



Metapopulation Biology Goes Evolutionary

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The Metamorphosis of Evo-Devo

Environment, Development, and Evolution: Toward a Synthesis. Brian K. Hall, Roy D. Pearson, and Gerd B. Müller, eds. MIT Press, Cambridge, MA, 2003. 304 pp., illus. \$45.00 (ISBN 0262083191 cloth).

Ryuichi Matsuda was an insect biologist both ahead of and behind his times. This book, a tribute to Matsuda and his ideas, came from a workshop in 1996 and is very much in the same vein. Matsuda was born in 1920 in Japan; earned a bachelor's degree from Kyushu University in 1950; received his PhD in entomology from Stanford University, working with G. F. Farris; and then spent time at both the University of Kansas and the University of Michigan before moving to the Biosystematics Research Institute of Canada in 1968, where he remained until his death in 1986. At that time he was finishing *Animal Evolution in Changing Environments, with Special Reference to Abnormal Metamorphosis* (1987, John Wiley and Sons).

I confess that I was not familiar with Matsuda and his work before reading *Environment, Development, and Evolution*. My appreciation of him comes from the descriptions of his life and work by various contributors to this volume, the best of which is the brief, but personal, recollection of Mary Jane West-Eberhard, who first met him when she was a graduate student at the University of Michigan. My comments about his work are based on what I could glean from these indirect sources.

Matsuda was interested in the evolution of form, especially of insects. He recognized much earlier than most that the environment could play a large and creative role in that process. During the 1960s, few evolutionary biologists and

even fewer developmental biologists appreciated this fact and the other ideas that Matsuda eventually called “pan-environmentalism.” West-Eberhard sums up Matsuda's reaction to this lack of appreciation:

Matsuda may have been hindered in his quest for a synthesis by his annoyance with neo-Darwinism. At least that attitude compromised his ability to communicate effectively with those most likely to be interested in his ideas, some of them apt to be alienated rather than convinced by terms like “neo-Lamarckianism” or even “genetic assimilation.” But Matsuda was about twenty years ahead of his audience in thinking about development and evolution, and it is a great pity that he did not live to see his ideas appreciated as they are in this book. (p. 116)

Unfortunately, some of Matsuda's defenders in *Environment, Development, and Evolution* seem to share his attitude. The first third of the book reads like a 20-year-old text fighting a 50-year-old battle. Roy Pearson, R. G. B. Reid, and especially Eugene Balon attempt to portray evolution as a theory in crisis and Matsuda as its savior, but their presentation is both a caricature of evolutionary theory and severely out of date. Their central claim is that evolutionary theory (“neo-Darwinism”) ignores the pervasive effects of the environment. Yet I learned as a student nearly 30 years ago that phenotypic variation among individuals in a population can be partitioned: $V_p = V_E + V_G + V_{G \times E} + V_e + \text{Cov}(E, G)$, where V_E is the variation due to environmental effects, V_G is the variation due to genetic effects, $V_{G \times E}$ is the variation due to differences among genotypes in how they react to the environment, V_e is variation due to develop-

mental noise, and $\text{Cov}(E, G)$ is variation due to the nonrandom distribution of individuals among environments. Admittedly, all of the terms with “E” in them were mostly, but not entirely, ignored until the 1980s. Since then, however, numerous papers dealing with the empirical existence and theoretical implications of these factors have appeared. Indeed, hundreds of papers are now published each year on phenotypic plasticity and reaction norms. The past decade has seen a score of books and major reviews on these subjects. Nevertheless, the authors of these opening chapters write as if this spate of research had not been carried out.

