Abstract

Evolutionary shifts to bird pollination (ornithophily) have occurred independently in many lineages of flowering plants. This shift affects many floral features, particularly those responsible for the attraction of birds, deterrence of illegitimate flower visitors (particularly bees), protection from vigorous foraging by birds, and accurate placement of pollen on bird’s bodies. Red coloration appears to play a major role in both bee-deterrence and bird-attraction. Other mechanisms of bird-attraction include the production of abundant dilute nectar and the provision of secondary perches (for non-hovering birds). As a result of selection for similar phenotypic traits in unrelated bird-pollinated species, a floral syndrome of ornithophily can be recognized, and this review surveys the component floral traits. The strong convergent evolution evident in bird-pollinated flowers raises a question about the nature of the genetic mechanisms underlying such transitions and whether the same gene systems are involved in most cases. As yet there is too little information to answer this question. However, some promising model systems have been developed that include closely related bee and bird-pollinated flowers, such as Ipomoea, Mimulus, and Lotus. Recent studies of floral developmental genetics have identified numerous genes important in the development of the floral phenotype, which are also potential candidates for involvement in shifts between bee-pollination and bird pollination. As more whole-genome information becomes available, progress should be rapid.

Key words: Anthocyanin pigmentation, bird-pollination, candidate gene, developmental genetics, honey-eaters, hummingbirds, nectar, ornithophily, pollination syndrome, sunbirds.

Introduction

The concept of pollination syndrome, whereby specific floral traits are associated with particular pollination mechanisms, dates back to the work of the Neapolitan botanist Federico Delpino (1833–1905). The attraction and utilization of a specific group of animals for pollination, for instance, is associated with specific characteristics of flower morphology, colour, nectar, odour, and orientation (Faegri and van der Pijl, 1966; Proctor and Yeo, 1973; Fenster et al., 2004). However, pollination systems are often more complex than floral morphology would at first sight suggest, and this has led to criticisms of the pollination syndrome concept, mainly based on the evidence that flowers attract a broader spectrum of visitors than expected (Waser et al., 1996). Nevertheless, there is ample evidence supporting a strong association between certain floral traits and functional groups of pollinators that exert similar selective pressures (Fenster et al., 2004).

One well-recognized syndrome of floral traits is that associated with bird pollination (ornithophily). Ornithophilous flowers (Fig. 1) are very often red with copious dilute nectar. Furthermore they lack characters associated with other pollination syndromes, such as scent.

In this review the main phenotypic traits of bird-pollinated flowers are summarized and discussed. Bird-pollination has evolved many times (usually from bee-pollination) and the aim is to highlight the major phenotypic convergences in plants with this pollination syndrome. The convergent evolution of this floral phenotype raises questions about the genetic mechanisms underlying such transitions and whether the same gene systems are involved in all cases. Three promising model systems are considered in this review. The first is a transition in the genus Ipomoea, where changes in the
control of the anthocyanin biosynthetic pathway are associated with shifts in flower colour from purple to red, and shifts from bee to hummingbird pollination. The second system is the genus *Mimulus*, where changes of flower colour and shape underlie a transition to bird-pollination. In this case, a single quantitative trait locus (QTL) of large effect controls the pigmentation of the flower and influences relative visitation rates of bees and hummingbirds. Finally, a transition to bird pollination is described in the legume genus *Lotus*, associated with differences in colour, flower orientation, flower size and petal morphology. We conclude by highlighting candidate genes that could potentially shed light on the evolution of this syndrome.

The syndrome of ornithophily

The birds

Many birds will casually visit flowers in search of food, often primarily to seek insects concealed in inflorescences although they will take nectar if it is available. Flower visiting of some sort has been reported in as many as 50 families of birds (Proctor and Yeo, 1973; Proctor et al., 1996). However, three families of birds have evolved as major groups of flower specialists. These are the hummingbirds (Trochilidae), the sunbirds (Nectariniidae), and the honey-eaters (Meliphagidae) (Fig. 2).

Hummingbirds are exclusive to the New World, ranging from southern South America to Alaska with the highest diversity in the northern Andes (Grant and Grant, 1968). As hummingbirds visit flowers by hovering there is no need for a perch and, in consequence, some hummingbird flowers are long and pendulous. Hummingbirds have beaks that are highly specialized for nectar feeding, even though insects form a normal part of their diet, necessitating a remarkable flexibility of the jaw (Yanega and Rubega, 2004). They have undergone a major evolutionary radiation in South America and a secondary radiation in North America (Mayr, 1964). Fossil evidence from Europe, however, suggests that the early evolution of this group was not exclusive to the New World (Mayr, 2004).

Sunbirds and spiderhunters (Nectariniidae) are the major group of pollinating birds in Africa and Asia. The honeyeaters (Meliphagidae) are very important pollinators of staphyleoid Ericaceae (Epacridaceae), Myrtaceae and Proteaceae in Australia and they extend north to Wallace’s line and east to New Zealand and Hawaii. Other important groups include the American orioles (Icteridae) in North and South America, the honeycreepers (Thraupidae) in tropical America, and the Hawaiian honeycreepers (Fringillidae, subfamily Drepanidinae) in the Hawaiian Islands. In Africa the White-eyes (Zosteropidae) are another important group, as are the South African sugar-birds (Promeropidae).

