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Complex Dependencies

Plant–Pollinator Interactions: From Specialization to Generalization. Nickolas M. Waser and Jeff Ollerton, eds. University of Chicago Press, Chicago, 2006. 445 pp. $45.00 (ISBN 0226874001 paper).

Ecologists no longer expect that field studies of mutualisms will commonly reveal obligate coevolved dependencies between particular plant and pollinator species. Figs and fig wasps still stand as the best suite of examples of one-to-one coevolution of flowering plants and pollinators, but they are exceptions to the rule that few plant species depend entirely on a single pollinator species, and few species of pollinators depend entirely on a single plant species. The reality of specialization and generalization is vastly more complex. The reasons for real differences in pollinator and plant dependencies—and their consequences for understanding, conserving, managing, and using pollination systems in nature and in agriculture—are far too important to the ecology of populations and communities to relegate to tidy, oversimplified natural history lore.

Plant–Pollinator Interactions, edited by Nickolas Waser and Jeff Ollerton, is a masterful overview of a rich field in a stage of dynamic ferment. Thirty-eight contributing authors offer 18 chapters of experiences and perspectives ranging from those of new investigators to those of established scientists.

Waser's introduction (part 1) provides historical context. Although Sprengel (1793) expressed "certainty" that many plants are pollinated by single agents, Waser points out that specialization and generalization do not reflect dichotomies in nature, but instead a continuum of degrees to which particular taxa or functional groups of pollinators use and are used by particular taxa or functional groups of plants. Waser leaves it to his authors to define dependencies and asymmetries in different pollination systems and ecological communities. This historical overview frames, and promises to extend beyond the framework, the contemporary controversy about the degree to which pollination "syndromes"—defined by Stefan Vogel and others as suites of flower traits of color, shape, scent, nectar composition, and pollen rewards—reflect adaptation to and use by identifiable groups of pollinators. If specialization and generalization continue to be redefined by successive authors in this volume, this ambiguity reflects the field.

Part 2 ("Ecology and Evolution of Specialized and Generalized Pollination") explores how use and selection by pollinators or plants influence the evolution of pollination mutualisms. José Gómez and Regino Zamora give a theoretical overview of ecological factors that promote specialization and generalization in pollination. In the spirit of G. Ledyard Stebbins, they argue that pollinators that enhance plant fitness are selective agents, and that the more distinct different pollinators are in providing those fitness benefits for plants, the more likely it is that consistent use by those pollinators will promote specialization by plants. When different pollinators provide distinctive selective benefits for plants experiencing serious herbivory, the plants evolve complex life cycles that allow them to make generalized use of this array of pollinators. Gómez and Zamora distinguish this from adaptive generalization that occurs when effective pollinators vary in number or attention in space and time (e.g., the classic *Calathea* case; Horvitz and Schemske 1990). Nonadaptive generalization, in contrast, occurs when different taxa of pollinators do not differ in their fitness effects.

Other chapters consistent with the "Stebbins framework" explore selective and ecological effects of different pollinators on plants, or vice versa. Paul Wilson and colleagues discuss repeated shifts from insect to bird pollination among distantly related members of the genus *Penstemon.* By contrast, Robert Minckley and T'ai Roulston explore in the following chapter the distinction between evolved and incidental specialization of bee pollination of flowers. In rare cases, a single bee taxon has evolved to use a single plant taxon; more commonly, one or more bee taxa by chance use a given plant species at a particular place and time, with the plant adjusting, if at all, to multiple pollinators. Other bees remain unspecialized, using and pollinating a variety of plant taxa. This is a thoughtful exploration of the question posed by Janzen (1980): "When is it coevolution?" James Cane and Sedonia Sipes (chapter 5) are concerned with degrees of consistency in bee use of flower taxa, whether the interaction is evolved or not. Their revised lexicon of degrees of pollen specialization recognizes several levels of oligolecty but excludes nectar collection that occurs without pollen gathering.

