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Bird-Flowers: Hovering Versus Perching Exploitation

Chr. Westerkamp

Institut für Systematische Botanik und Pflanzengeographie, Universität Heidelberg, FRG

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Abstract

Usually, bird-flowers are classified into New World flowers (used by hovering hummingbirds) and Old World species (adapted to perching birds). Since there are many observations which violate this classification the proposal is made to distinguish between blossoms adapted to hovering birds and those providing a well-defined perch. Characters and examples are given for both groups including the different ways a perch is provided by the plant and the distinct methods of hover-flight in birds. The diverse adaptive solutions for bird pollination within some taxa are exemplified. To understand bird-flowers the actual functioning of flowers must be in focus, and not the geographic distribution nor the systematic affiliation of their visitors.

Key words

Pollination, bird-flowers, flower-birds, hovering, perching, New World, Old World

Nectar-drinking is a widespread behaviour among birds. The figures of species involved range from 10% (Wolf and Gill, 1986: 103) to 30% (Schuchmann, 1987: 107), belonging to some 50 families (Meeuse, 1987: 22). Most of them belong to Passeriformes where foraging for nectar has evolved in at least 12 different groups (Sibley and Ahlquist, 1974: 24). In spite of these large numbers of birds only two different methods of exploitation are in use: hovering and perching. For most people hummingbirds (Trochilidae) are the only flower-birds known to hover-feed. As they are confined to the New World, it became a kind of "dogma" that New World bird-flowers are exploited by hovering birds while Old World flowers are generally utilized by perching birds (Knuth, 1905: 549; van der Pijl, 1937). However, (1) hummingbirds perch whenever possible (Wolf, 1985: 479), (2) there are flower-birds other than hummingbirds in the Americas, which normally perch when visiting flowers, and (3) Old World birds sometimes

hover when drinking nectar – although not as elegantly as trochilids. Consequently, blossoms adapted to perching exploitation exist in the New World and it is open for discussion whether there are hover-bird flowers in the Old World.

Trochilids not only perch whenever possible, but there are species which regularly sit when feeding. These include relatively heavy birds like *Eutoxeres* spp. (> 10 g) (Stiles, 1985: 773, Hinkelmann, 1985: 113; Snow, 1981: 390), *Oreotrochilus estella* and *Oxypogon* sp. (Carpenter, 1976: 15), *Patagona gigas*, as well as *Atthis heliosa* (2.7 g), one of the lightest species (Pyke, 1980: 358). Especially large hummers, those living at higher altitudes in the Andes, and burglars are said to perch while feeding (Stiles, 1981: 331). Interestingly they have larger feet than do hover-feeding species of similar weight, an observation first mentioned by Gould, 1861: 17 – cited after Melin, 1935: 162). New World nectar-feeders further include species of, e.g., Parulidae and Emberizidae-Thraupini (formerly combined as Coerebidae, a family name no longer in existence; Meyer de Schauensee, 1982: 459), Icteridae, and Vireonidae (Beecher, 1951: 285). These are all birds which are said to be comparable to relatively unspecialized Old World nectarivores (Stiles, 1981: 345).

Before the "dogma" became settled that only hummingbirds hover when flower-feeding, there were numerous observations of hovering in Old World flower-birds like Nectariniidae (Volkens, 1899; Porsch, 1924: 569; Porsch, 1926: 222; Cammerloher, 1928: 53; Melin, 1935: 174) and Meliphagidae (Porsch, 1927: 499; Melin, 1935: 212). Only recently has it become obvious that the hovering habit is not rare in, e.g., nectarinids (H. Brieschke, pers. comm.; J. Brakel, in litt.), Meliphagidae (Pyke, 1980: 375; Pyke, 1981: 861) or even warblers (Sylviidae) (Prinzinger, 1972; CW, pers. obs.) and (New World) finches (Taylor, 1973).

