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BOOK REVIEWS

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Ravens in Winter—Bernd Heinrich. 1989. Summit Books, New York. 379 p. with illustrations by the author. $19.95 (hardback).

Some 35 years ago Niko Tinbergen published *The Herring Gull's World,* which is still considered to be one of the classic works in Ethology, principally because of its mixture of hard science, informed speculation about the evolution of behavioral processes, and readily readable text. *Ravens in Winter* by Bernd Heinrich is similar to Tinbergen's classic, in that it combines a fascination with the study organism, description of the trials involved in field research, discussion of how the experimental method is used to explore behavioral phenomena, and revealing insights based on both experimental results and long familiarity in a highly readable and entertaining text.

The questions asked by students of behavior have changed over the intervening decades. What initially led Heinrich to this long and complex study was the observation that although ravens are typically seen flying in ones or twos, they frequently feed in large groups on carcasses in winter. More interesting is the observation that at least some of these birds give loud vocalizations that appear to attract conspecifics to the food source. Classical natural selection would predict that an individual finding a rich food source should remain silent and even defend these food bonanzas against conspecifics and other competitors so that the individual discovering the food would reap all of the benefits from its discovery. The central question of Heinrich's work therefore was "Do ravens recruit conspecifics to food sources in winter and if so, why?"

Anyone who has tried to explore the evolutionary basis of altruistic-appearing behavior will sympathize with the difficulties that Heinrich was faced with and will appreciate the complex nature of the interactions that he observed in solving this problem. Along the way, he explores a number of possible models and theories that could allow him to interpret his observations, including Hamiltonian selfish herds, kin selection, reciprocal altruism (including "tit-for-tat" models), and the possibility that ravens are actually trying to attract larger carnivores that are capable of opening frozen carcasses when ravens are not. Heinrich's discussions of these concepts and the logical structure that underlies each of them serve as excellent introductions to the interested layreader (the book's likely intended target), but they are also superior to discussions of these topics in most undergraduate textbooks, being both lucid and appealingly jargon-free.

None of these sociobiological models proved adequate to explain the patterns that emerged from Heinrich's data. Kin selection appeared to be precluded by the tendency of young ravens to disperse after becoming independent of parents, which meant that feeding aggregations were invariably composed of non-relatives. Since many investigators simply invoke kin selection to explain cooperative or altruistic behavior, without having any evidence to support their claims, Heinrich deserves credit for both testing the applicability of this concept and rejecting this explanation when the evidence failed to support it.

Similarly, reciprocal altruism was not supported because the feeding groups of ravens are not stable, which reduces or eliminates opportunities for reciprocal interactions. Some of Heinrich's results appeared on occasion to provide equivocal support for selfish herds and for recruitment of carcass-openers, which suggests that such selective pressures may contribute to the general evolution of the observed patterns, but these phenomena did not appear to fit the majority of instances when ravens found food and appeared to recruit conspecifics.

The results obtained indicated that adult breeding ravens, which appear to defend large territories on a year-round basis, do not advertise the presence of food, and in fact defend carcasses and repel other adults and juveniles when possible. The birds that appear to advertise the presence of food by calling are typically dominant juveniles, who appear to benefit from this advertisement in two ways. First, attraction of large numbers of other birds to carcasses can swamp the defensive efforts of adult birds, which allows the juveniles to exploit these food bonanzas. This behavior appears to be similar to that of heterospecific "gangs" of coral reef fishes that invade territories of damselfish and cannot be displaced because of sheer numbers (Robertson et al. 1976). Second, Heinrich suggests that ravens that advertise the presence of food increase their status and attractiveness to potential mates, so that this behavior could even be the result of sexual selection. The concept of status enhancement is similar to the idea that all altruistic behavior evolved to signal social status which has been developed by Zahavi in recent years. An alternative explanation not considered by Heinrich could come from "delayed-return" altruism (Rothstein and Pierotti 1988), which argues that altruistic-appearing behavior will be selected for if it yields benefits to the altruist in the future, regardless of whether the behavior is actually reciprocated by any of the original beneficiaries. Heinrich's idea that advertising the presence of food to conspecifics enhances social status, and increases the chances of obtaining a high status mate, clearly falls into the category of reaping future benefits from altruistic behavior in the present.