Bird pollination is particularly common in relatively aseasonal tropical and subtropical regions as flowers and nectar are available year-round to support nectarivorous birds. It tends to be absent or rare in regions in which vegetation has a long dormant period. North America is an exception, as hummingbirds migrate north during the summer. The migration is particularly remarkable on the NW coast where hummingbirds migrate as far as Alaska.
Bird pollination is almost entirely absent in Europe and in Asia north of the Himalayas. In Europe, although there are reports that some passeriform birds occasionally feed on nectar (Kay, 1985; Proctor et al., 1996; Schwilch et al., 2001; Merino and Nogueras, 2003), there is only one report of a bird-pollinated native plant, *Anagyris foetida* L. (Leguminosae). In Spain this is apparently pollinated by three warblers, *Phylloscopus collybita* Vieillot, *Sylvia atricapilla* L., and *S. melanocephala* Gmelin (Ortega-Olivencia et al., 2005).

**Ecology of bird pollination**

Some attributes of birds, such as long flight distances and high visual acuity, make them excellent pollinators, especially valuable during inclement weather conditions when other pollinators, such as bees, are inactive. Birds may, therefore, be important supplemental pollinators in environments where insects have low population densities, such as high altitude ecosystems (Van der Pijl and Dodson, 1966), dry environments (Stiles, 1978), isolated islands where insect colonization has been poor (Dupont et al., 2004; Micheneau et al., 2006), and for plants flowering during winter months when insects are few (Kunitake et al., 2004).

However, birds are large and require more energy than insects. For this reason plants with bird-pollinated flowers tend to put more energy into nectar production and often produce larger flowers to accommodate their avian...
pollinators. Bird-pollinated plants may also deploy more resources in floral structures that protect against thieves of their abundant nectar (Stiles, 1978). Environments with low plant productivity may be limiting for nectar production, and for this syndrome in general. The tropical forest understory, with limited photosynthetic rates, has relatively few bird-pollinated plants (Stiles, 1978) and the same appears to hold true for cold, hyper-arid, and nutrient-poor environments. The syndrome is particularly common in tropical and subtropical shrublands, open woodland, and riverine communities.

**Perching versus hovering**

The behaviour of those birds associated with ornithophily can be broadly divided into two types, hovering and perching. The hovering behaviour is found mainly in hummingbirds, but is also present in some families of passeriforms. In hovering, birds collect nectar without landing on the plant, which may therefore have hanging or pendant flowers. On the other hand, perching birds land on stems, leaf stalks, adjacent branches, and flower buds, which must provide an adequate perch. Low herbaceous plants may be pollinated by birds that perch on the ground, and they usually orient their flowers vertically erect. Examples include *Lotus berthelotti* Masf. and its relatives in the Canary Islands (Olesen, 1985), and *Gastrolobium praemorsum* (Meisn.) G. Chandler & Crisp in southwest of Western Australia (Keighery, 1982).

Among birds, flower foraging by perching is more widespread and involves fewer specialist adaptations than foraging while hovering. Flower visiting has evolved in several families of perching passeriforms both in the New World and the Old World. Unlike hummingbirds, passeriforms tend to forage and travel in groups and can be effective in cross-pollinating even large trees (Stiles, 1981). In the New World, pollination by perching passeriforms appears to have evolved recently, usually, although not always, involving plant species in genera already adapted to hummingbird pollination (Toledo, 1975; Cruden and Toledo, 1977).

**Hermit versus non-hermit hummingbirds**

Bird behaviour is important in determining the nature of bird–plant interaction. The vast majority of bird-pollinated species in the Neotropics, are herbs, shrubs, small trees, and epiphytes, and rarely large canopy trees. Solitary behaviour and territoriality in hummingbirds do not allow the levels of pollinator saturation or cross-pollination necessary for the effective pollination of large canopy trees (Stiles, 1975), which therefore tend to be bee-pollinated. Hummingbirds may be divided into two subgroups, hermits and non-hermits, and this division has important implications for pollination.

The majority of hermits have long, curved bills and a tendency to forage on flowers with long, curved corollas. They inhabit the understory of the tropical forest and decrease in abundance and diversity at higher elevations and in dry habitats. Hermits are non-territorial with a traplining method of foraging. Traplining involves visiting many plants sequentially for short visits, flying from plant to plant, often over some distance, and is highly effective in promoting cross pollination (Snow and Snow, 1972; Stiles, 1975, 1981).

Non-hermits have short straight bills and a tendency to hold territories and thus non-hermit pollination behaviour favours self-pollination. Non-hermits are widely distributed but have their greatest diversity in the tropical highlands (Snow and Snow, 1972; Stiles, 1975, 1981). The North American hummingbird fauna comprises a fairly homogeneous assemblage of non-hermit hummingbirds and probably for this reason North American ornithophilous plants are fairly uniform in floral form compared to those of South America (Grant, 1966; Stiles, 1981).

