BOOKS: ANIMAL BEHAVIOR

Song Science from Physiology to Fitness

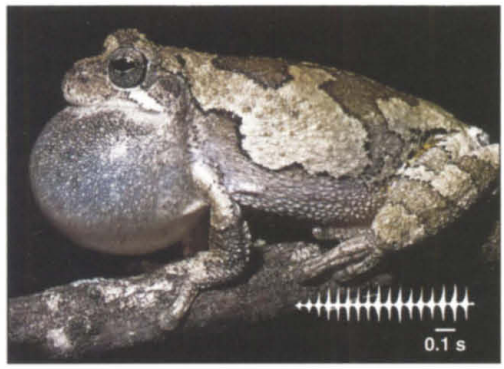
Darryl T. Gwynne

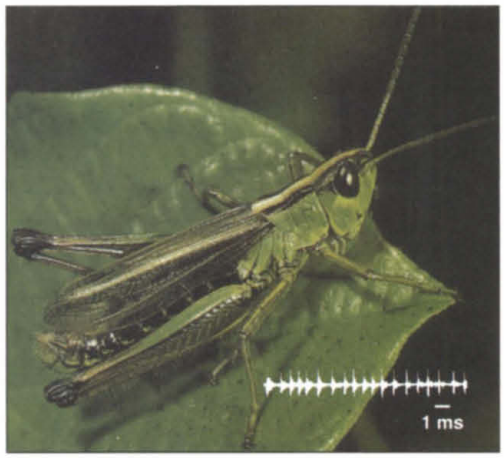
One could argue that nature's most acclaimed vocalists—the birds—are outsung by the ever-present and sustained croaking, buzzing, and whining of mate-seeking male frogs, toads, and insects. The insect songsters are mainly Orthoptera (crickets, katydids, and grasshoppers), but also include cicadas (in the order Hemiptera). The novelty of *Acoustic Communication in Insects and Anurans* lies in its coverage of these two quite disparate groups of animals that turn out to share more than their (literally) monotonous singing. Both groups encounter similar acoustical problems as a result of their ectothermy and relatively small body size, and both possess communication systems that, for the most part, are uncomplicated by parental care and song learning. Carl Gerhardt and Franz Huber, both experienced researchers in animal communication, approach singing in the two taxa using two levels of analysis. First, they address the mechanisms of sound communication, offering detailed coverage of the physics and physiology of how these animals generate, hear, and respond to sounds. Then the authors focus on evolutionary consequences, in particular how acoustical communication increases reproductive success (fitness).

Acoustic Communication in Insects and Anurans
Common Problems and Diverse Solutions
by H. Carl Gerhardt and Franz Huber

University of Chicago Press, Chicago, 2002. 543 pp. $100, £70. ISBN 0-226-28832-3. Paper, $35, £24.50. ISBN 0-226-28833-1.

The book provides case histories and up-to-date reviews for anyone interested in the physiological underpinnings or adaptive significance of behavior. One highlight is a thorough review of reproductive character displacement, in which the authors discuss how the fitness-decreasing consequences of responding to signals of other species can change female preferences that in turn lead to sexually selected changes in male calls. Gerhardt and Huber also cover more widely applicable models of adaptive female choice for male displays. Their examples include a tree frog (*Hyla versicolor*) that offers one of the few convincing demonstrations that preferences can result in genetic benefits for offspring. The chapter on female choice also reviews the more direct, material benefits of female call preferences. Such benefits should loom large in the mating habits of singing insects because orthopterans are well-known not only for calling but also for the nutrient gifts provided by males of most species. Thus, I was quite surprised to find no discussion of the hypothesis that females assess signals of male ability to supply these services (*1*).





Monotonous but meaningful. Calls are critical for species recognition in the gray tree frog (*Hyla versicolor*) and the meadow grasshopper (*Chorthippus montanus*).

