A Savage Approach to Tropical Biology

Author: HANKEN, JAMES

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A Savage Approach to Tropical Biology

Ecology and Evolution in the Tropics: A Herpetological Perspective. Maureen A. Donnelly, Brian I. Crother, Craig Guyer, Marvalee H. Wake, and Mary E. White, eds. University of Chicago Press, Chicago, 2005. 584 pp., illus. $45.00 (ISBN 0226156583 paper).

I've never been a fan of hero worship. I don't even take the day off on Presidents' Day. But in the case of this particular Festschrift, which honors biologist Jay M. Savage, I concede that the cause is awfully compelling. Renowned tropical ecologist and biogeographer, herpetological systematist, and accomplished university administrator, Savage has published more than 200 scholarly papers and three books. His 2002 book, *The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents between Two Seas,* is regarded already as the definitive summary of Costa Rican herpetology and a benchmark of quality against which all future faunal treatments will be measured. The recipient of numerous distinguished awards for academic achievement and international service in promoting the study of tropical biology (among other things, he helped found OTS—the Organization for Tropical Studies—in 1963), Savage also served as major professor for 39 PhD and 25 MS students.

Clearly, there is a lot of raw material here to work with, and workers to process it. The result is the volume *Ecology and Evolution in the Tropics: A Herpetological Perspective,* edited by five of Savage's former students (Maureen A. Donnelly, Brian I. Crother, Craig Guyer, Marvalee H. Wake, and Mary E. White) and comprising most of the presentations at a symposium convened in his honor at the 2000 joint meeting of the American Society of Ichthyologists and Herpetologists, the Society for the Study of Amphibians and Reptiles, and the Herpetologists' League in La Paz, Baja California, Mexico.

The 18 chapters are organized in two parts: "Evolution and Biogeography" and "Ecology, Biogeography, and Faunal Studies." There is also a foreword by Luis Diego Gómez, former director of Costa Rica's Wilson Botanical Garden and Las Cruces Biological Station, and founding member of that country's National Academy of Sciences (which in 1998 inducted Savage as an honorary member in recognition of his contributions to the scientific development of Costa Rica and his role in establishing OTS). The chapter authors, all of whom are former students of Savage or their collaborators, range from newly minted PhDs to prominent senior scientists. Savage himself coauthored one chapter. As is typical of University of Chicago Press products, the volume is carefully produced. Literature citations are not included in individual chapters but instead are gathered together in a single references section at the end of the book, along with a list of contributors and extensive subject and taxonomic indices. There are numerous black-and-white illustrations, although for the most part these are graphs, histograms, cladograms, or distribution maps. There are relatively few images of organisms, or indeed photographs of any kind. Color photographs are confined to the chapter by Scott and Aquino, which includes four plates that depict frogs of the Paraguayan Chaco. Presumably the paucity of color illustrations reflects at least in part a desire to keep the volume affordable; the cloth edition can be had for under a hundred dollars, and the paper edition costs less than half that.

Individual chapters vary considerably in their breadth and level of detail. Thus, whereas Emerson provides a concise (11 pages) yet very effective overview of the physiology of sexual dimorphism in Old and New World frogs, McDiarmid and Donnelly provide a comprehensive (100 pages) review of the herpetofauna of the Guayana highlands, focusing on the complex of tabletop mountains and other isolated massifs (*Pantepui*) that evince extreme floral and faunal endemism. More than half of the latter chapter is occupied by five lengthy appendices that identify individual tepuis (flat-topped, sheer-walled mountains) as well as their plant formations, herpetofauna, and history of exploration. Each chapter stars amphibians and reptiles of one sort or another, mostly tropical frogs, lizards, snakes, salamanders, or caecilians, and primarily from the New World; one notable exception is Bickford's report on frog monitoring in Papua New Guinea. Topics range from food habits to karyology, and from biotic surveys to the molecular systematics. Several chapters address similar topics, such as neotropical biogeography, but I was surprised at how little such chapters have to do with one another, insofar as they rarely evaluate or even cite each other's data or conclusions. Kluge's chapter proposing a new phylogenetic system of taxonomy is the most synthetic and in many ways the most impressive and ambitious chapter in the volume; it may outlast all other contributions. Unfortunately, it's also the most incomprehensible of the 18 treatments and is likely to defeat all but the most committed and dedicated—and jargon-hungry—phylogenetic systematists.