Interestingly, the existence of these two types of hummingbird has had a strong influence on patterns of floral diversity in the genus *Heliconia* (Heliconiaceae) (Stiles, 1975, 1981). *Heliconia* species that are pollinated by hermit hummingbirds usually have long, curved corollas, and grow in the forest understory where light is limiting. They grow in small, scattered clumps and produce a few flowers over a long flowering period. Daily nectar production is low with usually moderate to high nectar concentration (Stiles, 1975), and hermit hummingbirds trapline between clumps.

By contrast, non-hermit associated *Heliconia* species grow in large clumps with highly synchronous flowering, producing many flowers during a definite flowering period. These *Heliconia* species usually have short straight corollas and are usually found in highly productive environments of forest gaps or along rivers with abundant light (Stiles, 1975). They produce a large quantity of relatively dilute nectar. Territorial non-hermit hummingbirds will defend these clumps because of their abundant nectar reward, which is beneficial for pollination intensity but not for cross-pollination between clumps.

**Major groups of angiosperms with bird pollination**

Bird pollination is widespread in the flowering plants and appears to have evolved many times. It is present in some 65 flowering plant families and in most of these it probably represents a separate origin, usually from a bee-pollinated precursor. However, bird pollination is notably absent in some of the largest families of flowering plants. In Asteraceae, for example, only the South American genus *Muisia* is bird pollinated (Buzato et al., 2000; Proctor et al., 1996). On the other hand, there are some large clades in which bird pollination is particularly common, such as in the monocot order Zingiberales.
Families of this order are Cannaceae, Costaceae, Heliconiaceae, Lowiaceae, Marantaceae, Musaceae, Strelitziaceae, Zingiberaceae, and bird pollination occurs in all. Genera such as Canna (Cannaceae), Strelitzia (Strelitziaceae), Heliconia (Heliconiaceae), and Costus (Costaceae) are well known for their showy bird-pollinated species. In the Costaceae, for instance, ornithophily associated with hummingbirds evolved several times in the neotropics from bee-pollinated ancestral species (Specht, 2006).

Ornithophily has also evolved several times, mainly from bee-pollinated ancestors, in many families of the eudicots. A common pattern within these groups is the parallel evolution of the traits associated with ornithophily among non-closely related groups of plants. For example, within Gesneriaceae many Columnnea species have similar morphological traits—trailing epiphytes with fairly large and showy red flowers—with another group, Aeschynanthus. Columnnea is distributed in Central and South America and is pollinated by hummingbirds, whereas Aeschynanthus is distributed in the Paleotropics.

The multiple origin of bird pollination in the flowering plants raises the question of what pre-adaptations promote this evolutionary transition. Two features, commonly associated with bee pollination, appear to be permissive of a transition to bird pollination. One is floral zygomorphy (monosymmetry or asymmetry) and the other is the possession of a floral tube. Bird-pollination is common in many families with strongly zygomorphic flowers (e.g. Scrophulariaceae, Heliconiaceae, Gesneriaceae, Leguminosae). This feature is generally considered to be an adaptation to bee pollination and allows precise placement of pollen on the body of the bee. It seems that these adaptations may also be important for bird-pollination.

The same applies to the character of perianth segments being connate into a tubular corolla (or the presence of a tubular hypanthesis in Passiflora and Fuchsia). Tubular flowers originally evolved for insect pollination but are equally suitable for the probing foraging of bird’s beak. Hummingbird flowers in North America are predominantly sympetalous dicots and it has been suggested that this corolla condition, with its tubular shape, is another pre-adaptation to hummingbird pollination (Grant and Grant, 1968).

The floral phenotype

Types of floral adaptation

Floral adaptations to bird pollination fall into four broad types: (i) attraction mechanisms; (ii) exclusion mechanisms; (iii) protection mechanisms; and (iv) pollination mechanisms (Grant and Grant, 1968).

Attraction mechanisms are those such as copious nectar and vivid floral display that attract birds to flowers. The floral display may be just red or orange, or a combination of contrasting colours, including orange, yellow, green, and blue (‘parrot colours’). Strelitzia reginae W. Aiton, for instance, presents a striking display of orange and blue.

Exclusion mechanisms are those features that help to deter illegitimate flower visitors that might otherwise interfere with pollination and rob nectar. Red colour, long and narrow floral tubes, and the absence of insect landing platforms are the most obvious of these and are discussed further below. Pendent flowers, as in Aquilegia formosa Fisch. ex DC., are difficult for insects to work but easy for hummingbirds. Recurring petals, as in Ipomopsis aggregata (Pursh) V. Grant, or the short and recurved lower lip of Mimulus cardinalis Dougl. ex Benth., serve to deny insects a landing platform and similarly make the flowers difficult to work except by hummingbirds. In Trichostema lanatum Benth., the long-exserted stamens are recurved to block entrance to the tube.

Protection mechanisms are also important, as birds are large and potentially destructive pollinators. A common form of protection is provided by mechanical strengthening of the flower by the formation of sclerenchyma or collenchyma tissue in various floral parts. The ovary and ovules, often situated near to the nectaries, are particularly vulnerable to the probing of bird’s beaks. Protection of ovules takes many forms. There may be separation of ovary and nectary, either by the sheathing of the ovary by a staminal tube, or by a stalked or inferior ovary. Alternatively, there may be a groove formed by the corolla to guide birds’ beaks to the nectary without causing damage, or ridges of the corolla to provide direct protection to the ovary. In addition, the style may be protected in a groove formed from ridges of the upper petals, as in Justicia californica (Benth.) D. Gibson. In Penstemon it is the nectaries rather than the ovary that shift. In bird-pollinated species, the nectaries are displaced upwards from the base of the ovary to the outer bases of the upper pair of stamens.

