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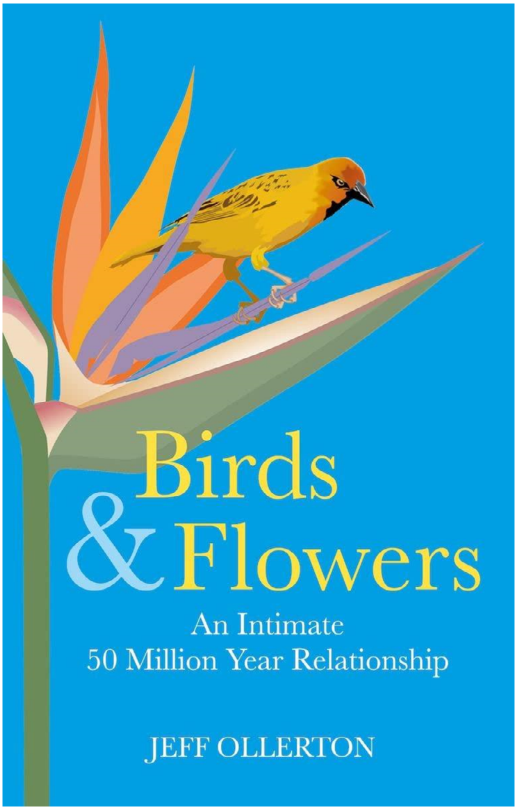
AN INTERESTING SYNTHESIS ON THE EVOLUTION OF PLANT POLLINATION BY BIRDS



Ollerton J. 2024. Birds & Flowers. An Intimate 50 Million Year Relationship. Pelagic Publishing, London. 312 pp., 28 color plates.

Jeff Ollerton is an expert in the field of biodiversity; he has worked extensively on the pollination of plants, in particular by birds, and has already published two books, *Plant-Pollinator Interactions: from specialization to generalization* (2006, N.M. Waser ed.) and *Pollinators & Pollination: Nature and Society* (2021, Pelagic publ.), other than many scientific papers on this subject. Writing *Birds and flowers*, the purpose of Ollerton is treating two aspects of the natural world with which people are most familiar, bringing together the global diversity of these two distinct, but often interdependent, groups of animals and plants.

The book is structured according to three main themes, the evolution and subsequent diversification of the relationships between flowers and birds, the present knowledge (and also unknowledge) on the ecology and interactions between birds and flowers, and finally the relationships between birds, flowers and humans.

Following Ollerton, in the Jurassic period, perhaps 170 million years ago, a group of dinosaurs evolved a set of novel traits that allowed them to exploit a semi-arboreal lifestyle that included the ability to glide between trees. The evolution of wings, provided with feathers, resulted in more or less 11,000 species that some scientists now recognize as the only living dinosaurs, the birds. Also, in the Jurassic, 145 million years ago or possibly much earlier a distinct group of seed plants (angiosperms) appeared; it had an incomparable ability to evolve into '*endless forms most beautiful and most wonderful*', Ollerton's citing a Charles Darwin's phrase. These flowering plants continued to diversify during the Cretaceous and overcame the mass extinction event about 66 million years ago that interested all of the dinosaurs, but not the birds and other groups of plants and animals.

Known pollinators per excellence are insects, reliable flower visitors whose life histories are linked to flowers which provide them with sugary nectar rich in minerals, amino acids and organic compounds. However, no animal could subsist for its entire life on just nectar, it is impossible to build bones and muscles from such a limited diet; even insects like some butterflies, which appear to survive only on nectar, obtain most of their food from the plant materials that they consume as caterpillars, and as adults will often suck inorganic nutrients from dung, urine and mud.

Ollerton highlights that also most birds shifted between feeding on different types of food, insectivory possible was at the origin of behaviors which gave rise to the exploitation of flowers by birds. Nevertheless, birds, compared to insects are much less numerous; for example, in comparison to the c. 360 species of hummingbirds (Trochilidae), there are at least 2,000 neotropical hoverflies (Diptera Syrphidae) and 5,000 bees (Hymenoptera Apoidea)! The flowering plants are about 30 times more diverse than the birds.

Likely, more than 50 million years ago, insectivore birds visiting flowers to prey upon insect, began to change behavior and evolved into bird pollination. According to the present assessment of current knowledge, of 253 recognized taxonomic families of birds, 74 (29.2%) include birds that visit flowers and are known or presumed pollinators. Even if we accept that the this percentage is twice that number, the scale of bird diversity is very small compared to insects, which are counted in the millions of species. The world holds 300,000 (possibly 400,000) species of angiosperms, but a significant fraction has co-opted birds to move their pollen around, as either their sole pollinators or in concert with other animals such as insects, bats or lizards. However, there are wide geographical differences; for example in the Americas, there are plant families with a high proportion of species (whole genera), that are hummingbird-pollinated, including groups with thousands of species, such as the families of Acanthaceae, Asteraceae, Bromeliaceae, Cactaceae, Gesneriaceae, and many more. As Ollerton writes, avian pollination is widespread, ecologically important over much of the world, and has evolved many times in different groups of plants. He also proposes to keep the use of '*ornithophily*' to simply refer to '*bird pollination*'. Bird pollination is very rare on European continent, and this is considered a real puzzle, there is no easy answer. Very few European birds are plant pollinators; *Anagyris foetida* (Fabaceae) is bird-pollinated, the first that has been demonstrated for any native European plant. In addition, the author records that the Canary Island chiffchaff *Phylloscopus canariensis* is presently considered an excellent pollinator of at least three plant species; this could be an insular specialization. However, there have been many previously published observations, over the last 100 years, showing that small passerines in Europe probe flowers for nectar. It is also not uncommon for migrant warblers to arrive in their north European lands loaded with amounts of southern European pollen on their faces (*pollen horns*) and bodies.