Insert:

The Different Ways of Hovering in Birds

It is necessary to make a clear distinction between the "Schwirrflug" (whirring flight) of trochilids and the "Trillerflug" (trilling or fluttering flight) of other birds; these are completely different. In the wings of hummingbirds the hand is enlarged at the expense of the arm. The wing thus can be more freely moved in all directions

(Snow, 1985: 239 f.). Upper and lower surfaces show about the same profile (Nachtigall, 1985: 107) so that the wing is more or less symmetrical in transect (l.c.: 65). As shown by Stolpe and Zimmer (1939), using slow-motion pictures, the wing is rotated after the downstroke, making the upstroke an upside-down downstroke. During one wing-beat cycle the wing-tip describes a lying figure-eight. Forward and backward thrust are compensated in this way and hence annihilated. This, and the high wing-beat frequency (up to > 50 Hz), allow the bird to keep every position in space without any shaking of the body.

All other birds achieve hovering in the air by simply increasing their wing-beat frequency (to up to 10 Hz). They cannot totally avoid a forward thrust but have to interrupt their wing-beats every few cycles – a manoeuvre which led Zimmer (1943) to coin the term “Trillerflug” (trilling flight) for this method of hovering. During an upstroke the bird folds its wings against the body and remains for a short while in this position. The diminished uplift makes the bird fall a little backward and the cycle starts anew. The hovering is thus somewhat irregular and for physiological reasons can be maintained only for a short period.

Nectar-feeding birds, which are among the smallest birds and the largest flower visitors (Brown et al., 1978: 687), seem to be weight-dependent in their “decision” to hover or perch while feeding (Pyke, 1981: 864), 9 g being a threshold around which both alternatives are feasible (Pyke, 1980: 358). Sometimes birds display a behaviour intermediate between hovering and perching (e.g., *Oreotrochilus* (Trochilidae) at *Chuquiraga* (Asteraceae) – film by K. L. Schuchmann), similar to the “Rüttel-Klammer-Flug” (hovering-clasping flight) in some flower-feeding bats (Dobat and Peikert-Holle, 1985: 154).

Blossoms Adapted to Hovering Birds

These bird-flowers show an orientation toward free space. Visitors not only need a gate of approach but also space for their wing-beat immediately in front of the flower. An alighting place is not provided. Solitary flowers prevail, and in inflorescence blossoms only single flowers are in anthesis* on any given day. Strengthening of hover-exploited flowers seems to be taxon-dependent as there is “no good evidence that the delicate and exact probing of the bill of a hovering hummingbird damages even soft-tissued flowers” (Snow and Snow, 1980). The floral tubes are narrow and straight and achieve exclusiveness more via prolongation than by curvature. The longer the bird's bill and the longer the tube, however, the greater is the difficulty of “threading” the beak (e.g., *Ensifera ensifera* [Trochilidae] in *Datura* sp. [Solanaceae]). By their outward orientation hover-bird flowers can neither be reached nor pollinated by perching animals, e.g., non-flying mammals.

Blossoms Adapted to Perching Birds

In contrast to the previous group, these blossoms provide a well-defined perch towards which the single flowers are oriented (for perch provision see next paragraph). In some flowers the final adjustment is reached only during the very last phase of ontogeny by an over-tilting of the pedicel as in, e.g., *Phygellus capensis* (Scrophulariaceae), where the lower lip functionally becomes the upper lip (Goebel, 1920: 287 f.), a movement relative to the perpendicular, independent of the orientation of the perch (the main axis) (pers. obs.).

