

number of cases are known whereby anthropogenic habitat alteration is effectively reversing the speciation process. As Price points out, changed agricultural practices may be driving the breakdown of speciation in Snow Geese, which once maintained geographically distinct blue and white races, but which now are hybridizing and may be collapsing into a single gene pool. Several other examples are given (chapters 16, 17) in which human activity may be causing a reversal of speciation. At a minimum, a better understanding of the breakdown of reproductive isolation may provide insight into the genetic and demographic mechanics of how hybridization contributes to the loss of biodiversity.

On the whole, this is an excellent and highly readable book that bears on one of the most important questions in all of science: the origins of biological diversity. The author has an uncanny ability to tie the biology of speciation to traditionally separate fields, including community and behavioral ecology. As such, the book has something to offer evolutionary biologists and ecologists of any stripe. Moreover, the seamless integration of natural history with a sophisticated body of speciation theory will appeal to anyone with an interest in understanding the inspiring diversity in the world around us, avian and otherwise.

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The Meaning behind Malformed Frogs

Malformed Frogs: the Collapse of Aquatic Ecosystems. Lannoo, M. 2008. University of California Press, Berkeley, California. 270 pp. \$65.00 (hardcover). ISBN 978-0-520-25588-3.

For more than a decade, reports of grotesquely deformed frogs have

caused public concern and scientific controversy. Following the 1995 discovery of frogs with missing, extra, and malformed limbs by a group of Minnesota middle-schoolers, scientists have invested considerable time, energy, and resources toward understanding the causes and implications of amphibian malformations. Are malformations a threat to amphibian populations, which continue to decline in many parts of the world? Could malformations in frogs be indicative of an insidious threat to human health? Although significant progress has been made addressing these questions, many outstanding issues remain, and the mystery of deformed frogs has neither gone away nor has it been entirely solved.

Over the last decade, advances in the study of amphibian malformations have occurred on 2 primary fronts: quantifying the extent of the issue and identifying its likely causes. To date, severe malformations have been recorded in 71 amphibian species in over 40 U.S. states, with particular concentrations in the western United States, upper Midwest, and northeastern United States into southern Canada. Reported malformations primarily affect the hind limbs of frogs and toads that recently emerged from standing water habitats, such as lakes, ponds, and wetlands. The frequency of malformations can be extremely variable over time and across space, with individual wetlands acting as hotspots in some years but not in others. Investigations into the causes of malformations, which at times have led to inspired debate, have focused primarily on UV-B radiation, chemical contaminants, predator attacks, and trematode parasitism. It is now clear that all these factors are capable of causing limb abnormalities in amphibians, particularly when administered in laboratory experiments. With respect to limb malformations, probably the most extensively studied causative agent is infection by the trematode parasite *Ribeiroia ondatrae*, which attacks the developing

limb tissue of larval amphibians. Integrated laboratory experiments and field surveys reveal that trematode infection is a widespread cause of limb malformations in the western United States and some areas in the Midwest. In other areas, however, *Ribeiroia* has not been detected or occurs only at low levels, leaving open the question about what factor is responsible for observed malformations. Several recent studies suggest that the levels of UV-B exposure in amphibian habitats are often too low to directly induce abnormalities, which has caused focus to shift toward the potential roles of chemical contamination and predator attacks.

In his new book, *Malformed Frogs: the Collapse of Aquatic Ecosystems*, scientist Michael Lannoo draws renewed attention to the issue of amphibian deformities and its unanswered questions, offering his own perspective on the successes and failures underlying the investigation. This is only the second book to focus on malformed frogs, and it is the first to be written by a scientist. Over the course of 7 chapters, Lannoo guides his readers through a diverse collection of topics related to malformed amphibians, including amphibian development and morphology, chemical contaminants and toxicology, the causes of human malformations, and how each topic informs the study of amphibian deformities. Throughout, Lannoo employs a casual and entertaining writing style that makes this book an easy read for both scientists and the lay public. He draws heavily on quotations from eclectic sources, ranging from the Bible to Supreme Court briefs, which often provides a novel perspective, but at times can be distracting. The book is illustrated with extensive radiographs of deformed frogs and offers the most up-to-date accounting of which amphibian species have been reported with malformations in the United States. In a generous tribute, Lannoo asks that all proceeds from the book go to the Memorial Fund for Dr. Daniel Sutherland

(1952–2006), a parasitologist who, while making valuable contributions to the study of deformed frogs, is best remembered as a loving father, a dedicated husband, and a remarkable friend.