Pollination mechanisms are those that enhance the precise deposition of pollen on bird and stigma. These include both spatial and temporal relations of the reproductive organs to the position of pollinating birds. The long exserted stamens of bird-pollinated species of Aquilegia (e.g. A. formosa), Fuchsia, and Ribes (e.g. R. speciosum Pursh) dust birds’ heads or even backs, with pollen. In the radially symmetrical Ipomopsis aggregata the ring of five stamens place pollen all around the base of the birds’ beaks. Zygomorphic flowers, on the other hand, tend to place pollen on the top of the beak or on the top of the bird’s head.

Why red?

Explanations for the remarkably consistent association of bird-pollination with red or reddish flowers take two forms, either avoidance of bees (and other insect pollinators), or attraction of birds.
It seems that red colour is not necessary to attract birds. There are examples known where birds are effective pollinators of species with orange, yellow, and white flowers (and less frequently reddish violet and blue flowers) (Proctor and Yeo, 1973; Ortega-Olivencia et al., 2005; Micheneau et al., 2006). This has led to the suggestion that avoidance of bees (which cannot see red) is more important than attraction of birds (Proctor and Yeo, 1973; Proctor et al., 1996). Birds perceive colour over wavelengths ranging between 300 nm and 660 nm, whereas bee vision is in the range 300–550 nm. In the neotropical forests bird-pollinated flowers have been shown to have typical median reflectance greater that 585 nm, outside the visual range of bees (Altshuler, 2003). However it should be noted that bees can perceive (and do visit) some flowers seen as red by humans, if they have at least some reflectance in the shorter wavelengths as well (Chittka and Waser, 1997).

However, as well as its invisibility to bees, the fact that red is very readily detectable by birds is also likely to be significant. For instance, the visual prominence of red may be important for migratory hummingbirds, which can easily detect red flowers when entering a new habitat and associate it with reward (Grant, 1966). Indeed, the association of red flowers and bird pollination may be explained via optimal foraging theory and the relative efficiency of bees and birds in detecting red (Rodriguez-Gironés and Santamaria, 2004), with red flowers acting as a signal of high caloric reward (Raven, 1972). With the association between high energetic rewards and the colour red already well established, there may be strong selective pressure for other bird-pollinated flowers to adopt this ‘common advertising strategy’. However, there is a curious twist in Fuchsia excorticata L.f. of New Zealand, in which a developmental change, from green to red flower colour, signals lack of nectar reward in post-reproductive flowers (Delph and Lively, 1989). Birds, therefore, avoid the red flowers in favour of green.

Flower colour and its perception

Flowers that appear red to humans are of three types (Chittka and Waser, 1997). Some species have an additional peak that stimulates the blue receptor of bees; for example, the red flowers of Dianthus carthusianorum L. are perceived as blue by bees, as this species has a reflectance peak that stimulates the blue receptor of bees. The red flowers of field poppies (Papaver rhoes L.) have a reflectance peak below 400 nm and are perceived by bees as ultraviolet. However, typical red hummingbird flowers, such as Ipomopsis aggregata and Justicia rizzinii Wassh., will be perceived as green by bees (Chittka et al., 1994; Chittka and Waser, 1997). These flowers only stimulate the green receptor of bees, and there is no additional peak of reflectance in other wavelengths. This type of flower, with a peak only in the red, and with no blue or UV reflection, is more difficult for bees to detect than flowers of other colours (Chittka et al., 1994; Chittka and Waser, 1997).

On the other hand, birds are tetrachromatic and they have an additional UV receptor compared to humans, making colour perception in birds more complex than in mammals (Bowmaker, 1977). Further, they have oil droplets that can act as filters that increase the complexity of colour perception. Birds can see, in theory, twice the number of colours compared with trichromats (Ödeen and Hästad, 2003). It seems that birds do not have an innate preference for the red colour, although most of them have their greatest spectral sensitivity and hue discrimination towards the long wavelength end of the spectrum (Stiles, 1981). Experiments with hummingbirds have shown that they learn to associate a range of colours with rewards and that this behaviour can be modified (Proctor et al., 1996).

Floral pigments (anthocyanidins and flavonols) have the major impact on the wavelength of light reflected from flowers. There are three major types of anthocyanidin pigments: pelargonidin (generally red), cyanidin (typically magenta or blue depending on pH) and delphinidin (generally blue). Bird-pollinated flowers are much more likely to contain pelargonidin and much less likely to contain delphinidin than flowers generally (Scogin, 1988). A general predominance of pelargonidin in tropical floras (Beale et al., 1941) has been attributed to the tropical distribution of hummingbird pollination (Harborne, 1976). A difference in pigment composition has been reported in comparisons between perching-bird and hummingbird-visited flowers (Scogin, 1988), with a greater prevalence of cyanidin, as opposed to pelargonidin, in perching-bird flowers.

