BOOK REVIEW

REVISTA DE Biología Tropical

Demystifying Orchid Pollination: back to the basics of Natural History

Karremans, A. P. (2023). Demystifying Orchid Pollination. Kew Publishing, Royal Botanical Gardens, Kew, Richmond, Surrey, TW9 3AB UK, 440 pp.

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Natural history is a multidisciplinary science that combines evolutionary biology with ecology and other fields, such as comparative anatomy, paleontology, biogeography, and biosystematics. Merging fields is essential to understanding the patterns of distribution and abundance of organisms, as this requires the integration of evolutionary and ecological time. The beauty of natural history lies in its multidisciplinary nature, which sets no boundaries to scientific inquiry. This condition is fundamental in generating scientific knowledge through the stimulation of human curiosity (Nanglu et al., 2023). This emphasizes the importance of natural history in knowing whether a question is relevant and could be applied to a system, and in calibrating experiments to hypothesis testing (Travis, 2020). This process (a.k.a. the scientific method) involves detailed observations, hypotheses testing, developing experiments, and collecting once again, more observations and evidence. The ordered chaos of identifying relevant questions and suitable systems to answer them is far from being linear. Classic natural history is what emerges from the pages of Adam Karremans' book "*Demystifying Orchid Pollination*".

This book is a tour de force and a testament to the rich history of exploring the mysteries of pollination focusing on the most diverse Angiosperm family, Orchidaceae (with over 30 000 species worldwide, Christenhusz & Byng, 2016). Orchid flowers have a remarkable complexity and intricate variations in morphology and function, and thus, it is not surprising that they have captured the imagination of naturalists since the beginning of civilization. *Demystifying Orchid Pollination* shows that Natural History, as a scientific method, still has plenty to contribute to ecological and evolutionary theory.

Karremans presents a very comprehensive compilation of cases of orchid pollination erroneously explained by myths. The subtitle (*Sex Stories, Lies and Obsession*) could be interpreted, with some sarcasm, as synonymous with *pollination* since it describes the nature of the biological interactions that the process involves, which includes deception, pollen exchange and fertilization (sex), and many times, the human obsession with sticking to myths as simple but erroneous explanations of phenomena with fragmentary evidence. Karremans draws on classical natural history to

resolve these myths and crack the riddles of orchid pollination. This involves gathering scattered evidence through an exhaustive literature review, conducting arduous and laborious field observations and experiments, and consulting with colleagues. Although this process may seem simple, detailed observation of nature requires great perseverance, patience, work capacity, a detective mind… and yes, a considerable number of hours in the field.

The book is organized into seven chapters. Chapter 1 (Plot) provides the foundation and starts with a summary of the history of research on orchid pollination studies, then describes orchid diversity and flower structure, and ends with a revision of the discussion of pollination syndromes. Early naturalists focused on describing the structure and anatomy of flower parts rather than unraveling the ecological mechanisms involved in pollination and fertilization. Christian Konrad Sprengel (1750 to 1816) was the first to scientifically explore pollination biology. His most significant contribution, *The newly revealed mystery of nature in the structure and fertilization of flowers*, published in 1793, was known by Charles Darwin and certainly inspired his interest in orchids.

Since then, orchids have provided compelling systems to explore evolutionary questions. Darwin was the first to describe in detail reproductive strategies such as protandry in terrestrial orchids and the production of imperfect flowers. He analyzed the causes of cross-pollination and recognized its importance for the evolution of species (Yim et al., 2009). Additionally, Darwin demonstrated that flowers had diverse strategies to attract pollinators, and that many species avoid self-fertilization. Darwin´s main contributions were the article "*Fertilization of Orchids*" (1862) and the book "*The Various Contrivances by Which Orchids Are Fertilized by Insects*" (1862), dedicated to the description of floral morphology and pollination of orchids from temperate and tropical regions. In these works, Darwin showed a laborious, precise, and specialized work where he demonstrated how orchid flowers and their pollinators matched in form and function setting the stage and questions for future work on orchids.

Also in chapter 1, Karremans pays homage to the seminal works of Calaway Dodson and Robert Dressler (researchers to whom the book is dedicated). Dodson and Dressler made significant contributions to the ecological, taxonomic, and evolutionary knowledge of orchids. Dodson and L. Van Der Pijl updated Darwin's book after a century with the book "*Orchid flowers: their pollination and evolution*" (Van Der Pijl & Dodson, 1966). The collaborations of Dodson, Dressler, Van Der Pijl, and many others, stimulated studies on orchid pollination, especially after the 1960s. However, the field is still dominated by research on terrestrial orchids, particularly those of temperate regions. Despite their sheer diversity, tropical epiphytic orchids have been little explored in terms of their interactions with pollinators.

Chapters 2 (Deceit) and 3 (Reward) provide examples of species interactions and present riddles, not only to pollination ecology but to evolutionary biology. One can only speculate how such intricate interactions between species, as well as between groups of species sharing phylogenetic relationships and common pollinators, gave rise to coevolution and group selection, guild mimetism, diffuse coevolution, and other evolutionary mechanisms that are just beginning to be explored. The evolutionary origin of pollination relationships remains a constant question throughout the book.

