

Ethology and Behavioral Ecology of Marine Mammals

Series Editor

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The aim of this series is to provide the latest ethological information on the major groupings of marine mammals, in six separate books roughly organized in similar manner. These groupings are the 1) toothed whales and dolphins, 2) baleen whales, 3) eared seals and walrus, 4) true seals, 5) sea otter, marine otter and polar bear, and 6) manatees and dugong, the sirens. The scope shall present 1) general patterns of ethological ways of animals in their natural environments, with a strong bent towards modern behavioral ecology; and 2) examples of particularly well-studied species and species groups for which we have enough data. The scope shall be in the form of general and specific reviews for concepts and species, with an emphasis especially on data gathered in the past 15 years or so. The editors and authors are all established scientists in their fields, even though some of them are quite young.

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Editor

Ethology and Behavioral Ecology of Odontocetes

 Springer

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Cover illustration: On the left: Part of a subgroup of rough-toothed dolphins, *Steno bredanensis*, off Kona, Hawai'i. They have very large brain to body size ratios, and sophisticated rapid learning. Photo by Deron S. Verbeck. On the right: Short-finned pilot whales, *Globicephala macrorhynchus*, socialize in the waters off Tenerife, Canary Islands. Photo by Teo Lucas.

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Dusky dolphin (*Lagenorhynchus obscurus*) males “scramble competing” for a female below and in front of them, with males leaping high to home onto the female, and very rapidly to out-leap/out-distance other males. These races and leaps take much energy, can go on for more than one hour, and are part of the multi-male/multi-female system of sexual strategy quite common in delphinid society. While several males inseminate a female during her estrus, they also have large testes and compete not only by behavior as shown here but by sperm competition of volume of sperm in one female at one time of estrus. Researchers are just now beginning to unravel aspects of behavioral and possible physical/physiological female choice that must be very important in scramble competition strategy (Photo by B. Würsig, reprinted from cover of *Aquatic Mammals* 2018, 44(6), with permission)

*Dolphin, leaping high in the sky
Diving deeply, far past our sight.
You seem quite joyful, and adventurous. . .
And yet, we hardly know you.*

*Decades of research
Following in small boats.
Documenting behaviors from oceangoing
ships
Tracking and observing from high cliffs.*

*We immerse ourselves in water
To chance upon an intimate glimpse of life.
What is your fabric of society?
How do you relate to others; what do they
mean, to you?*

*What clues of life can we learn
To study foraging, social, sexual, calf rearing,
predator avoidance behaviors?
These are, in so many ways, mysteries. . .
And so, in we dive.*

**Robin Vaughn-Hirshorn
Mt. Airy, MD, USA**

Introduction to the Series

We are pleased to provide the reader with a series on ethology and behavioral ecology of marine mammals. We define ethology as “the science of animal behavior” and behavioral ecology as “the science of the evolutionary basis for animal behavior due to ecological pressures.” In our assessment, those ecological pressures include us, the humans. We determine, somewhat arbitrarily but with some background, that “marine mammals” are those mammals that habitually feed in the sea, but also include several mammals that went from saltwater oceans back into rivers, as seen in the chapter by Sutaria et al. in the first book of the series (Odontocetes).

Thus, we include toothed whales (the odontocetes) as Book 1; baleen whales (the mysticetes) as Book 2; sea lions and fur seals (the otariids) as well as the walrus as Book 3; true seals (the phocids) as Book 4; the special cases of sea otters and polar bears as Book 5; and manatees and the dugong (the sirens) as Book 6. Now, each of our chosen editors and their chapter authors have their own schedules, so the series will likely not arrive in the order given above, but we have full faith that within the next 5 years, i.e., 2019–2023, all six marine mammal books on “Ethology and Behavioral Ecology of Marine Mammals” will have seen the light of day, and you, the readers, will be able to ascertain their worth and their promise, as to present knowledge and to accumulating data while our fields of science advance.

For those of you paying close attention, we admit that not all mammals that occur in marine waters are represented, nor all who have gone back to freshwater. Thus, there is nary a mention of marine-feeding bats, marine-feeding river otters, those aspects of beluga whales who foray way up into major rivers, seals living in land-locked lakes at times thousands of kilometers from the ocean, and other species that occasionally make the marine environment or—as generally accepted marine mammals—adjacent freshwater systems their home. Such are the ways of a summary, and we apologize that we will not be able to please all.

