CHAMPION POLLINATORS

Long-proboscid flies in a biological system unique to southern Africa.

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Southern Africa abounds in plants that have flowers with long, slender floral tubes and in an unusual range of animals with long mouthparts that feed on the sugar-rich nectar in the base of the tubes. The animals that feed on the nectar, all potential pollinators of these plants, include sunbirds with long bills and tongues and a variety of different groups of insects with elongated mouthparts. Among these insects are butterflies and moths, flies, including bee flies (Bombyliidae) and acrocerid flies (Acroceridae), and some bees. These flies and bees have mouth parts up to 8-12 mm long and visit flowers with floral tubes of moderate length, usually in the 10-15 mm range. Such pollinators are not uncommon and they occur all over the world.

Southern Africa is also home to a special group of long-proboscid pollinators: flies with mouthparts mostly exceeding 20 mm, one of only a few kinds of organisms capable of taking nectar from plants with super-long, narrow floral tubes that exceed 20 mm in length. Such flies are remarkable among pollinators for their needle-like mouthparts are longer than their bodies, sometimes up to three times as long. Many of the plants that they visit to forage for nectar have slender floral tubes exceeding 30 mm in length and sometimes up to 70 mm. Clearly, these long-proboscid flies and the plants with which they are associated have co-evolved and form a close ecological mutualism.

Champion among long-proboscid flies is the Cape west coast species *Moegistorhynchus longirostris* which has a tongue as long as 70 to 80 mm. Several other flies have tongues up to 40 mm, still amazing when one considers that the fly has no way to retract its prodigious appendage, but must fly with it extended forward or tucked loosely below its body. Flies with these super-long mouthparts include some twelve known species in two fly families, the Nemestrinidae (tangle-veined flies - a fairly uncommon animal) and the Tabanidae (horseflies - short-proboscid species which bother cattle and humans alike as the females painfully bite the skin to obtain the blood meal they require to complete their life cycle). The cast of long-proboscid flies includes the two horseflies, *Philoliche gulosa* and *P rostrata,* and several nemestrinids, including six species of the genus *Prosoeca,* one of *Stenobasipteron,* and at least two species of the genus *Moegistorhynchus.* These flies with super-long mouthparts occur throughout southern Africa, their collective range extending from southern Namibia to the Cape Peninsula in the west, along the mountains of the southern Cape and through Lesotho and KwaZulu-Natal into Mpumalanga, Northern Province and Swaziland. None of these flies is known from tropical Africa, which also seems to lack plants associated with long-proboscid fly pollination.

Active in the spring in the Western Cape and Namaqualand, Prosoeca *peringueyi* is the sole pollinator of a range of wild flowers with long floral tubes and bright red to purple petals, such as *Lapeirousia silenoides.* Photo: J. Manning.

Our interest in long-proboscid fly pollination began with an investigation of the taxonomy, biology and evolution of the genus *Lapeirousia,* and subsequently that of the genus *Gladiolus,* both members of the plant family Iridaceae. These genera exhibit major radiation and speciation in southern Africa, and in both there has been significant adaptive radiation for a variety of pollination systems. Many species of both genera have flowers with particularly long tubes and secrete relatively large amounts of nectar that is rich in sucrose. Our work on *Lapeirousia* gave us the first indications of the presence of guilds (see accompanying box) of plant species using particular long-proboscid fly species to achieve their pollination.

In Namaqualand, in the interior west coast of South Africa, we discovered that the carmine-red flowers of *Lapeirousia silenoides*

(Springbok painted petals) were pollinated exclusively by one species of fly, *Prosoeca peringueyi*. At particular times of the day and in sunny, warm weather this large fly, which has mouthparts 30 to 40 mm long, could be found foraging for nectar on the flowers of *1. silenoides*. Its violet-coloured pollen deposited all over the face of the flies can often be seen with the naked eye. We soon noticed that *Properingueyi* also visited similarly coloured and shaped flowers of other plants that grew nearby. Often the flies would visit the brilliant magenta flowers of *Pelargonium incrassatum*, a species of the Geraniaceae fairly common in Namaqualand. Flies would also visit the flowers of *Babiana* species (Iridaceae) with long-tubed, dark blue-violet flowers and *Hesperantha latifolia* with deep red flowers. It gradually dawned on us that a wide range of spring-blooming, intense red, purple or bluish flowers with pale coloured markings, complete absence of scent, and a long floral tube containing sugary nectar were visited solely, but indiscriminately by *Prosoeca peringueyi*.