Ravens in Winter is a book that can, and should, be read by ornithologists and behaviorists at several levels and for several reasons. One major reason is that the Common Raven, *Corvus corax,* is widely credited with being "the most intelligent species of bird in the world," and for this reason alone, the dynamics of its social behavior warrant attention. Heinrich mentions a professor attempting to discourage a student from undertaking a project similar to his by saying "Ravens are smarter than you are, and it will take you years to

outwit them enough so that you can begin to get meaningful data." It should also be noted, however, as Heinrich points out, that no proof of the raven's singular intelligence has yet been published, and although it did take years, Heinrich collected large amounts of meaningful data.

Ironically, *Ravens in Winter* provides no compelling new evidence of a singular intelligence. The picture that Heinrich presents is of a somewhat social and clever species which is capable of complex social interaction, and which shows both apparent cooperation and conflict among individuals. This mixture of conflict and cooperation is worth emphasis, for many hardcore sociobiologists and behavioral ecologists often talk as if organisms were always cooperative or always competitive. Rarely are mixed strategies in which competition and cooperation are context dependent discussed, even though real organisms are much more likely to pursue mixed strategies. Many species of birds (and mammals), many of which are not credited with a "singular intelligence," show levels of cooperation comparable to ravens. For example, gulls, genus *Larus,* which are often compared unfavorably with ravens (Heinrich cites a gull biologist who observed ravens and Herring Gulls together on a colony, as stating that "in comparison to ravens, gulls acted like vegetables," p. 111), show all of the cooperative foraging behavior described by Heinrich for ravens, including recruitment, vocalizations that appear to attract conspecifics, and behavior that appears to attract heterospecific predators that enhance feeding rates of the gulls themselves (Hoffman et al. 1981; Gotmark et al. 1986; Pierotti 1988a, 1988b). This behavior is almost certainly related to the fact that gulls at sea typically exploit ephemeral food patches, such as schools of fish, which are more efficiently exploited by groups than by individuals. The principle remains, however, that gulls show recruitment and group coordination comparable, if not superior, to that described for ravens by Heinrich.

Observations on cooperation in gulls, however, do not detract from either the supposed intelligence of ravens, or the significance of the results described by Heinrich. Quite the contrary, this actually points out one of the strengths of *Ravens in Winter,* and why it is an important book for all ornithologists and behavioral ecologists. Heinrich's careful elucidation of his research methods including (1) the way in which he presents questions and hypotheses and proceeds to test them, (2) his demonstration of how equivocal or even negative results lead the committed field biologist to new questions, hypotheses, and experiments, and (3) the detail in his observations and data, permit an understanding of field methods and data interpretation that can act as a standard for both students and professionals. In addition, the wealth of information provided allows readers to make direct comparisons with their own study systems, and yields potential insights into the complexity underlying social behavior in a way that many lesser volumes do not permit.

Despite the title, *Ravens in Winter* deals with far more than the winter ecology of ravens. Included are a general introduction to corvid social behavior, descriptions of reproductive behavior, and descriptions of vocal and visual displays that would warrant publication on their own in professional journals. This yields an overall picture of the life of *Corvus corax* that is unrivaled in the literature.

Heinrich's motivation for writing this book appears to have developed from the frustration that many of us feel when forced to shorten manuscripts or eliminate interesting observations for the sake of publication. Originally, Heinrich felt he could run a few simple experiments, prove that ravens behaved in an altruistic manner, and get a quick publication in *Science.* Unfortunately the birds did not simply cooperate (in any sense of the term), and he was forced to conduct numerous experiments and observations over a four-year period. When he finally did publish his results in *Behavioral Ecology and Sociobiology,* he laments that "it is hard to leave out and still retain coherence, much less a flavor of the ramifications." We can be grateful that he has had the opportunity and has chosen to expand upon his results, for *Ravens in Winter* is one of the best books published on field ornithology, behavioral ecology, methods in field research, and even science itself in many years. In addition, it is a bargain at the price.—RAYMOND PIEROTTI, Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701

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Dynamic Modeling in Behavioral Ecology—M. Mangel and C.W. Clark. 1988. Princeton University Press. 317 p. Cloth: ISBN 08505-6 $45.00; Paper: ISBN 08506-4 $15.95

The limitations of simple analytical approaches to modeling foraging behavior have been known for years (Zach and Smith 1981, chapter 5 in *Foraging Behavior,* Garland STPM Press, New York), but the replacement of static models with dynamic ones has been a slow process. Marc Mangel and Colin Clark provide a user's guide to a computer method which should increase the

rate at which dynamic models are incorporated into behavioral ecology.

Dynamic Modeling in Behavioral Ecology attempts to take the reader all the way from first principles of probability theory and computer programming to actually constructing computer solutions for a wide range of applications in behavioral ecology. If read seriously, this book is intended to show students and professionals how to use dynamic modeling in their own work.