Floral form is often moulded in relation to the direction and movement of the bird's beak; in cases of nototribic pollen deposition the functional lower lip is sometimes removed. Blossoms adapted to perching birds are often composed of a large number of flowers many of which are in anthesis at any given time. In this way, visitors are able to reach several flowers from a single perch without considerable additional movement (Pyke, 1981: 865). The inflorescences must be strong enough for the bird to perch on (Siegfried et al., 1985: 153) and, more importantly, to land on (Rebelo, 1983: 24). Such flowers are often of a stronger fabric since they are strained more heavily than hover-exploited flowers. Exceptions to this exist, e.g., *Leonotis leonurus* (Lamiaceae) and *Lotus berthelotii* (Fabaceae) with delicate flowers. As these frequently are wide open, flowers adapted to visits by perched birds are accessible not only to a multitude of birds but in many cases to non-flying mammals as well. Exclusiveness cannot be achieved by a rectilinear lengthening of the blossom without becoming curved at the same time (Baumberger, 1987: 10). Fixed to a perch, birds with a very long straight beak would be unable to insert it (e.g., *Ensifera ensifera* [Trochilidae]). The stronger the curvature, however, the more precise the positioning of pollen and stigma in relation to the visitor becomes (Holm, 1988: 30).

Perch Provision

Perches may be grouped as follows:

- outside the inflorescence
 - on the ground
 - on a neighbouring structure
- within the inflorescence
 - proximally
 - distally

In rare cases only a perch is provided by the flower itself, as in *Strelitzia* (Strelitziaceae). Here, two of the inner petals which envelope anthers and style serve as a perch. A bird alighting on it releases the enclosed anthers by the action of its feet which become entangled in the pseudo-viscin threads connecting the pollen grains (Waha, 1984). Often one foot tries to obtain a hold on the long, unstable, sticky stigma where it leaves behind some pollen (Rowan, 1974; Frost and Frost, 1981: 382). Similarly, birds foot-pollinate some *Norantea* species (Marcgraviaceae) (*N. sessilis* – Perry, 1986: 61; *N. goyazensis* – Malme, 1923: 449 f.) when stepping into the small flowers in search of the nectar-containing bracts below them. Sometimes birds grip the corolla not designated for this purpose when another perch is not

* applied in its conventional sense (e.g., Bischoff, 1839: 16) describing the whole active phase of the flower.

available [e.g., *Canarina canariensis* (Campanulaceae), see below].

Some plants produce their flowers near the ground [e.g., *Hyobanche sanguinea* (Scrophulariaceae) – pers. obs.; *Anigozanthos humilis* (Haemodoraceae) – Holm, 1988: 100], others lay down their inflorescences, e.g., some species of *Aloe* (Asphodelaceae) (N. Jürgens, pers. comm.; W. Barthlott, pers. comm.; CW, pers. obs.) or have a prostrate growth habit, e.g., *Lotus berthelotii* (Fabaceae) (Olesen, 1985: 406); they all are visited by ground-perching birds (see Keighery, 1982: 82 for a list of Australian ground-pollinated species). Only rarely, do plants utilize neighbouring or foreign structures as perches for legitimate pollinators: in some pendulous species of *Heliconia* (Heliconiaceae) *Eutoxeres* species (Trochilidae) perch on the lower (= next upper) branch bract (sensu Daniels and Stiles, 1979) when feeding from the flowers above them (Snow, 1981: 390) and in some climbers (e.g., *Canarina canariensis*) the supporting plant is the support for the flower visitor too.

In most other cases, of course, perches are provided either proximally or distally to the inflorescence concerned. Only rarely are both possibilities realized in the same inflorescence (e.g., in some Myrtaceae: *Verticordia grandis* – Holm, 1988: 123; *Callistemon* spp.). Most frequently perches are provided proximally to the inflorescence or to the flowers in anthesis. Often the blossoms are somewhat remote from the leafy zone so that the scape literally offers a perch for the visitors, as in, e.g., *Fritillaria imperialis* (Liliaceae), *Cyrtanthus carneus* (Amaryllidaceae), *Burbridgea nitida* (Zingiberaceae), and *Erythrina latissima* (Fabaceae). As flowering proceeds in large inflorescences, birds have to alight on faded flowers as in



Fig. 1 *Philemon* sp. (Meliphagidae) on *Spathodea campanulata*, an Australian bird working an African plant correctly: perching on the central buds the bird bends its head outward-downward into an anthetic flower. (Photo courtesy of H. Kunze).