Do the trade-offs assumed by most discussions of specialization and generalization exist? Are some generalist pollinators or flowers disadvantaged by being jacks-of-all-trades and masters of none?

Do the trade-offs assumed by most discussions of specialization and generalization exist? Are some generalist pollinators or flowers disadvantaged by being jacks-of-all-trades and masters of none? Paul Aigner (chapter 2) models how specialization might evolve without trade-offs in "fine-grained" environments in which mutualists depend on far fewer partners than they encounter. Trade-offs have not been addressed carefully in pollination biology; little evidence of reduced fitness from generalization seems to exist. In a clear departure from the Stebbins framework, Aigner suggests that trade-offs are not necessary for special-

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ization. He hypothesizes that pollinators responsible for plant specialization need not be either the most numerous or the most effective ones for a plant if they supply marginal gains or deficits in fitness for the plant, and he offers a fascinating speculation about how to test the idea.

The studies discussed in part 3 leave us free to wonder what quantitative patterns of plant and pollinator association actually exist across communities, regions, and continents. Pedro Jordano and colleagues (chapter 8) probe nested structure in pollination in a wide array of systems, finding that all show a structure characterized by "nodes" of common plants, visited by common and rare pollinators, with the probability of pollinator interaction declining as the number of plants increases. In the same spirit but with different methods, Diego Vázquez and Marcelo Aizen (chapter 9) ask whether the probability of interaction is equal among plant and pollinator species within 18 communities. The answer is a clear no, with frequent asymmetric associations of plants and pollinators. Theodora Petanidou and Simon Potts (chapter 10) compare real and apparent specialization, judged by the number of plant species visited, in Greece, Israel, and Spain. They find that evolved specialization is rare, but that at any place and time, selectivity of insects for plants and vice versa may be quite high. Few extreme generalists are obvious. Using evidence from Greece and Argentina, Diego Medan and colleagues (chapter 11) argue that generalization must be understood through time, offering analyses of pollination systems that are active throughout the year.

Are tropical systems different? Ollerton and colleagues find, not surprisingly, more pollination systems in tropical than in temperate communities, with more diverse floras and faunas and therefore more opportunities for specialization. Within plant groups, it is not clear that greater specialization in pollinator systems exists in the tropics, although the open question of what defines specialization contributes to this continuing ambiguity.

Do pollinators consistently select for reward strategies of plants? Scott Armbruster compares arctic *Saxifraga,* which exhibits little specialization, with degrees of specialization in species of temperate *Collinsia* in California, *Stylidium* in Western Australia, and *Dalechampia* in the tropics. Repeated evolution of pollen or resin collection in the latter system of neo- and paleotropical vines presents a classic study of selection for specialization reverting in some lineages to generalization.

Part IV examines the relevance of specialization and generalization to agriculture and conservation. Sarah Corbet offers a typology of flower presentation and another of insect use, which together are more operationally useful for agricultural systems than are Vogel's syndromes. Suzanne Koptur has a similarly useful message concerning the endangered plants of vanishing pine rocklands in southern Florida; many endangered species appear to secure adequate polli-



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nation because their insect mutualists are maintained by residential gardens. Manja Kwak and Renee Bekker provide a unique contribution by calculating vulnerability indices for plant species used in European community restorations. Ingolf Steffan-Dewenter and colleagues address the effects of habitat fragmentation on bee pollination. These authors explore the consequences of fragmentation for common asymmetrical pollination systems that lie between rare one-to-one mutualisms and rare extreme generalization. Their chapter is especially interesting in pointing out that effects of fragmentation consist of much more than increased pollen limitation.

Ollerton (last chapter, part 5) closes with what may prove to be a seminal synthesis. Interactions between organisms are usually modeled as means of optimizing currencies of energy or nutrients. Ollerton promotes the idea of a "biological barter" economy, in which rewards may be exchanged for services that are sometimes reasonably modeled by energy optimization (nectar as food for bees), but in many cases not (resin for bee nest construction, flower fragrances for bee courtship). Ollerton is out of step with the parade here, but in my view the parade has been going in the wrong direction for some time. His chapter develops the idea that specialization occurs when exclusive mutualisms become "intimate through trophic, physiological, and/or physical integration."