The predicaments of and prospects for the world's natural populations of reptiles and, especially, amphibians today are much different from when an innocent young assistant professor named Jay Savage made his first collecting trip to Costa Rica more than 40 years ago. The serious plight of global amphibian populations has been convincingly documented and is now widely accepted, less than 20 years since "declining amphibians" were first brought to the world's attention (Wake 1991, Stuart et al. 2004, Mendelson et al. 2006). Indeed, it's astonishing how quickly we have adjusted to this harsh reality. Declines and even disappearances affecting many species are routinely discussed as a matter of fact. In this light, those chapters that in-

ventory faunal assemblages and population trends from once intact or even "pristine" sites are both immensely valuable and poignant. Perhaps the most stirring example is McDiarmid and Savage's firsthand account of the herpetofauna of Costa Rica's Osa Peninsula and their descriptions of how this region has changed over the course of their study: "At the present rate of cutting and development, within the first two decades of this century nearly all of the Central American humid lowland evergreen forest habitats, products of millions of years of evolution, seem certain of destruction" (p. 366). And later, "Most of the forests in which our work was accomplished have been cut" (p. 413).

From the get-go, the editors unabashedly and proudly identify this book as a testament to taxon-oriented biology, and this claim is more than substantiated by the content and scope of its individual contributions. This raises questions of a broader nature regarding the future of organismal biology—and especially taxon-oriented biology—and how it will be pursued in coming years. Will another such volume be possible 50 years from now? If possible, will it be desirable? Does the taxon-oriented approach respond favorably and satisfactorily to the imperatives of "modern biology"? These questions are not answered here; indeed, they aren't really even broached, either implicitly or explicitly.

To some extent this is understandable; the main topic of the book is the biology of amphibians and reptiles, and especially the ecology and evolution of tropical species. Someone, however, had better start asking these questions publicly, and offering compelling answers, because the time when one could take for granted widespread support of organismal biology—both financial and otherwise—is long past. Many taxon-based professional societies are struggling to remain viable in the face of declining membership. Taxon-based hires also are increasingly rare in many college and university biology departments, including some associated with natural history museums. These are serious problems that require meaningful and creative solutions. My own view is that there is an important—indeed, an indispensable—role for organismal and taxon-oriented approaches in contemporary biology, but that to remain viable (at least in an academic setting), such work needs to be much more effectively and extensively integrated with molecular biology, genetics and genomics, physiology, and other disparate fields than it has been to date. Few of the treatments in *Ecology and Evolution in the Tropics* embrace such a forward-looking posture, which remains an appropriate and necessary goal of future education and research.

JAMES HANKEN
James Hanken (e-mail: hanken@oeb.harvard.edu) is Alexander Agassiz Professor of Zoology and director of the Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

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A GUIDE FOR SPATIAL ANALYSIS IN ECOLOGY

Spatial Analysis: A Guide for Ecologists. Marie-Josée Fortin and Mark Dale. Cambridge University Press, Cambridge, United Kingdom, 2005. 365 pp. $60.00 (ISBN 0521009731 paper).

