December 14–18, 1981, categorized by affiliation of the first author. Based on abstracts published in Marine Mammal Information, December 1981 and July 1982, B. Mate, Editor, Oregon State University. Abbreviations: National Marine Fisheries Service (NMFS); Bureau of Land Management (BLM); National Park Service (NPS).

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1 Academies, centers, surveys and observatories.

Naval Research in 1963. The proceedings were later published as an influential book, edited by Kenneth Norris, entitled Whales, Dolphins and Porpoises. The U.S. Navy developed a special interest in dolphins (Wood 1973) when it was discovered that they were easily trained and were capable of echolocating. At present the Office of Naval Research and the National Science Foundation support most basic research on marine mammals in the United States. The findings resulting from this extensive funding on diving capabilities and physiology, vocal behavior and echolocation and reproductive physiology serve as an excellent base for ecological studies in nature.

There are more people doing research on marine mammals today than ever before and research interests span multiple disciplines. The research abstracts from the IV Biennial Conference on the Biology of Marine Mammals in San Francisco in 1981 (Table 1) show that the majority of reports, 71 percent, was given by people outside government and state agencies. Moreover, the variety of affiliations suggests a diversity of research approaches and values such as: public display, husbandry in captivity, training to perform, material for study by future generations, rehabilitation of the sick, testing biological theory and assessing human generated impacts on the marine environment. Another point gleaned from inspecting these abstracts is that 21 studies were collaborative efforts between people in and out of government, i.e., between investigators
engaged principally in basic and applied research. Clearly, the research picture is far different today than it was prior to 1950.

What is the effect of all of this new activity? We predict a change for the better for numerous reasons, some of which are listed below:

*More Ground Can Be Covered by Many Than by Few*

For example, a number of researchers with diverse affiliations have recently obtained information on California sea lion (*Zalophus californianus*) feeding habits. These studies were conducted in the Gulf of California (D. Aurioles and co-workers from Centro de Investigaciones Biologicas in La Paz, Mexico), in the Channel Islands in the southern California Bight (J. Francis, C. Heath and M. Lowry of the University of California at Santa Cruz and the National Marine Fisheries Service) and the Farallon Islands in central California (D. Ainley and colleagues from the Point Reyes Bird Observatory). Similar examples exist for baleen and toothed whales. The behavior of humpback whales (*Megaptera novaeangliae*) has recently been investigated in the North Atlantic (Whitehead 1983; Tyack and Whitehead 1983), off Hawaii (Tyack 1981, 1982, 1983; Darling 1983) and in southeast Alaska (Baker and Herman 1983). Researchers in each area are identifying animals by natural marks and exchanging identification photographs, cooperation which is beginning to elucidate movement patterns between summering and wintering grounds. Studies of bottlenose dolphins (*Tursiops truncatus*) in Argentina (Würsig and Würsig 1977), Texas (Shane 1977; Gruber 1981) and Florida (Wells *et al.* 1980) reveal differences in behavior and group size that are evidently specific to habitat and place.

*Many Different Species Are Being Studied, Not Just Those That Are of Commercial Value*

This is well-illustrated by the assessment and impact studies of marine mammals and birds contracted by the Minerals Management Service (formerly the Bureau of Land Management) during the past 10 years. Equal attention is given to all species in air and ship surveys. Some species are relatively inaccessible, and study of them would not have occurred without the substantial funding made possible by this federal agency. For example, bowhead whales (*Balaena mysticetus*) have been the object of an intensive five-year study of summer feeding and social behavior in the Beaufort Sea. The study was commissioned to investigate the possible effects of disturbance associated with proposed oil and gas development activities. However, results have gone beyond these narrow confines and have uncovered a wealth of information about this little known species (Richardson 1983). We have learned that bowhead whales forage cooperatively at times, they sometimes feed near the bottom like gray whales (*Eschrichtius robustus*) and social activity occurs even during the primary feeding season. Similar behavioral work, funded because of concerns about industrial activity, have taught us much about feeding in gray whales and the benthic
ecology of their feeding grounds in the Bering Sea (Thomson 1983). Moreover, this approach yields useful information for making comparisons between species and provides a potentially important perspective on the commercially valuable species (Bonnell et al. 1978).

