SOUTH AFRICAN BLUEBELLS

Wasp and bees, stars and bells: an intricate pollination study of *Wahlenbergia*.

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South African bluebells, *Wahlenbergia*, like the Scottish bluebell *Campanula rotundifolia*, belong to the family Campanulaceae. There are about 200 known species of *Wahlenbergia*, of which nearly 150 occur in southern Africa, the greatest concentration of species being in the south-west. The plants are mostly annual or perennial herbs, the majority of which are erect, though some are straggling. Some have woody bases.

The flowers, as both the family name and the common name suggest, are bell shaped. In most species the bells do not hang down but are held erect. In colour they are not true blue, most are shades of bluish-violet. More unusually some species of *Wahlenbergia* (including *Lightfootia* species) are pinkish violet, white or yellowish. In most species there is a distinct corolla tube with short free lobes but in some species the tube is shortened to the degree that the flower appears star-like (stellate).

The stamens are five in number, like the petals, and alternate with them. In most of the tubular species the anthers are fused to the petals but in the stellate flowers they are free. In the bud the anthers form a tube through which the style grows after the anthers have ripened and are ready to shed the pollen. The style and the outer surfaces of the closely appressed stigmatic lobes are clad in pollen-collecting hairs so that as the style grows up through the tube the pollen is brushed out and is presented in the open flower on this central column.

After the flower has been open for some time the pollen collecting hairs wither and any pollen which has not been removed by insect visitors falls. The stigmatic lobes then open and are ready to receive pollen from another flower.

Nectar is produced on top of the ovary which is inferior to sub-superior. In the erect tubular flowers the pool of nectar is securely cupped and is somewhat protected, for example, in *W. paniculata* it has a small surface area resulting from the base of the tube being very narrow, in *W. pilosa* there are long hairs arising from the style, and in *W. psammophila* the bases of the filaments are expanded. In stellate flowers, such as *W. annularis* and *W. sanderi* in which the cup is very shallow, expanded filament bases completely cover the nectar, not only protecting it from evaporation but also from spilling.

I have watched nectar-drinking visitors coming to *Wahlenbergia* flowers throughout the south-west. Year by year these visitors were usually pollen wasps (*Marsarnia*) if the flowers were tubular, or melittid bees (*Melittidae*) if the flowers were stellate. A casual
observer may disagree with this observation because the tubular flowers in some years and in some places are visited by large numbers of other insects. There have been, for example, times when, on the slope above the Clanwilliam Dam, I have seen W. paniculata visited by large numbers of bee flies (Bombyliidae) in addition to pollen wasps and tissues, in the Geopap Reserve, when butterflies were noticeable visitors to W. pilosa together with pollen wasps. The bee flies and the butterflies did not enter the flowers but merely inserted their long ‘tongues’ to drink the nectar. The pollen wasps, three species of Celonites (C. wahlenbergiae, C. bergeriwhalgiæ and C. lotteriis, recently described by Fred Gess), Masarina mixta, and several species of Quatinia and Quartiniiides (Masarinae) alight on the outwardly curved free corolla lobes and enter the flowers to reach the nectar. In doing so the three Celonites and Masarina mixta brush against the central column so that, when a flower is in the pollen presenting phase, pollen is deposited on their backs. When such a pollen-laden wasp enters a flower with receptive open stigmatic surfaces, pollen is deposited and thus pollination takes place. In the larger flowers the Quatinia and Quatiniiides species can come and go without pollinating the flowers but in smaller flowers they are effective. Melittid bees are less commonly associated with the tubular flowers than are pollen wasps but when and where they are regular visitors, they will also successfully pollinate the flowers. Unlike the pollen wasps, they enter the flowers without first alighting on the lip, with the underside towards the column. Pollen is therefore wiped onto the underside and not the back of the insect.

This difference in behaviour by pollen wasps and melittid bees is extremely important to them when they visit stellate Wahlenbergia flowers in which the bases of the filaments cover the nectar. The melittid bees are positioned for inserting their ‘tongues’ under the cover whereas the nectar is closed to a pollen wasp. The difference is also important to the flowers as in the open flower it is only a relatively large melittid which makes contact with the pollen clad column and therefore only these bees will be effective pollinators. There are induced species of Capicola (Melittidae) which are restricted in their choice to these flowers and are therefore closely associated with them. They receive as a reward not only nectar but also pollen which, unlike the pollen which they receive accidentally and which services the flowers, is deliberately collected and carried to their nexts packed on their hind legs.

Pollen wasps collect pollen for provisioning their nest cells from both tubular and stellate flowers. This pollen is ingested directly from the column and is carried to the nest in the wasp’s crop.

Towards the end of the afternoon when the Wahlenbergia flowers start to close, males of both Capicola and Masarina that, unlike the females, do not sleep in the nests, stay in the flowers which close over them giving them shelter for the night.

To the south of Springbok in Namaqualand and to the west of the Olifants River Valley extensive areas have been ploughed for the opportunistic production of wheat. Such replacement of the species-rich vegetation with a single graminaceous species results in an almost total insect species loss. When such lands are left fallow or abandoned, pioneer plants start to grow. Initially a limited range of annuals predominates, often forming almost pure stands. These annuals are species that are present but uncommon in the species-diverse communities of the surrounding undisturbed areas. An increase in population size of the insect species associated with these plants as compared with that of the surrounding area results. This effect is strikingly demonstrated by the wasp and bee species associated with Wahlenbergia. Areas in which the deep-flowered Wahlenbergia species were formerly abundant and W. annularis was uncommon have been cultivated and allowed to lie fallow. In these areas W. annularis is now the dominant plant, which has resulted in the displacement of the masarines and an unnatural abundance of melittids.

Acknowledgements


A further reading list is available on request from the Publications Manager, Botanical Society, Private Bag X19, Newlands, 7725, fax (021) 707 2376.