A glossary would have helped readers unfamiliar with the mechanisms of sound communication through the frequent bioacoustical and neurophysiological jargon. Another minor quibble concerns the use of confusing common names for higher taxonomic groups of singing insects, such as "crickets" for Gryllidae. "Locust" has been used in other literature for both cicadas (Cicadidae) and grasshoppers (Acrididae). Moreover, katydids (Tettigoniidae) have elsewhere been called "bush-crickets" and "long-horned grasshoppers."

To a large extent, the four pairings of taxa and levels of analysis that are covered in the book have previously been separate fields of inquiry. Thus, Gerhardt and Huber do a great service in combining them. The authors share a philosophy that the study of communication should integrate the mechanistic and evolutionary levels. Consider, for example, the bizarre case of green tree frogs, *Hyla cinerea*. Females prefer male calls of low frequency (pitch) only during cool temperatures, whereas call frequency of individual males remains constant. One might conclude that a mating advantage gained by deep-croaking, heavyweight males during cool weather is due to adaptive female choice. However, studies of metabolically dependent mechanisms in frog hearing point to an alternative, nonadaptive explanation.

Despite this and several other examples, the author's integration of the two levels of analysis falls short, primarily because the book's mechanistic and evolutionary sections are too segregated. The mechanisms underlying behavior need to be linked to some sort of adaptive model. Gerhardt and Huber imply this with their inclusion of "biologically significant acoustic signals" (which I take to mean adaptively significant signals) in early chapter headings. The survival benefits of sound localization or recognition of predator noises are obvious, but the adaptive advantages of conspecific song recognition and identification are more elusive.

The authors must have evolutionary models in mind when they refer to "suboptimal signals," an expression that implies there are fitness consequences in responding to signals. Because species recognition is occasionally referred to in the early chapters, it appears that fitness costs of interacting with the wrong species is the main (only?) concept associated with the physiological analysis of song recognition. But, as the later chapters reveal, there are other hypotheses for adaptive female discrimination of calls. Although central to evolutionary studies of behavior, these hypotheses rarely seem to turn up in physiological discussions. For example, what mechanisms might underlie female preferences? The authors discuss one possibility, "neural-network" hypotheses for female choice of novel signals. However, there appears to be little research on the recognition of call parameters that indicate male ability to supply fitness benefits such as good genes or important services.

In considering sexual selection, a mechanistic approach could extend beyond premating communication because females can influence paternity at later stages. As Gerhardt and Huber point out, when females store sperm from several males there are opportunities to favor certain ejaculates. For instance, vibrations by mating male in-

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sects can be displays that enhance paternity (*2*). Links between male copulatory vibrations and the response of females through contraction of sperm storage organs (*3*) would be fertile ground for further research.

There is much work to be done in linking mechanistic and adaptive approaches to the study of animal communication. Gerhardt and Huber's book will provide a critical foundation for this research.

References

1. R. Thornhill, *Am. Nat.* **110**, 153 (1976).
2. W. G. Eberhard, *Female Control: Sexual Selection by Cryptic Female Choice* (Princeton Univ. Press, Princeton, NJ, 1996).
3. J. Clark, A. B. Lange, *J. Insect Physiol.* **46**, 191 (2000).

BOOKS: ECOLOGY

A Herpetological Treasure Trove

Tim Halliday

The Amphibians and Reptiles of Costa Rica is a very large book about a small country. Despite its limited area, Costa Rica hosts a rich flora and fauna. Geographically positioned between two vast continents with very different biotas, the country is quite important to our understanding of biogeography and evolution. Its well-developed programs for conserving its biodiversity and for developing ecotourism provide a model for other parts of the world, particularly tropical regions. Costa Rica also occupies a singular position in the history of herpetology as the place where many generations of researchers and students have learned, often from the book's author, about tropical reptiles and amphibians. It is home to no less than 396 species of anurans, salamanders, caecilians, lizards, snakes, turtles, and crocodilians. The majority of these species are also found in neighboring countries, thus extending the relevance of the book as a reference text for Central America. Moreover, the book's scholarly coverage of almost every aspect of the biology of amphibians and reptiles in a tropical country makes its publication a landmark in the development of herpetology.

