Conservation aside, the book includes some comprehensive and elegant reviews of carnivore biology. Morphology, biogeography, and phylogeny are some of the themes for which the contributors have assembled data encompassing the entire order Carnivora to extract useful "take-home" messages. It can be an unenviable task to plunge into the disparate and extensive datasets on the carnivores and distill meaningful patterns in their extraordinary morphological, behavioral, and ecological diversity. However, as in the first volume, editor John Gittleman has assembled some of the leading thinkers to tackle this unwieldy assignment, with results that are frequently complementary. For example, Lars Werdelin's effort (chapter 17) to steer perception of carnivore ecomorphology away from traditional taxonomic constraints balances evenly with a functional analysis of spectacular dental weaponry of the extinct "megacarnivorans" (Audrine Biknevicius and Blaire Van Valkenburg, chapter 12). Similarly, two papers on carnivore genetics, one at the individual level (Matthew Gompper and Robert Wayne, chapter 13) and the other at the population level (Wayne and Klaus-Peter Koepfl, chapter 14), are united in illustrating common processes.

A few chapters, notably those discussing reproductive endocrinology in dwarf mongooses (Scott Creel, chapter 2) and spotted hyenas (Laurence Frank, chapter 3), narrow the focus slightly. The study of gregarious carnivores has yielded some of the most remarkable discoveries about mammalian behavioral ecology, and both contributions illustrate well the payoff to be had from long-term study. Although both chapters repeat already published results, this work is fascinating, and the authors have incorporated new theories on the extraordinary relationships between reproduction and behavior in the complex societies of group-living carnivores. This theme is explored subsequently by Peter Waser (chapter 8), who reviews patterns of dispersal in social carnivores; not surprisingly, dwarf mongooses and spotted hyenas are two of the six well-studied species that feature in his analysis.

Despite the themes and topics that unite the book, this volume suffers slightly from uncomfortable organization. Although the book is indeed about behavior, ecology, and evolution, its division into these subsections results in unnecessary awkwardness. For example, a thought-provoking essay by Marc Bekoff and Dale Jamieson on the ethics of studying carnivores is slotted into the behavior section, as is an analysis of the adaptive significance of coloration (Alessia Ortolani and Tim Caro, chapter 4), which is as ecological as it is behavioral. Conversely, Gus Mills's review (chapter 6) of capture, census, and diet-study methods heads the ecology section, although it deals primarily with behavioral considerations that are important for success in carnivore field studies.

The book's diverse assemblage of topics may have rested more harmoniously by eliminating the subdivisions carried over from the first volume. However, this complaint is minor and certainly does not diminish the quality of contributions. This book is a valuable addition to the understanding of the carnivores and will stimulate further interest in this fascinating group. Gittleman has established a worthy tradition of assembling current research on the carnivores into a single accessible work.

I am already looking forward to Volume III.

LUKE HUNTER
Mammal Research Institute
University of Pretoria
Pretoria 0002, South Africa

References cited

SIGNALING, HANDICAPS, AND EVOLUTION


Intra- and interspecific signaling between organisms has been known from the time of the earliest naturalists; indeed, Darwin considered signaling carefully in the development of his evolutionary ideas. With the rise of ethology and its incorporation into evolutionary theory over the past several decades, many workers have discussed the role of signals in the life and evolution of organisms, but with limited success because it was not clear how to accommodate the possibilities of false signaling and cheating. (False signals and cheating are the knowing transmission of an untrue signal from an individual to the advantage of the sender and the disadvantage of the receiver.) To a large extent, these concerns reflect the fact that evolutionists have often approached the question of signals from a theoretical viewpoint and have lacked a firm foundation in empirical analyses of actual signaling between real organisms.

In 1975, Amotz Zahavi provided a clarification for the problems of false signals and cheating that was novel and brilliant, and it demonstrated how best to approach solutions to evolutionary problems. The handicap principle, as Zahavi called this solution, states that when sending out signals, animals impose a handicap, or extra burden, on themselves that puts the individual organism in extra danger. Thus, an animal that sends such a signal clearly indicates to the receiver that it is in good physiological condition and can afford to assume the extra burden and danger. The handicap principle thus ensures that the signals sent out are honest, not false or cheating.

Perhaps more important than the actual concept of the handicap principle is how the Zahavis developed the concept. Again, the method was a simple one, but it involved much work. Basically, the handicap principle developed as an outcome of a
long-term study by Amotz Zahavi and his students and associates of the Arabian Babbler, *Turdoides squamiceps*, in which they learned almost everything about the life of this social bird, which inhabits the drier areas of Israel, including its inter- and intraspecific signaling.

