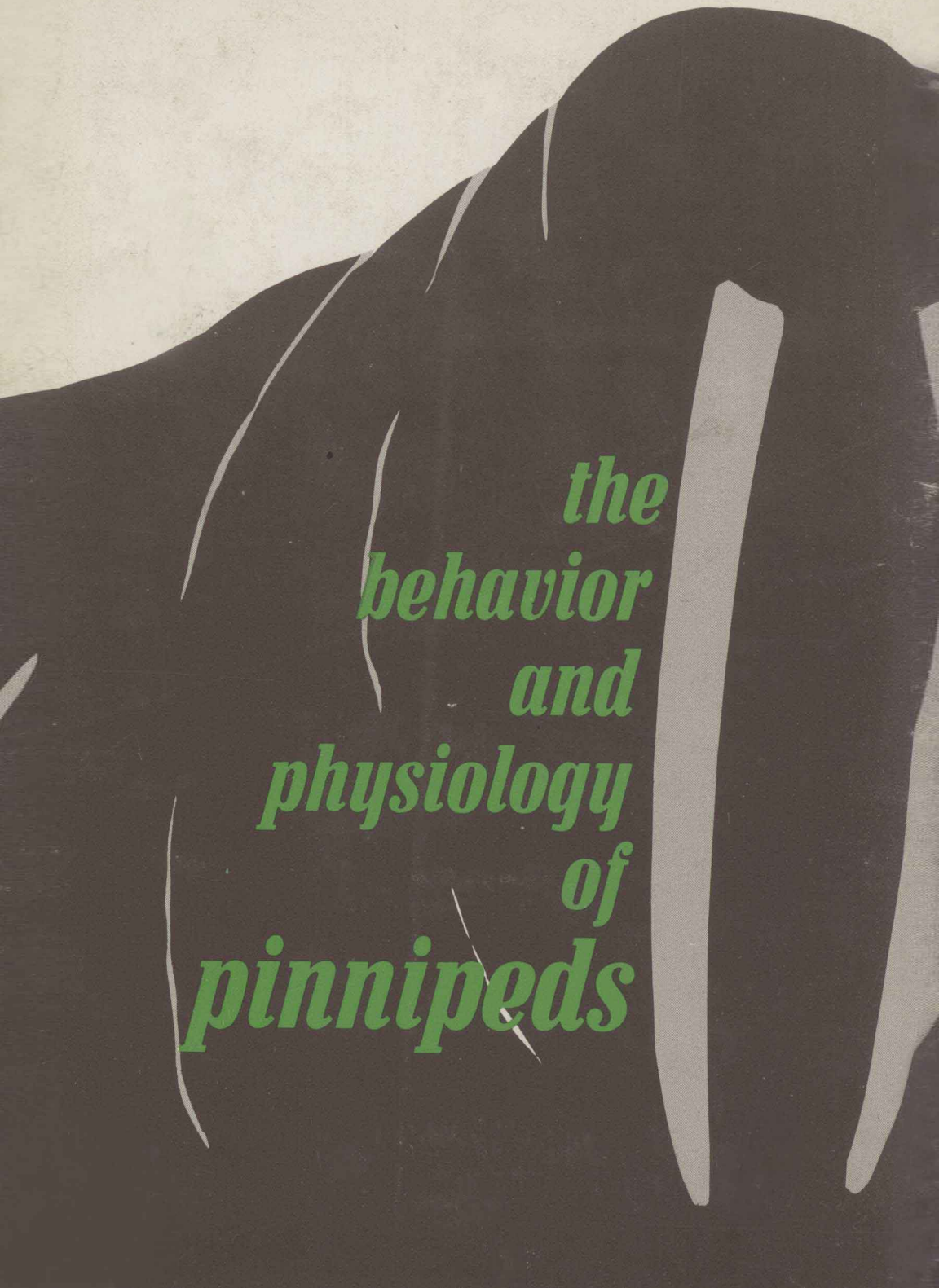
Harrison Hubbard Peterson Rice Schusterman



the behavior and physiology of pinnipeds

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Preface

During the past decade, scientific and public interest in marine mammals has experienced a sharp growth. Most notable has been the popularization of the porpoises and whales in general. This book is about another order of marine mammals, the Pinnipedia, which includes the seals, sea lions, and walrus. Previously no single volume has been available to serve as a foundation for current and future research with the pinnipeds. To meet this need, this book seeks to provide broad basic information about accomplishments in pinniped research, as well as insights into current methodology, recent research results of particular significance, and practical information concerning the health and husbandry of laboratory colonies of pinnipeds.