This collection of essays is stimulating, but will not suit all needs. The antagonistic roots of pollination mutualisms are apparent in Susanne Renner's comprehensive discussion of the pollination of flowers that offer no rewards—the ultimate plant "cheaters." The collection would have profited from a theoretical discussion of the evolution of mutualism from antagonism (e.g., Bronstein 2001). Moreover, the phenomena examined are mostly temperate and might not be good models for tropical forests, where flower displays are often huge and high above the ground, and could conceivably attract thousands of pollinators—or very few.

Plant–Pollinator Interactions will define much of the debate on the central issue of specialization and generalization in pollination biology. I recommend it to all students of pollination, as well as to those interested in broader issues of plant and animal interactions. My guess is that a volume of similar depth and reach with a tropical slant will change the debate again.

HENRY F. HOWE
Henry F. Howe (e-mail: hfhowe@uic.edu) is a professor in the Department of Biological Sciences at the University of Illinois at Chicago.

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BLAZING A BIOGRAPHIC TRAIL

Francis Crick: Discoverer of the Genetic Code. Matt Ridley. HarperCollins, New York, 2006, 214 pp. $19.95 (ISBN 006082333X cloth).

In 2004, HarperCollins launched "Eminent Lives," a series of brief biographies of important historical figures. Gifted writers were assigned to write engaging profiles of important historical figures such as Thomas Jefferson and Machiavelli. The first scientist to join these august ranks is Francis Crick, the Nobel Prize–winning biologist who codiscovered the structure of DNA and led the successful search for the genetic code. What makes this achievement all the more striking is that this biography, by the award-winning science writer Matt Ridley, is the first one ever written about Crick, brief or long.

How is it that such an important figure in the history of science has been so neglected? Many of the other scientists who were involved in the discovery of DNA—James Watson, Rosalind Franklin, and Maurice Wilkins, to name three—have had their life stories told. And Crick's accomplishments have been well documented in books such as Horace Judson's *Eighth Day of Creation.* But there's something about Crick's life as a whole—a long one, which ended in 2004 after 88 years—that has eluded the embrace of biographers.

Frankly, having read Ridley's enjoyable biography, I'm stumped. Crick's life had a fascinating arc. He was not a scientific Mozart, his greatness tediously obvious from childhood. As a child, he was bright, but not brilliant. He studied physics at University College London, beginning a PhD research project on the viscosity of water, which he later called the "dullest problem imaginable." In World War II, he designed new mines that had a major impact on the naval struggles between Britain and Germany. He might have well gone into intelligence work after the war, but he had little taste for the bureaucratic sparring that came along with the job. Instead, Crick underwent a remarkable transformation at age 30. He decided that he would become a biologist, and that he would solve two of the biggest puzzles biology had to offer: life and consciousness. Ridley argues that these twin goals reflected Crick's long-running atheism. He would seize both nature and the soul from religion.

Crick went to Cambridge to follow through on his hubris, but it didn't go well at first. Ridley describes him at the time as "this loudmouth with the braying laugh who was much better at telling [his colleagues] what was wrong with their science than actually making measurements himself." What his colleagues didn't realize was that Crick had developed an exceptional ability to visualize molecules and mathematical problems. He could translate the mysterious hieroglyphics of X-ray crystallography into the atomic structure of proteins. And when James Watson arrived at Cam-

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bridge, the two scientists quickly seized on the problem that would make them legends: the structure of DNA.

Ridley does an excellent job of escorting readers on the intellectual roller coaster ride that followed. Anyone who has read about the discovery of DNA in James Watson's *The Double Helix* or other accounts will be familiar with the outlines of that work. But Ridley explores the nuances of the breakthrough—including the uneasy relationship between Watson and Crick and others studying DNA—with both care and verve. And somehow he succeeds in telling that story in only 31 small pages.

