# Pollination ecotypes of *Satyrium hallackii* (Orchidaceae) in South Africa

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Intraspecific variation in floral traits may reflect adaptive shifts in the pollination system of a plant. This idea was tested by examining the pollination biology of *Satyrium hallackii* H. Bolus., an orchid which has spurs varying from 8 to 36 mm among populations in southern Africa. Field observations showed that the short-spurred form (*S. hallackii* subsp. *hallackii*) in coastal fynbos habitats is pollinated by bees, while the long-spurred form (*S. hallackii* subsp. *ocellatum*) in grassland habitats is pollinated primarily by hawkmoths and, secondarily, by long-tongued flies. The shift between hawkmoths and bees as pollinators may have been promoted by an ecological gradient in South Africa: carpenter bees are common in coastal fynbos habitats, but rare in grassland habitats where there are few available nesting sites. On the other hand, hawkmoths are common in grassland habitats, but rare in fynbos where there are few palatable host-plants. The formation of pollination ecotypes across pollinator gradients has probably been a major factor in the diversification of South African plants with specialized pollination systems.

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ADDITIONAL KEY WORDS:—flora of southern Africa – hawkmoths – carpenter bees – long-tongued flies – speciation.

## CONTENTS

## INTRODUCTION

According to models developed largely by Dodson (1962), Grant & Grant (1965) and Stebbins (1970), speciation in plants could result from the formation of ecotypes adapted to the local pollinator environment. When availability of a specialist

pollinator is geographically patchy, fitness may be pollinator-limited in some plant populations, resulting in selection for floral traits which attract different, more effective pollinators. Such shifts between pollinators, depending on their local abundance and effectiveness, could lead to the formation of pollination ecotypes (Miller, 1981; Inoue & Amano, 1986; Pellmyr, 1986; Johnson, 1996a; Johnson & Steiner, 1997). Despite their plausibility, models of speciation through the formation of pollination ecotypes have received only meagre empirical support.

In one of the first studies to examine the link between pollinators and speciation, Dodson (1962) found repeated shifts between pollination by *Euglossa* and *Eulaema* bees among closely related species of *Stanhopea* (Orchidaceae). This formed the basis for Dodson's so-called 'leapfrog' model of speciation. More recently, Robertson & Wyatt (1990) found that differences in the spur length of mountain and lowland populations of *Platanthera ciliaris* could be attributed to differences in the proboscis length of butterflies in the two regions. Johnson (1994) described a similar basis for ecotypes in the butterfly-pollinated South African orchid *Disa ferruginea*. Grant & Grant (1965) discussed several possible examples of differentiation of geographical races in the Polemoniaceae, including shifts between bee-flies and bees in *Gilia leptantha*. They also mentioned several closely related sister species which differ in their pollination systems. In Ranunculaceae, Pellmyr (1986) described the existence of three 'pollination morphs' of *Cimifuga simplex* occurring at different altitudes. Armbruster (1985) attributed the origin of ecotypes in *Dalechampia scandens* (Euphorbiaceae) to reproductive interference with sympatric *Dalechampia* species in some populations. Several other possible pollination ecotypes have been proposed in the literature (e.g. Arroyo & Dafni, 1995; Susuki, 1992), but in most of these the basis for floral variation is obscured by a lack of correspondence between observed pollinators and floral morphology.

Some biologists have argued that plant-pollinator relationships are generally too diffuse to allow the evolution of specialized ecotypes (Feinsinger, 1983; Howe, 1984; Herrera, 1988; Horvitz & Schemske, 1990). This is supported by studies which show that taxa pollinated by a wide spectrum of insects may not undergo strong selection on floral characters (e.g. Herrera, 1987). However, the assumption that all pollination systems are diffuse and unspecialized is misleading. Highly specialized pollination systems are well documented, especially in plants from the tropics and temperate regions of the southern hemisphere (e.g. Wiens *et al.*, 1983; Nilsson, Jonsson & Randrianjohany, 1985; Steiner & Whitehead, 1988; Johnson & Bond, 1994; Goldblatt, Manning & Bernhardt, 1995).