Nectar

Bird-pollinated flowers generally produce a large quantity of dilute nectar as the main pollinator reward. Nectar characteristics, such as (i) volume, (ii) sugar concentration and viscosity, (iii) sugar composition, and (iv) amino acid composition, are extremely important in determining the success of plant–pollinator interactions (Baker and Baker, 1983a; Proctor et al., 1996) and nectars of bird-pollinated plants tend to be recognizable as such.

The volume of nectar in flowers is generally correlated with the size of the flower (Baker, 1978). However, size for size, bird-pollinated plants tend to secrete larger quantities of nectar relative to bee-pollinated species. The same is true in bat-pollinated species. Some bat-pollinated Bombax species, for example, can produce between 200–300 µl of nectar daily (Baker, 1978).

Nectar concentration is a characteristic often inversely linked to nectar volume. This holds true in bird-pollinated flowers, which produce relatively dilute nectars but in
large quantities. Mean sugar concentrations in nectars of bird-pollinated flowers range between 20% and 26% (Pike and Waser, 1981; Stiles and Freeman, 1993; Proctor et al., 1996) with extremes between 10% and 34% (Baker, 1975). The sugar concentration of nectar determines its viscosity, which is an important physical property that is thought to affect the ease of uptake of nectar by birds. Large quantities of nectar at low concentrations have therefore been explained on the basis of constraints of its uptake associated with viscosity (Baker, 1975), and nectar viscosity tends to remain constant even under different environmental conditions (Proctor et al., 1996). However, dilute nectar with low sugar concentration is less optimal for bees, and so this trait may be more anti-bee than pro-bird (Bolten and Feinsinger, 1978). Nectar with sugar concentration below 18% is not beneficial to honeybees because of the high energetic cost of evaporating water in order to produce honey (Percival, 1965).

**Nectar sugar composition** is also important. Nectar is mainly composed of fruit sugars such as glucose and fructose (hexoses), and/or the disaccharide sucrose. Based on composition, the following types of nectar have been distinguished: (i) sucrose-dominant nectar, (ii) sucrose-rich, (iii) hexose-rich, and (iv) hexose-dominant (Baker and Baker, 1983a). Hummingbird-pollinated flowers generally have sucrose-dominant nectar, whereas flowers pollinated by passerine perching birds tend to have hexose-dominant nectar (Baker and Baker, 1983b, 1990; Freeman et al., 1984; Lammers and Freeman, 1986; Elisens and Freeman, 1988; Stiles and Freeman, 1993; Baker et al., 1998; Perret et al., 2001). Bee-pollinated flowers characteristically have sucrose-rich or sucrose-dominant nectar (Baker and Baker, 1983a), so such nectar composition in hummingbird-pollinated flowers that have evolved from bee-pollinated flowers is not surprising. More difficult to explain are the hexose-rich nectars. Passerine birds often feed on fruits as well, and it has been suggested that the ‘taste’ for hexose fruit sugars derives from this (Baker and Baker, 1983b). Also, there is evidence that some Old World birds (such as Sturnidae, which includes some facultative nectarivores) have difficulty digesting sucrose (Schuler, 1977).

**Amino acids** are another important constituent of nectar. They provide a source of protein-producing substances, perhaps affect the ‘taste’ of the nectar (Baker and Baker, 1983a) or stabilize the sugars in the nectar, i.e. avoid crystallization (Baker and Baker, 1983a). Surveys have reported between 2–24 amino acids on nectar from different species (Baker, 1978). Bird-pollinated flowers contain low concentrations of amino acids, which is because birds have additional sources of protein-building amino acids (Baker and Baker, 1986). One exception to this trend has been studied in *Erythrina* (Leguminosae) pollinated by territorial orioles and tanagers, whose uptake of amino acids mainly depend on this plant (Baker and Baker, 1982).

**Corolla morphology in bird-pollinated flowers**

Flower morphology associated with ornithophily can divide bird-pollinated flowers into five major groups (Proctor et al., 1996). In the **brush-flower** the flowers are arranged in clusters, usually in spheres or cylinders, with protruding stamens, and pollen placement is generalized. The Australian flora is particularly notable for its brush flowers, for instance in Proteaceae and in *Acacia* species (Lara and Ornelas, 2001). Another common flower trait is the **hanging bell**, producing copious nectar. Examples of this are found in *Canarina* (Campanulaceae) (Dupont et al., 2004; Valido et al., 2004), *Fritillaria* (Liliaceae) (Burquez, 1989; Peters et al., 1995), and *Cadia* (Fabaceae) (Citerne et al., 2006).

However many ornithophilous flowers have long sympetalous corolla tubes. Such corolla tubes differ from those of bee-pollination by being long and narrow (the shape of a birds beak rather than a bees body) and the inconspicuous size and position of the corolla lobes. Rather than forming a landing platform, as in bee-pollinated flowers, the lower corolla lobes are often reflexed under the flower so preventing the alighting of insects. This has been termed the ‘dogfish’ flower-type (Proctor and Yeo, 1973) from a fancied resemblance to the backwards-sloping snout of elasmobranch fish. The long, narrow tubular corolla is important in deterring bees from accessing nectar. However, this trait may be circumvented by nectar robbing (Lara and Ornelas, 2001) if the base of the corolla tube is not protected by a robust calyx. The corolla tube may also be downcurved (arcuate) in a similar way to many bird beaks. There is also a benefit to being downwardly directed in that insect access is more difficult. However, most North American hummingbirds have relatively short straight beaks and, probably in consequence, most North American ornithophilous flowers have rather similar short straight and narrow corolla tubes (Fig. 3).