As the series editor, I confess to having been a science party to all of the major taxonomic entities of this series, but this is only because I have been in the marine mammal field for about 50 years now, with over 65 graduate students who—in aggregate—have conducted research on all continents, and in no manner do I

pretend to have kept up with all aspects of diverse fields of modern enquiry. It is a special privilege (and delight) to have multiple up-to-date editors and their fine authors involved in this modern compilation, and I am extremely grateful for this. I am learning, still and ever.

I confess to lending only a minor hand to all but the first book on odontocete cetaceans. At first, it was envisioned that each book be similar to the structure of that first book, with a general section on patterns of ethology, and several in-depth species-specific chapters after that. But chosen coeditors for the other books soon told me that this would not work—the knowledge base of other-than-odontocetes is simply not the same for those other taxa, and the books need to represent this. I (at first reluctantly) agreed. We are here to provide the reader with up-to-date excellent new summaries of the state of the art of these taxa, and it would be inefficient to stick to a particular formula of presentation for all. Each chapter is excellently reviewed by the book editors, peer reviewed by other scientists as chosen by the editors, and perused and commented on by me. If you learned something new and imparted that to your colleagues and students, then the series and sections of it shall have been worthwhile.

With respect and best wishes

Tortolita Desert, AZ, USA
December 2018

Bernd Würsig

Preface

It is tremendously satisfying to help put together a book of this nature, an up-to-date summary of data and thoughts about ethology and behavioral strategies of odontocetes, the toothed whales. Choosing the authors (who chose their own coauthors, if any) was a challenge—each and every subdiscipline of our wonderful field could have had other talented authors, from overall topics such as mating strategies, mom-calf rearing, and foraging to specifics of a chosen few species with goodly amounts of data (and many more would have been possible to represent), and could have gone in many different ways. But the authors who said “yes” rose to their task in an admirable and timely fashion and produced what I (in an admittedly biased view) consider to be a wonderful compendium, suitable as a “kick-off” (chose either traditional football or the US version as analogy) to other editions to come forth, on the same topic with 2, mysticetes; 3, otariids and walrus; 4, phocids; 5, sea otter and polar bear; and 6, sirens. I am pleased by the results from this first volume on odontocetes and hope that you may be as well.

The layout of this book is in two parts: (1) general patterns and (2) species examples. Chapter 1 (Gowans) discusses grouping patterns and potential reasons for these, and somewhat laments the present state of our science, where we are learning much about overall patterns but are still in early steps of delving into individuality of dolphin societies, i.e., how does each dolphin—with its own uniqueness—adapt and survive within the society. I will come back to this point in the final short chapter of this volume, as I believe it important in addressing our concept of “dolphin” as an individual interacting with others in a complex society. Chapter 1 lays the groundwork for all chapters to follow, and there are references of all other chapters in this one. I regard it seminal to the flow of the book.

Chapter 2 (Tyack) provides us with a primer to modalities of communication, with the understanding that communication is of vital importance in the flow of information of societal creatures. Chapter 3 (Vaughn-Hirshorn) takes us into a discussion of one of the most important requisites to sustain life—feeding, and Chapters 4 (sexual strategies, Orbach) and 5 (maternal care, Mann) discuss what comes out of successful feeding—the capability and promise of making new life.

Chapter 6 (Bräger and Bräger) discusses how odontocetes move relative to requisites of food, predator avoidance, and social-sexual rearing of young, and Chap. 7 (Srinivasan) reminds us that neither feeding nor sex nor calf rearing will work successfully if a dolphin is maimed or killed by a predator. “The ecology of fear” is indeed a major guidance for sociality of odontocete cetaceans.

The final three chapters of this first section illustrate diverse parts of odontocete cetacean life. Chapter 8 (McHugh) summarizes the excellent knowledge we now have of social strategies and tactics of odontocetes close to shores, and Chap. 9 (Mesnick et al.) discusses the amazing “other” needs of dolphins and multi-species societies of delphinids in deep waters, far from shores, with the eastern tropical Pacific as a major rather well-studied paradigm. Both authors highlight that dolphins near shore and in deep oceanic waters have been and are subject to intensive (and very different) human-caused influences. This topic is admirably taken up in the final chapter of this session, Chap. 10 (Bearzi et al.), with a cogent and up-to-date discussion of odontocetes adapting—as much as may be possible—to human activities, and we humans attempting to do likewise.