To test the idea that intra-specific variation in floral results from the formation of pollination ecotypes, the pollination of an orchid species which exhibits considerable variation in spur length was studied. The study species, *Satyrium hallackii* H. Bolus, occurs in marshy habitats across southern Africa. There have been no previous studies of pollination in this species.

The phenetic variation within *Satyrium hallackii* was studied by Hall (1982), who recognized two subspecies, differing primarily in the length of the floral spurs. *Satyrium hallackii* subsp. *ocellatum* (H. bolus) A. V. Hall (= *Satyrium ocellatum*) has spurs 20–36 mm in length and occurs in the northern and eastern regions of southern Africa. *Satyrium hallacki* subsp. *hallackii* has much shorter spurs (8–15 mm) and occurs in a few scattered populations along the southern coastline.

The genus *Satyrium* exhibits a classic pattern of floral radiation, characterized by the evolution of numerous pollination systems in a relatively small clade (Johnson,

1996b,c). By examining the basis for intraspecific variation in one species, I hoped to gain at least some insights into the evolutionary processes which led to adaptive radiation in the genus as a whole.

## MATERIAL AND METHODS

### Spur length measurements

*Satyrium* flowers have two spurs derived from the labellum. To establish the patterns of geographical variation in spur length of *S. hallacki*, the spur lengths of all specimens in South African herbaria were measured to the nearest 0.1 mm. For this purpose, spur length was defined as the distance between the tip of each spur and the point where the two spurs are joined. In addition, the distance between the spur tip and the stigma in 5–26 fresh flowers from each study population was measured. This latter measurement more accurately reflects the functional depth of the flower.

### Study sites and pollinator observations

A population of the short-spurred form, *S. hallackii* subsp. *hallackii*, was studied at Bettys Bay (34°17′S 18°56′E), about 40 km east of Cape Town. This population of about 200 plants occurs in a permanently wet dune slack, about 500 m from the coastline. The vegetation at this site consists of small sclerophyllous bushes typical of the Cape fynbos. Observations were made from 10:00–15:00 on 5 January 1995, 10:00–20:00 on 10 January 1995 and 10:00–15:00 on 29 December 1995.

The long-spurred form (*S. hallackii* subsp. *ocelattum*) was studied at Verloren Valei Nature Reserve (25°17′S 33°09′E), in the Mpumulanga Province, about 1500 km north-east of the Bettys Bay study site. The vegetation at this site consists of treeless montane grasslands with several permanent wetlands. The study population consisted of several hundred flowering individuals in a large wetland. Observations were made between 10:00 and 20:00 on 2 and 3 February 1993.

At both study sites, all possible pollinators were caught, identified and examined for the presence of pollinaria. The volume of nectar in the spurs was measured with micropipettes and the nectar concentration was determined with a refractometer. Samples of nectar from five flowers at each population were spotted onto filter paper for later analysis of the constituent sugars using standard HPLC techniques.

The levels of pollination success in each population were determined by examining stigmas for the presence of pollen massulae. The frequency of pollinaria removal from the flowers was also recorded.