Differences between corolla tubes of bee and bird-pollinated species are well illustrated in the genus *Streptocarpus* (Gesneriaceae) (Harrison et al., 1999; Hughes et al., 2007). Between the bee-pollinated *S. rexii* Lindl. and the bird-pollinated *S. dunnii* Mast. there are five major floral differences associated with pollination syndrome. *S. dunnii* has small flowers that are massed into large inflorescences, while in *S. rexii* the floral display is provided mainly by the large individual flowers. *S. dunnii* has a cylindrical corolla tube suitable for probing by a bird’s beak, whereas *S. rexii* has an open funnel-shaped flower allowing for ingress by relatively large bees. The orientation of the flowers is varied in *S. rexii*, while in *S. dunnii* all the flowers on the inflorescence face the single, large leaf that probably serves as a perching surface for birds. *S. dunnii* has red flowers without nectar-guides, whereas *S. rexii* has pale violet flowers marked with the
dark nectar-guides that are often found in bee pollination. Finally, *S. dunnii* has a slightly longer adaxial than abaxial corolla tube length, producing a straight or slightly down-curved flower. This morphology is suitable for an ascending approach by a bird perching on the foliage below. *S. rexii*, on the other hand, has a shorter adaxial than abaxial corolla length, giving a swept-back flower, so providing an insect landing platform.

**Other characters associated with bird pollination**

Whereas red flower colour and characteristic nectar are nearly universal in ornithophily, a number of other characters are more minor or associated only with specific examples of ornithophily. These include: (i) floral posture, (ii) secondary perches, (iii) protection, (iv) floral cluster-, (v) prominent nectar, and (vi) absent characters.

**Floral posture** is closely correlated to pollinator behaviour. Nodding flowers without perches such as *Fuschia* and bird-pollinated *Aquilegia* species are invariably hummingbird pollinated, as hummingbirds have the ability to hover under a downward facing flower and direct their beaks upward into what is generally a long nectar path. This posture effectively excludes other pollinators by making the flower difficult to access.

Bee flowers, by contrast, are often horizontally oriented, in accordance with the generally horizontal approach flight of bees and have horizontal or near-horizontal lower lips for alighting. Flowers pollinated by perching birds that probe from above for nectar are often upwardly oriented. The genus *Tillandsia* provides examples of both types: short inflorescences with upwardly directed flowers for foraging by birds perching on the stiff leaves, or long arching inflorescences bearing pendulous flowers for hummingbird pollination. The bird-pollinated *Streptocarpus dunnii* has a single leaf, which probably functions as a perch for foraging birds and the flowers are unidirectionally oriented and down-curved towards the single leaf. Related bee-pollinated *Streptocarpus* species have flowers oriented in all directions. The South African *Phygelius capensis* E. Mey. ex Benth. has flowers that are somewhat resupinate, turning back towards the stems from where they may be easily probed by perching birds. By contrast, insect pollinated and hummingbird pollinated flowers tend to face outwards towards the incoming flight path of the pollinators.

**Secondary perches** are important for facilitating pollination by birds requiring a perch for floral foraging. The most striking example is provided by the ‘rat’s tail’ babiana (*Babiana ringens* Ker Gawl.) (Anderson et al., 2005). This produces completely sterile robust inflorescence stalks functioning exclusively to provide a perch for foraging by the malachite sunbird [*Nectarinia famosa* (L.)]. The stiff inflorescence bract of *Strelitzia* provides a strong perch for birds working the *Strelitzia* flowers with their feet.

**Protection.** Large vertebrate pollinators can be damaging to all but the most robust of flowers. Perching birds are frequently highly destructive of flowers and may destroy them in the search for insects and nectar. For this reason many flowers have protection in the form of tough construction of parts. *Strelitzia reginae* is an example of a flower in which the floral parts are rather cartilaginous in texture and robust enough to survive rough foraging by pollinating birds.

**Floral clustering.** Dense inflorescences are frequently associated with pollination by perching birds in the Old World. Rather than flying from single flower to single flower as bees and hummingbirds do, perching foragers will exploit flower clusters by probing several flowers from the same perch. A good example is provided by the robust, multi-flowered inflorescences of *Banksia*, which are pollinated by honey-eaters and other animals.

**Prominent nectar** is frequently associated with bird pollination in those flowers wide enough for the nectar to be seen. Birds have great visual acuity and often nectar is presented to birds with striking visual cues. The ‘nectar globes’ often found at the base of hanging bell shaped flowers are an example of this. In *Fritillaria imperialis* L., a plant known since the 18th century to attract birds to feed on the nectar (White, 1789), these take the form of prominent white depressions in the bases of the perianth segments that fill with large drops of nectar. *Nesocodon maureitianus* (I.B.K. Richardson) Thulin has nectar that is prominent for a different reason, it is coloured red with an aurone pigment, a phenomenon which is surprisingly
common and generally associated with bird or reptile pollination (Olesen et al., 1998; Hansen et al., 2006).

