NEW BIOLOGICAL BOOKS

The aim of this section is to give brief indications of the character, content and cost of new books in the various fields of biology. More books are received by The Quarterly *than can be reviewed critically. All submitted books, however, are carefully considered for originality, timeliness, and reader interest, and we make every effort to find a competent and conscientious reviewer for each book selected for review.*

Of those books that are selected for consideration, some are merely listed, others are given brief notice, most receive critical reviews, and a few are featured in lead reviews. Listings, *without comments, are mainly to inform the reader that the books have appeared; examples are books whose titles are self-explanatory, such as dictionaries and taxonomic revisions, or that are reprints of earlier publications, or are new editions of well-established works.* Unsigned brief notices, *written by one of the editors, may be given to such works as anthologies or symposium volumes that are organized in a fashion that makes it possible to comment meaningfully on them.* Regular reviews *are more extensive evaluations and are signed by the reviewers. The longer* lead reviews *consider books of special significance. Each volume reviewed becomes the property of the reviewer. Most books not reviewed are donated to libraries at SUNY Stony Brook or other appropriate recipient.*

The price in each case represents the publisher's suggested list price at the time the book is received for review, and is for purchase directly from the publisher.

Authors and publishers of biological books should bear in mind that The Quarterly *can consider for notice only those books that are sent to The Editors,* The Quarterly Review of Biology, *C-2615 Frank Melville, Jr. Memorial Library, Stony Brook University, Stony Brook, NY 11794-3349 USA. We welcome prepublication copies as an aid to early preparation of reviews.*

WOLVES ARE CONSUMMATE PREDATORS

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A review of

WOLVES: BEHAVIOR, ECOLOGY, AND CONSERVATION.

Edited by L David Mech and Luigi Boitani. Chicago (Illinois): University of Chicago Press. $49.00. xvii + 448 p + 16 pl; ill.; author and subject indexes. ISBN: 0–226–51696–2. 2003.

The gray wolf (*Canis lupus*) is the consummate predator—highly intelligent, adaptable, and widely distributed. As such, this species is a model for understanding adaptations of a predator, as well as the biology and ecology of predation. L David Mech and Luigi Boitani have collected 13 chapters by 22 authors into the most comprehensive review of literature on wolves since Mech's (1970) single-authored book. Chapters include reviews on wolf behavior and social organization (Chapters 1 through 3), predator-prey interactions and population dynamics (Chapters 4 through 6, and 12), physiology (Chapter 7), genetics and systematics (Chapters 8 and 9), and relations among humans and wolves, including conservation (Chapters 12 and 13). Chapter 11 deals exclusively with recovery efforts for another species, the red wolf (*C. rufus*). The book contains a thorough 40-page index, 73 tables, 79 black-and-white figures, 50 color photographs in 16 glossy plates, and a goldmine of 56 pages of references. The book also includes an author index, which researchers

always find useful. Each chapter starts with a personal anecdote by one of the authors, apparently to entice lay readers. The volume begins with a brief foreword by George Rabb, an ethologist who studied wolf behavior in the 1960s, and the book is dedicated to U S Seal, a senior research biologist who died in 2003. Although of large format, this is not a coffee-table book, but a serious attempt to review everything known about wolves.

A remarkable amount of natural history information has been compiled on wolves in the past 30 years, facilitated a great deal by the development of radiotelemetry, and more recently DNA technologies. Telemetry has revealed many details about territoriality, pack structure and composition, dispersal, habitat selection, predation, and interactions of wolves with other species. Molecular genetic technology is beginning to unravel patterns of relatedness within and among packs, evolutionary history, hybridization, and even population estimation (Chapter 8). Sophisticated technologies have been necessary to demystify the wolf because wolf populations, pack composition, spatial distribution, and predation are remarkably dynamic, a fact that occasionally delights but sometimes befuddles the various authors.

As is always the case in a multiauthored volume such as this, writing styles and scholarship vary enormously among chapters, although the editors clearly have attempted to minimize overlap in content. Review chapters can be extremely useful, but students should be cautioned to seek out primary references. For example, I went searching for sex ratio data in *Wolves* prompted by an 1869 letter from George Cupples to Charles Darwin (see *Darwin Correspondence Online Database*; http://darwin.lib.cam.ac.uk/) only to find conflicting reports citing the same source. Kreeger (Chapter 7, p 195) cites Mech (1970) as reporting that the sex ratio among adult wolves favors males, whereas Fuller et al. (Chapter 6, p 170) cite Mech (1970) as indicating that the sex ratio is either equal or slightly biased toward females.