## RESULTS

### Variation in spur length

Analysis of the available herbarium material showed that spur length varies enormously among populations of *Satyrium hallackii* in southern Africa (Fig. 1).
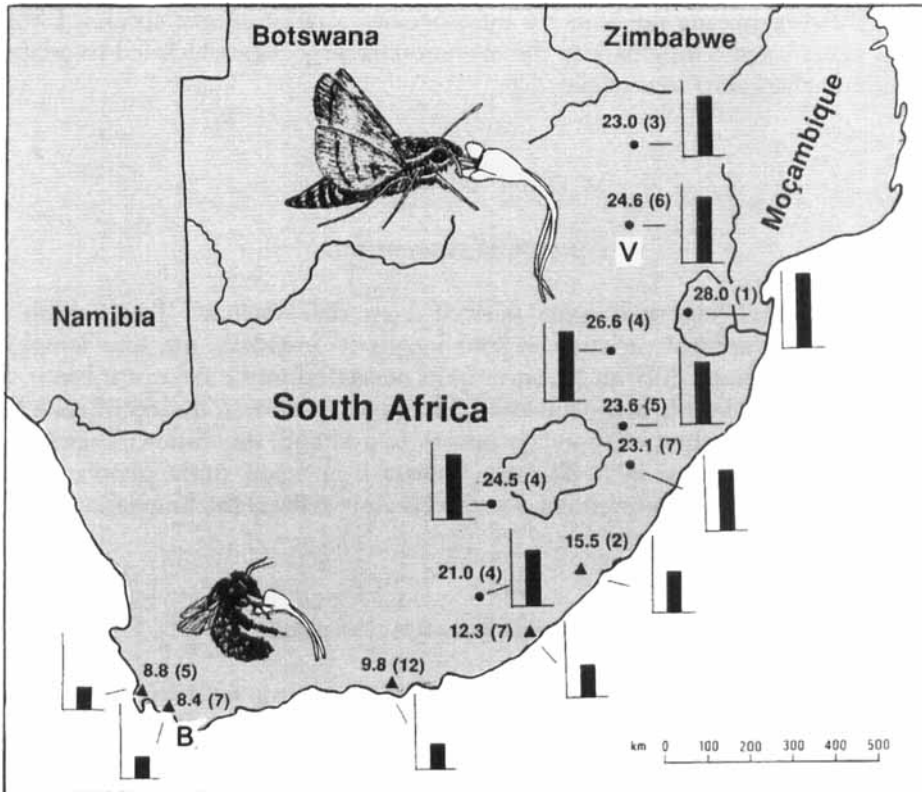
Figure 1. Variation in spur length among populations of *Satyrium hallackii* in South Africa. (▲) *S. hallackii* subsp. *hallackii*; (●) *S. hallackii* subsp. *ocellatum*. The mean spur length is given for each locality with the sample size (number of plants measured) in parentheses. A graphical illustration of spur length at each locality is provided by bar graphs where the height of the y axis represents 30 mm. The data were obtained from 67 specimens in South African herbaria. Localities of the study sites are indicated by the following abbreviations: B - Betty's Bay, V - Verloren Valei Nature Reserve.

Populations near Cape Town have spurs of only 8–9 mm, while the spurs exceed 20 mm in most populations in the northern and eastern regions of South Africa. Spur length shows a clinal tendency and some populations in the eastern province cannot easily be assigned to one subspecies or the other.