**Characters conspicuous by their absence.** These include scent, night blooming, and nectar guides. In contrast to bats, which visit flowers that often have a rancid or mousey smell, many birds appear to have a poor sense of smell and bird-pollinated flowers are usually odourless. Not all birds have poor olfaction and exceptions include vultures, tube-nosed Procellaridae (storm petrels and albatrosses) and the nocturnal kiwis (Apteryx spp), all of which rely heavily on olfaction for foraging. However, nectar-feeding birds do not belong to this type and appear to forage by sight, and strictly diurnally. Nectar guides (markings under visible or ultraviolet light that guide insects to floral rewards) are generally absent in bird-pollinated flowers. This is unsurprising as, while the insect compound eye is optically crude, bird vision is excellent (with good depth perception) rendering foraging within flowers easy.

**The molecular basis for the evolution of ornithophily**

The bird-pollination syndrome appears to have evolved independently very many times in a wide variety of plant families and genera (Stiles, 1981; Thomson et al., 2000). The syndrome may be initiated with birds experimentally foraging for insects or other sources of food into the flowers (Proctor and Yeo, 1973; Proctor et al., 1996), followed by selection of mutations that increase flower visitation and effectiveness of pollen transfer by birds. The molecular basis for these mutations has been addressed using model systems, in which a shift from one syndrome to another is examined in closely related species with contrasting flower morphology.

**Some model systems**

**Ipomoea:** The genus *Ipomoea* (morning glories) has tubular flowers in a wide variety of colours associated with different pollinators. The ancestral colour in this group is blue/purple and together with other traits (broad floral tube, moderate nectar production, inserted stigma, and non-versatile anthers) this indicates an adaptation to bee pollination (McDonald, 1991). In one clade, however, there has been a shift to red flowers and hummingbird pollination, encompassing some six species (including *I. quamoclit* L.). Generally, the anthocyanin cyanidin, and its derivatives, produces purple flowers whereas pelargonidin and its derivatives result in red flowers. The gene flavonoid-3’-hydroxylase (*F3’H*) is important in controlling pigment production, and the flower colour shift in the *I. quamoclit* lineage has been shown to be due to a down-regulation of the *F3’H* enzyme (Zufall and Rausher, 2003, 2004). *F3’H* is directly responsible for the hydroxylation of anthocyanidin precursors at the 3’ position that is required for the production of cyanidin rather than pelargonidin. Furthermore the enzyme dihydroflavonol 4-reductase (*DFR*), with a role downstream of *F3’H*, seems to have lost its substrate affinity in this species.

Although the major change in this case is a shift in flower colour, other flower traits, such as stigma position, flower tube width, and the amount of nectar produced, also distinguish the two pollination syndromes.

**Mimulus:** In this genus two closely related species, *M. lewisii* Pursh and *M. cardinalis* Douglas ex Benth., display a great differences in floral characteristics. The former is pollinated mainly by bumblebees and has pink flowers with a wide corolla, nectar guides, and a modest amount of nectar; the latter is associated with hummingbird pollination and has red flowers with reflexed corolla lobes, a narrow corolla tube, and copious production of nectar (Ramsey et al., 2003). A major QTL for flower colour is associated with the allele YELLOW UPPER (*YUP*) that controls yellow pigment concentration (Bradshaw et al., 1995, 1998). In *M. lewisii* the dominant allele *YUP* prevents carotenoid deposition, thus petals have only their pink anthocyanin pigments; whereas in *M. cardinalis*, the recessive allele *yup* allows carotenoid deposition and flowers with red coloration. Flower colour is known to have a very marked effect on pollinator visitation (Schemske and Bradshaw, 1999), and when the allele of *M. cardinalis* *yup* allele is introgressed into the *M. lewisii* background, hummingbird visitation increases dramatically, whereas bee visitation is considerably lowered (Bradshaw and Schemske, 2003). This suggests that an adaptive divergence in pollination syndrome can be initiated by a major change in flower colour alone. No gene has yet been cloned as responsible for *YUP* and its molecular identity still remains unknown.

**Lotus:** *Lotus* is a large genus in the Fabaceae, containing about 130 species divided into 14 sections. *Lotus* flowers are zygomorphic and typical of the papilionoid legumes. There are five petals: one dorsal (the standard) usually large and conspicuous, two lateral petals (wings) and two ventral petals (keel petals) that enclose the stamens and the ovary. Pollination takes place when a bee lands and depresses the wings and the keel, forcing out a string of pollen from the stamens located beneath the keel and placing it in the underside of the visitor. Other floral features of *Lotus* that are associated with bee pollination are the horizontal position, yellow colour, sucrose-dominant nectar composition, and scent production.