As in any compendium of this sort, there are editorial needs of regret, and I will not hide mine. I am sorry that we did not get into the lovely topic of dolphins and other toothed whales diving (they spend most of their lives underwater, after all). We are learning about social communication, potential coordination, and affiliation needs of odontocetes somewhat and way below the surface of the water, and we have inadequately represented this topic here. As well, there are details of certain societies, such as those of isolated islands and atolls, which show us strong indication of operating differently simply because of such isolation. While there are references to such excellent works, it would have been good to have a separate chapter on “insularity,” but this did not happen due to author constraints on time. Similarly, we are missing a chapter on intelligence and cognition, including the topic of grieving. Much ink has been spilled elsewhere on topics related to potential mental experiences, and we do attempt to lead the readers to that vast literature, especially in Chap. 23 (Würsig). Finally, the concept of culture—of passing on learned traits from generation to generation (and, at times introducing new behaviors, “fads,” rapidly within one generation)—could have had its own chapter. Much has also been written about it, and I hope that references to culture throughout the book will help give the reader a flavor of the importance of this topic.

The second part of this volume, on examples of odontocete knowledge, largely follows a species by species plan. We move from matriarchal societies (Chaps. 11, 12, and 13, with authors Ford, Cantor et al., and Boran and Heimlich, respectively) to two examples of beaked whales (Chap. 14, Baird, of animals believed to be not so social), to our best examples of long-term research on dolphins, the common bottlenose (Chap. 15, Wells) and Indo-Pacific bottlenose (Chap. 16, Connor et al.) dolphins of generally near-shore waters. These two chapters provide much of the informational depth to discussions of sociality for the rest of the book, represented well by Chap. 1 (Gowans). Again, other species and species groups could have been chosen, such as on our quite large knowledge of humpback dolphins (*Sousa* sp.), common dolphins (*Delphinus* sp.), Risso’s dolphins (*Grampus griseus*), bottlenose

whales (*Hyperoodon* sp.), Atlantic spotted dolphins (*Stenella frontalis*), and narwhals and beluga (Family Monodontidae). Each of these species discussions would have further enriched the book, but then there is a time and need to say “enough,” and we have here a summary of important species, never mind what could have been.

Chap. 17 (Lammers) on spinner dolphins and Chap. 18 (Pearson) on dusky dolphins have similar trajectories to each other, with data and discussions about near-shore small and highly gregarious cetaceans that live relative to feeding in an efficient manner while needing to be ever vigilant about predators that can wipe them out “at any moment” (see also Chap. 7, Srinivasan). Chap. 19 (Sutaria et al.) discusses the special case of riverine dolphins and porpoises, with a developing model of potential sociality as related to evolution, and possibilities and constraints of habitats. Chapter 20 (Constantine) discusses the New Zealand Hector’s dolphin that lives close to shore in small societies and is beleaguered by human attention wherever it goes. Chapter 21 (Teilmann and Sveegard) does similarly with harbor and other porpoises the world over, excellently weaving through diverse aspects of their behavior and ecology. Chapter 22 (Jefferson) reminds us that no matter what knowledge we have or are gaining, this will not do the animals (or us!) much good in the face of multiple examples of known risks of population and species demise due to human actions. Chapter 10 (Bearzi et al.) and this one might be taken as the most important ones of this book—present and rational discussions of dangers and needed conservation actions of social animals in the seas. The final short Chap. 23 (Würsig) is an attempt at a synthesis of the excellent information of this volume, with personal insights as to what may be important to study as we advance our knowledge of odontocetes, and of other marine mammals of oceans, bays, and rivers.

It is always a pleasure to thank the numerous people who have made such a compilation possible. First and foremost, hearty thanks go to the authors, from 15 different countries and all major continents. You have provided us with gifts of fine science and thought, and I am grateful. I also thank the numerous authors and others who are eagerly (and for free!) sharing your beautiful photos and illustrations of animals in nature. I thank over 50 anonymous reviewers who helped to make the present contributions better by your wise comments; and the editors and advisors of Springer International, with special commendations to Éva Loerinczi, Uma Periasamy, and Bibhuti Sharma. As always when I help to put a book together, Melany Würsig has been a stalwart companion to critique, advise, and simply listen. Thank you.

Submitted with respect

Atawhai, Kaikoura, New Zealand
January 2019

Bernd Würsig



Hector's dolphin, *Cephalorhynchus hectori*, mother and calf surfacing off Kaikoura, New Zealand. These little nearshore dolphins are endangered in much of their range around the south island of New Zealand, and critically endangered for their subspecies relative, the Maui's dolphin, *C. h. maui*. Photo by Bernd Würsig

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