This pattern was also evident to the south in the Olifant's River and Bidouw valleys where *Prosoeca peringueyi* could be found visiting the flowers of *Lapeirousia jacquinii*, *1. violacea* or *1. pyramidalis*, different species of *Babiana*, *Sparaxis variegata* (Iridaceae), and *Pelargonium magenteum*, all having violet to dark reddish flowers with pale markings and a long, nectariferous floral tube in common. On the Bokkeveld Plateau near Nieuwoudtville in the Northern Cape Province we found a local variation of what was becoming a familiar pattern. Purple-flowered and long-tubed *Lapeirousia oreogena*, *1. jacquinii*, *Babiana framesii* and *B. sambucina* were being visited by a second species of *Prosoeca* as yet not named. And on the Hantamsberg near Calvinia, in the western Karoo, *Babiana flabellifolia* and *Romulea hantamensis*, which also have long-tubed, purple flowers, were visited exclusively by this species of *Prosoeca*. The puzzle as to why long-tubed purple or magenta flowers are so common only north of the Olifant's River valley was explained. They are adapted for pollination by these two flies which are found only north of Clanwilliam.

With the longest proboscis of any fly, *Moegistorhynchus longirostris* is the only insect able to reach into the base of the floral tubes of plants like *Lapeirousia anceps* to feed on the ample nectar located there. *Moegistorhynchus* appears to be attracted particularly to cream and pink flowers with darker markings. Photo: J. Manning.

A second group of Namaqualand and Cape west coast plant species formed another guild with flowers adapted for pollination by different species of long-proboscid flies. They also have long-tubed flowers with ample amounts of sweet nectar, but the flowers are white to pale pink and have red to purple markings that seem to function as a visual signal. We first saw the nemestrinid fly, *Moegistorhynchus longirostris* on a species of *Lapeirousia*, *1. fabricii* in Namaqualand. This fly had already been recorded as a visitor and probable pollinator of another *Lapeirousia*, *1. anceps* (by the entomologist, A. J. Hesse, and reported by the German biologist, Stefan Vogel in 1954). We later found this fly pollinating not only *1. anceps*, but several plants with similarly shaped and coloured flowers with long floral tubes. Near Yzerfontein on the Cape west coast M. *longirostris* also pollinates *Pelargonium stipulaceum*, and other species of Iridaceae with cream flowers, including *Babiana tubulosa*, *Geissorhiza exscapa*, *Gladiolus angustus* and *Ixia paniculata*. The cream-flowered orchid, *Disa draconis* is also part of this guild. In the Olifant's River valley near Clanwilliam we again found this fly, this time pollinating both *1. anceps* and *1. fabricii*, as well as *Geissorhiza exscapa* and *Tritonia crispa*.

A second fly, the tabanid *Philoliche gulosa*, shares this same series of plants, but mainly outside the range of M. *longirostris*. *Ph. gulosa* has slightly shorter mouthparts than M. *longirostris* and presumably is at a slight disadvantage in competing with M. *longirostris* for nectar. Their ranges overlap only to a small extent, however, and both species are able to utilize the same set of plants. It is notable that the length of the floral tube usually tracks very closely the length of the visiting insect's mouthparts. The floral tube in the plant species is much longer in populations visited by M. *longirostris* than in those visited only by *Ph. gulosa*, graphically illustrating this phenomenon.

In the mountains of the Western Cape, including the Cape Peninsula, we have seen some of the same plant species that we found being visited by *Moegistorhynchus longirostris* and/or *Philoliche gulosa*, as well as others with a very similar appearance, being visited by other flies including *P. rostrata* and *Prosoeca nitidula*. These plants evidently belong to a greater *Moegistorhynchus Philoliche* pollination guild in the southern African winter-rainfall zone that involves cream to pink-flowered plant species that flower in the spring and early summer, September to November or December.