The discovery of the structure of DNA was an iconic moment in scientific history, in part because the double helix was such a good icon, a molecule with photogenic curves. More abstract, but no less important, was the code by which DNA's genes were translated into proteins. Ridley rightly stresses the importance of this work, and he demonstrates that in its own cryptographic way, Crick's solution to the genetic code was just as graceful as his work on DNA.

And then he was done. After 1967 Crick never found another subject in which he could make such great discoveries. He mulled over the idea that life on Earth was seeded by aliens. He tried his hand at the question of why humans and other eukaryotes have so much DNA. In the early 1980s, Crick took up the other great question he had wanted to answer as a biologist: consciousness. It is astonishing to imagine a scientist in his late 60s teaching himself neuroanatomy, but Crick did it. Consciousness was not ready for a reductionist solution, Crick realized, and so he instead organized scientists to make it so. He argued that consciousness was not just a philosophical question, but one that could be studied at the molecular level. He was writing papers about the brain right until his death. Today consciousness remains far from solved, but with molecular atlases and functional neuroimaging and other experimental approaches now maturing, it's not silly to think that someday it might be.

Despite the short length of the biography, Ridley has taken great care in its research. Not only has he sifted through Crick's writings, but he has also interviewed many of the people who knew Crick. While I heartily recommend the book, I couldn't help wishing that the author had not tried to squeeze this heavyweight body of work into the petite format of "Eminent Lives." Ridley's narrative has to make sudden turns, veering from the fine points of protein structure to Crick's wedding and then back. Ridley does not create a fully fleshed-out human being, but a collection of traits: scientist, party thrower, atheist, and so on. There's not much attention to the times in which Crick lived—the turbulent late 20th century, in which science and society were undergoing massive changes, many of which Crick helped create.

One thing does come out clearly from Ridley's portrait: Crick himself would not have been a fan of this book. He hassled James Watson over the *Double Helix,* considering it a sensationalistic account of their work. To Crick, people were less important to the history of science than the ideas and discoveries themselves. This attitude may make Crick an unattractive subject for a biographer in search of a major new project. But perhaps Ridley's slender account will encourage someone to produce a fine doorstop.

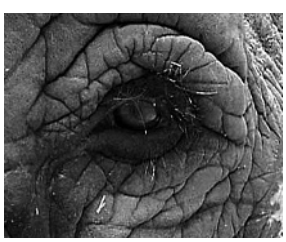
CARL ZIMMER
Carl Zimmer (e-mail: carl@carlzimmer.com) is the author of Soul Made Flesh: The Discovery of the Brain and How It Changed the World *(Free Press, 2004) and* Evolution: The Triumph of an Idea *(HarperCollins, 2001).*

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FEELINGS DO NOT A SCIENCE MAKE

Pleasurable Kingdom: Animals and the Nature of Feeling Good. Jonathan Balcombe. Macmillan, New York, 2006. 256 pp. $24.95 (ISBN 1403986010 cloth).

Jonathan Balcombe has broken what he describes as the scientific taboo on discussing animal feelings. In *Pleasurable Kingdom: Animals and the Nature of Feeling Good,* he argues that most scientists are still much too reluctant to talk about animals feeling happy or experiencing pleasure because of an unjustified fear of being considered anthropomorphic. He criticizes those who insist on sticking to observable behavior and refuse to take what he sees as the obvious next step of attributing conscious emotions to the animals they study. For him, it is implausible in the extreme to argue that we humans enjoy our food, the touch of companions, or sex and at the same time to argue that other species, showing similar behavior, do not. One of the photographs illustrates his point succinctly. The caption could have been "Red kangaroos copulating." In fact it is "Red kangaroos enjoying sex."



Balcombe invites us to make our choice. When we watch animal behavior such as eating or mating, are we watching "just" behavior, or are we watching a combination of behavior and pleasure? He is full of praise for those scientists who do shake off their behaviorist shackles and unashamedly talk about animals consciously experiencing pleasure. He also supplies a wealth of fascinating information about animal behavior to support his idea that much of what animals do is pleasurable to them. He is particu-

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larly impressed by the capacity of many animals to play (engage in activity for pure enjoyment) or to do things such as masturbate or engage in nonreproductive sex that cannot be related to biological function in any simple way. It must be, he argues, because they enjoy it.