Chapter 2 deals with the many ways in which orchids manipulate their pollinators through deceit. In general, orchids have been divided into those that provide rewards, and those that deceive their pollinators, although the difference is not obvious and there is continuous variation between both extremes as reflected in the diverse assemblage of visitors to orchid flowers. In the plant kingdom, the Orchidaceae has the most species on record with deceptive pollination mechanisms. In this chapter, Karremans describes different pollination syndromes, from ornithophily, myophily, myosaprophily, and psychophily. The concept of *syndrome* refers to similar suites of flower

traits found in evolutionarily unrelated taxa that result from convergent selection by targeting the same pollinating agent (Faegri & van der Pijl, 1979; Dellinger, 2020). This may sound like another oversimplification (another myth?), but the concept has worked as a suitable model to establish patterns among groups, both plants and pollinators, and Karremans simply uses the term without entering the controversy of whether it has been a useful concept (Rosas-Guerrero et al., 2014). This chapter provides compelling examples and spectacular scenarios for the exploration of evolutionary stable strategies. The book includes examples of orchids that mimic the appearance of spiders to deceive predatory and parasitoid wasps looking for spiders, or orchids that generate an aroma to attract male euglossine bees which will then use it as a perfume to attract females, or orchids that produce the scent of a fungus deceiving flies looking for a reproductive site but that then pollinate these orchids. The evolution of these impressive strategies requires a fragile balance between the frequency of deception versus true rewards and the cleverness of the flower visitor falling for the trick. For the trick to work the frequency of the trickeries must be lower than the negative impact on pollinator fitness. The type of rewards is also very diverse and vary from the absence of rewards and pollination by deception, the presence of traces of nectar that lure pollinators to visit flowers without obtaining sufficient nectar, to flowers whose aroma resembles rotting meat, which offer both nectar and a sweet smell. One can only wonder about the population dynamics that must be at work for the evolution of these deception strategies.

Three insect orders (Hymenoptera, Diptera, and Lepidoptera) dominate orchid pollination. Chapter 4 (Misfits) tackles the subject of pollination misfits, this is, groups of pollinators that do not fit the classic role of orchid pollinators and include outliers such as beetles, crickets, trips, and hummingbirds. Outliers provide suitable systems to evaluate traditional hypotheses on pollination biology.

Chapter 5 (Redesign) concentrates on the variation of the pollination mechanisms, however, this adds to more bizarre cases of pollination as an "improvement" of the already not-so-regular cases, such as the mildly toxic nectar of orchids of the genus *Epipactis*, where wasps become drowsy after drinking the toxic nectar and spend more time in the flower doing erratic movements that eventually accomplish pollination.

Chapter 6 (Fallacies) deals with even more specific and often bizarre cases of interactions around orchid flowers, such as lurking predators (called *antipollinators*) that use orchid flowers as suitable sites for predation, or the pseudo-antagonism interactions between male bees and orchid flowers that mimic male bees and are thus attacked by the males. It is not clear in what instance the attack results in a successful pollination. Karremans also tackles some well-established myths about the high specificity of pollinators, since most orchid species do not have a well-documented fauna of pollinators, and for those that do, high specialization is the exception.

Chapter 7 (Change) tackles the effect of anthropogenic disturbances on orchid conservation. Being the most diverse angiosperm family, it is not surprising that Orchidaceae holds good and bad records, such as being the family with the highest speciation rate but also showing the highest extinction rate. Like most organisms nowadays orchids are threatened by anthropogenetic factors such as habitat loss and fragmentation, over-collection, and climate change, to name a few. Karremans discusses the shifting seasons of pollinator emergence vs blooming influenced by fluctuating temperatures, whose lack of overlap is endangering many pollination systems. Since habitat change is a multifactor process the impact of climate change on orchid pollination is understudied. The book ends with a positive message fostering the need to maintain biodiversity even in the toughest places such as cities. Nature will find a way.

Final remarks

The book highlights the crucial importance of fieldwork, which is evident from the first pages but is especially clear in the accompanying videos. These are research videos, so they do not feature fancy background music or an entertaining narration. They are linked to a QR code, which represents one of the great contributions of the book as it becomes a multimedia resource. The videos are excellent at capturing pollinators at the right time to illustrate a behavior and provide the evidence needed to solve the puzzle of a particular pollination mechanism. Technology can help to resolve some myths around the pollination mechanism by amplifying the researcher's observation capacity, but it will not replace scientific inquiry, which is stimulated by spending considerable time in the field. The book is illustrated with beautiful photographs, which not only fulfill the didactic objective of helping to understand the text but also provide a high-quality aesthetic element, which takes place right from the beginning with the magnificent book cover, evidence of the Lankester the Botanical Gardens´ registered trademark of excellence in nature photography.

The book is intended for a wide audience, from biologists with specialized interests in pollination biology to the public interested in understanding orchid pollination and the challenges it faces due to habitat loss, fragmentation, and climate change. The book is filled with specialized terms but is written in a very accessible way relating topics peppered with the titles of pop and rock songs. The reader gets progressively acquainted with specialized terms. In summary, Karremans´ book fills a void in the natural history of orchid pollination since Dodson and Dressler´s book. It highlights the beauty of evolution maintaining a fragile equilibrium between the conflicting interests of plants and their pollinators and leaves many questions to be resolved by population and evolutionary biologists. As a pure, classic work of natural history, Karremans' book provides a broad perspective on orchid diversity, pollination biology, and the resilience and adaptation of natural systems.

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