Pearson, Reid, and Balon do lay out the components of Matsuda's theory, but one problem with the way they frame the argument is that no evolutionary biologist that I know would call herself a “neo-Darwinian.” We are all just evolutionary biologists. Reid, at least, recognizes the rhetorical folly of argument by label. More important, the theory as presented is empty. The central tenet of pan-environmentalism is that the environment affects the phenotype of individuals. This principle is so obviously true that no evolutionary biologist would dispute it. However, the theory as presented goes little beyond that claim, although it is the details of how those effects occur that matter. For example, if the environment is strictly random, the effects on evolutionary processes will be very different than they would be if the environment were completely predictable. Over the past 20 years, an entire domain of evolutionary theory has arisen that deals with these issues, namely, plasticity theory—the evolution of development under environmental uncertainty. None of that theory is referenced here. (What is referenced, however, by Balon,

is Michael Behe's *Darwin's Black Box*, which is cited as proof of the failure of evolutionary theory; apparently Balon fails to appreciate that Behe is a creationist and a proponent of intelligent design.)

I also find incongruous Pearson, Reid, and Balon's claim that pan-environmentalism is a universal theory of evolution. As presented in their chapters, this theory apparently applies only to Kingdom Animalia, and primarily to Phyla Chordata and Arthropoda. Even within those bounds, the theory seems to deal mostly with morphology and the timing of a few critical life history events, such as metamorphosis and the onset of reproduction.

The book does have some strong points. The best parts are the chapters dealing with evolution and metamorphosis in fish, herptiles, and insects. Most of these are written by people who were unfamiliar with Matsuda's work or who came upon it after his death. The chapter by John Youson on fish metamorphosis—at 40 pages, one of the longest in the book—shows clearly how Matsuda's views fit into modern ideas of plasticity and the evolution of development. The chapter is primarily a review of Youson's own work on lampreys, but Youson repeatedly links this work back to Matsuda's key ideas. Marvalee Wake's chapter on the evolution of viviparity makes a similar effort. Other chapters, such as the one by Christopher Rose on amphibian metamorphosis and the one by Barry Sinervo and Erik Svensson on the origin of novel phenotypes, also provide excellent reviews, although they make little or no attempt to tie directly into Matsuda's ideas.

All told, the last two-thirds of the book constitute a nice review and an interesting look forward at a corner of the field of the evolution of development. Of particular note is West-Eberhard's chapter; in a little over five pages she very concisely and clearly summarizes her theory of genetic accommodation, a process that takes several hundred pages in her magnum opus (*Developmental Plasticity and Evolution*, Oxford University Press, 2003).

Overall, this book has merit for those interested in the narrow topic of the evo-

lution of development and metamorphosis in vertebrates and insects. Don't get too discouraged by the first third of the book—it eventually redeems itself. For those interested in more synthetic works, I recommend Massimo Pigliucci's *Phenotypic Plasticity: Beyond Nature and Nurture* (Johns Hopkins University Press, 2001); West-Eberhard's *Developmental Plasticity and Evolution*; and my own book, coedited with Thomas Dewitt, *Phenotypic Plasticity: Functional and Conceptual Approaches* (Oxford University Press, 2004).

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Samuel M. Scheiner is a federal employee; this critique represents his own views, however, not those of the US government.

CLEAR-EYED OBSERVATION OF WILD, UNRESTRAINED ANIMALS

Winter World: The Ingenuity of Animal Survival. Bernd Heinrich. Harper-Collins, Ecco, New York. 2003. 368 pp., illus. \$24.95 (ISBN 0060197447 cloth), \$14.95 paper (ISBN 0060957379 paper).

Bernd Heinrich, an emeritus professor of zoology at the University of Vermont, applied his understanding of animal physiology and behavior to meet the challenges of the North American 100-Kilometer Championship race in Chicago and become the ultramarathon champ, as he wrote in *Racing the Antelope*. His superb books—15 to date—also garner medals: the L. L. Winship/PEN New

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England Award, the Rutstrom Authorship Award for Conservation and Environmental Writing, the New England Booksellers' Award, and the John Burroughs Medal for Natural History. Heinrich's *Bumblebee Economics* was nominated for the National Book Award in science.