A significant portion of the scientific interest in pinnipeds has centered around their evolutionary adaptation from a terrestrial to an amphibious existence. Man's curiosity in this area is especially stimulated by the invidious comparison to himself. When moving from land to water, man is severely handicapped and has had to develop elaborate artificial devices to allow even limited occupancy of the seas, whereas the pinnipeds are equipped to move freely from the water medium to air and return with remarkable facility. Under water, man is hard of hearing and his vision is extremely poor; recent research indicates that at least some pinnipeds can see and hear well in both media. Man can stay submerged unaided for a minute or so before requiring respiration, but the many pinnipeds stay beneath the surface for much longer and expend a great amount of energy before surfacing for air. Man is often adversely affected by the pressure changes encountered two or three meters below the surface, whereas pinnipeds have been known to dive to depths beyond 100 meters and return quickly to the surface with no ill effect. These and other facts have aroused the curiosity of scientists of many disciplines, particularly the physiologists, who would like very much to understand the elaborate diving physiology of this animal.

To regard their behavioral and physiological adaptations to amphibious life as the exclusive reasons for studying these animals would be unfair. Ethologists have long been interested in pinniped social structures, communication techniques, and ecological roles, and each of these subjects is still causing heated discussion and enlightening research. Valid information of this kind can only be obtained in the natural surroundings of the undisturbed animals. Therefore, from

almost pole to pole and from above and below the surface of the sea, man is actively observing and recording the behavior of pinnipeds.

Some studies, however, require that the animal be observed in a controlled experimental environment. This is true of both physiological and behavioral research, and in the past few years more and more laboratories have acquired and kept pinnipeds for research purposes. The comparative psychologist, for example, has studied the visual, auditory, and problem-solving abilities of pinnipeds under rigidly controlled conditions. These studies have enabled us to obtain a clearer picture of the pinnipeds' position among animals. Similarly, the psychologists' laboratory studies of social behavior have provided useful checks of hypotheses formulated by the ethologists' observations in the natural habitat.

Both laboratory research effort and the expanding number of commercial exhibits have increased the number of pinnipeds held in captivity. It is vitally important that the animals being studied or exhibited be healthy. Yet up to very recent times, little veterinary research had been conducted with pinnipeds. It is also true that there was relatively little known about appropriate diet, caging, and husbandry. Many contradictory views were held as to best procedures for keeping animals, and mortality rates were high. This dearth of factual information still prevails, but currently a serious effort is being made to obtain a foundation of sound animal care practices. A section of this book serves as a first step in that direction. Although admittedly only a beginning, the best judgments available are offered and they are based on practical experience and a thorough review of the existing literature.

The organization of the book deserves some clarification. There are four sections: two sections on behavior, one being largely ethological under the leadership of Richard Peterson, the other primarily laboratory studies of behavior under the supervision of Ronald Schusterman; a section on general physiology, developed by Richard Harrison; and a section on husbandry and animal care, directed by Richard Hubbard. Each of these authors was responsible for writing a chapter designed to provide a broad fund of information in his general field of pinniped research and to delve more deeply into his particular research problems. Several shorter papers representing useful and recent developments that are relevant to specific sections of the book have been contributed. We are grateful to these authors for helping to sharpen the focus on several research areas of considerable recent interest.

It is a pleasure to acknowledge with gratitude the work of those who have made the book possible. Since it is reproduced by photo offset, the production work for the finished chapters was largely done before the final copy was sent to Appleton-Century Crofts. Special thanks goes therefore to Stanford Research Institute for the services of an excellent staff. Those who worked, hard, long, and well to produce the text were Marlene Adams, Ellen Brandt, Merle Holmwood, Patricia Howard, Charlotte Matthews, Frances Maurier, Terri Paquette, and Valera Peterson.