The biosphere is spectacularly diverse and beautiful, thanks to the fact that things are not randomly arranged. Instead, the world is "patchy," with nonuniform spatial structures. Spatial heterogeneity, manifested in various forms of interwoven patchiness and gradients, is both a cause and a consequence of biodiversity and ecosystem functioning. Underlying this tremendous heterogeneity in nature is spatial autocorrelation: Things that are closer to one another are more similar. Ecology, the study of the relationship between organisms and their environment, is replete with phenomena in which patterns and processes are spatially autocorrelated or dependent. Thus, ecology is really the study of the interrelationship between pattern and process on different organizational levels ranging from individual organisms to the entire biosphere. Quantifying patterns, then—particularly in the spatial domain—is a critical step toward ecological understanding.

Yet ecological theory has long been dominated by nonspatial perspectives, and only in recent decades have spatially explicit views begun to take a central place in ecology. This may be seen as something of a paradigm shift, which owes much to the rapid development of landscape ecology, whose goal is to understand the relationship between spatial patterns and ecological processes on multiple scales. However, dealing with spatial patterns can be conceptually complicated and technically challenging. Although various spatial analysis methods are available to ecologists, a guide to the proper use of these methods, particularly in ecology, has been elusive. *Spatial Analysis: A Guide for Ecologists,* by Marie-Josée Fortin and Mark Dale, is intended to fill the gap. The two authors are outstanding Canadian ecologists with exceptional background and experience in spatial statistics. Some of their previous publications on spatial pattern analysis of vegetation are well known to plant and landscape ecologists who are keen on spatial issues.

The book consists of seven chapters: an introduction, five core chapters organized largely around data types, and a conclusion. The introductory chapter is a concise but informative overview of some fundamental concepts of spatial analysis (e.g., stationarity, spatial autocorrelation versus dependence, sampling design). Commonly used methods of spatial analysis are covered in the next two chapters: Chapter 2 describes dozens of methods for analyzing completely censused population data for point patterns (the authors recommend those based on Ripley's K function and wavelets), and chapter 3 covers methods of analyzing surface patterns that are suited for sample data, as well as maps of continuous variables, including join count statistics, spatial autocorrelation indices, fractal dimension, Mantel statistics, variograms, and various interpolation techniques. In this chapter the authors discuss at length whether and how to analyze global as opposed to local spatial statistics to deal with the problem of nonstationarity in data sets encompassing large, heterogeneous areas.

Two sets of techniques for patch identification (spatial clustering) versus boundary delineation (edge detection) are compared in chapter 4. Chapter 5 is devoted to the problems of spatial autocorrelation: its mathematical nature, underlying assumptions, statistical solutions, and ecological interpretation. Chapter 6 tackles what is arguably the most challenging topic covered by this book—spatiotemporal analysis, in which autocorrelation in both space and time must be taken into account. Finally, chapter 7 concludes by highlighting several key issues discussed in the previous chapters.

The overall organization of the book makes a lot of sense. The writing is generally good, and at times enthusiastic and engaging. Many technical books on spatial statistics seem mathematically complicated and ecologically terse (dry and boring, in plain English), but this is not the case here. The authors never forget their target audience—ecologists—in the discussion of any topic, and throughout the book their numerous examples and illustrations make connections between statistical details and ecological interpretations. I also found the concluding remarks at the end of each chapter quite useful, because they not only summarize main elements of the chapter but also contain valuable pointers and thought-provoking ideas. I particularly liked chapter 5, which is probably the most informative and useful reading on dealing with spatial autocorrelation in ecology.

There are, however, a few things that seem less impressive. For example, it is hard to find any conceptual logic in chapter 6, which is more of an agglomeration of seemingly disparate methods. The somewhat superficial discussions on cellular automata and chaos seem to detract from, rather than add to, the strength of the book. There is little discussion on landscape pattern metrics, which have been widely used in ecological studies. Also, spatial scaling is a central issue in ecology and environmental science, and it would have been interesting to include some discussion as to how spatial statistics can help revealing scaling patterns and quantifying scaling uncertainties.