In his latest book, *Winter World: The Ingenuity of Animal Survival*, Heinrich explores the strategies that enable animals to survive icy days and numbing nights in their natural habitat. Through clear-eyed observation of wild, unrestrained animals, complemented by his own ingenious experiments, Heinrich unravels the evolutionary innovations that allow diverse species such as butterflies and bats, flying squirrels and frogs, kinglets and caterpillars, and many others to endure such extreme climatic conditions, within behavioral and physiological constraints. His explanation of the physiological ecology of winter adaptation will delight and inform scientists and naturalists.

Winter World opens with a brief chapter on definitions and terms that relate to activity and body temperature. The 24 chapters that follow focus on the diversity of mammals, birds, reptiles, amphibians, and insects living in the forest beyond Heinrich's homemade log cabin—and sometimes inside the cabin—in western Maine. He supplements his own field observations with the research findings of other scientists to amplify our understanding that in the northern woods heat means life, but cold does not necessarily spell death.

Where do northern animals dwell in winter if they cannot migrate south, as certain of our own species do? How does a 5-gram golden-crowned kinglet cope on nights with a chill factor near -50° Celsius (C)? When does being fat translate into being fit? Adaptations to winter are as diverse as the species Heinrich describes.

For example, the star-nosed mole digs in for the winter below the frost line. When snow insulates the ground, moles can hunt for winter food closer to the surface because the subnivian space (the zone above the soil and below the snow) usually remains close to 0° C. The name of the game is warmth and fuel.

Heinrich guides us into the woods to unfold the mystery of how the kinglet nests successfully in late winter. A kinglet hangs its cup-shaped nest like a hammock, within spruce or fir twigs that shield the birds from wet and cold. The nest is lined with lichen, moss, strips of paper birch, and caterpillar silk, and insulated with feathers and snowshoe hares' downy fur. Feather counts of 2486, 2674, and 2672 in three individual nests attest to the coziness of these small shelters—thus the kinglet supplements its own feathery insulation by creating a favorable microclimate. Moreover, Heinrich observes that kinglets forage nonstop all day, explaining how a kinglet, weighing no more than two pennies, can find sufficient daily fuel, up to three times its body weight. A kinglet's gut contents reveal the bird's winter energy source: inchworm (geometrid moth) caterpillars. Caterpillars in winter? Whack a tree; caterpillars shower down. Do kinglets overwinter with adequate fat reserves? Probably not, posing an unanswered question of just how cold a kinglet becomes in severe winter. Perhaps it goes into overnight mini-hibernation, like a hummingbird.

Torpid turtles pile up in a communal hibernaculum (Graham et al. 2000). Map turtles and softshell turtles congregate from November through March, stretched out on the river bottom. Inactive, not even breathing, turtles most likely take up sufficient oxygen from the 0.1° C water (Graham et al. 2000).

Amphibians evolved diverse winter strategies in different habitats. Heinrich finds toads when he turns garden soil in the autumn; the Manitoba toad (*Bufo hemiophrys*) hibernates in gopher mounds (Tester and Breckenridge 1964). The wood frog hibernates beneath leaves, and the winter habitats of spring peepers, gray tree frogs, and chorus frogs await discovery. All four frog species pack their cells with glucose that serves as antifreeze. Ice in intercellular spaces crystallizes on protein. Breathing halts. Hearts stop. Metabolism plummets until spring.

What animals get fat to be fit (to paraphrase a line from *Racing the Antelope*)? The skunk, jumping mouse, black bear, woodchuck, and raccoon plump up when

the food supply dips in autumn; their body is their fuel tank. In contrast, an obese flying squirrel lugging excess fat in flight would be at a disadvantage. The flying squirrel remains active in winter—it does not hibernate, store food, or fatten. To investigate how well the nest of a flying squirrel insulates, Heinrich heated a potato to 60° C. Within the nest the potato cooled to 42° C in 35 minutes; outside it cooled to 15° C in -13° C air. Flying squirrels also cuddle in groups Heinrich has counted as many as 10 flying squirrels leaving a tree hollow. *Glaucomys volans*, the southern flying squirrel, appears to form even more impressive winter aggregations—up to 50 individuals (Weigl et al. 1999).