All these long-proboscid flies have'a random foraging behaviour. They will visit flowers of the different members of their respective guilds quite indiscriminately, and thus carry pollen of several species on their bodies, a feature easy to determine with the naked eye by the heavy deposits of differently coloured pollen, and by microscopic analysis of pollen removed from their bodies. The problem of pollen clogging (see accompanying box) however, does not occur. This is because at sites where plant species use a particular fly for pollination each species has anthers so positioned that pollen is consistently deposited on a different part of the fly's body. For example, at sites in Namaqualand, pollen of *Lapeirousia silenoides* is deposited on the frons (front part of the head) of *Prosoeca peringueyi*, that of *Pelargonium* on the lower thorax and of *Babiana dregei* or *B. pubescens* on the upper thorax. A similar pattern is repeated in guilds using *Moegistorhynchus* and *Philoliche*.

Our studies of the biology of *Gladiolus* in southern Africa has led us to identify two more completely separate guilds of plants species using quite different long-proboscid fly species to achieve their pollination. In the Drakensberg of KwaZulu-Natal and Lesotho the fly, *Prosoeca ganglbaueri*, with mouth parts 20 to 35 mm long, is active in the late summer and early autumn and appears to visit, indiscriminately, long-tubed cream or pink flowers, usually with darker

Moegistorhynchus longirostris about to insert its elongated proboscis into the slender tube of *Ixia paniculata*. Photo: J, Manning.

OF POLLINATION AND GUILDS

Pollination by flies with extremely long mouthparts has been called rhinomyophily, a tough name to rem!ilmber. The term includes pollination by all flies with slender, sucking mouthparts, simply to distinguish it from the more general myophily, or pollination by flies with short mouthparts. Sapromyophily, pollination by flies with lapping mouthparts is a completely different pollination syndrome, typically associated with rank-smelling flowers without tubes and readily accessible nectar. Long-proboscid flies feed primarily on nectar and they may visit almost any flower that offers this reward. However, it is only from flowers with very long tubes that an adequate supply of nectar is assured. Other insects are prevented from exploiting this resource because their mouthparts are simply too short. Nectar in short-tubed flowers is available to a host of insects and is readily depleted by common insect visitors including honey-bees, butterflies and wasps. It is then in the best interests of the energetic needs of insects with longer mouthparts to confine their foraging to flowers with long tubes because they benefit from the lack of competition for this food resource. Long-tubed flowers produce a generous food supply and store it in sites that are only accessible to a few highly specialized visitors.

Only those plant species with very long-tubed flowers actually benefit from the visits of the flies because as these insects forage for nectar they brush against the anthers. Pollen is then dusted onto their bodies and is carried to another flower where it can, in turn, be brushed against the stigma, so accomplishing cross-pollination, essential for the life cycle of the plant to be completed. Insects often learn rapidly to recognize important sources of food and the form and colour of a particularly valuable source of food becomes imprinted on their memory. A consequence of this is that plants with flowers closely resembling the primary nectar source or sources will also be visited with some frequency, particularly if they also offer a reward. Thus it is typical of long-proboscid fly pollination systems for the several plant species in a particular area that use the same insect for their pollination to have flowers of similar colour, and sometimes shape and overall appearance. These plants are said to form a guild, that is, a group of organisms using a particular resource in a similar way, in this case a highly specific pollinator.

Long-proboscid flies have a random foraging behaviour, visiting flowers of the different members of their respective guilds quite indiscriminately, and thus carrying pollen of several species on their bodies. The problem of pollen clogging, that is the deposition of foreign pollen on the stigma of a flower, thus preventing pollen of the right species reaching the stigmatic surface and eventually effecting fertilization, however, does not occur. This is because at sites where plant species use a particular fly for pollination each species has anthers so positioned that pollen is consistently deposited on a different part of the fly's body.