The Same Phenomenon Is Being Observed from Different Perspectives

"Scabby molt" is an aberrant condition of the pelage and skin in northern elephant seals and is observed most frequently in yearlings during the winter. Individuals with extreme cases of it may exhibit exudative cracks in the skin. Despite their sickly appearance, these animals do not die during their two- to four-week stay on land. However, when taken into rehabilitation centers, given antibiotics and fed, many of them die (as do some apparently healthy animals). The probability of death is related to the apparent severity of the condition. From these observations, it is likely that many of these animals which are dying in nature go unobserved. One approach provides the incidence and epidemiological context of the condition in nature; the other confirms that morbidity is involved. The two independent observations indicate a problem warranting research.

The Aims, Values and Associations of Some Organizations Working with Marine Mammals Appeals to the General Public and the Good Will Derived Helps Promote Research

Wild animal zoos and menageries have a long history of providing public entertainment and education. Thousands of people go through the turnstiles of aquaria and oceanaria every year for similar reasons that people during the renaissance flocked to view the curiosities accumulated by the Medicis in their "gardens of knowledge." Although most of the visitors may never see a marine mammal in the ocean, seeing them in captivity makes the animals more meaningful. Jacques Cousteau's television programs have made whales, seals and sea otters more familiar to the general public (albeit sometimes incomprehensible to the scientist). Similarly, the efforts of people working in rehabilitation centers for beach-stranded animals receive public attention. The visibility, interest and good will gained from these endeavours, some of which are only marginally related to science or management, work to the benefit of all people working with marine mammals. Popular books extolling, if not documenting, dolphin intelligence (the earliest and most widely read being those of John Lilly) enhanced the appeal of these animals to the general public, making it easier to justify study of their perceptual and mental abilities. An informed, sympathetic public is more apt to donate funds for marine mammal research or support allocation of funds for this purpose by the federal government.

Interaction of Individuals with Different Backgrounds and from Different Organizations Can Lead to Scientific Breakthroughs

When individuals with different orientations work together on a common problem, the whole achieved is often more than is accomplished by the indi-
individuals working alone. Excellent progress has been made in recent years on the diving behavior and energetics of free-swimming pinnipeds and marine birds using time-depth recorders or variants thereof. These units are attached to diving mammals and record all dives made over about a two-week period. Gerald Kooyman (1965, 1968) pioneered the use of these devices in his studies on Weddell seals. An improved design permitted employing the units on northern fur seals (Kooyman, Gentry and Urquhart 1976) and variations on this design (Kooyman, Billups and Farwell 1983) have been used on other species of fur seals, yielding detailed information on the time that feeding begins after departure from the rookery, circadian activities, diving effort and diving depths. A record has just been obtained substantiating the often-quoted suspicion that elephant seals are the deepest diving pinnipeds. Studies on whales will be attempted soon. The design, development and deployment of these devices resulted from the interaction of individuals affiliated with a university institute, the National Marine Fisheries Service and private industry. Moreover, various government agencies provided funds for research and development. This technological breakthrough promises to reveal a great deal about the elusive underwater behavior of marine mammals.

A New Paradigm

The second development involves what Thomas Kuhn (1970) calls a paradigm shift, a change in the accepted model for explaining a phenomenon. It is a monumental historical paradox that, after the publication of The Origin of Species, students of Darwin’s theory of evolution by natural selection adopted the idea that social traits served the good of the group or species rather than the individual. In spite of Darwin’s argument that natural selection operated on the level of the individual, the notion that the group level was more important became widespread and prevailed in biology and the social sciences from the early part of this century to about a decade ago. It was customary to attribute sex, death and reproductive cycles as being advantageous to the species rather than the individual. The issue came to a head in 1962 when Wynne-Edwards (1962) hypothesized the mechanism and rationale for group selection in his controversial book, Animal Dispersion in Relation to Social Behavior. He took as his starting point an analogy from the whaling and fishing industry. Noting that “overfishing reduces both the yield per unit effort and the total yield,” he argued that animals are no different in principle from fishermen. They must manage their own number to prevent overkilling their own prey. He hypothesized that animals did this by assessing their population number and density via social displays. This informed them about when to sacrifice personal survival or reproduction for the good of the group. Thus, according to this theory, social behavior evolved to sustain groups. The notion that animals unselfishly curtailed their own numbers became popular.

