

### REVIEWS

COMMUNICATION AND BEHAVIOR OF WHALES. R. Payne (ed.). American Association for the Advancement of Science, Selected Symp., 76:xii + 643 pp. 1983. (Westview Press, 5500 Central Ave., Boulder, Colorado 80301). Price \$37.00 (soft).

Advances in our knowledge of the lives of mammals and the forces that mold them have followed a similar progression for most taxonomic groups. Initial phases are based on inferences drawn from examination of specimens and anecdotal glimpses; intermediate stages involve quantitative field observations of behavior and ecology. The latter phases typically bear fruit in terms of the construction of numerous hypotheses, the predictions of which are tested through comparative studies and experimental manipulation to lead towards a conceptual synthesis. For a variety of reasons, progress along this path follows an uneven pace in different groups of mammals. Despite the breadth implied by its title, this book does not provide a conceptual synthesis on communication and behavior of whales, but such a phase may be premature. The book does, however, represent a large leap forward in that it heralds the entrance of a rigorous, analytical field approach to the study of whales. The editor (who also co-authored four of the papers) provides an introduction outlining the scope and development of the work covered by the volume, as well as subject and author indices. Most of the papers are based on data collected over a span of one to three field seasons (longer periods are covered in some of the right whale work) and share elements that have led to successful advances in field studies of other large mammals over the past two decades: logistically accessible but relatively unmolested study populations, an ability to recognize individuals based on natural markings, and a dedicated corps of researchers.

Part I, Vocalizations, consists of five chapters, the first three dealing with analysis of humpback whale sounds recorded around the Hawaiian Islands during the winter breeding and singing seasons. K. Payne *et al.* summarize the elaborate but orderly structure of humpback whale songs and define their components and dynamics. Songs are composed of single note units grouped into set phrases (often with subphrases) repeated variable numbers of times to form themes. Themes are repeated in a highly predictable sequence as songs of up to 26 min duration. An individual may link songs together continuously for several hours in song sessions. The authors show that songs regularly change at all levels of structure. Greater change occurs within seasons than between years, and within any season all individuals in the area seem to keep up with the course of these changes and produce the same song. The dynamic nature of humpback song may somehow be a result of female choice of singing males as mates. This paper concludes with a brief comparison of various kinds of animal "songs" and groups them based on methods of introducing variability; humpbacks rank among the most complex. Guinee *et al.* demonstrate that the seasonal changes in humpback song cannot be explained by different individuals entering and leaving the local population. They successfully recorded three individually distinctive whales at intervals of 39 to 329 days and show that changes in each animal's song parallel changes in the entire population. Frumhoff pays particular attention to features of "aberrant" songs for clues to general rules of structure and dynamics. Humpbacks consistently sing themes in the same order and almost invariably include certain "fundamental" themes. However, a few individuals employ sequences

that violate the population-wide order of transition and some also omit certain fundamental themes. The results are aberrant songs, which can be categorized based on the complexity of deviation from typical song. Frumhoff suggests that the aberrant singers may be young whales learning how to perfect this elaborate display. A fourth paper on humpback song is found in Part 3 where R. Payne and Guinee show that the complex changes in Hawaiian humpback song are also followed by humpbacks 4,700 km to the east near the Revillagigedo Islands, probably as a result of individuals travelling between the two areas carrying the changes with them. If this is true, authors conclude that genetic interchange can be implied by song similarity, particularly since the song appears to be a male breeding display.

Two papers on vocalizations of other species complete Part 1. Ford and Fisher present results of their study of structurally discrete categories of the pulsed calls of killer whales along the coast of British Columbia against a background of general information on the species' communication and social structure. Killer whale pods each possess repertoires of discrete pulsed calls which may remain stable for ten years or more. Closely-associated pods with overlapping ranges have calls in common, but distinct calls are found in the repertoires of less closely associated groups and widely segregated pods show no calls in common. These calls probably function to maintain pod cohesion and coordination of movement. Pods seem to consist of kin groups that remain stable for many years, but because they frequently mix in short-term association with other pods, the authors hypothesize that the existence of group-specific calls may be of importance in keeping pods intact. Clark presents results of a quantitative and methodologically unique descriptive study of the low frequency acoustic repertoire of the southern right whale. He provides good evidence that blows are modified to form harsh and growl-like sounds used as threats, that tonal calls with FM upsweeps are contact calls, and that complex calls with harsh and pulsive qualities are aggressive sounds. Broad results from this objective analysis follow developing generalized concepts of the structure and function of mammalian vocalization.

Part 2, Behavior on Breeding Grounds, consists of four reports. Darling *et al.* present their observations of individual humpback whales wintering off Maui. Photographic records of at least 264 individuals were compiled over three winters; sightings suggest a considerable flux of individuals as the season progresses. Information on composition of social groupings and behavior of individuals suggests that singers and escorts, which also show more abrasions and scars, are males competing for mates. Glockner and Venus present further data on individual humpbacks that winter off Maui, including details on features used for recognition, relative growth of calves, and cow-calf behavior. Norris *et al.* provide qualitative observations on the behavior and ecology of gray whales near Baja California and combine these observations with information in the literature to revise certain aspects of thought on the annual cycle of this species. R. Payne and Dorsey use photographic records to show that callosity coverage of certain areas of the heads of female southern right whales is less extensive and the callosities themselves are smaller than on whales suspected to be males (based on substantial circumstantial evidence). Right whales seem to avoid contacting each other with these callosities except during probable aggressive encounters, and resulting scrape marks are more prevalent on males. The authors present their findings as the first example of sexually dimorphic structures used for aggression in baleen whales. Some readers may find this conclusion premature due to the indirect methods of measurement and the assumptions involved in determining sex. Additionally, the dimorphism involved, although statistically significant, is minor (only a few percentage points in coverage) in comparison with typical sexually dimorphic features used as weapons in terrestrial mammals.