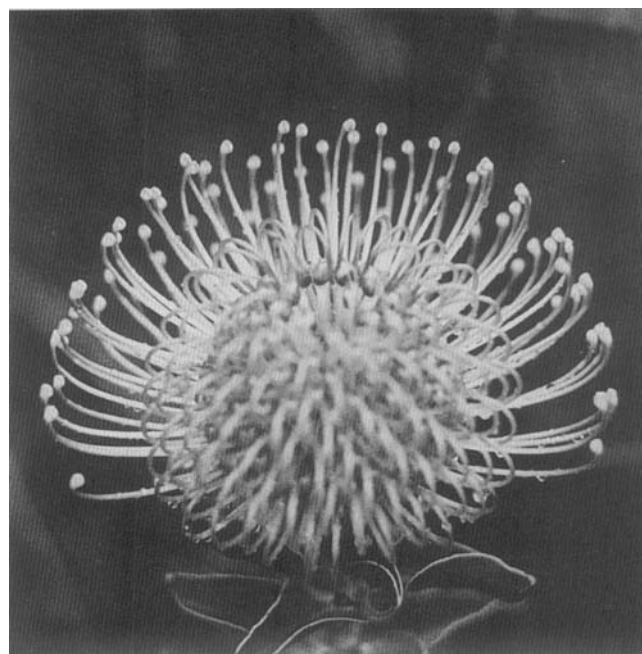


Fig. 2 *Leucospermum* sp. Inflorescence still providing a perch in its centre. When stretching of styles proceeds towards the centre, birds cannot find a hold there any longer – a situation already given at the periphery of the head.

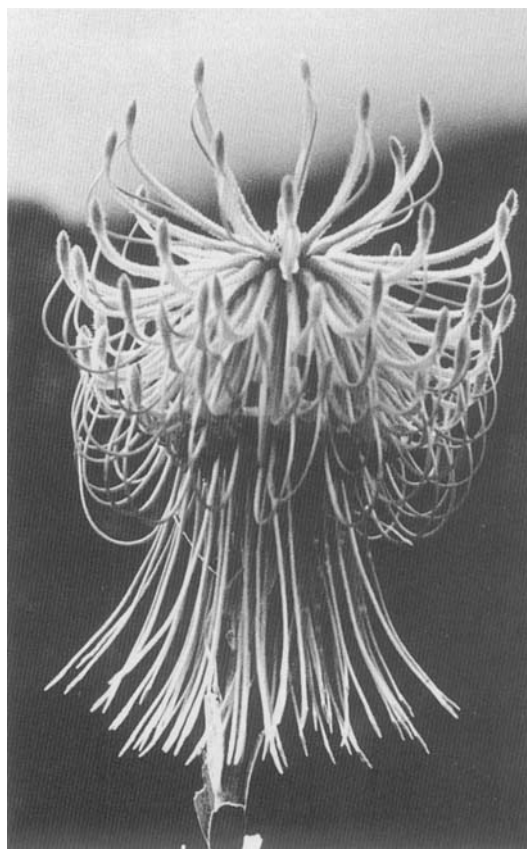


Fig. 3 *Leucospermum reflexum*. Functional pollen-presenters point to the perch proximally of the inflorescence, no foothold in the centre of the inflorescence (compare with Fig. 2).