Group selection had a great impact on marine mammalogy, both on those responsible for management and on individual researchers. The group selection notion of self-regulation of animal numbers by “self-destruction” for the good
of the group was in accord with management philosophy. It explained increases in mortality and, when high mortality was evident, implied that the population was at carrying capacity and justified culling. Culling saved animals the trouble of having to do it themselves. It was nature’s way and besides, it strengthened the stock! Even independent researchers with no population to protect were captivated by the argument. For example, in their paper on the breeding biology of grey seals, Coulson and Hickling (1964) concluded that the lower survival rate of calves reared under crowded conditions was self-induced, a mechanism to prevent their numbers from increasing beyond the limits of food resources.

In spite of its human appeal (the emphasis on altruism was more palatable than the selfish view of “nature red in tooth and claw”), the group selection argument was systematically and thoroughly shot down during the 1960s and replaced by the original Darwinian interpretation of reproductive survival of the fittest individuals. David Lack (1966) showed that group selection is unnecessary; all instances for which it was invoked were explained through natural selection and kin selection acting on individuals. G. C. Williams (1966) gave strong support to his argument that the goal of an individual’s reproduction is not to perpetuate the population or species but to maximize the representation of its own germ plasm relative to that of others in the same population. Perrins (1964) demonstrated that birds did not proliferate uncontrollably because individuals self-sacrificed for the group, but rather because parents could not feed more than a certain number of chicks, therefore they benefited by limiting egg production. Moreover, there were no data showing that animals received population feedback from social displays. Modeling studies during the 1970s showed that group selection is possible but not probable; the conditions for the evolution of an “altruistic gene” over a selfish one are stringent; and individual self-sacrifice for the good of the population is least likely to occur in large stable populations where social behavior is most highly developed (Wilson 1975).

The dragon was slain and the people explored the distant reaches of the kingdom freely. This involved taking Darwin’s survival of the fittest individuals to its logical end with respect to behavior. W. D. Hamilton (1964) showed that cases of apparent altruism in nature were explained on the individual level by kin selection; individuals maximize their reproductive success or their “inclusive fitness,” not only through their offspring but through relatives with whom they share genes. Individuals are selected to maximize their reproductive success and, hence, the degree of genetic relationship predicts selfishness, cooperation, altruism and spite in social encounters. Trivers (1972) showed that parental investment is important in the evolution of sex differences and in the reproductive strategies employed by each sex. The biology of social behavior, called social theory (Trivers 1976), behavioral ecology (Krebs and Davies 1981) or sociobiology (Wilson 1975; Barash 1982), became an exciting new discipline attracting many into its fold. New heroes surfaced and spokesmen made reputations for themselves as advocates (Dawkins 1976) or detractors (Gould 1980).

What are the consequences of this change in interpreting how natural selection operates? Several are listed below:
Stimulation of Research