### *Pollinator observations*

Solitary bees were observed to visit the short-spurred form of *S. hallackii* at Betty's Bay (Fig. 2A–D). *Xylocopa caffra* appeared to be the most important pollinator at this study site; 18 individuals carrying pollinaria were observed visiting the orchids. The mouthparts of *X. caffra* are *c.* 8 mm in length (Table 1). Although the functional flower depth in this population was *c.* 14 mm (Table 2), the bees partially insert their heads into the labellum chamber which enables them to reach most of the nectar in the spurs. Pollinaria were deposited on the frons and galea of the bees (Fig. 2C). Pollen massulae are brushed onto the stigma when the bee probes the flowers for nectar. Female bees alternated between visiting *Satyrium hallackii* for nectar
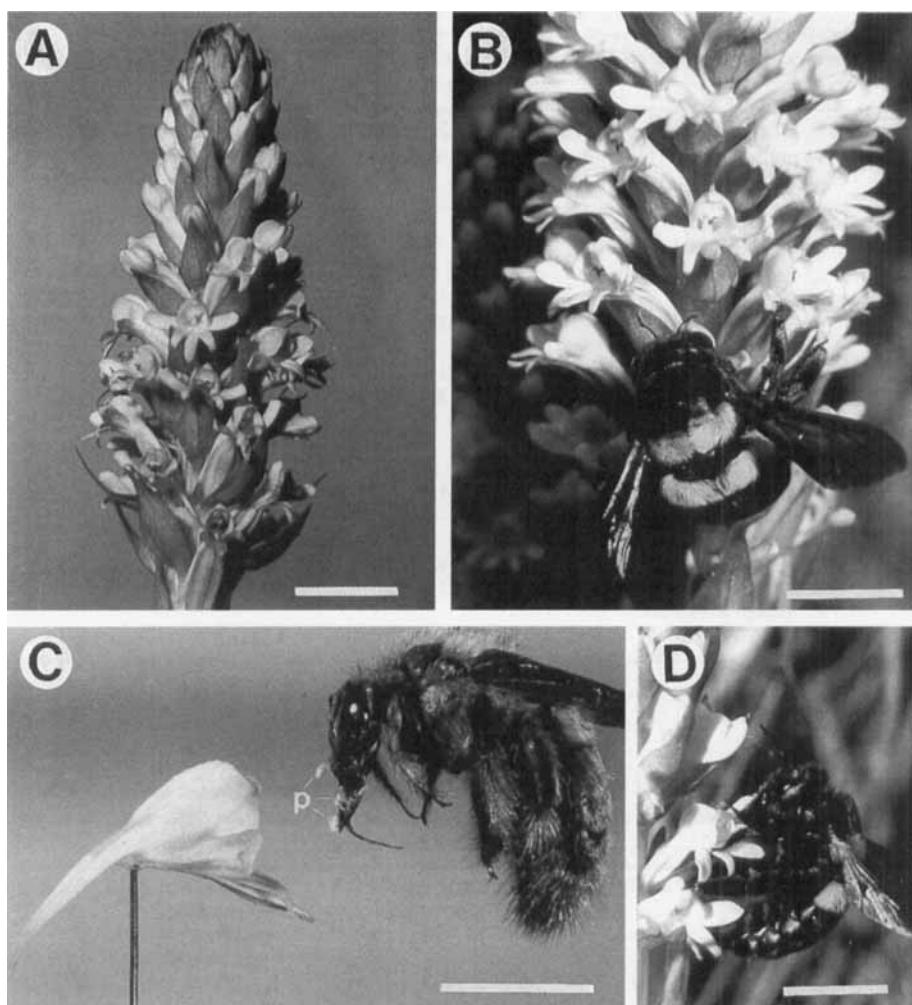
Figure 2A–D. A, inflorescence of *Satyrium hallacki* subsp. *hallackii* (short-spurred form). Scale bar = 20 mm. B, female carpenter bee *Xylocopa caffra* feeding on flowers of *S. hallackii* subsp. *hallackii*. Scale bar = 10 mm. C, male *X. caffra* positioned next to a flower of *S. hallackii* subsp. *hallackii*. Note the attachment of pollinaria (p). Scale bar = 10 mm. D, lateral view of female *X. caffra* feeding. Scale bar = 10 mm.

and buzz-pollinating the flowers of *Chironia jasminoides* (Gentianaceae) which grow intermingled with the orchid at this site. Male bees foraged solely on nectar from the orchids. Bees landed on the lower portion of the inflorescence of *S. hallacki* and foraged upwards, visiting several flowers before departing. One individual of the very large carpenter bee *Xylocopa capitata* was observed carrying two pollinaria. Smaller anthophorid bees (*Amegilla* sp.) also probed the flower for nectar, but most of the *c.*10 individuals observed did not carry pollinaria. On the other hand, allodopine bees, *Allodape panurgoides* Smith (Anthophoridae: Ceratinini), carried pollinaria despite their small size. No moths were observed at the study site during a warm evening.