Because this is a single-species treatise on the natural history of wolves, it suffers in generality and application of biological principles. Although predator-prey interactions are the quintessential core of the wolf, our understanding of basic wolf-prey dynamics remains weak. For example, fundamental to understanding the effect of wolves on prey populations is the functional response, defined to be the rate at which an individual predator kills prey (Turchin 2003). Very simply, this quantity when multiplied by the number of predators enumerates the number of prey removed by predation. Obviously, several variables must be considered in calculating a functional response, including prey density, prey vulnerability, and environmental conditions, such as snow depth, although frequently ecologists model the functional response solely as a function of the abundance of prey. Mech and Peterson (Chapter 5) present the disturbing view that the "functional response concept was inappropriate for application to wolf-prey systems" (p 150). They go on to explain how functional response is complicated by pack size and prey vulnerability, but then proceed to throw the baby out with the bathwater rather than adding these variables into the functional response equation. Such contempt for the basic principles of predator-prey theory is based on the fact that it was established by laboratory experiments with small mammals and invertebrate prey and is, therefore, poorly suited to describing wolf predation (p 150).

Such a naïve perspective may hold back researchers working on wolves from making meaningful contributions to our understanding of predator-prey systems. There is no excuse for dismissing ecological principles, and advances made by researchers studying smaller beasts have helped to lay a framework for wolf researchers. For example, recent papers have shown how prey vulnerability can be modeled in a functional response (Jeschke and Tollrian 2000). Likewise, it is an easy matter to make the functional response a function of environmental variables (see, e.g., Flinn and Hagstrum 2002) or multiple species of prey (Abrams and Allison 1982). Predator-prey theory has developed by adding complications to basic structural models of predator-prey interactions and then studying the dynamical consequences of this added complexity.

Views on predator-prey modeling are expressed in Chapters 5, 6, and 13, but students should be warned that many of these discussions are misguided. Because predator-prey interactions are so fundamental to understanding wolves, some of the issues merit specific mention. For example, we are presented with Eberhardt's view that differential equations are inappropriate for modeling wolf-prey systems because reproduction does not occur continuously throughout the year (p 151). Yet, adopting difference equations where we assume that nothing happens between year t and $t+1$ certainly does not add realism. In fact, we know that difference equations have emergent properties of complex dynamics that may or may not reflect nature. Furthermore, mortality is a continuous process occurring throughout the year, and this seasonal process is necessary for the existence of compensatory mortality (Boyce et al. 1999). Many aspects of wolf predation vary seasonally and can be modeled as time-varying functions and, again, a rich literature exists on seasonal forcing of continuous-time functions incorporated, for example, in the functional response (Allen 1990; Fulton et al. 2003).

Another example where readers need to be cautious is the implication on page 151 that ratio-dependent predator-prey models are useful for wolf-prey systems; however, this overlooks the biologically outrageous consequences of such an assumption (Abrams 1997). Again, it would be much better to develop detailed models of functional response to unravel the mechanisms behind predation rather than obfuscating the process with a ratio-dependent model. Abrams notes that widespread acceptance of ratio-dependent predator-prey theory "would set predator-prey theory back by decades" (Abrams 1994:1842); a key reference on this important debate is not provided (Abrams and Ginzburg 2000).

Another view that will trouble modelers is the suggestion by Fuller et al. that incorporating details of social behavior in a population model of wolves will more "faithfully simulate reality" (p 187). They then contradict themselves three paragraphs later, by stating that social factors are largely irrelevant, and the abundance of vulnerable prey is the key variable determining wolf population density. Despite the logical contradiction here, in general, effective ecological modeling uses the simplest model possible that captures the essential dynamics of the system (Starfield 1997). Adding complexity can make it more difficult to understand the dynamics of the model and consequently offers little or no insight into the mechanisms driving the natural system. And it certainly is not true that a more complex model will more "faithfully simulate reality." The task for the modeler is a balancing act to capture just enough complexity to help us to understand the system, but no more complexity than is necessary.

Readers are repeatedly warned that wolf-prey systems are too complex with too many factors to consider (p 152), and each wolf-prey situation is unique (p 157). Mech and Boitani contend: "Recent findings of a long-term study of northern ecosystems in the Yukon show the largely unpredictable interaction between simple species relationships and complex stochastic events that affect ecological processes at a variety of spatial and temporal scales (Krebs et al. 2001)" (p 159). Charles J Krebs and his coauthors on the Kluane Project will be disappointed to see their insightful work characterized so hopelessly. The fact is that there are patterns in nature, and it is the role of the ecologist to find them and to develop an understanding of the mechanisms that create them.