As Kuhn (1970) noted, a paradigm is not only important for its explanatory value but also because it directs research questions; the function of normal science is to further articulate the paradigm in view of the match between the paradigm’s predictions and the facts observed. A paradigm shift, such as the one we have described, changes the focus and priorities of behavioral research. Since selection acts on individuals, the new emphasis is on how individuals go about maximizing their reproductive success. Social behavior is the outgrowth of genetic differences which surface as conflicts of interest between different phenotypes. It is the manoeuvering, the probing, the parrying for position and the compromise in reproductive competition. Hence, the new perspective emphasizes questions about sexual selection and sex differences in morphology and behavior, major and alternate reproductive strategies of males and females, changes in strategy with development, apparent altruism and cooperation, kinship, nepotism and recognition of kin, parental care strategies with an emphasis on effort and investment, sex ratio variation, individual economic decisions in reproductive and survival behavior and the evolution and ecology of breeding systems. Researching these issues requires in-depth, long-term observations of marked individuals of known age living in natural conditions. Studies of this kind have always yielded some of the most useful information about pinnipeds (e.g., Laws 1956; Coulson and Hickling 1964; Peterson 1965; Stirling 1969, 1971; Le Boeuf 1974; Reiter et al. 1981). A similar approach is just now beginning to pay off with cetaceans. The increasing sophistication of cetacean field studies can be traced back to identifying individuals. In the early 1970s, a number of investigators began using photographs of natural markings to recognize individuals: R. Payne with southern right whales (Eubalaena australis) in Argentina (1976, in press), M. Bigg with killer whales (Orcinus orca) off Vancouver, British Columbia (Bigg et al. 1976), S. Katona, S. Kraus and others with humpback whales (Katona et al. 1979) and B. Würsig and M. Würsig with bottlenose dolphins in Argentina (1977). During the same period, Irvine and Wells (1972) began tagging bottlenose dolphins in Florida; subsequently they relied on the marks left by the tags after they were removed. Many other studies going on today utilize photographs of natural markings to recognize individuals, e.g., Dorsey (1983) with minke whales (Balaenoptera acutorostrata) and Darling (1978) with gray whales. As a result of this change in methodology, many aspects of social behavior are becoming apparent, the social behavior of cetaceans is being compared to well-studied terrestrial mammals, and cetacean studies are beginning to contribute to the prevailing social theories. Given the zeitgeist we have described, studies of this kind will be more important than ever in the future. Only in this way can one determine the form, diversity of strategies and outcome of reproductive competition.

Revision of Former Interpretations

With the old paradigm, the observation that males injure or kill females during mating attempts might have been interpreted as bad for the species, a
reflection of crowding, the presence of too many females and the necessity to weed out the weaker ones. In the new paradigm, conflict between males and females is to be expected. When a few males monopolize breeding, excluded males may employ alternate reproductive strategies that are injurious to females. This has been observed in pinnipeds, sea otters, primates and several other vertebrates (Le Boeuf 1981). Similarly, whale population models have assumed equal mortality rates for males and females of all species (Ohsumi 1979). However, Trivers (1972) predicts and marshals evidence to show that male natural mortality rates are higher than female rates in extremely polygynous species where the male is larger than the female. Mortality rates should be skewed to males in some sexually dimorphic odontocetes. Ralls, Brownell and Ballou (1980) report that the genera *Stenella, Globicephala* and *Physeter* form a series showing increasing degrees of sexual dimorphism (with presumed associated polygyny) and higher male mortality.