The authors and I wish to express our appreciation to our colleagues who have read and commented upon various chapters. The responsibility for the pub-

lished work remains with the authors, and the scientific endorsement of the content by those who have so kindly given their judgments is not implied. The official reviewers include George Bartholomew, Lawrence Irving, Ian McLaren, Victor Scheffer, William Schevill, and John M. Warren.

In addition, we wish to thank the following publishers for permission to reprint portions of previously published research material appearing in this book: *Journal of the Acoustical Society of America, Journal of the Experimental Analysis of Behavior, Journal of Zoology, Mammalia,* and *Science.*

Charles E. Rice
Coordinator and Editor

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PART I

Ethology and Ecology

1

Social Behavior in Pinnipeds

with Particular Reference to the Northern Fur Seal

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INTRODUCTION

Georg Wilhelm Steller, marooned on Bering Island in 1741, became mystified and intrigued by the elaborate social organization of the seals and sea lions that thronged the island. He built a small observation blind in the midst of one of the rookeries of fur seals and prepared a remarkably concise behavioral description, one of the earliest ethological analyses of any mammal (Steller, 1751; Stejneger, 1936; Ford, 1967). Steller's picturesque descriptions of the formal harems, raucous vocalizations, solicitous care of the young, and dense aggregations of thousands of animals soon aroused the curiosity of many naturalists. Why do these "cities of seals" occur? Can they provide insight into the workings of other mammalian social systems, particularly those of man?

Since Steller's time, literally hundreds of authors have published anecdotal descriptions of the behavior of pinnipeds. Few workers have yet been able to quantify their observations, to compare the various pinnipeds, or to

analyze the functions of the behavior patterns they have described. Many descriptions have been incidental to other work: to commercial exploitation, or to traditional biological studies such as anatomical or reproductive investigations. Three penetrating analyses are those of Nutting (1891), Bertram (1940), and Bartholomew (1952), all of whom have compared the pinnipeds and proposed theoretical explanations for their complex behavior.

Since these papers were written, considerable new information has been collected, and this chapter is an attempt to discuss the pinnipeds in light of recent work. Much remains unknown, and I have had to draw on many anecdotal accounts and preliminary investigations. Many generalizations are based on a few species, particularly those that I have studied. The best known pinnipeds are the fur seals, especially the northern form, *Callorhinus,* and the elephant seals, *Mirounga.* It should be noted that the fur seals and the elephant seals are, in some respects, more highly specialized than other pinnipeds. It is entirely possible that comparisons based on these atypical species are misleading. I hope that my generalizations, even when incorrect, may stimulate in some small way further investigations of pinniped behavior.

Methods of Study

Pinnipeds generally come ashore on desolate islands, reefs, or ice floes. If a man can gain access to one of these places, as Steller did, he can learn a great deal, since the animals tend to be relatively unafraid of man, rather immobile, and often remain in plain view on open beaches for long periods of time (Fig. 1). Anyone who has attempted to watch wild mammals knows that these characteristics are typical of very few other groups.

Nevertheless, analyses of the social and reproductive behavior of pinnipeds have not yet progressed as rapidly in obvious directions as might be hoped. For example, some of the most accessible species have received little attention, while exotic forms living near the poles have attracted investigators. Thus the first behavioral study of gray seals (*Halichoerus grypus*) in the western Atlantic has only recently been completed (Cameron, 1967), and the California and Steller sea lions (*Zalophus californianus* and *Eumetopias jubata*) have likewise received little attention despite the proximity of their rookeries to North American cities.

A number of special problems present themselves in study of pinniped behavior and offset the ease of the observational aspect of study. The primary problem is study of behavior when the animals are at sea (see "The

Fig. 1 PORTION OF KITOVI ROOKERY, ST. PAUL ISLAND, ALASKA, USED FOR AUTHOR'S BEHAVIORAL STUDY OF NORTHERN FUR SEALS FROM 1961 TO 1963.