The author's graceful black-and-white sketches evoke the nature of winter beautifully—for example, a grouse tunneling deep under the snow and a flying squirrel peeping from a maple. Readers inspired to learn more about winter adaptations will appreciate that the references are sorted by chapter. Many readers will wish to dip into *Winter World* repeatedly, but an index is lacking, a blemish that the publisher could have remedied.

Heinrich credits a nature guide published in 1922 (Hans Wagner's *Taschenbuch der Käfer* [Pocketbook of Beetles]) as the first book he read that linked the contents of paper pages with something concrete in nature (Cannon 1999). *Winter World* provides readers a similar link between the book and the natural world. Although not produced as a textbook, *Winter World* might serve as an undergraduate supplemental text for a course in animal ecology, evolutionary biology, or vertebrate physiology. For a course in science writing, it would serve well as a source of well-crafted writing. *Winter World's* audience will range from those who venture out only to a city park to those who, like Heinrich, climb an 80-



foot-tall spruce to see life from a treetop perspective.

Swallows migrated to the moon, asserted naturalist John Morton in the late 18th century. Heinrich's splendid book gives us a more informed view of animals' adaptations, in this case, the adaptations that enable survival in winter. It is the rare book that teaches us to see more clearly even as it delights us. *Winter World* will impel you to take a walk in the winter woods.

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METAPOPULATION BIOLOGY GOES EVOLUTIONARY

Ecology, Genetics, and Evolution of Metapopulations. Ilkka Hanski and Oscar E. Gaggiotti, eds. Elsevier Academic Press, London, 2004. 696 pp. \$54.95 (ISBN 0123234484 cloth).

The notion that discrete populations interact through the exchange of individuals (and hence genes as well) is certainly not new, and is easily traced back through the writings of such

authors as Levins, Mayr, Dobzhansky, Wright, Harper, Elton, and many others. However, the study of interconnected populations has attained more prominence in recent years through the emergence of metapopulation biology as a distinct research area. In 1991, Michael Gilpin and Ilkka Hanski jump-started this new specialty area with the publication of the edited volume *Metapopulation Dynamics*. Six years later, prompted by the rapid proliferation of research in this area, the two editors edited a sequel, *Metapopulation Biology* (Hanski and Gilpin 1997). Thus, *Ecology, Genetics, and Evolution of Metapopulations (EGEM)* represents the third publication in this series of edited volumes focusing on the biology and dynamics of metapopulations. It is important to note that *EGEM* is not a revision of either of the earlier two books; rather, it is an entirely new book, containing all new chapters.

As suggested by its title, the 2004 publication differs from its predecessors in

that it covers more than ecological dynamics, the primary focus of the first two books. *EGEM* adds an explicit emphasis on genetic and evolutionary patterns and processes of metapopulations. In the preface, Hanski and Gaggiotti describe their intention: to provide readers with a diverse collection of up-to-date reviews on a wide variety of metapopulation topics. In this, they have succeeded. The book is divided into five parts: an introductory section on metapopulation dynamics, one section each on metapopulation ecology, genetics, and evolutionary dynamics, and a final section on integration and applications. Three contributions compose each of the first four sections, and eleven sections (approximately half the book) make up the final section.

The editors have succeeded also in compiling a diverse set of reviews, and this represents a major strength of the publication. A total of 37 authors from 11 countries contributed. European contributors outnumbered North American

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Hanski and Gaggiotti, along with the other 35 contributors, have produced an excellent compilation on metapopulation biology. I suspect that the book's emphasis on genetics and evolution will serve as an important catalyst, stimulating more metapopulation research in these areas.

contributors by nearly two to one, reflecting the strong interest and significant contributions from European scientists in this area during the past 15 years. Some chapters are largely theoretical in nature while others are primarily empirical. Some are organized around case studies, and others describe modeling efforts. Some focus directly on practical applications of metapopulation theory and knowledge (e.g., in conservation efforts). As for focal organisms, different chapters address in depth plants, insects, mammals, and pathogens.