Part 3, Migratory Destinations and Stock Identification, consists of the paper by Payne and Guinee on humpback songs as indicators of stocks and a paper by Darling and Jurasz, which documents movements of seven individually identifiable humpbacks from Alaska in summer to Hawaii in winter. Some individuals were seen together in close proximity in both places, one was seen again in Alaska to complete a round trip, and an

eighth was found near the Revillagigedo Islands in winter two years after being photographed in Hawaii.

Part 4, Research Techniques, contains two papers. R. Payne *et al.* describe in great detail their methods for identifying individual right whales in the field, based on 16,000 photographs taken off Peninsula Valdes, Argentina. Individuals can be identified based on callosity characteristics and location, pigmentation patterns and wounds. There are also probable differences in callosity patterns among right whales from different oceanic regions. This chapter is a reprint of a Marine Mammal Commission contract report which has been available as a National Technical Information Service publication (PB81-161093) since 1981. Glockner describes methods for determining the sex of humpbacks based on underwater lateral views of the area posterior to the genital slit. She also provides information on sexual differences in pigmentation patterns and behavior and on the even sex ratio in 33 calves.

Part 5 is an annotated bibliography on humpback and right whales compiled by Bird. It will be of great value to workers in this field, and covers 390 references on humpbacks and 194 on right whales, grouped separately for each species. Each entry is numbered and annotated. Separate author, subject, geographic and journal indices are provided for each species.

I liked this book, learned a great deal from it, and am inspired by the obvious devotion of the investigators. There are points about the book, however, that may annoy or disappoint some readers. In the Introduction, Payne strongly emphasizes the virtue of field studies over the dissection of specimens. Workers who have salvaged carcasses will be somewhat dismayed at this position, particularly because much of the basic framework of ideas about whales rests on their labor. Field studies are an advance, but examination of specimens is an important antecedent. For example, the assumptions that the winter singing season is the breeding season for humpbacks, that postpartum estrus can occur, or that sex can be determined in the field all are founded on prior analysis of the reproductive tracts of salvaged specimens or the examination of whales taken in fisheries.

There is an uneven quality to the papers reported here. Perhaps this is due to differences in the extent of the internal review: some chapters acknowledge the help of outside experts, others only a few co-workers in their own narrow fields, and some acknowledge no review at all. Although there is no question as to the scientific rigor involved in the collection and analysis of the data presented in the paper, I felt that some discussion could have benefited had it been steered more towards functional and theoretical perspectives. For example, it would have been more profitable, in my view, to see greater exploration into the functions of humpback song and its dynamics than a ranking on a continuum from crickets to humans or comparisons with the structure of the songs of largely monogamous and territorial birds. However, this book was a long time in the making (the symposium was held the first week in January 1980 and the book published December 30, 1983) and some of the discussion lacking on this particular topic has appeared prior to its release (*see*, for example, Tyack, 1981. *Behav. Ecol. Sociobiol.* 8: 105-116 and Tyack and Whitehead, 1983. *Behaviour* 83:132-152).

There is some very rich information here waiting to be treated within the framework of what we currently know about the evolution of mammalian mating systems, sexual selection theory, and various determinants of social structure, behavior, and life history strategies. However, the book does not contain summaries that try to tie the basic information presented together. This would have been useful, particularly for the studies done by the same teams at the same sites and times that were reported as separate chapters. The sequence of information was also difficult for me to follow. Research techniques were covered in the last section of papers, and chapters skipped around among species. I ended up reading all the chapters on humpbacks together, for example, to get a more coherent picture of their biology. I would also have preferred more objective substitutes for terms like "corpses" and "culture" that were not edited out. However, the book was otherwise generally well-edited and I noted only a few misspellings and other errors. Reproduction of a few of the photographs was not suitable for clear illus-

tration of individual features. The reprint of the NTIS report and the bibliography may not be of interest to all readers, but together they constitute more than one-third of the book. Summary discussions might have more profitably utilized some of this space.

As pointed out earlier, the work presented represents a welcome new era in the study of whales and the value of the book far outshadows the above criticisms. I do not hesitate to recommend this book for the libraries of all marine mammalogists. Others interested in mammalian behavior and communication will also appreciate many of the contributions it contains. Graduate students would do well to spend many hours discussing the book and the points of conjecture it raises. There is no doubt that much of the information found in this book will be considered landmark material that will be cited for many years to come, and the efforts of all the contributors are to be applauded.

THOMAS J. O'SHEA

U.S. Fish and Wildlife Service  
Denver Wildlife Research Center  
412 N.E. 16th Avenue  
Gainesville, Florida 32609