Spatial Analysis is a guide, not a recipe book. In today's quest for ecological understanding of spatial patterns, recipes of methods clutter bookshelves, and an insightful guide like this one is much in need. I agree with the authors that ecologists are not adequately cognizant of the issues of scale and the consequences of spatially autocorrelated data for sampling design, data analysis, and ecological interpretations, and commend them for having done an admirable job in alleviating this situation. Without any hesitation, I highly recommend this book to anyone who is interested in spatial analysis in ecology and environmental sciences. However, although only a basic grasp of statistics is assumed, the readers should not be surprised to find out that,

to fully comprehend the materials covered in this book, it will require both broad knowledge in ecology and in-depth understanding of spatial statistics.

JIANGUO (JINGLE) WU
Jianguo (Jingle) Wu (e-mail: Jingle.Wu@asu.edu) is a professor in the School of Life Sciences and the Global Institute of Sustainability, Arizona State University, Tempe, AZ 85287.

THE PRESENCE OF WILD THINGS

Pilgrim on the Great Bird Continent: The Importance of Everything and Other Lessons from Darwin's Lost Notebooks. Lyanda Lynn Haupt. Little, Brown, New York, 2006. 276 pp. $24.95 (ISBN 0316836648 cloth).

The present is brought to us by the past. In *Pilgrim on the Great Bird Continent,* Lyanda Lynn Haupt constructs a tangled and intricate temporal web of evolutionary, philosophical, and ecological threads. These threads connect the scientific and personal events of Charles Darwin's life to issues that burn for Haupt today. But Haupt does not just use Darwin's diaries, journals, and ornithological notes as a springboard for her own issues; she is a passionate scholar for whom these works shine with modern relevance.

The book is structured by the life of Darwin and, more particularly, by his development as a naturalist. We see him seasick and anxious to prove himself, sailing off in *The Beagle* as little more than a gentleman's companion to Captain Fitzroy; we see him writing home, tentatively soliciting his sister's criticism of his diary-writing style; we witness his gradual conversion on the South American continent into a scientist who recognizes, as Haupt notes, that "nothing in the natural world is beneath our notice" (p. 15); and finally we see him rooted back in the soil of his garden at Down House, musing on worms, barnacles, pigeons, and God, and congealing his theory of natural selection from a huge volume of seemingly unconnected observations.

From these plotlines, Haupt emerges as another character. Like a good teacher, she imbues scholarly material with personal investment. When Darwin sweats over his youthful prose (it is florid and imitative of earlier travelogues), Haupt confesses that her own college papers mimicked the style of books she happened to be reading at the time; she compares her own reaction to the gait of black-winged stilts to Darwin's description; she contrasts Darwin's religious views with her own, and resurrects the word *agnostic* in the process. The only time this exchange between Darwin and Haupt seems contrived is when his specimen-collecting sensibilities are shoehorned into a discussion of current animal-rights positions.

Haupt is herself an excellent writer, and this is no more apparent than in her telling of Darwin's discovery of the lesser rhea. I won't spoil the reader's surprise, except to say that this is a delectable story that deserves a place in every biologist's crock of rattling good yarns. Indeed, it is the combination of her gifts as both a writer and a scholar that enables the fruition of the scientific, philosophic, and even poetic dimensions of this book. In a world overpopulated with specialists, Haupt's ability to grasp and describe the whole revitalizes Darwin's promise of "grandeur in this view" of evolution.

Haupt shares a strong kinship with Darwin. She is a woman of ideas, scholarly and acute. But she is, like Darwin, a person who is most at home observing nature "in patience, in stillness," where living creatures are "revealed, animal to animal, with a kind of earthen *familiarity,* on the forest soil" (p. 86). Darwin's recorded observations touch Haupt: "Come, these [ornithological] notes say, be expectant, do not be dull, but bring the lost fullness of your intelligence to this endeavor, as you come quietly in the presence of wild things" (p. 87). And she urges us all, whether "as activists, as scientists, as bird-watchers, as homespun

naturalists, [or] as everyday humans whose lives constantly brush the perimeter of a wilder, natural world" (p. 16), to pay attention.