Evolutionary biologists reading this book will discover that interpretations of wolf-prey systems easily and unwittingly invoke group-selection arguments. For example, presumably "wolves could not kill every prey individual they wanted to" (p 142) because they would deplete their prey. Elsewhere we are told that wolves "coexist with their prey by exploiting the less fit individuals" (p 131). This suggestion can be misleading, and it certainly is not clear that natural selection necessarily leads to coexistence via selective predation. For large ungulate prey, such as moose (*Alces alces*), bison (*Bos bison*), and elk (*Cervus canadensis*), there is excellent evidence that wolves indeed select young and old ages (p 188), and there is much variation in the vulnerability of prey. But this is not necessarily what permits coexistence, except if

some prey are truly invulnerable to predation (Abrams and Walters 1996). Some prey populations have been decimated by wolves, so it is not universally true that prey populations contain invulnerable members. A more universally effective mechanism perpetuating coexistence is density-dependent predation, as has been documented for wolves preying on moose (Messier and Joly 2000). Likewise, wolf predation varies spatially in complex ways that can contribute to coexistence, as illustrated by the ability of white-tailed deer (*Odocoileus virginianus*) to persist in the interstitial spaces between wolf-pack territories (Mech 1977; Lewis and Murray 1993).

There can be no challenge to the concluding main points of Chapter 5 on wolf-prey relations (by Mech and Peterson) that wolves can reduce prey abundance and contribute to regulation of some prey populations. It is, however, not so clear to me that "wolves have their greatest demographic effects on prey via predation on young-of-the-year" (p 157). No evidence is presented to substantiate this view, which might be true (see Gaillard et al. 1998) but requires careful analysis. For long-lived species such as ungulates, which are usually the prey for wolves, adult mortality yields the greatest sensitivity to population growth (Gaillard et al. 2000). So even though young and old ungulates are selected as prey by wolves, they must kill more of them to have a demographic consequence. Vulnerability of prey by age varies seasonally (Molinari-Jobin et al. 2004) and as a function of group dynamics (Lett et al. 2004). For moose in Alaska and the Yukon, and elk in Yellowstone, bears (*Ursus arctos*) have been found to take more neonates than wolves (Gasaway et al. 1992). As pointed out by Mech and Peterson, calf mortality might be compensatory, so further work is needed to conclude that wolves have their greatest demographic consequence by preying on calves.

Genetics is wonderfully complex in wolves and provides some exceedingly difficult challenges for conservation biology. Apparently these challenges shaped the composition of the book, with Chapter 8 on Molecular Genetic Studies of Wolves (Wayne and Vilà), followed by a more traditional view on Wolf Evolution and Taxonomy (Nowak) in Chapter 9. Molecular genetic studies have revealed that hybridization between wolves and coyotes (*C. latrans*) is common in the Great Lakes region of North America, and recently it has been suggested that the wolves that have been hybridizing are of a different species, *C. lycaon,* perhaps closely related to the red wolf, *C. rufus.* Whether this hybridization is a natural process is unclear. Wayne and Vilà suggest that if *C. lycaon* exists because of human-caused habitat alterations and predator control, *C. lycaon* may have no "conservation merit" (pp 236–237). If, on the other hand, such hybridization is a consequence of natural expansion of wolves (or coyotes), one might argue that such hybridization is part of a natural process that merits conservation attention.

The same dilemma exists for the red wolf, which DNA analysis suggests is not a valid species, but instead may be a hybrid between gray wolves and coyotes. Yet, the red wolf is the subject of a major effort by the U.S. Fish and Wildlife Service to reintroduce the large canid to the southeastern United States (see Chapter 11 by Phillips et al.). Nowak (Chapter 9) takes a strong position that the red wolf is a valid species threatened because of hybridization with coyotes that during recent decades have expanded their distribution throughout the former range of the red wolf. The conservation ramifications of red wolf and wolf-coyote hybridization are interesting. On the one hand, a primary objective of the Endangered Species Act is to preserve genetic diversity, and the species concept is fundamental to its implementation (Agapow et al. 2004). Yet, one might argue that there are ecological and aesthetic values to having a large canid represented in these areas, irrespective of the purity of genetic origin. We do not know if there are ecological "benefits" to having wolves shaping community structure (see pages 158 to 160 by Mech and Boitani), but it seems like a reasonable postulate. Despite conflicting DNA evidence, the official position of the U.S. Fish and Wildlife Service (and Nowak) is that the red wolf is a valid species that is being threatened by hybridization with coyotes.