*Clarifies Unexplained Data or Former Puzzles*

Previously incomprehensible data now make sense to us. For example, Clutton-Brock et al. (1982) point out that not so long ago some ecologists were puzzled that polygynous mammals produced about equal numbers of male and female offspring despite the fact that a single male is able to fertilize many females. Females should conceive more female than male offspring, they reasoned. This was logical with the group selection paradigm because this would be the most economical use of resources by the population. With the paradigm shift, we restate the question in terms of individual advantage. That is, what proportion of male and female offspring should an individual produce to maximize his or her own reproductive success? Fisher (1958) showed that the answer is 50:50 when the cost of producing males and females is about the same. Coulson and Hickling (1961), with grey seals, and Stirling (1971), with Weddell seals, observed that despite a 50:50 sex ratio at birth, more males were born early in the season and more females later in the season. These investigators had no explanation for their results. In a seminal paper, Trivers and Willard (1973) argued that females are selected to bias the sex of their young to males when rearing conditions are optimal and they stated the general conditions which would select for deviations from a 50:50 sex ratio. If this hypothesis is correct, it suggests that the deviant sex ratio in the seals mentioned above may be due to older, more fit females giving birth early in the season and younger, less fit females giving birth at the end of the breeding season. In a similar vein, a vast amount of data on fetal sex ratios of slaughtered whales has lain fallow for much of this century, unexplained and apparently uninteresting to many. Seger and Trivers (1983) have examined these data on five species of mysticete whales. They find sex ratios (males to females) of the following order: 0.531 (humpback), 0.513 (blue), 0.510 (minke), 0.506 (fin) and 0.458 (sei). The decline in sex ratio values as the season progresses indicates that male mortality is higher than females *in utero*. Most interestingly, the two species with the highest sex ratios (humpback and blue) show the highest rates of differential
male mortality, an association predicted by R. A. Fisher's model (Fisher 1958). Moreover, high sex ratios and high male mortality in utero are associated with polygyny in adulthood. Recent field data show clearly that extensive aggressive competition occurs among humpback males for breeding females, suggesting that they are polygynous. Seger and Trivers' analysis suggests that similar behavior might be observed among blue whales but the observations to test this idea have not yet been conducted.

Shifts Emphasis to Different Animals

The new social biology puts a priority on studies of some marine mammals that did not exist previously. It is well known that some animal groups weigh more heavily in the theory of the day than others. During the heyday of learning theory it was the white rat (Bower and Hilgard 1981). Ethologists based many of their concepts on studies of three-spined sticklebacks, chicks and ducklings, and herring gulls (Eibl-Eibesfeldt 1970). Ecological theory owes much to work on herbivores and birds (Morse 1980). Many animals will contribute to sociobiological thinking. In company with the social hymenopterans, bullfrogs, red deer and various species of birds will be some of the land-breeding, polygynous pinnipeds. That is because the latter display to a remarkable degree the consequences of sexual selection such as sexual dimorphism. Polygyny, the most common mating system among mammals and most vertebrates, is extreme in these animals. Students, imbued with the neo-Darwinian logic, see them as excellent subjects for the study of the evolution of these traits; they provide tests for predictions and theories (Alexander et al. 1979). Along these lines, Connor and Norris (1982) have reviewed numerous, diverse reports of epi­meletic behavior of dolphins and conclude that these toothed whales exhibit a high degree of reciprocal altruism, a characteristic they share with human beings. This conclusion seems warranted by the following traits, which characterize dolphins: the need for grouping for predator defense; long life; extended parental care; low dispersion rates coupled with fluid associations between groups; and multiple opportunities for reciprocation.

Puts Emphasis on Question-oriented Research as Opposed to Description for Its Own Sake as Was Characteristic of Some Ethological Work during Its Heyday

Cetaceans, which are notoriously difficult to study, are being researched in an increasingly sophisticated way. Within the past 10 years, long-term natural history studies have been initiated on right whales (Payne 1976, in press), humpback whales (Katona and Whitehead 1981), bottlenose dolphins (Irvine and Wells 1972; Tayler and Saayman 1972; Würsig and Würsig 1979) and spinner dolphins, Stenella longirostris (Norris and Dohl 1980). These studies have yielded considerable information about sociality and foraging strategies. Recently, Clark (1983) showed that right whales have different vocalizations for different purposes. Tyack (1981, 1982) hypothesizes that humpback whale
song plays a part in reproduction similar to that played by vocalizations in insects, birds and primates. Based on an impressive group effort and utilizing the results of many previous investigations on feeding ecology, sexual physiology and behavior, a strong case is made that males compete aggressively to escort females (Tyack and Whitehead 1983), and males sing to communicate their readiness to mate and to keep other males away. It is suggested that female choice is responsible for the complicated nature of the song, what Wilson (1975) called "the most elaborate single display known in any animal species." Darling (1983) advances a similar hypothesis but emphasizes the importance of song in male-male competition. He likens the function of humpback whale song to horns on ruminants; the song signals the maturity and age category dominance of the male singer. Norris and Mohl (1983) have advanced a stunning hypothesis; odontocetes capture their prey by immobilizing it with narrowly focused high intensity sound. These hypotheses await testing, but the very fact that they are being advanced is cause for rejoicing and for anticipating new developments in the future. It appears that behavioral studies of cetaceans are coming of age and the data being gathered are generating interest among non-specialists.