Like *Moegistorhynchus*, the eastern escarpment fly, *Stenobasipteron wiedmannii* is attracted to pale pink flowers. One is seen here pollinating the rare *Gladiolus macneilii*.
Photo: J. Manning.

markings, of *Gladiolus microcarpus*, *Hesperantha scopulosa*, *Zaluzianskya microsiphon* (Scrophulariaceae) and species of Orchidaceae including *Disa oreophila*. At sites along the Mpumalanga Escarpment *Pr. ganglbaueri* or two other long-proboscid flies, *Pr. robusta* and *Stenobasipteron wiedmannii*, visit and appear to pollinate several more plants with long floral tubes including several species of *Gladiolus* and *Watsonia* (Iridaceae), some orchids, and a few members of the mint family, including *Orthosiphon* species. Another plant that appears to use a long-proboscid fly for its pollination is the large, pink-flowered *Nerine angustifolia* (Amaryllidaceae) which, although it doesn't have a long floral tube, has stamens over 20 mm long that brush the underside of a long-proboscid fly as it feeds on nectar at the base of the tepals. Other species at these sites with similarly coloured, long-tubed flowers include the orchid, *Disa amoena*, which also appears to be adapted for pollination by long-proboscid flies. At all these sites too, pollen is deposited by each member of the guild on a different part of the fly's body. The problem of pollen clogging of the stigma thus appears to be a primary consideration in long-proboscid fly pollination and a factor limiting the local occurrence of two or more species that use the same sites of pollen deposition on a fly.

So far some sixty plant species have been identified that appear to be pollinated exclusively by one or no more than two species of long-proboscid fly. A review of southern African plant species with similar flowers to those now known to be pollinated by long-proboscid flies brings the list of species potentially pollinated by these flies to at least 150 species, and there are certainly more. This makes pollination by nemestrinid and tabanid flies with mouthp~rts exceeding 15 mm one of the most significant pollination systems in the subcontinent, and one of particular importance in families such as the Geraniaceae and Iridaceae. It is surprising then, that until recently this pollination system was virtually unknown.

A disturbing aspect of long-proboscid fly pollination is that it is a highly specialized system. Numerous plant species depend on just one or two organisms for their pollination and thus for their ultimate survival. Such organisms have been termed keystone species for good reason. The conservation of plants depending on long-proboscid flies for their pollination depends ultimately on the survival of these flies. Unfortunately the survival of the flies is not assured. Tabanid flies have the larval stages of their life cycle in wetlands, not always close to the sites where the plants that they feed upon grow. The females are also believed to require a blood meal from a large mammal before she can lay eggs. Farming and urban development activities can damage and destroy wetlands and reduce habitat for the mammals on which tabanid flies feed. No wonder then that at some sites where species depend on *Philoliche* for their pollination one can find populations of plants that no longer produce seeds. Their specialized pollinator is locally extinct.

Unlike the tabanid flies, the life cycles of the southern African nemestrinids, *Moegistorhynchus*, *Prosoeca*, and *Stenobasipteron* are completely unknown. The few nemestrinid flies whose life cycles are known have larvae parasitic on other insects including locusts. With such complex life cycles nemestrinid flies are probably especially vulnerable to environmental disturbance and loss of habitat. Again we have found populations of plants with flowers adapted for pollination by both *Moegistorhynchus* and *Prosoeca* that set no seed at all in years when we have studied them. It is not yet known whether the emergence of the flies from their pupae had failed to coincide with the flowering time of the floral guilds they feed upon or whether they were extinct locally. Nevertheless, we are convinced that in the long term, all these specialized long-proboscid flies will become eliminated from much of their original ranges, and that several of the plant species which depend on these flies for pollination will soon be eliminated locally because of the absence of their pollinators. Some plant species with small ranges will probably face total extinction.

It is extremely important, then, that we learn about the life histories of such specialized pollinators. Until this information is available, reserves for the conservation of plants with specialized pollination systems will have to be made as large as possible and must include a variety of habitats so that the complex webs that allow the lives of these organisms to be sustained will be preserved. ®