The long-spurred form of *S. hallackii* at the Verloren Valei site was visited by large numbers of hawkmoths during late afternoon and evening (*c.* 16:00–19:00) (Fig. 3A,B). Examination of 12 captured hawkmoths, representing four species,

TABLE 1. Insects observed to pollinate *S. hallackii* at two localities. The long-spurred form (*S. hallacki* subsp. *ocellatum*) occurs at Verloren Valei and the short-spurred form (*S. hallackii* subsp. *hallackii*) occurs at Bettys Bay

| Study site | Observed pollinators | Individuals observed | Individuals captured | Mean number of pollinaria (range) | Proboscis length in mm (X ± SD) |
|---|---|---|---|---|---|
| Verloren Valei | LEPIDOPTERA Sphingidae *Basiothia schenki* (Möschler) | >20 | 5 | 6.0 (1–13) | 41.0 ± 0.6 |
| | *Hippotion celerio* (L.) | >20 | 3 | 8.0 (3–13) | 39.0 ± 1.2 |
| | *Nephele comma* (Fabricius) | 1 | 1 | 8.0 | 39.0 ± 0 |
| | *Agrius convulvuli* (L.) | >20 | 3 | 3.6 (2–7) | 89.0 ± 3.5 |
| | DIPTERA Nemestrinidae *Proseca ganglbauri* (Lichtwardt) | 1 | 1 | 5.0 | 33.0 ± 0 |
| Bettys Bay | HYMENOPTERA Anthophoridae *Xylocopa caffra* (L.) | 18 | 4 | 2.6 (2–4) | 8.2 ± 0.5 |
| | *X. capitata* Smith | 3 | 1 | 2.0 | 10.0 ± 0 |
| | *Allodape panurgoides* Smith | 7 | 7 | 3.5 (1–5) | 2.8 ± 0.4 |

TABLE 2. Floral characteristics of the two subspecies of *Satyrium hallackii*. Nectar sampling times were 12:00 (*S. hallackii* subsp. *hallackii*) and 16:00 (*S. hallackii* subsp. *ocellatum*). Asterisks indicate significant differences (*t*-test, two tailed)

| | Functional spur length (mm) | | Nectar volume in both spurs (µl) | | Sugar concentration (g.100 g$^{-1}$) | | Sugars (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{X} \pm SD$ | $n$ | $\bar{X} \pm SD$ | $n$ | $\bar{X} \pm SD$ | $n$ | Glu | Fru | Suc |
| *S. hallackii* subsp. *hallackii* | 13.6 ± 1.3 | 26 | 0.35 ± 0.1 | 26 | 23.1 ± 3.6 | 8 | 19 | 19 | 62 |
| *S. hallackii* subsp. *ocellatum* | 32.8 ± 3.6*** | 5 | 0.50 ± 0.3** | 23 | 18.9 ± 1.8* | 10 | 13 | 14 | 73 |

*$P<0.05$, **$P<0.01$, ***$P<0.001$.