PROTECTING MARINE MAMMALS BY LAW

The Marine Mammal Protection Act of 1972 makes the United States government responsible for long-term management of marine mammal populations. This means conserving and protecting these populations and doing research on them to see that it is done wisely. Numerous unquestionable benefits accrue from this legislation. First, there are more likely to be marine mammals in the future if the law is upheld and enforced. Had similar legislation been enacted early in the past century, there might be research programs today on sea mink, green turtles, heath hens, Labrador ducks and great auks. Secondly, research is being financed on monk seals, manatees, dugongs, bowhead whales and sea otters—species with populations that are low or in decline—and this may yield information important to their continued survival. Third, the responsible agencies conduct or contract broad-based research programs on numerous other marine mammals with an emphasis on maintaining the populations at maximum net productivity (Anonymous 1982). The positive effects, from a scientific point of view, are that money is allocated for applicable research on phenomena important in managing populations. Although the research mandated appears to be tied closely to management's charge of keeping populations near optimal levels, the information gained is likely to be of general interest.

Potential Positives and Problems

Both positive and negative consequences may result from the developments we have described. We enumerate a few examples of each.
Outcrossing and Hybrid Vigor

The interaction of these two developments promises to stimulate new and varied research especially across "management–non-management" lines. Management scientists have a charge to protect populations and to maintain them at a certain level. Hence, their efforts are applied to a specific goal giving priority to the population. Non-management scientists are not bound by a single priority and a unified goal; their efforts are "pure" in the sense that immediate applications of their findings are not required. Historically, the most important questions to managers have been how many animals are there, how many can be harvested and do they cross political boundaries. Only the first and a variation of the third (animal distribution) are apt to be of direct interest to the non-manager. The principal questions of non-managers are more diverse, their important questions may wax and wane with vicissitudes in theory, and many of their questions may not be relevant to management. Examples of the latter are: What is the function of singing in humpback whales? Are dolphins reciprocal altruists? Under what circumstances does adoption occur in elephant seals and what are the proximal and distal explanations? In short, scientists from the two sectors are operating with different paradigms and, consequently, will tend to do different things. Indeed, the two different worlds or cultures of managers and non-managers is obvious by simply comparing marine mammal articles in the Journal of Mammalogy with Reports of the International Whaling Commission. We think both groups can learn something from each other.

The focus on individuals necessitated by the paradigm shift will not only provide a check on theory; the data collected will provide a more in-depth understanding of population phenomena of interest to managers. By this we mean that understanding populations is ultimately a matter of understanding the behavior of the individuals that compose them. Thus, there are two ways to study populations. The one that has been used most often in the past is to emphasize measurement of population parameters such as population number, giving second shrift to efforts at studying individuals. This is often necessary when dealing with large populations or where it is difficult, dangerous or too time-consuming to focus on individual behavior. Managers can rarely afford to conduct long-term studies of populations in which marked individuals of known age are observed for long hours over many years. This second approach, focusing on individuals, is most often done by independent researchers, each one investing several years on a project. The manner of study yields data that are useful in this respect even when the intention of the study is not primarily to elucidate understanding the population. For example, individual female seals marked at birth and monitored for several years on their natal and adjacent rookeries can provide a wealth of information beyond, say, original intentions of simply observing changes in maternal behavior with age (Reiter et al. 1981). Some things that would come out of such a study would be: age-specific survival, age at primiparity, age-specific fecundity, changes in reproductive value with age, and age-specific reproductive success (measured as giving birth). If the pups of these females were also monitored, additional useful information would
be obtained such as age-specific reproductive success (weaning a pup, having a pup survive to one year of age or to reproductive age). Of course, these are critical variables in modeling the behavior of populations. These data should fall out from the long-term studies of researchers primarily bent on testing theory, but the data also redound to the benefit of those concerned with predicting the vicissitudes of populations.