Malformed Frogs approaches the issue primarily through 2 complementary approaches: interpretation of the published research on malformed frogs coupled with empirical data from 17 Minnesota ponds. The use of raw field data from Minnesota gives the reader an on-the-ground experience of investigating amphibian malformations, that is, often lacking in primary scientific literature. Based on a critical review of the previously published research on malformed frogs, Lannoo argues, as have others, that no single factor can explain all amphibian malformations.

In what is probably the most important contribution of the book, Lannoo focuses on solutions to the malformed frog problem. He suggests that the variety of causes of the problem becomes almost irrelevant because a major factor in most causes appears to be agricultural runoff (which contains pesticides and parasite-enhancing fertilizers). Hence, reducing runoff is the simple answer to curbing malformations. He calls this the “not so funny joke” underlying the malformed frog issue. Because scientists have focused primarily on possible causes and have generated disturbingly few recommendations about how to reduce the frequency of amphibian malformations in affected wetlands, Lannoo’s effort provides a welcome shift toward seeking solutions.

Alongside its novel contributions, this book has some weaknesses. Primarily these involve insufficient attention to the complex ecological aspects of the investigation and a failure to define the problem adequately. For example, by classifying potential causes into “natural” versus “manmade” categories, the book largely ignores the multifaceted ecological interactions among these

factors that underlie this issue. Moreover, by narrowly focusing on Minnesota wetlands alone, excluding the hundreds of malformed amphibian reports from the U.S. West, North-east, and parts of Canada, Lannoo misses a genuine opportunity to develop broad conclusions about the landscape-level patterns of malformations and to synthesize available information on the regional causes of malformed amphibians. And although Lannoo deserves praise for his emphasis on solving the malformed frog problem, the notion that science has failed in the study of deformed frogs or that the collection of data comes at the expense of management action are oversimplified.

Conservation biologists, having wrestled with the challenges of acting in the face of inadequate data, have pioneered the field of adaptive management for just such situations. Because management actions can also come at a cost to society, additional data are imperative to understanding the implications behind deformed frogs and assessing what resources should be dedicated to reducing them. Even if we halted the use of pesticides and fertilizers, which play important roles in our nation’s agro-economy, it would be difficult to say whether this would reduce malformations in the short term. Nutrients such as phosphorus (and some chemical contaminants) can persist or recycle in the environment for years, such that run-off reductions may require decades to become effective. Thus, although Lannoo is right to emphasize the need for more active management, best management practices will be built on sound research that elucidates the consequences of malformations for amphibians and the remediation(s) necessary to alleviate such risks.

A critical weakness of the malformed-frog investigation generally and of this book specifically is a failure to adequately define the “malformation problem.” Stated another way, what is normal or expected in an amphibian population versus

what is abnormal and therefore of concern? Lannoo states that “malformed frogs are unholy things” and that every account of malformed frogs should “raise deep concerns.” Some malformations, however, are expected in every population, be it frog, human, or otherwise. If you examines enough frogs, you will always find malformations, typically owing to mutation, trauma, developmental errors, or rare alleles. In humans this baseline frequency of malformations hovers between 3% and 5%. Strange as it sounds, this is normal. Concern arises when the frequency swells significantly above this baseline, as was observed following the use of thalidomide in morning sickness medication from 1956 to 1962 and as continues to be observed in Kazakhstan 40 years after Soviet nuclear testing. Lannoo, however, argues that imperfections in our ability to precisely quantify the frequency of malformations in a population preclude the use of malformation frequency as a metric to assess severity. Thus, even if only 1 frog out of 100 in a pond is abnormal—within the expected baseline frequency—Lannoo suggests there may have been far more malformed individuals that died before they could be observed (and this pond could therefore still be considered a “hotspot”). Indeed, despite an entire chapter entitled “Hotspots,” the book offers no information on how to differentiate a hotspot from a normal pond.

