Cognitive Ecology of Pollination

Animal Behavior and Floral Evolution

Important breakthroughs have recently been made in our understanding of the cognitive and sensory abilities of pollinators: how pollinators perceive, memorize, and react to floral signals and rewards; how they work flowers, move among inflorescences, and transport pollen. These new findings have obvious implications for the evolution of floral display and diversity, but most existing publications are scattered across a wide range of journals in very different research traditions. This book brings together for the first time outstanding scholars from many different fields of pollination biology, integrating the work of neuroethologists and evolutionary ecologists to present a multidisciplinary approach. Aimed at graduates and researchers of behavioral and pollination ecology, plant evolutionary biology, and neuroethology, it will also be a useful source of information for anyone interested in a modern view of cognitive and sensory ecology, pollination, and floral evolution.

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Preface

The idea of making this book arose from a symposium at the XVI International Botanical Congress in St. Louis, USA in August 1999, which brought together some of the contributors of this book. The idea, then, was to inform botanists of important recent developments in pollinator behavior, cognition, and sensory biology. These new findings and perspectives have numerous implications for the evolution of plants and the shaping of plant community structure. Our rationale for such a symposium was that we thought that many botanists are hard-pressed to keep up with the literature concerning pollinator neuroethology and behavioral ecology. Therefore, the field of plant–pollinator interactions is somewhat hobbled by stereotyped, anachronistic, scale-limited, or just simplistic views of how animals really interact with flowering plants.

Our discussions during the symposium (and with other contributors outside the symposium), however, revealed much more profound gaps than just the one between botanists and zoologists. Pollination biology is poised at the boundary between two different traditions, those of proximate and ultimate reasoning in biology. On the one hand, evolutionary ecologists tend to seek *adaptive* explanations for biological characters – how do the observed traits benefit the animal or plant? Physiologists and neuroethologists, on the other hand, prefer to consider the *mechanisms* by which environmental stimuli provoke or modify behavior. Unfortunately, these two groups of scientists have little commerce; they publish in different journals, attend different conferences, and tend to disparage each other's views. This was how the biological world was divided until a few years ago.

In recent times, however, many workers have realized that we cannot fully understand the operation of an animal's senses, learning, and cogni-

tion without knowing under what conditions these functions evolved; we cannot understand how flowers (and other biological signals) evolve without understanding mechanisms of information-processing on the receiving side. Attempts to bridge the gap between the two traditions have become fashionable in the past few years. It is in these attempts that the real shortfalls are revealed. Many physiologists will "round up" a paper's discussion by adding a paragraph on the adaptive significance of the traits they describe, where the existence of the trait is usually regarded as sufficient evidence for its adaptive nature. Standard evolutionary tools, such as phylogenetic analyses or measurements of fitness, are generally deemed unnecessary. Evolutionary biologists, on the other hand, do nowadays often discuss behavioral mechanisms, but their understanding of such mechanisms is sometimes rudimentary. The result is that mechanisms, in such papers, seem often tailored to fit *any* kind of observed behavior, rather than being based on what we actually know about them from physiological work. Finally, behavioral ecologists are sometimes guilty of both sins: pan-adaptionism without rigorous tests of evolutionary hypotheses *and* naïveté about neural mechanisms underlying behavior. Because papers in each of these traditions are largely refereed by other workers within the same field, the review process seldom forces authors to adjust their views. This, in turn, antagonizes scientists in the other fields. Each of us knows that our own field of research is a difficult one that demands knowledge of a specialized education and training in certain rigorous ways of thought. When an "outsider" offers a contribution to our field, we are quick to note the imperfections and inadequacies that are virtually inevitable. Perniciously, we may further decide that the inadequacies of outsiders must extend to their performance in their own fields, while they – of course – reach the same conclusion about us. We fear, therefore, that well-intentioned attempts to link ultimate and proximate perspectives, when done clumsily, will further the antagonism between these traditions, rather than smooth it out.

Pollination biology is a field that might serve as a link to tie these fields together, because it involves workers from all of the traditions above, all working on the same or similar experimental subjects. But readers should be warned from the start that our book does not represent the successful reconciliation and fusion of these viewpoints. Rather, we selected authors from different traditions whose work seemed to us most stimulating and innovative in *initiating* the process. Several of our chapters

present controversial views that highlight the discrepancy between traditions, but it is our sincere hope that by encountering these views side by side, readers will realize the necessity of *careful* links between proximate and ultimate reasoning.

Our emphasis in selecting authors was to find work that stimulated us intellectually, rather than attempting a complete survey of the field of the sensory, behavioral, and cognitive processes involved in flower visitation, and its implications for floral evolution. The chapters are organized so that we move from the more zoological work to the more botanical (but naturally, a clear distinction is not possible). We start with several chapters on the implications of cognition, memory, and perception for pollinator foraging behavior, then move through several sensory modalities involved in flower detection and recognition (color vision, pattern vision, olfaction, echolocation), at the same time discussing several important classes of pollinators (bees, bats, birds, butterflies, etc.). This is followed by one general chapter on the importance of recognizing pollinators as individuals and another on the influences of predators on pollination systems. The last third of the book has a stronger emphasis on the consequences of pollinator behavior and cognition for the evolution of floral traits, covering frequency dependent selection, assortative mating, speciation, and the influences of floral traits on patterns of pollen movement.

In selecting the contributors for this volume, it was of particular importance for us not to be biased towards age and eminence. We thought that fresh ideas are likely to come from young scientists, and so many of our authors are still in the early stages of their careers. As we received the chapter manuscripts one by one, we became more and more enthusiastic, because we felt that this approach has worked out very well. If this book turns out to be a success, this is due in no small part to the energy and creativity of its contributors, their support in reviewing chapters by other authors, and their patience in dealing with endless suggestions for revisions by two rather censorious editors. We are also extremely grateful to the following external referees: John Allen, Elizabeth A. Bernays, Thomas S. Collett, Catherine L. Craig, Heidi Dobson, Robert Dudley, Ted H. Fleming, Lee Gass, Wayne Getz, Andreas Gumbert, Carlos Greco, Carlos M. Herrera, Katherine Hinman, Almut Kelber, Peter Kevan, Susan J. Mazer, Randall J. Mitchell, Douglass H. Morse, Daniel R. Papaj, Gene Robinson, Flavio Roces, Sharoni Shafir, Sara Shettleworth, and Paul Wilson. Tracey Sanderson and Sarah Jeffery, who handled our manuscript at Cambridge University Press, have been extremely helpful in guiding us

through assembling this book. Its completion would have been impossible without Barbara Thomson's meticulous editorial help.

We sincerely hope that the efforts of all the individuals contributing to this work will foster new and innovative work on the interaction of animals and plants, and provide fruitful stimulation for all the biological traditions involved.

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