Kniphofia (Asphodelaceae) and *Melanthus major* (Melianthaceae). At first sight, distal (or central) perches seem to fall into two clear-cut categories: sterile and fertile. *Puya chilensis* (and other species; Bromeliaceae) is a classical (New World!) example of a sterile perch distal to the anthetical flowers in each partial florescence (Johow, 1898), while in *Antholyza ringens* (Iridaceae) the main axis ends in a sterile portion with flowers on a side-branch adjusted to this perch, well depicted already by Marloth (1915: pl. 44). In *Deplanchea tetraphylla* (Bignoniaceae) (Weber and Vogel, 1986: 244), *Brunsvigia* div. spp. (Amaryllidaceae) (S. Vogel, pers. comm.), and in *Pelargonium fulgidum* (Geraniaceae) internodes or pedicels serve as foot-holds. Fertile central perches are provided by buds in, e.g., *Spathodea campanulata* (Bignoniaceae) (Winkler, 1907: 261 ff.) (Fig. 1), *Etilingera* (= *Nicolaia*) *elator* (Zingiberaceae) (Classen, 1987) and most Proteaceae. Birds here grasp the buds themselves, their bracts, or – in many Proteaceae – the immature styles arching out of the buds before dehiscence. On closer inspection it remains to be investigated if these inflorescences are indeed fertile up to the ultimate flowers, as these no longer have a perch (compare, e.g., *Leucospermum* div. spp. (Proteaceae), Fig. 2). Birds cannot alight and thus cannot pollinate. Consequently, are these terminal flowers – functionally – only perches? Observations in Proteaceae (Collins and Rebelo, 1987: 409) have demonstrated that birds strongly prefer partly opened inflorescences. In order to keep pace with the proceeding anthesis, an equally steady elongation of the axis is observed in *Etilingera elator* (Classen, 1987), thus offering open flowers at a constant distance from the perch during most of the flowering time of an individual inflorescence.

As proximal and terminal perches are sometimes available within a single genus (e.g., *Leucospermum*, see below; Figs. 2, 3), it would be interesting to know if any transitional stages exist. To my knowledge, a putative continuum has only been suggested for *Deplanchea* by Weber and Vogel (1986: 246 f.), admittedly on purely morphological grounds.

Examples for Diversification

It is instructive to examine some taxa containing many bird-flowers, especially when they are distributed over more than one floristic kingdom.

Erythrina (Fabaceae) (data from Neill [1987] unless otherwise stated). This pantropical genus is entirely ornithophilous (Vogel, 1980: 32). Forty-two Old World and 15 New World species are adapted to perching birds, 65 New World species to hovering exploitation. In the former, the inflorescence axis is held horizontally, the flowers are wide open, herkogamous, homogamous, and have more or less sticky pollen. In the New World this group includes (with authors describing pollination) *E. breviflora* (Cruden and Toledo, 1977), *E. megistophylla* (Steiner, 1979), *E. oliviae* (Toledo and Hernandez, 1979), *E. poeppigiana* (Feinsinger et al., 1979), and the pantropical (Krukoff and Barneby, 1974: 340) *E. fusca* (Morton, 1979). *E. crista-galli* is thought to be pollinated by perching birds by Baker and Baker (1979) because of its hexose-dominated nectar, while Arroyo (1981: 749) interpreted the resupination of this flower as an adaptation to hovering birds. One

could even imagine pollination by hummingbirds perching on the standard (CW). There clearly is an urgent need for observations. Interestingly, hummingbirds intending to drink from perch-possessing *Erythrina*s have to sit down (Cruden and Toledo, 1977).

Hover-bird adapted *Erythrina* species evolved convergently in several lineages (Hernandez and Toledo, 1982: 77). They display a vertical inflorescence axis with flowers pointing outward. The standard forms a narrow pseudotube enclosing anthers and stigma which are at about the same level. The flowers are protandrous and have dusty pollen (Hemsley and Ferguson, 1985). Only a few Old World species (from sect. *Humeanae*, with narrow, tubular flowers) exhibit a similar pollen condition.