This seemingly subtle omission creates an enormous problem in the study of deformed frogs. Without an operational definition of what is normal, almost any wetland can be classified as a hotspot, and many disagreements about the relative importance of different causes stem from differences in exactly how the problem is defined. Ecologists routinely struggle with the problem of uncertainty in data collection; rather than throwing the data out, scientists should strive to quantify such uncertainties and use statistics to determine whether

the observed malformation levels significantly exceed the expected baseline value (a null hypothesis of <5%). Although such approaches are not foolproof and may exclude some accounts that warrant attention, they provide an essential first cut between what is normal and what is a potential problem. For example, although the fatality rate of Ebola Zaire in Africa (approximately 90%) is often inflated owing to incomplete estimates of surviving patients, it is nevertheless recognized that Ebola has a much higher fatality rate than annually circulating strains of influenza (<1%). Some malformations will always occur in amphibian populations because this is a fundamental tenet of natural selection, but scientists need to recognize and incorporate a clear definition of what types and levels of malformations should be considered “normal” if the investigation is to move forward.

Finally, while many have argued that amphibians represent the proverbial canary in the coal mine, acting as early-warning bioindicators of risks to human health, this metaphor has limitations. As suggested by the book's alarmist title, *The Collapse of Aquatic Ecosystems*, and an entire chapter devoted to human malformations, Lannoo believes malformations in amphibians may forewarn of a health problem for humans. Evidence to support this link is rather thin, however. It is true that the limb-development pathway is strongly conserved among vertebrates, potentially supporting the notion that whatever causes amphibian malformations could also affect human development, but one must consider major differences between these groups that influence malformation patterns. For example, human fetuses develop within a protective womb, whereas amphibian larvae develop in a dynamic wetland environment where they are exposed daily to threats from predators, limited food availability, and infectious disease. Lannoo often draws on human medicine to argue

that traumatic injury (e.g., predator attack) cannot explain missing limbs in frogs. If an adult human were to lose an entire limb, the person would almost certainly bleed to death, particularly in the absence of modern medical care. But the situation is very different for a larval amphibian, in which the developing limbs are small, incompletely vascularized, and capable of partial regeneration. This is not to say that insights cannot be achieved by comparing human and amphibian development—and indeed developmental biology has advanced in just this way. Rather, scientists should refrain from making conclusive judgments on the basis of analogies; instead, ideas need to be tested experimentally under realistic conditions.

This book—and this review—each illustrate that today, more than a decade after that fateful day in Minnesota, many unanswered questions about deformed frogs remain. Science has made great strides in understanding some of the causes of observed malformations, but there are many pressing issues that still need to be addressed. Foremost among these is identifying the consequences of malformations for affected amphibians and other wildlife. Growing evidence indicates that malformations are detrimental to amphibian survival and reproduction, but their long-term impacts on amphibian population viability and whether they contribute significantly to population declines remain open questions. Anecdotal data strongly suggest that high-frequency malformations incur population-level impacts, but the lack of quantitative information makes it nearly impossible to assess the severity of the malformation problem and allocate resources toward solutions. Overcoming these obstacles requires more intensive and longer-term population monitoring of malformation hotspots, including replicated mark-release-recapture studies of malformed and normal frogs over multiple timescales.

Progress in the study of amphibian malformations also will require that scientists move beyond single-factor explanations to incorporate field and experimental studies capable of detecting interactions among causative agents. Rather than seeking to create simplistic explanations regarding the relative importance of parasites and pesticides, for example, researchers should embrace the diverse and likely ubiquitous mechanisms through which these factors will interact to affect amphibians. This approach is fundamentally challenging because it requires extensive collaboration among scientists of diverse disciplines and perspectives and because it requires a shift away from the current approach of ranking the importance of causes and toward developing a predictive framework that specifies under what conditions certain cause(s) will predominate. Because it is known that malformations vary both regionally and temporally, this framework must dynamically incorporate spatiotemporal variation. Providing the necessary data for this endeavor will require a resurgence in efforts to monitor malformations, which have waned in recent years.

It is vital that ongoing research on malformations concurrently contribute to mitigating the impacts of abnormalities on amphibian populations, which are now the most threatened vertebrates on the planet. Field experiments, particularly at large spatial scales, represent one of the most powerful demonstrations of causal control in science. The use of such experiments to reverse or reduce the effects of malformations could, therefore, provide a clear demonstration of causal understanding while advancing solutions to an applied conservation problem. Field manipulations are particularly effective when conducted alongside more controlled laboratory studies, which provide the mechanistic insights lacking from large-scale, in situ efforts. Definitive evidence linking malformations and

declines in amphibians may be currently lacking, but such information often requires decades to be compelling, during which time amphibian populations already in decline could disappear. If the last decade has been characterized by research into the causes of malformations in amphibians, conservationists let us endeavor to characterize the next decade by its progress in reducing their impacts.