In many ways, the release of inhibitions on talking about the conscious emotional experiences of animals is to be welcomed. Thirty years ago, Donald Griffin argued that we should start asking questions about animal awareness in the context of cognition. Extending that inquiry to animal emotions is equally important. But there are also good reasons for not throwing caution entirely to the winds when it comes to the question of whether animals actually experience pleasure as we do. First, behaviorism—the belief that only observable behavior and physiology can be studied scientifically—does not deny the existence of animal consciousness altogether, as is sometimes claimed. It just says that the existence of conscious feelings cannot be tested empirically, and so the study of conscious emotions is outside the realm of science. There is a profound sense in which behaviorism is right: Theories about physiology and behavior make predictions that can be tested against the real world in a way that theories about consciousness cannot. As John B. Watson put it nearly a hundred years ago: "One can assume the presence or absence of consciousness anywhere in the phylogenetic scale without affecting the problems of behavior by one jot or tittle and without influencing in any way the mode of experimental attack upon them" (1913). This is not the same as denying consciousness in animals. It just points out the enormous difficulties of investigating it scientifically.

Although Balcombe repeatedly acknowledges that we cannot know for certain whether animals actually experience pleasure, he gives the impression of dismissing or underestimating the problems that behaviorism highlights in ascribing consciousness to animals. Consciousness is still the "hard problem." We do not understand how it arises from within our own brains and so have no idea at all what to look for in the brains of other animals to decide whether they too are conscious. We cannot even say what would count as evidence for or against it. But in Balcombe's chapters on play, food, sex, love, and other pleasures, he seems to be being asking us to believe that there is no hard problem anymore, no need at all for philosophers and neuroscientists to be still scratching their heads and saying how profoundly mysterious consciousness is. The mind–body problem seems to have vanished in a simple mental switch from copulation to pleasurable sex.

Second, this book left me with an oddly depressing feeling that we were being urged to abandon all standards of scientific reasoning. The argument that we can't prove that animals consciously experience pleasure, but should assume they do anyway because it's so plausible, leaves no hurdles to be overcome, no standards by which a theory can be tested against reality. Anyone's guess or intuition about animal feelings becomes as good as anyone else's. Worse, there appears no longer to be any distinction between the anthropomorphism of Bambi and the scientific study of animal behavior. Those of us who do try to study animal behavior objectively would seem to be redundant, swept away on a tide of anthropomorphism. Balcombe has opened the floodgates and left us with no criteria for judging what might be true and what might be false.

I'm all for asking questions about animal consciousness. It is a biologically fascinating area, and one that is profoundly important for our ethical treatment of animals. But I also think it should not be done at the cost of abandoning the scientific method altogether, or of underestimating the implications of the fact that we don't understand the physical basis of our own consciousness, let alone that of other species. If we do wish to make a leap of analogy from our own experiences to those of other species and use anthropomorphism in our interpretation of their behavior, we should do this knowing what we are doing. A leap of analogy is just that—a leap away from what we can discover by scientific means. Behaviorism isn't wrong. It is just cautious, and shows us where the boundaries of hypothesis testing and evidence lie. Abandon those standards if you wish to. Follow Balcombe in using anthropomorphism to understand animal behavior if you feel that is the most fruitful way forward. But don't, please, confuse the two.

MARIAN STAMP DAWKINS
Marian Stamp Dawkins (e-mail: marian.dawkins@zoo.ox.ac.uk) is a professor of animal behavior in the Department of Zoology at the University of Oxford and a fellow in biological sciences at Somerville College, Oxford, United Kingdom. She is the author of Animal Suffering: The Science of Animal Welfare, Unravelling Animal Behaviour, *and* Through Our Eyes Only? The Search for Animal Consciousness.

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