On the other hand, the focus on populations required by managers challenges theory-driven researchers to assess the biological implications of management policies and actions. For example, in their efforts to keep a population number near optimum, managers may decide to cull individuals. An example of the rationale from the northern fur seal operation in the Pribilofs is typical: "In the management of the fur seal herd, the Federal Government has adhered to a policy of taking pelts from seals considered surplus to breeding requirements (Baker, Wilke and Baltzo 1963)" or "the surplus males in excess of the reproductive needs of the population are harvested when they are between the ages of 2 and 6 years of age (Anonymous 1982)." The logic is impeccable if the population's interests are primary and that is the case for the manager. But most non-management scientists live in another world whose orientation begins with the study of individuals. To the latter, differential reproduction based on individual competition drives the system. We suggest that they take the manager's cull as a "natural" experiment, predict the results from theory and interpret the data. Ask what is the effect of artificially selecting out a large segment of the young male population annually. Competition for territories and access to females will certainly be reduced because there will be fewer males in competition. Is the sample of males culled biased in any way? This would have additional implications for subsequent genetic variation among males. Ask what is the effect of removing a portion of the subadult male population on females, their pups, and on the variance in the reproductive success of territorial males. Does management in the process of culling "... quiet(s) the very struggle for existence that has shaped these magnificent creatures over millions of years (Scheffer 1974, pp. 63)?" Observations on southern sea lions (Otaria byronia) are interesting in this regard. Vaz-Ferreira (1965, 1975) observed that males subordinate to those holding females during the breeding season, primarily subadults and juveniles, periodically invade as a group the harems ruled over by the dominant males. He reports that the raiders interfere with copulations in progress, abduct females and pups, copulate with females, and in the process injure and sometimes kill females and pups. Claudio Campagna and B. Le Boeuf observed similar behavior in Argentina and noted the importance of the number of peripheral males surrounding female groups. Does this behavior occur in northern fur seals? Perhaps it is not observed on St. Paul Island because culling subadult males occurs annually. However, the behavior has been observed recently on St. George Island where culling stopped in 1973 (Gentry, personal communication). The point is that systematic culling can have important effects on the population and the "experiment" can be interpreted on many levels. To the degree to which these effects can be specified, they provide another useful bit of information for the manager.
Although each development described is predicted to have an overall wholesome effect on future studies of marine mammals, there are potential problems to consider.

A considerable increase in the number of people doing research on marine mammals could give rise to two problems. Researchers could get in each other’s way. This is certainly a possibility in the long-term studies conducted on or near small islands or in the study of animals that appear predictably at the same place at sea on an annual basis. Cooperation and coordination of activities are required to avoid overlap of effort and interference. Marking animals can be a problem when many people are doing it. Ten years ago, a single group tagged northern elephant seals on islands off the coast of California and Mexico; today five different agencies are involved. To maximize the return for these independent efforts, there must be a network for standardizing procedures and communication of information. The Southwest Fisheries Center of the National Marine Fisheries Service is in a good position to coordinate this particular activity. Another problem stemming from the increase in research activity is disturbance to the animals under investigation. Unfortunately, we know little about the degree to which research activities are disruptive as each project and each species under study presents a different case. Marking and disturbance are two areas where federal monies earmarked for management of marine mammal populations might be well spent.

There is the danger that with a shift in theory everyone will go out and investigate only those behaviors relevant to the new paradigm. Indeed, this is the normal science, which Kuhn speaks of, that makes science go forward. Unfortunately, it also often blinds us to other things and alternate interpretations. There is another drawback. The underpinnings of social biology are genetics and the hiatus between the gene and behavior is immense. This has led to a flurry of armchair theorizing that far outstrips the data necessary for theory verification. Theory often explains data, but straining too hard for a fit is unwise. Theories come and go; the data do not change. This lesson is all too clear in reading some excellent data papers of two decades ago that are marred by time-locked interpretations espoused in the discussion sections.