Apart from her enthralling scholarship, as a contemporary naturalist Haupt appears to have three objectives: to examine and advance the discussion of animal rights, to promote observation of nature in the natural state (as opposed to what she sees as an increasing emphasis on atomizing it in the lab), and to provide justification for conservation. Her argument is that if people become more familiar with nature, they will be more likely to conserve it. But as much as I crave to be in the presence of wild things, and as much as I support efforts to bring children closer to nature, I am skeptical that these strategies alone can propel the conservationist spirit as far and as fast as it needs to go. Nature is running out of time. I agree with Haupt that those who know nature are more likely to protect it. Yet nature is becoming more estranged: For many of us, our most intimate contact is from television! Other strategies for conserving species exist, and I wonder that Haupt, who holds a master's degree in environmental ethics and philosophy, doesn't employ them. Still, her contribution, while not comprehensive, inspires fidelity to the latent naturalist sensibility in us all.

Haupt's first love is the quiet observation of nature. One hopes that her brilliant prose and scholarship will inspire current and future generations to share her passion. As for me, I am moved by *Pilgrim on the Great Bird Continent* to arise from my couch and venture beyond, to penetrate the wild perimeter.

JOHN BOIS
John Bois (e-mail: jbois@verizon.net) teaches advanced placement biology, biology, microbiology, and physiology at Northwestern High School, Hyattsville, MD 20782. He also teaches biology at Prince George's Community College, Largo, MD 20774.

A BLIND WATCHMAKER MODEL OF HUMAN EVOLUTION

Simulating Human Origins and Evolution. Ken Wessen. Cambridge University Press, New York, 2005. 241 pp., illus. $120.00 (ISBN 0521843995 cloth).

Modeling has become coequal with experimentation and theory building as part of the scientific process. Nonetheless, critics of modeling seem highly dubious that a string of zeros and ones can possibly contribute significantly to our understanding of complex processes, especially human evolution. Yet Richard Dawkins's "blind watchmaker" model captured, and still captures, a wide following: It became the subject of BBC and NOVA specials, popular scientific magazine articles, Web sites with alternative implementations and visualizations, and, of course, the ire of creationists and intelligent design adherents. On the other hand, Dawkins's scientific critics were skeptical of his model, which used only a few genes and artificial selection of individuals rather than populations. These critics wondered whether those parameters were appropriate simplifications of organisms with thousands of genes evolving in complex environments with frequency- and density-dependent selection; demic structure; epistatic gene interactions; and rugged, dynamic adaptive landscapes that gainsay monotonic hill climbing.

Ken Wessen has studied these critics well, even though his book *Simulating Human Origins and Evolution* refers neither to Dawkins nor to the ensuing related literature. Instead, Wessen brings together the dual perspectives of his two PhDs, one in human evolution and one in theoretical physics. He maintains a hybrid career, with one foot in quantitative finance and the other in academia (at the School of Anatomy and Human Biology at the University of Western Australia). Wessen starts with a simple string of characters—25 instead of Dawkins's 9—and invokes selection, thereby making his model extraordinarily richer. The phenomena he invokes are spatial (immigration and emigration between up to four continents), temporal (gradual versus punctuated evolution, with generation times of species—not individuals—frequently 250,000 to 2 million years long), and phylogenetic or genealogical (different demographic processes and monophyletic, paraphyletic, or polyphyletic models). He also invokes multiple other evolutionary complexities, such as interbreeding, coalescence, fossilization, and extinction. Furthermore, Wesson's basic strings of characters are both heritable and nonheritable and are subject to both mutation and selection; his unit of analysis is a phylogenetic tree visualizing historical relationships, not individual morphology.