Ollerton shows the copious nectar spilling from the center of the flower, below the orange petals, and allows to taste its sweet promise of a reward for services rendered, explaining where the stigma is located, a sharp point standing out from the bloom, waiting for pollen to arrive. Pollen may be dry and dusty or wet and sticky, it varies hugely in shape, and in size from microscopic to individual grains that can be seen without the aid of magnification. Also, cohesive masses of pollen known as '*pollinia*' have evolved independently in two plant families (Orchidaceae and Asclepiadaceae); units comprising the pollinia, together with accessory structures for attachment to the pollinator, may remain onto the bird's tongue. They are able to do this because the tips of the tongue are finely frayed and narrow enough to act as points of attachment for the pollinaria. They need a lot of energy, and, according to Ollerton, 'nectar can provide a very quick boost, much like a glass of lemonade after a period of hard graft in the garden. Nectar contains more than carbohydrates, however, and it cannot be emphasized enough just how complex it is both as a substance and as a tool in a plant's strategy for reproduction'.

Other than a reproductive function, pollen of some flowers is a reward for those pollinators that can digest its protein-rich contents. In addition, in bird pollinated flowers, pollen often remains on the feathers of the bird visitor, captured by the barbs and barbules. Even though feathers would seem to be possible evolutionary choice for where to place pollen, really there are many alternative flower strategies in which beaks, feet or even tongues are involved.

Flowers are very variable and diverse; some are long and tubular in form, and bright red, fitting the expectations of the hummingbird '*pollination syndrome*', others are funnel- or bowl-shaped, and variously white, yellow, orange or pink. Flowers that are bird-pollinated, such as the fuchsias (Onagraceae), kniphofias (Liliaceae) from South Africa and New Zealand, are larger, more robust, and more brightly colored, and unscented. The penstemons (Pantaginaceae) include 270-300 species, most bee-pollinated, but perhaps 39 (13-14%) are pollinated by hummingbirds. Red flowers are less conspicuous to bees, but they certainly are not invisible to them, and these insects will find and keep visiting them if they offer appropriate rewards. Birds, which have a tetrachromatic vision, are equally capable of detecting flowers of any color and searching for the flowers that are most rewarding in a community. Vision is not the only sense at play for avian flower visitors, however, and in some respects smell is a more puzzling aspect of bird pollination.

Following Ollerton, when viewed phylogenetically, it seems clear that some degree of hummingbird pollination had evolved from exclusive bee pollination on a minimum of 13, and possibly as many as 25, occasions during the past history of this group of plants. These switches from bee to bird pollination correlate with changes in the flowers; for example, bee-pollinated flowers tend to be purple, bluish or yellow in color, whereas penstemon flowers that use birds are usually red, orange, magenta or rose-colored to human eyes. The bees exploit the flower in two ways: by making holes at the base into which they can insert their tongues, or by crawling past the dangling sexual parts of the flower and entering from the front. The latter technique may occasionally result in pollination, but really the flowers have evolved to be effectively serviced by hovering buzzers rather than crawling bumblebees. The Bird of Paradise (*Strelitzia*) employs a sophisticated mechanism which, in its native Southern Africa, ensures seed set via its main pollinators, perching birds such as the Cape weaver *Ploceus capensis*.

Concerning the nectar, in addition to water, most abundant chemicals are energy-rich sugars, such as hexose sugars (six carbon atoms), glucose and fructose (monosaccharide sugars), and sucrose (disaccharide sugar formed from a combination of glucose and fructose molecules). Hummingbirds are completely dependent on nectar to provide energy, but not for essential amino acids and minerals, so all species include insects, spiders and other arthropods in their diet.

According to Ollerton, there is a clear difference between specialists and generalists pollinating birds; generalists are typically characterized by beaks and tongues that are well adapted to consuming nectar from flowers, specialists often have narrow and pointed beaks, ideal for probing within the deepest of flowers, and the tongues may be highly fringed, to act as a mop, or partially tubular, to pump up the bird's fluid diet. From the physiologist point of view, there are specialized enzymes for breaking down sugars; this is undoubtedly an evolutionary adaptation. Concerning adaptations, the nectar of tree tabacco (Solanaceae) contains nicotine and the chemically similar anabasine, both powerful insecticides. The capacity of sunbirds (Nectariniidae) to deal with nicotine and anabasine seems to be mediated by the bacteria in their guts; the same is almost certainly true of hummingbirds, highlighting the importance of microbes in the ecology and evolution of bird-flower relationships. Interestingly, the Palestine sunbird *Cinnyris osea*, which pollinates the plant in the eastern Mediterranean, have a limited capacity to cope with these toxins, and in the absence of alternative nectar sources, it may remember the location of plants that produce lower amounts of these alkaloids and visits their flowers preferentially.

This fascinating book concludes with interesting ecological considerations on the consequences of interactions between different species not only from different families, but from different kingdoms. As the ecologist Dan Janzen put it in 1974, 'what escapes the eye is a much more insidious kind of extinction: the extinction of ecological interactions'. What happens when one of the partners is lost from a community? What if a bird loses an important nectar source or a plant loses its bird pollinator? When a bird becomes extinct, also specialized bacteria, fungi and parasites with which it is associated end up the same way. Species do not occur in isolation, and the biodiversity of species interactions is fundamental to the ecology of the planet.

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