Protecting animals by law and knowing them through scientific study are different values whose aims are implemented in different ways. The two are in conflict. Studying animals is potentially disturbing and interferes with protection; protecting animals limits their study. The law takes precedence. Scientists must compromise their principles and submit to the law. However, the scientific enterprise is delicate and the law is not sensitive to scientific exigencies. There is historical cause for concern. Presently, transgressions by a scientist are treated in the same way as unlawful dealing in walrus tusks or a fisherman shooting sea lions, despite the different motives of the scientist and the profiteer. This is ironic insofar as protecting animals depends on knowing them, which necessitates studying them. Furthermore, controlling the activities of scientists is such
a trivial matter when contrasted with the thousands of marine mammals that fishermen kill annually, with permission, incidental to catching fish.

The combination of recent protective legislation for marine mammals, rising public demand for animal rights and the popularity of the environmental movement is such that studying animals in the field and in the laboratory is not as simple a matter as it was a few decades ago. Conducting marine mammal research in the laboratory is much more costly today in large part because of the legal husbandry requirements. Tank dimensions must be proportional to the animal's size and expensive veterinary consultation is required. Consequently, outside of commercially self-sustaining oceanaria, not much behavioral work is being done on captive animals during this period of cutbacks in federal research funding, and future prospects do not look good. Obtaining permission to conduct laboratory and field work requires considerable time, energy and foresight, and inflexible rules in the permit procedure constrain research programs. Completing the permit procedure satisfactorily months in advance of the work is especially difficult for a researcher starting out on a new project. He must anticipate conditions and contingencies to which he has not yet been exposed. He must speculate about all manner of outcomes and inflate the numbers in his plan to cover all possible outcomes because, if the permit is granted, deviations from the stated program are not allowed without additional notification and review. This is a serious drawback, especially to the scientist in the field. The critical element of judgment is removed from his repertoire—the option of trying something else on the spot after getting feedback or following a lead that was not anticipated, *i.e.*, taking advantage of serendipity. The danger is that the deliberate, centralized permit procedure screens out what might be the most exciting discoveries, the unexpected ones. In looking back over his long illustrious career, the noted behavioral psychologist, B. F. Skinner, remarks, "I had a fundamental rule when I was doing experiments. If something interesting turns up, drop everything and go for it (San Francisco Chronicle, November 7, 1983)." The anarchy of science is most important for its successful conduct. If this kind of freedom is not preserved, many potential young marine mammalogists may end up studying other animals that are not being "managed" or that are too lowly to be "saved." We must address the fact that the Marine Mammal Protection Act, and the manner in which it is enforced, play an important role in determining the way in which marine mammalogy develops or does not develop. Only a small amount of tinkering and tweaking of the permit process is necessary to give the scientist the flexibility required to do his job well. In the long run, this would enhance our understanding of marine mammals.

**Conclusion**

We think the future study of marine mammal behavior is on the whole promising. Invaluable long-term studies of whales and seals involving individual marking and life history study are in process. These will complement the valuable research programs being conducted in the laboratory on ontogeny, imprint-
ing, habituation, sensitization, associative and complex learning, learning within a social context, perceptual sharpening and motivation. The study of some land-breeding pinnipeds will be important for testing predictions from current social theory and this promises to increase our understanding of sexual selection and the evolution of polygynous breeding systems. Cetacean research is in the process of going beyond simple description to question-oriented research. Many different species are being studied from a variety of points of view and the federal government is financing this research along broad lines. The two worlds inhabited by management and non-management science must be integrated; increased communication and exchange would be mutually beneficial. Marine mammals bring together many people with different values and specific interests. The distance that separates the diverse positions of sealer, manager, scientist, conservationist and preservationist is vast and perhaps unbridgeable (Busch 1984). If connections can be made, it is on the common ground of understanding the marine mammals through study while respecting the different approaches and the ultimate goals of each party.

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