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Carson's Legacy

Rachel Carson. Legacy and Challenge. Sideris, L. H., and K. D. Moore. 2008. State University of New York Press, Albany, New York. 287 pp. \$24.95 (paperback). ISBN 978-0-7914-7472-3.

Rachel Carson's place as one of the giants in the history of the U.S. environmental movement is secure. The national attention that followed the publication of *Silent Spring* in 1962 likely played no small part in motivating the rich suite of environmental laws that moved through the U.S. Congress in the late 1960s and early 1970s. Carson's place in the academic pantheon as a philosopher, a writer, and a subtle thinker who boldly, if perhaps not deliberately, located her work at the tortuous intersection of the sciences and the literary arts, the academic and the activist communities, and the terrestrial and marine environment is less fully theorized. Work done in this area is important to ensure that Carson's legacy and challenge continue to inform and inspire the general environmental public, professionals and interested bystanders who might be curious to dissect the rhyme and reason behind the writings of any figure who can claim credit for changing a national discourse. The essays col-

lected by Sideris and Moore in this book are a valuable offering in that direction.

Like Carson herself, the collection eludes to the danger of becoming trapped in any single genre of thinking or criticism. The contributors are philosophers and ecologists, writers and entomologists, poets and historians. One of the reasons the book works so well is the diversity of voices and the brevity—and sometimes humility—of the contributions. None of the essays exceeds 16 pages. Each of them provides a single insightful snapshot taken from a different angle, with different lights and filters, of a figure whose descriptions of the natural world and the moral imperatives it places on humanity are so skillfully composed that her work seems to occupy all of these genres and none of them at the same time.

The opening section of the book contains three essays on Carson's legacy as an activist and an advocate, the face for which she is perhaps most well known. Tempest Williams, Lubchenko, and List describe Carson's role as a catalyst for change in both the public and their own private spheres. The second section invites environmental ethicists (Cafaro, Bratton, Callicott and Back, and Kroll) into the discussion to chart the contours of the moral landscape that emerges from Carson's work. Carson's three books on the sea provide the ethicists as much material here as her more well-known call to arms about the profligate use of pesticides in agriculture.

Part III (Sideris, Hazlett, and Smith), titled "Reflections on Gender and Science," investigates Carson's approach to the occupation and the presentation of science. It details how she moved with apparent ease between the pivots of reason and emotion. The authors discuss how Carson demonstrated simultaneously both detached observation and an emotional attachment to her research subject. This section lays out the well-documented misogynist re-

sponse to *Silent Spring* from many in the scientific and the industrial communities and how her persistence in the face of this criticism opened up new ways of being a scientist for those who followed.

The fourth part of the book examines the theme of toxic pollution so central to *Silent Spring* in order to discover how—or if—things have changed in the last half century. Pimental, McGuire, Merrill, and Steingraber mix ecological science with personal narrative and social constructivist analysis to warn against the continued power and presence of DDT and other pesticides, even since Carson's death from cancer in 1964. Finally, the closing section of the book contains essays by Sideris, Norwood, and Moore on the role of the religious and the significance of wonder. The essay published after Carson's death under the title *The Sense of Wonder* was never to be the book-length treatment Carson had hoped. This section illuminates the significant role of wonder and of religious feeling in transforming Carson's careful observations of the natural world into something that might inspire.

Readers who hope to come away from the book with a definitive picture of Carson's philosophy, her ethics, and her understanding of the relationship between science, literature, and philosophy might find themselves disappointed. There is no definitive judgment made about which academic labels stick best to Carson and her legacy. The contributors do not sing with one voice about whether she was an ecofeminist or not, whether she was an environmental justice advocate or a nature romantic, whether she rejected or cautiously embraced the human ability to manipulate nature, whether she thought the mighty oceans exceeded the power of human endeavor, and whether she believed it was facts or the emotional response to those facts that spoke the loudest. The authors of the essays in this collection are far from unanimous in their answers to these questions.