showed that they carried an average of six pollinaria attached to the upper surface of the proboscis (Table 1, Fig. 3C). The spur length of the orchid at this site was *c.* 24.6 mm (Fig. 1), but the functional flower depth was *c.* 33 mm (Table 2). Most of the hawkmoths had medium length tongues (39–41 mm), but one of the moths, *Agrius convolvuli*, was an effective pollinator of the orchid even though its proboscis is more than twice the length of the orchid's spurs. A long-tongued fly, *Prosoeca ganglbauri* (Nemestrinidae), with a proboscis 33 mm in length also effectively pollinated the orchid at this site (Fig. 3D). Hawkmoth pollination of *S. hallackii* in the Verloren Valei Nature Reserve has also been regularly observed by G. van Eede (pers. comm.) during 1992 and 1994.
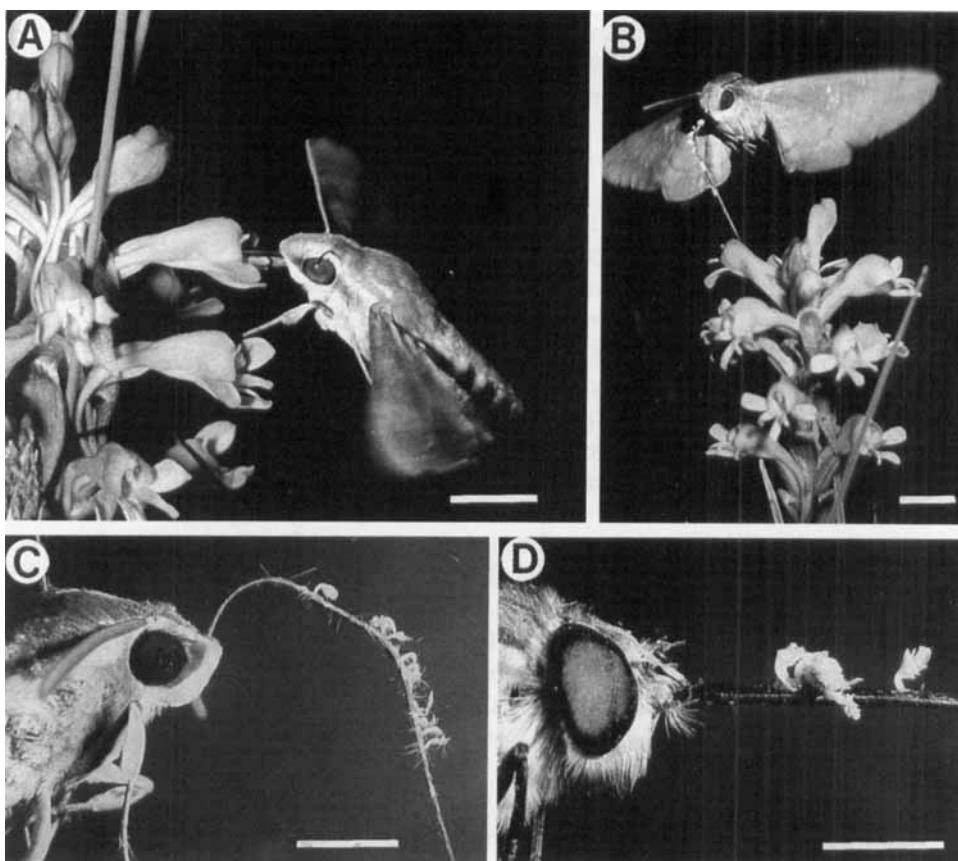
Figure 3A–D. A, hawkmoth *Nephele comma* feeding on the flowers of *Satyrium hallackii* subsp. *ocellatum* (long-spurred form). Scale bar = 10 mm. B, *N. comma* hovering over a flower of *S. hallackii* subsp. *ocellatum*. Note the large number of pollinaria attached to the proboscis. Scale bar = 10 mm. C, hawkmoth *Basiothia schenki*, with pollinaria of *S. hallackii* attached to the proboscis. Scale bar = 5 mm. D, long-tongued fly *Prosoeca ganglbauri* with pollinaria attached to the proboscis. Scale bar = 5 mm.

## Nectar

The standing crop of nectar in the spurs of *S. hallackii* subsp. *hallackii* at midday was only *c.* 0.4 µl with a sugar concentration of 23.1% (Table 2). The standing crop of nectar in the spurs of *S. hallackii* subsp. *ocellatum* was *c.* 0.5 µl with a sugar concentration of 18.9% (Table 2). The sugar composition differed slightly between the subspecies, with *S. hallackii* subsp. *ocellatum* having a slightly higher proportion of sucrose in the nectar (Table 2).

## Pollination success

At both study sites, the high levels of insect activity resulted in almost full pollination success. Of the 261 flowers examined on 12 plants of *S. hallackii* subsp. *hallackii*, every flower (100%) had one or more pollinaria removed and 259 flowers (99%) had pollen massulae on the stigma. Of the 112 flowers examined on 20 plants

of *S. hallackii* subsp. *ocellatum*, 98% had pollen massulae deposited on the stigma and also had one or both of the pollinaria removed. Thus both male and female function of flowers in the study populations did not appear to be limited by pollinators.

DISCUSSION

This study clearly shows the existence of distinct bee- and hawkmoth-pollination ecotypes within the South African populations of *S. hallackii*. Very long-spurred forms of *S. hallackii* in Zimbabwe may represent yet a third ecotype pollinated by very long-tongued hawkmoths (S. D. Johnson, unpublished data).