The Amphibians and Reptiles of Costa Rica
A Herpetofauna between Two Continents, between Two Seas
by Jay M. Savage
University of Chicago Press, Chicago, 2002. 954 pp., illus. $75, £52.50. ISBN 0-226-73537-0.

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Forty years of research in Costa Rica have provided Jay Savage with an unmatched and encyclopedic knowledge of its herpetofauna. He has distilled his experience into the detailed species accounts that provide the core of the book. The amount of information in these accounts varies considerably, depending on how much is known about each species. The text covers diagnostic traits, morphology, and coloration as well as aspects of the ecology, life history, and behavior. Accompanying distribution maps show the locations of specimens and other authoritative records. The numerous keys can be used to identify species in the field, though the sheer weight of the book precludes its use as a conventional field guide. Each species is illustrated with at least one color photograph, and these are supplemented with drawings of important morphological characters. The photographs, the majority of which are by Michael and Patricia Fogden, are of exceptionally high quality.

Midnight snacking. *Imantodes cenchoa* is a common arboreal snake that preys on frogs and anole lizards (such as this *Norops*); the spider is just passing by.

In the book's introductory section, Savage reviews the principals of systematics and nomenclature, and he describes the basic techniques of field and museum herpetology. He also provides thorough surveys of Costa Rica's geography, climate, biota, and history (including the remarkable conservation efforts in the country). The last section of the book presents a detailed analysis of the biogeography of Costa Rica's amphibians and reptiles. With this, Savage seeks to explain the evolution of present-day distribution patterns in relation to what is known of plate tectonics and the paleoclimate of Central America. He offers a complex but fascinating story. Together, these general sections broaden the book's appeal and make it valuable as a general text in herpetology and tropical ecology.

Leaf litter loiterer. *Eleutherodactylus gollmeri* is a relatively common inhabitant of lowland and premontane humid forests.

Although Costa Rica has been more thoroughly studied than other tropical countries, we are still filling gaps in our knowledge of its herpetology. The book lists eight species that were described while the manuscript was being edited for publication. A curious irony of the current heightened interest in worldwide declines among amphibians is that intensive exploration (much of which is motivated by the need to document biodiversity before it disappears) and the application of modern molecular techniques have led to new species being described at a higher rate than ever before. As a result, our appreciation of the extant diversity of reptiles and amphibians, particularly in the tropics, is expanding very rapidly.

Costa Rica was home to the now extinct golden toad (*Bufo periglenes*), a spectacularly beautiful and very unusual creature that has assumed an iconic status in the context of global amphibian declines. It is particularly significant that the golden toad, along with several other species of amphibians and reptiles, has vanished from a reserve intended to protect biodiversity. Despite considerable research, the causes of this and other recent extinctions among amphibians remain elusive. What is clear, however, is that conservation through the creation of protected areas is simply not sufficient to protect many species. The only disappointing feature of this book is that Savage does not really address the issue of amphibian declines. One searches in vain for evidence that his unrivaled field experience in Costa Rica, which extended well into the period of population crashes, gave him some insight into the geographical and taxonomic distribution of declines and into their possible causes.

In an ideal world, *The Amphibians and Reptiles of Costa Rica* would serve as a model for the study and documentation of biodiversity throughout the tropics. It took Savage a lifetime to collect and compile the vast quantity of information he presents in the book. Unfortunately, the many and diverse threats to the continued existence of the world's reptiles and amphibians are so severe that it is unlikely anyone will have the time to repeat his achievement elsewhere.

PHOTOS BY MICHAEL FOGDEN AND PATRICIA FOGDEN/COURTESY UNIVERSITY OF CHICAGO PRESS