Dynamic Modeling is not intended as a book on behavioral ecology, but rather as an introduction to a modeling technique. As such the impressive range of examples from the biological literature will give the reader a good idea of the types of applications which are amenable to this approach. Because the biological information is presented in each case as an introduction to the models, it is best that the reader be familiar with at least some aspects of behavioral ecology beforehand. This should not be a problem for most biologists, since the applications include such diverse topics as foraging behavior, parental allocation and clutch size in birds, migrational patterns, and social behavior.

Mangel and Clark suggest having a trusted computer close by when reading this book, and we would add that the reader should have a pencil and paper ready as well. *Dynamic Modeling* should be viewed as a workbook, organized to teach a methodology. It is not designed to provide an overview of models used in behavioral ecology, nor is it intended to convince the skeptical reader that this is the best approach. Rather, it is a demonstration of the ways in which a traditional engineering technique can provide insight to a wide variety of biological problems.

The primary computational method Mangel and Clark develop in this book is in fact one of several techniques commonly used by management engineers to solve resource allocation problems. Historically, techniques for optimal management of resources were developed in the 1940s as part of the war effort; together with game theory and discrete-event simulation these techniques form a body of theory known among engineers as "Operations Research." From an engineer's viewpoint, the models presented in this book will seem unremarkable. Because he understands the models, the engineer may be misled into believing that he therefore understands the biology.

On the other hand, any biologist who can follow Mangel and Clark's advice to "think deeply about the biology" will likely find the techniques presented in this book to be strange and perplexing—not because the methods are overly difficult, but because they have traditionally been taught only to engineers. However, we remind ethologists that game theory has become useful, familiar, and understandable despite the fact that it was originally developed by engineers; and we predict that dynamic modeling will, in time, also become a familiar and understandable biological technique.

The dynamic modeling approach is not difficult to justify. Decision processes for which precise and fixed criteria for success exist can be handled reasonably well by marginal analysis; Charnov's "Marginal Value Theorem" is a good example of a situation where diet choice is determined by the simple and consistent rule that the rate of energy gain will be increased whenever possible. When the criteria of success are less precise, when success is a distant outcome of a sequence of decisions, or when a minimum value must be reached, then more intricate methods are called for; the dynamic modeling technique presented by Mangel and Clark is one of a small group of methods that are designed to handle the general problem of stochastic decision networks. Dynamic modeling is thus an appropriate technique for answering many questions in behavioral ecology.

Because the methodology will be unfamiliar to most biologists, we advise readers to page through one of the several "applications" chapters before committing themselves to the in-depth discussions of probability theory and programming technique presented in the opening chapters. These summaries coherently present all the probability theory and computer programming concepts used throughout the remainder of the book. However, we feel the opening chapters alone will not be adequate preparation for readers who lack experience with these topics. In addition, we found the epilogue to contain an enlightening discussion of the philosophical motivations behind a dynamic modeling approach—an overview ordinarily found in introductions. By all means read the epilogue *first*.

We have found that this book works best for graduate students who already have a basic understanding of probability theory (from an introductory statistics course) and some prior computer programming experience.

Dynamic modeling approaches promise to be very useful to future theoretical developments in behavioral ecology, freeing us from the severe limitations of static analytical models. Trade-offs, differing currencies, complexities imposed by field situations, and the effects of short-term individual behavior on populations have not been successfully treated in behavioral ecology because of the difficulties inherent in constructing and solving analytical models. By using a computer modeling approach, we will be able to incorporate currently available analytical models in more elaborate dynamic models, and so explore the interactions between many aspects of animal behavior (e.g., predation and patch-choice, nutrient limitation and energy demands, reproductive consequences of diet choice).

Mangel and Clark have managed to present dynamic optimization theory in a form that is immediately useful to biologists, primarily in a classroom setting at the graduate level. Unfortunately, the methods are neither intuitively obvious nor simple to program. This book is not to be "read," but rather carefully studied. Thus, we recommend *Dynamic Modeling* to serious students of behavioral ecology who not only wish to learn an unusually powerful computational technique, but are willing to change their entire view of how ecology and behavior interact.—DAVID J. STEWART, Department of Biological Sciences, University of Arkansas, Fayetteville, AR; CYNTHIA ANNETT, Arkansas Cooperative Fish and Wildlife Research Unit, Department of Biological Sciences, University of Arkansas, Fayetteville, AR.