The editors emphasize that they did not try to impose a particular approach on the authors, a decision that contributed both to the diversity of contributions and to the book's inability to become much more than a collection of contributions, as excellent as many of them are individually. The two editors did write an outstanding introductory chapter, which gives the reader an informative historical perspective on the development of metapopulation biology and an overview of more recent developments in the areas of genetics and evolution. I wish they had made a similar effort at the end of the book and written a concluding chapter identifying and emphasizing some of the common themes, problems, and prospects elucidated in the preceding material. In this reviewer's opinion, the benefits of such a chapter in helping to create an organizing conceptual framework would have far outweighed the costs of writing it.

I suspect the editors might respond that their decision to let the individual contributions stand on their own was intentional. It is true that a synthesis is not needed to meet the first of the editors' stated goals for the book, which is to serve as a reference to researchers. The number and range of contributions give researchers abundant food for thought.

One thing I particularly liked was that all the references are consolidated in a single bibliography at the end of the book. I have always found it frustrating to look up a reference I know was cited somewhere in an edited volume when all the references are appended to individual chapters. The lack of an organizing theme or common approach, however, seriously hampers the book's ability to meet the editors' second goal, which is to provide a textbook for advanced students in ecology, genetics, evolutionary biology, and conservation biology. By "textbook," I mean a book that presents a subject in a coherent, consistent way and has an explicit scheme of organization. By this standard, *EGEM* falls short.

It would be difficult to imagine any population ecologist or population geneticist who couldn't find some of the chapters informative and stimulating. But the breadth of the material is even larger than the book's title suggests. The relationship of metapopulation biology to landscape ecology is discussed by Kimberly With, as well as by Hanski and Gaggiotti. The extension of the concept of metapopulations to the notion of meta-communities is developed in a thought-provoking chapter by Matthew Leibold and Thomas Miller. Life history evolution in metapopulations is discussed by Ophélie Ronce and Isabelle Olivieri. The metapopulation dynamics of infectious diseases are discussed in a chapter by Matt Keeling and Ottar Bjørnstad. Prospects of climate change impacts on metapopulation dynamics are presented by Chris Thomas and Hanski. And the relevance of metapopulation theory to refuge design is covered by Mar Cabeza, Atte Moilanen, and Hugh Possingham. This is just a sampling of the book's richness.

The text is easy to read and logically formatted with frequent headings and

subheadings. Most, but not all, chapters end with a section called "Conclusion" or "Concluding Remarks," which the reader can skim to determine whether a particular chapter might be worth reading. The figures are clearly presented. The chapters differ in their accessibility, although, as suggested by the editors (who state that probably not many "would find all the chapters easy bedtime reading"), the challenge of some chapters may be more attributable to a reader's unfamiliarity with the topic than to poor writing or editing. The book has a soft, cloth cover and the price is reasonable, given the exorbitant cost of so many edited volumes these days.

In sum, Hanski and Gaggiotti, along with the other 35 contributors, have produced an excellent compilation on metapopulation biology. I suspect that the book's emphasis on genetics and evolution will serve as an important catalyst, stimulating more metapopulation research in these areas, just as the 1991 Hanski and Gilpin volume did for metapopulation ecology. At the same time, I could not help feeling a bit disappointed as I turned the final page of text. I found myself mumbling the title words of Peggy Lee's hit, "Is That All There Is?" Perhaps it was unrealistic to expect that the third volume in this series, published 13 years after the first volume, might be more synthetic than its predecessors. Perhaps my conception of a textbook differs from that of the editors. In any case, it is clearly time for someone to write a real metapopulation textbook, an overview of the field written by one or just a few authors. The related field of landscape ecology has benefited from several such books in the past (Forman and Godron 1986, Forman 1995) and currently is benefiting from one just published (Turner et al. 2004). I encourage Hanski and Gaggiotti, as well as other metapopulation biologists, to consider such an undertaking before publishing the next in the current series of edited volumes.

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NEW TITLES

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