Marine Environment," next section). In addition, there are numerous problems associated with marking individual animals for behavioral study. Such markings must not interfere with the animal's normal behavior, and should be visible from a distance. Scheffer (1950) summarizes various techniques that have been tried for marking fur seals. I know of no method that satisfies all the requisites, but new techniques are developing rapidly. High-temperature branding tends to be injurious, but cryogenic branding may be satisfactory (M. Keyes, personal communication). Bleaches, paints, and dyes can be used for temporary marks and do not necessarily require capture of the animal (Peterson and Bartholomew, 1967). Small tags of noncorrosible metal can be used for permanent marking but may lead to slightly increased mortality (Roppel et al., 1965, p. 19) and are generally not satisfactory for identification of animals from a distance. Some animals can be easily approached or captured for marking; others, such as fur seal bulls, are too large and dangerous. Experiments in immobilizing large pinnipeds with drugs have been undertaken on several species (Peterson, 1965a; Ling, et al., 1967).

Phylogeny

There are three families of pinnipeds: the Phocidae or "true seals," the Otariidae or sea lions (including fur seals), and the Odobenidae or walruses. The interrelationships of these families are not yet fully understood since the fossils that have been found are inadequate to provide a clear picture of their evolution. A few generalizations are possible, however. The Phocidae may have descended from an otter-like ancestor, and the other two families from a bear-like carnivore (McLaren, 1960). Fossils thought to be counterparts of the present-day families (Mitchell, 1966) have been taken from strata deposited in the early Miocene (20 to 25 million years ago), suggesting that the seals, sea lions, and walruses have evolved separately for a very long time (see Fig. 2 for one interpretation of pinniped phylogeny).

From the viewpoint of comparative behavior, the rather ancient origin of the different families is important. The parallels in behavior, such as the widespread "polygynous" breeding pattern, may reflect convergent evolution of different stocks inhabiting similar ecological niches. Comparison of the ecology of the modern forms may, then, lead to a better understanding of the significance of the puzzling behavior patterns they exhibit. Because of the prolonged phylogenetic separation of the groups, there is less reason to suspect that similar behavior is simply a reflection of common ancestry.

THE INFLUENCE OF ECOLOGY

General

There can be little doubt that the elaborate systems of social organization seen in pinnipeds have appeared, first and foremost, as adaptations to an amphibious mode of life. In other words, the combination of marine and terrestrial environments has imposed many kinds of unusual selective pressures on pinnipeds. Some correlations between ecology and behavior are immediately apparent: for example, the use of isolated islands for breeding certainly relates to the presence of predators on the mainland and the terrestrial immobility of animals with limbs adapted for swimming. Again, the extreme density of breeding aggregations may be related to specialization of the eyes and ears for underwater use; it is reasonable to guess that short-distance aerial communication would be simpler than long-distance signalling with aquatic-adapted organs, hence selection for compact breeding colonies.