The approach used by the Zahavis in developing the handicap principle is the naturalist one, involving long-term field studies. The Zahavis demonstrated that the best way to understand evolutionary problems and to derive new explanations is by careful, detailed studies of organisms in the wild, not by sitting inside an office doing theoretical analyses and adding unchecked assumption after assumption to account for inconsistencies. And, indeed, this approach was the one used by Darwin in formulating his ideas about evolution—ideas that had escaped his laboratory biologist colleagues. Once the Zahavis postulated the handicap principle for the Arabian Babbler, they were able to reanalyze many additional examples of honest signaling from the literature, providing additional support for the handicap principle.

*The Handicap Principle* draws on these examples to analyze signaling between organisms and its evolutionary role. The book, which was originally written in Hebrew, has been translated into clear, flowing English. All references and explanatory comments are provided as endnotes, and there is a comprehensive bibliography. A few graphs are included, but most of the illustrations are charming vignettes showing or alluding to the point being made in the neighboring text. Reading this book was a real pleasure, and I was sorry when I came to the end. New ideas, supporting evidence, and discussions about signaling are presented clearly, with full documentation. Most interesting is that the Zahavis do not hesitate to extend their analyses to humans. The human examples of signaling discussed certainly fit well into the general framework of their presentation.

I am especially pleased that the Zahavis have come down strongly on the side of individual selective demands, rather than group selection, as the evolutionary mechanism controlling the evolution of true signaling via the handicap principle. I am also pleased that the Zahavis have not restricted their discussion to higher animals; their inclusion of lower animals, plants, and microorganisms demonstrates the broad application of intra- and interspecific signaling and the handicap principle to most, if not all, organisms.

My major complaints with *The Handicap Principle* lie with the term “signal selection,” which I feel is unnecessary, and with the discussion of possible conflict between the handicap principle and sexual and kin selection. I see no reason to postulate a large number of different types of individual selection to cover each different type of interaction between organisms and their external environments. Although I agree with the Zahavis that the concepts of sexual and kin selection have been overused and applied erroneously to many examples, I do not agree that the concept of the handicap principle (and honest signaling) is in conflict with selection—be it individual, sexual, or kin—on organisms. The handicap principle and honest signaling, as I understand these ideas, represent functional explanations in biology, and the resulting selection, whether individual, sexual, or kin, represents evolutionary explanations in biology. Nevertheless, evolutionary explanations, such as the type of selection that may be involved in the evolution of a particular feature, must be firmly supported by functional explanations. And this approach is exactly what the Zahavis have accomplished in this book.

I strongly recommend *The Handicap Principle* to specialists in evolutionary biology, to students of animal behavior and of the many other disciplines in biology that deal with intra- and interspecific interactions between organisms, and to the interested layperson, all of whom will find this book as interesting as I have. Furthermore, *The Handicap Principle* fills a rare niche in scientific books—namely, a book in which the scientific ideas are presented honestly and accurately, in a clear and interesting way, without talking down to non-specialists. Special mention should be made of the excellent translation into English of the original Hebrew text by Naama Zahavi-Ely and Melvin Patrick Ely. I applaud the Zahavis for a job very well done.

WALTER J. BOCK
Department of Biological Sciences
Columbia University
New York, NY 10027

**UPS AND DOWNS OF UV-B**


Life as we know it would not exist were it not for a diaphanous layer of pale, blue gas high in the stratosphere. This gas is ozone, the atomic form of oxygen, and it protects most life on Earth from the destructive effects of biologically active solar ultraviolet radiation (UV-B and UV-C). Approximately 90% of the atmosphere’s ozone is distributed through the stratosphere in a band some 15–50 km above the surface of the earth, but the apparent thickness of this layer is misleading because the ozone molecules within it are few and far between. If the average amount of ozone in a vertical column through the atmosphere were brought to the surface at standard temperature and pressure, it would form a layer only approximately 3 mm thick. However, most plants and animals owe their existence to the efficiency with which the ozone layer absorbs virtually all the UV-C wavelengths (shorter than 280 nm) and most of the UV-B (280–315 nm) within sunlight. The UV-B radiation that does manage to slip through the ozone layer can be both beneficial and harmful, because the same wavelengths that kill *Escherichia coli* in water and stimulate the