Using two computer simulation programs he developed, Specialist and Genie, and manipulating the parameters of all of these variables, Wessen investigates such controversies as (a) the "out of Africa" (recent replacement) versus the "multiregion" (regional continuity) hypotheses of human origins; (b) scientists' ability to gather sufficient human fossil data to sort out lineages derived from morphology and from sequence (mitochondrial matrilineal inheritance, Y-chromosome DNA patrilineal inheritance, and diploid nuclear markers); and (c) the potential use of macroevolution modeled with deterministic, logistic, and stochastic extinction to examine phylogenies that appear in the shape of a vase or amphora, or truncated severely by a mass extinction. He invokes singularities in event-driven models and also considers continuous models with only sustained minor fluctuations.

Wessen is a careful and humble modeler. His primary premise is attributable to Oxnard (2000): "A whole organism morphogenetic average reinforces the phylogenetic information while minimising functional parallels and convergences in local anatomical units, because the former is additive over different anatomical units, but the latter is independent across anatomical units" (p. 26). His epistemology is Popperian. He proceeds by falsifying one assumption or hypothesis after another. Thus, his major conclusions cast doubt on the work of others who had insufficient data, used

inappropriate reconstruction algorithms, depended upon too few parameters, or did not thoroughly investigate the sensitivity and robustness of their models to slight perturbations or deploy multiple runs to mediate problems of extrapolation.

Thus, Wessen's exclamatory conclusions include these: "After 15 generations, there is never an overall common ancestor, and in more than 98% of the cases there is no common ancestor for any individual continent" (p. 115). "This serves to illustrate the difficulty in constructing a phylogeny from incomplete information, even in such a highly idealized case as provided by the simulation, where the characters are largely unambiguous and fossilisation is high" (p. 68). And, startlingly, "In a sense, it seems you have to know the answer to get the answer!" (p. 126). The reader should not be discouraged from tackling the modest amount of mathematics, the extensive tables and figures, and the painstaking thoroughness with which Wessen navigates his material.

Although I have emphasized Wessen's cautions, readers would be well advised to appreciate his positive findings. Thus, he frequently notes that often one is better able to trace a lineage, or to find a most recent common ancestor, than one might have expected a priori, and that it is still possible to coarsely reconstruct the timing of migration events even in the face of too few fossils. Furthermore, he invites readers to play with the interactive colored versions of his Windows XP simulations, which are available for free downloading from his Web site (*http://school.anhb.uwa.edu.au/personalpages/kwessen*). He also provides detailed manuals for each package, also in color.

The simulation program Specialist lets users test phylogenetic hypotheses subjected to numerous evolutionary forces. In similar fashion, Genie allows users to test genealogical hypotheses in the face of demographic factors such as overpopulation, population bottlenecks, breeding patterns, sex ratios, and extensive coalescence.

Wessen's insights about models, data, and methodologies (both algorithms and heuristics) are well worth heeding. John

Casti, in *Would-Be Worlds: How Simulation Is Changing the Frontiers of Science* (1997), argues that the primary power of simulation is surprise. Only when we are confronted with counterintuitive results are we sufficiently intrigued to explore further or to change our basic notion of what seems warranted and what are reasonable assumptions. In the light of Bill Wimsatt's (1987) famous article "False Models as Means to Truer Theories," Wessen's simulation of human evolution will be a useful reference for phylogenetic systematicists, human geneticists, physical anthropologists and primatologists, and paleoarchaeologists who want to think deeply about both the power and limits of reconstructing human history from currently available data and with contemporary tools. It is not an easy read, because it is quite technical.

Yet this book puts all of the public rhetoric that Dawkins's simple model inspired into better perspective. *Simulating Human Origins and Evolution* presents a "blind watchmaker" model on steroids.

JOHN R. JUNGCK
John R. Jungck (e-mail: jungck@beloit.edu) is the Mead Chair of the Sciences at Beloit College in Wisconsin and the editor of the BioQUEST Library, a collection of over 80 biological simulations, tools, and databases.

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CHICAGO BOTANIC GARDEN

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