Inbreeding has been a concern in several wolf populations, especially in Europe (Chap-

ter 8). Although the population of wolves on Isle Royale, Michigan has rebounded, we almost lost wolves there about a decade ago, and speculation was that loss of genetic diversity made this insular population especially vulnerable to disease (Peterson 1995). Wolves in southern Sweden and Norway originated from a single pair and remained at low abundance for approximately ten years until a lone male, apparently from Karelia, dispersed from the north in 1991 (p 232). Since then, the Scandinavian wolf population has increased by 29% per year (Vilà et al. 2003) to the point that protocols for wolf control are being debated. One hypothesis is that the influx of fresh genetic material from this one wolf was sufficient to allow the population to expand.

The chapter, Wolf Interactions with Nonprey (by Ballard et al.), is a useful synthesis that fills a void in the literature. Much of the review examines the interaction between wolves and other carnivores. Of particular interest was the dramatic upheaval in coyote social structure that followed wolf recovery in Yellowstone National Park (pp 266–268). Another fascinating case study is the remarkable dependence by ravens (*Corvus corax*) on wolf kills in Yellowstone National Park and elsewhere (pp 269–270).

Chapter 12 is an exceptionally comprehensive synthesis on wolves and humans by Fritts et al. Much has been done during the past 20 to 30 years to foster more responsible management of wolf populations, and I thought that Fritts et al. did a superb job of characterizing human attitudes and effective management strategies. Few people realize that wolves continue to kill children in some rural areas of India, on the order of 50 to 60 per year. Finding ways to reduce livestock depredations will be crucial to the success of effective wolf recovery in many areas of the world. Engaging local trappers and hunters to assist in wolf-control programs is being used increasingly as a cost-effective and publicly more acceptable method of reducing wolf populations than poisoning or aerial gunning.

Mech and Boitani have added a four-page conclusion after the last chapter in which they make several interesting points about the management of wolves in a world with an ever-increasing human population. Management cannot work if it engages either extreme of strict protection or ruthless control. We were successful in nearly eliminating the wolf from the conterminous United States during the early decades of the 20th century. We have been remarkably successful at restoring wolves to the Greater Yellowstone ecosystem and central Idaho. Wolves continue to depredate livestock throughout much of their distribution and are consequently controlled by killing. Recognizing the conflicts with humans and controlling wolves in areas where livestock depredations occur can go a long way toward reconciling resentment about conservation of wolves.

Students will appreciate the suggestions for future study that appear near the end of several chapters. These suggestions are useful despite a bizarre digression where we learn that "the significant factors affecting wolf population trends are well studied" (p 189) and that our knowledge is reasonably detailed and "unlikely to get much better" (p 189). In fact, the book would have benefited enormously from a broader perspective, asking what is it about wolves that improves our understanding of biology. Specifically, one might fairly ask what has all of this research on wolves done to enhance our understanding of the biology and ecology of predation? No wild species has attracted more controversy, hatred, love, fear, passion, or research dollars. We have indeed learned a great deal about the natural history of wolves; but after reading this enormous tome I find that we are still waiting to see contributions of this knowledge to the basic principles of biology. Although I found points to criticize in this book, I also found much to praise. There is no single source that compiles more information about wolves, and this compendium will stimulate a new generation of field biologists to design studies to fill the many gaping holes in our understanding of wolves and predator-prey interactions in general. For its price, this is a bargain of a book.

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Wolves are Consummate Predators A review of. Wolves: Behavior, Ecology, and Conservation. Edited by L David Mech and , Luigi Boitani. Chicago (Illinois): University of Chicago Press. $49.00. xvii + 448 p + 16 pl; ill.; author and subject indexes. ISBN: 0â€“226â€“51696â€“2. 2003. Mark S. Boyce. Night had fallen over Winterfell and the howling of wolves could be heard out in the wolfs wood. The wind was loud and cold but that was the North, always cold even with winter over. Tonight, though it was especially cold for death and war was upon the horizon.Â The cold penetrated even the Godswood of Winterfell but the wind and the howls of wolves did not, leaving only silence for the only Stark in Winterfell. Being the new Lord of Winterfell and the last male stark of Rickardâ€™s line was a duty that Benjen never thought would happen to him, being the youngest of the pack and yet it did. Losing them all should have brought him grief but rage and the wolfâ€™s blood was all that dominated Benjenâ€™s very being. 4 starks killed in the South and one abducted in the span of a moonâ€™s turn! The primary predators of wolves are humans. We use guns, traps, poison, snares, dogs, and eagles. Yes, I just said eaglesÂ Steve Bodoi wrote it up in his book, which Amazon suggests is excellent (Eagle Dreams: Searching for Legends in Wild Mongolia.). However, as you can imagine, most eagles arenâ€™t eager to take on a wolf and. Continue Reading. Wolves arenâ€™t hunted as food by any animal. Other predators will still kill them given a reason. The primary predators of wolves are humans. We use guns, traps, poison, snares, dogs, and eagles. Yes, I just said eagles