Bird pollination occurs in four species of *Lotus* from the Canary Islands (Olesen, 1985; Valido et al., 2004). In this group (also known as *Rhyyncholotus*) the flowers are red-orange in a vertical position, with hexose-dominant nectar, and no scent production (Dupont et al., 2004). However, the most striking differences are the size and shape of the petals (Fig. 4). In the bird-pollinated species the flowers
are about twice the size of those of typical bee-pollinated species and the dorsal petal is bent backwards while the ventral petals point up. The floral mechanism is effective in depositing pollen either on the top of the head or on the throat of a foraging bird (Fig. 4), but the original bird pollinator appears to be extinct.

This system is a promising one in which to study the role of petal identity in transitions between pollination systems. The genes responsible for dorsal petal identity have been identified in *Lotus japonicus* (Regel) K. Larsen. These are the legume CYCLOIDEA-like genes (Citerne et al., 2003; Cronk, 2006; Feng et al., 2006), which have already been shown to be involved in the shift to bird-pollination in the papilionoid legume *Cadia* (Citerne et al., 2006).

**Candidate genes and future prospects**

As noted above, the major trait associated with ornithophily is red colour, implicating genes of the anthocyanin biosynthetic pathway. So far, only one gene, flavonoid-3′-hydroxylase (*F3′H*) in *Ipomoea*, has been linked with shifts to bird pollination (Zufall and Rausher, 2004). Another gene, ANTHOCYANIN-2 (AN2) of *Petunia*, has been linked with shifts in pollinators, although from bee to hawk-moth pollination (Quattrochio et al., 1998, 1999). However, the anthocyanin biosynthetic pathway is well characterized and further genes involved in this pathway will doubtless be linked to the evolution of bird pollination in the future.

*MIXTA*, a transcription factor of the MYB family, has also been related to changes in flower colour perception. However, the effect is not on the pigments itself; this gene controls the production of conical cells of the epidermis (Noda et al., 1994; Glover and Martin, 1998). Although this gene has not been examined between a pair of species with contrasting flower morphology and different pollination syndromes, the bird-pollinated *Lotus* species has substantial differences in papillose conical cells and trichomes on the dorsal and lateral petal compared with the bee-pollinated *Lotus* species (I Ojeda and Q Cronk, unpublished data), and *MIXTA* is under investigation for a role in the evolution of this pollination syndrome in *Lotus*.

No gene linked to scent control has yet been studied in the context of loss of scent in bird-pollinated species. However, one gene, *S-LINALOOL SYNTHASE* (*LIS*), has been identified in shifts to moth pollination in some *Clarkia* species. Different expression patterns are observed between *C. breweri* Greene, a moth-pollinated species, and other bee-pollinated *Clarkia* species (Raguso and Pichersky, 1995; Dudareva et al., 1996). Another scent gene, *ODORANT 1*, has been cloned and analysed in the control of the synthesis of benzoid compounds in the moth pollinated *Petunia axillaris* (Lam.) Britton (Verdonk et al., 1995).

**Fig. 4.** Flowers of *Lotus* species. Bird-pollinated species of (A) *Lotus berthelotii* Masf. and (B) *L. maculatus* Breitfeld, two members of the subgenus *Pedrosia* s.l. (D) The model legume *L. japonicus* GIFU B129 and (E) *L. arenarius* Brot. a closely related species of the bird-pollinated species within the subgenus *Pedrosia* s.l. (C, F) Diagrammatic representation of the hypothetical mechanism by which a bird seeks nectar in flowers of *L. berthelotii*. Arrows indicate the direction in which the dorsal petal is pushed. a, Dorsal petal; b, lateral petal; and c, ventral petal. (C, F) Modified from Olesen (1985).
et al., 2005). However, as scent is absent in ornithophilous species, the transition to bird pollination will probably involve the loss or down-regulation of genes.

So far, no gene has been identified in the control of nectar production and composition. Two QTLs have been identified as involved in controlling these traits in Mimulus and Petunia (Bradshaw et al., 1995; Stuurman et al., 2004).

Recent studies in the control of petal identity and shape in Lotus japonicus have identified two genes (CYCLOIDEA-like genes) in the control of dorsal and lateral petal (Cronk, 2006; Feng et al., 2006). Papilionoid legumes are generally bee-pollinated but the genus Cadia, with pinkish-red, hanging, open bell-shaped flowers with no scent and copious nectar, displays the bird-pollination syndrome. The evolution of the hanging bell from a papilionoid ancestor is due to the over-expression of CYCLOIDEA genes, reconfiguring petal identity and restructuring the flower (Citerne et al., 2006).

Tubular bird-pollinated flowers are often narrower than their bee-pollinated relatives. While the molecular control of this difference in corolla form has not been investigated with respect to a transition in pollination syndrome, mutants in the gene CINCNATATA show how such morphological differences could be controlled by a single gene. In Antirrhinum flowers, expression of CINCNATATA promotes corolla growth, apparently through a positive effect on cell proliferation. Some cincinnata loss of function mutants have rather narrow corolla tubes and small corolla lobes somewhat reminiscent of the ornithophilous phenotype (Crawford et al., 2004).

The previous examples use a candidate gene-based approach, comparing closely related species with contrasting flower morphology and different pollination syndromes. A genomics-based approach will soon be possible as two complete genome sequences are due to be released shortly in genera with both bee and bird pollination (Lotus and Mimulus), which should allow rapid progress in these two systems.

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