In the south-hemispheric Proteaceae ornithophily is said to have evolved several times independently (Johnson and Briggs, 1975: 443). Although operated by birds from different families (Meliphagidae in Australia, Promeropidae in the Capensis), most of them work in the same way – with birds perching in the centre of the inflorescence stretching outward-downward while inserting their bills into the freshly opened flowers. This holds for *Protea* and *Leucospermum* as well as for *Banksia* (Holm, 1988: 44; Ramsey, 1989) and *Grevillea*. Similar observations were made on nectar-drinking mice and marsupials (Turner, 1982: 57 – but see Carpenter, 1978). In a film on *Protea*-pollinating mice by J. Rourke (Kirstenbosch), they always worked the inflorescences from the centre, trying to turn their heads by 180° in order to enter the lower flowers of a head lying on its side. Interestingly, uninitiated young already demonstrated the same behaviour at their first trial. Birds working *Leucospermum* inflorescences from below – as do, e.g., *Nectarina* spp. – only steal nectar but never contact pollen-presenters nor stigmas – with one notable exception: in *Leucospermum reflexum* (Fig. 3) this position is the only way to pollinate the flowers, with anthetical flowers pointing downwards. Another example of the caution required when trying to infer pollination from a visitor's pose was demonstrated by Collins (1983) for *Mimetes hirtus*: although *Nectarinia violacea* (Nectariniidae) is often observed (and depicted: Marloth, 1913: pl. 32) working the compound inflorescences from below, it does not contact the pollen-presenters/stigmas. The actual pollinator *Promerops cafer* (Promeropidae) perches on the landing platform on top of the inflorescence and reaches down over the distal ends of the pollen-presenters and thereby brushes them with its throat. An interesting case still to be studied is *Embothrium* with ornithophilous species in Patagonia and Australia. Did it invade Australia from the New World (Vogel, 1980: 35) or vice versa (Johnson and Briggs, 1975: 443), and did ornithophily evolve once or repeatedly?

A situation similar to that in *Leucospermum*, but just the other way round, is met with in *Aloe* (Asphodelaceae): while many ornithophilous Aloes are worked from below (e.g. *A. striata*) or by ground-perching birds (see above), one species at least (*A. longistyla*) depends on birds perching on top of the inflorescence (Rebelo, 1987: 85).

In *Anigozanthos* (Haemodoraceae) Hopper and Burbidge (1978) not only demonstrated a seasonal dif-

ference between the blooming peaks of two species growing in the same place, but they also showed that *A. humilis* is visited by ground-hopping and -perching individuals of *Anthochaera carunculata* (Meliphagidae) which become dusted on the base of the beak; *Anigozanthos manglesii*, on the other hand, provides a perch on the recurved stem below the inflorescence. In the latter species pollen is deposited on the top of the head and the nape of the neck up to 8 cm from the bill tip in birds of the same species which mostly fly from inflorescence to inflorescence.

In *Canarina canariensis* (Campanulaceae) visiting birds perch on neighbouring twigs, but if no perch is available they exploit the flowers on the wing or by grasping the corolla, leaving traces of their claws. The wide mouth of the corolla enables the birds to enter the flower from this position. The bells of *C. eminii* are more narrow (Hedberg et al., 1961: 27) and the flowers hang freely from their supporting branch (E. Fischer, pers. comm.). I cannot imagine birds clasping the corolla rim and entering the flower from this perch because of the narrowness of the floral tube. Claw marks have never been observed (E. Fischer, pers. comm.). Thus, hovering exploitation – and pollination – seems to be the only way feasible in this species. Further examples of Old World flowers adapted to hovering birds include the Himalayan *Agapetes* spp. (Ericaceae) (J. Martens, pers. comm.) and *Impatiens sakeriana* (Balsaminaceae) from Cameroon (S. Vogel, pers. comm.).

Conclusions

Because of the undoubted ability of nectar intake on the wing in non-trochilid flower-birds, we should be prepared to find more hover-exploited bird-flowers which have not been influenced in their evolution by hummingbirds. Thus we must discard the "dogma" of a clear-cut partition between New World and Old World bird-flowers. On the other hand, almost all flowers adapted to birds that perch while exploiting flowers are provided with one well-defined perch only, most other perching positions not being effective for pollination. To understand bird-flowers the actual functioning of the flowers must be in focus, and not the geographical distribution nor the systematic affiliation of their visitors.

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Chr. Westerkamp

Institut für Systematische Botanik
und Pflanzengeographie
Im Neuenheimer Feld 345
D-6900 Heidelberg
Federal Republic of Germany