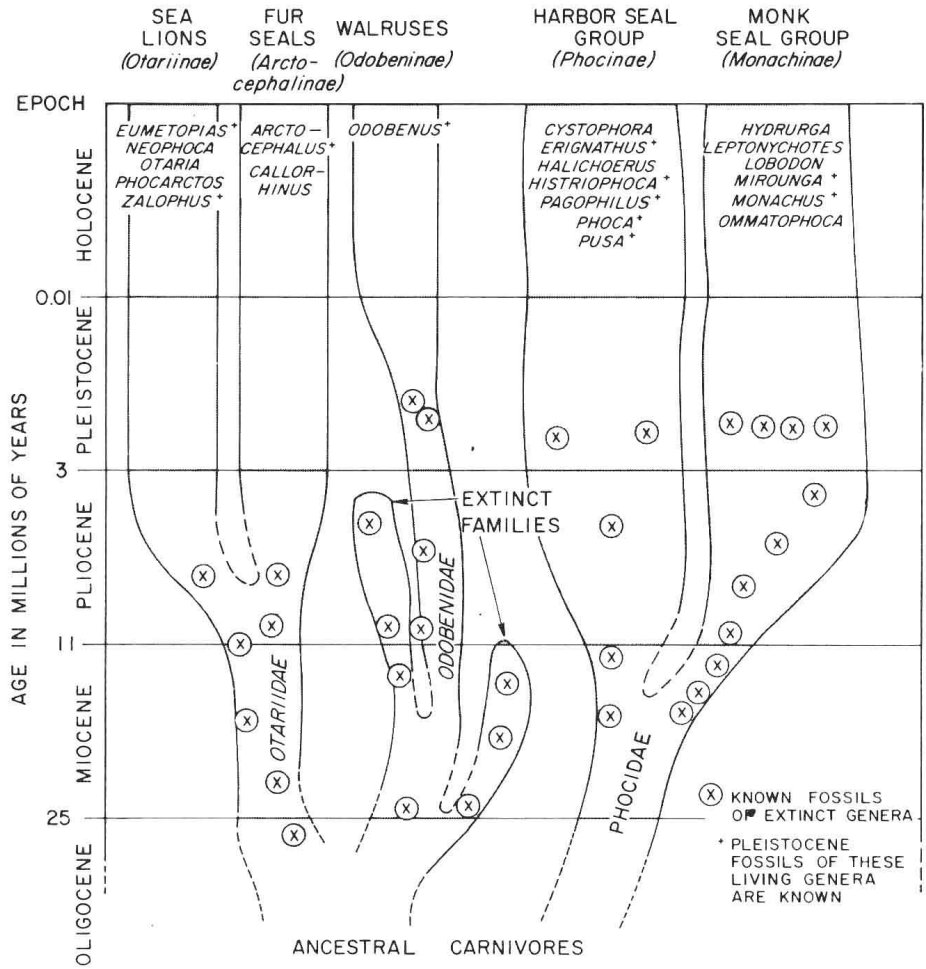

Fig. 2 AN INTERPRETATION OF THE RELATIONSHIPS BETWEEN DIFFERENT KINDS OF PINNIPEDS, BASED ON FOSSIL RECORDS. The exact times of the divergences between different groups are still open to speculation; this chart represents a current view. Thanks to Charles A. Repenning for preparation of this figure.

Because of relationships of this kind, a consideration of pinniped ecology and ecological history is needed as a basis for a realistic examination of social behavior.

Ecological History

The fossil record of the pinnipeds has many major gaps, and it is therefore very difficult to infer what environmental factors led primitive land mammals to begin seeking food at sea. It seems logical to suppose that protopinnipeds found abundant food along the shores of the sea, lakes, or streams, and most authors who have considered this subject (see Howell, 1930; Davies, 1958; McLaren, 1960) hypothesize that the early pinnipeds were lacustrine, or inshore animals. The otariids, for example, are thought by Scheffer (1958) to have evolved in the protected, food-rich kelp reefs of the North Pacific, inhabiting an environment similar to that of present-day sea otters. Adaptations may have appeared gradually or suddenly (Downs, 1956; Davies, 1958), which permitted the early pinnipeds finally to exploit the open seas.

Many behavioral patterns seem to have been modified or developed anew as the animals evolved more amphibious habits, but some patterns clearly reflect their land-carnivore ancestry. For example, as pinnipeds became adapted to life at sea, the mammalian pattern of sexual reproduction may have been a critical limiting factor. Reproductive processes are closely related to social behavior. Internal fertilization of the ovum, intrauterine development of the embryo, and nourishment of the newborn young with milk are adaptations which few aquatic animals exhibit, and it seems likely that these processes evolved in land animals partly as adaptations to life in air. Thus, as a terrestrial mammal entered the sea, rather profound alteration of the behavioral patterns accompanying reproduction would probably be necessary. Whales, which give birth, suckle, and mate at sea, evolved elaborate adaptations, but not the pinnipeds, which give birth to their young on shore (or on ice). In most species, nursing is a terrestrial activity, and in many, copulation is also confined to land. Except for the existence of ocean-dwelling whales, it might be theorized that the restrictions of pinnipeds were related to an inflexible mammalian reproductive pattern tying them to land for parts of their lives. Since the whales are phylogenetically older, one could theorize that the seals are in a transitory evolutionary stage, and in their present form