Pollination ecotypes of *S. hallackii* in South Africa can be attributed to differences in the distribution of hawkmoths and carpenter bees. Hawkmoths are relatively abundant in the grasslands where the long-spurred populations of *S. hallackii* occur. Many grassland orchids are adapted to pollination by hawkmoths (Johnson, 1995). On the other hand, hawkmoths are rare in the Cape region, presumably because plant families such as Apocynaceae, Convolvulaceae and Rubiaceae, which contain many of the host-plants for African hawkmoth larvae, are not well represented in the Cape flora (Bond & Goldblatt, 1984). In addition, Cape fynbos plants generally have sclerophyllous and nutrient-poor leaves which discourage feeding by lepidopteran larvae (Johnson, 1992). Only one Cape orchid, a forest species, is known to be pollinated by hawkmoths (Johnson & Liltved, in press).

In contrast to hawkmoths, carpenter bees are relatively scarce in grassland habitats, apparently because the lack of woody shrubs poses severe limitations on the availability of nesting sites (Watmough, 1974). However, these bees are plentiful in the Cape region where they commonly nest in the stems of dead *Protea* shrubs (Watmough, 1974). Carpenter bees are responsible for the pollination of many Cape plants, including several orchid species (cf. Johnson, 1993).

It seems plausible, therefore, that floral differentiation in *S. hallackii* occurred in response to unequal geographic distribution of its pollinators; this is what Grant & Grant (1965) referred to as changes in the 'pollination climate'. In the absence of a phylogeny for *Satyrium* it is difficult to know whether bee or hawkmoth pollination is more recently derived in *S. hallackii*. If we assume, for example, that the ancestor of today's *S. hallackii* was short-spurred and bee-pollinated, then the following sequence of events can be envisaged: (1) short-spurred populations in the grasslands were bee-pollinated, but also received occasional visits by hawkmoths which are more abundant in the grasslands; (2) selection favoured individuals with relatively long spurs because they were more effectively pollinated by hawkmoths (cf. Nilsson, 1988).

It would have been of great interest to investigate populations along the coastline which have spurs of an intermediate length (Fig. 1). Unfortunately, the few intermediate populations represented by herbarium specimens appear to have been eliminated by development. Coastal habitats have been rapidly transformed and even the Bettys Bay study population, which may be the last remnant of the short-spurred form, is on land zoned for housing.

Other putative examples of both bee- and hawkmoth-pollinated ecotypes evolving in a single species include *Capparis spinosa* (Capparaceae) (Eisikowitch, Ivri & Dafni, 1986), *Calyophus hartwegii* (Onagraceae) (Towner, 1977) and *Aquilegia caerulea* (Ranunculaceae) (Miller, 1981). Although both hawkmoths and bumblebees visit *Aquilegia*

*caerulea* in North America, Miller (1981) argued that geographical variation in this species was associated more with shifts between different hawkmoth species and that bumblebees act only as secondary pollinators.

One factor which may have facilitated the shift from bee to hawkmoth pollination in *S. hallackii* is the light pink colour of the flowers which is attractive to both bees and hawkmoths. Carpenter bees in the coastal fynbos frequently visit pink flowers (Johnson, 1992) and hawkmoth pollination of pink flowers is known in other African orchids e.g. *Cynorkis uniflora* in Madagascar (Nilsson *et al.*, 1992). The long-tongued fly *Prosoeca ganglbauri* which pollinated *S. hallackii* in the grasslands is also known to be attracted to pink flowers (Johnson & Steiner, 1995). The lack of a discernable scent in the long-spurred form of *S. hallackii* may indicate that hawkmoth pollination is not fully developed in this species or that long-tongued flies (which are not known to respond to scent) have been important in the floral evolution of the long-spurred form.

The volume and concentration of nectar does not seem to have been markedly affected by the shift in pollinators (Table 2). The slightly lower concentration of nectar in the hawkmoth-pollinated form is consistent with the prediction that flowers pollinated by long-tongued lepidoptera should have relatively dilute nectar (Kingsolver & Daniel, 1979). Sucrose-rich nectar, as found in both subspecies of *S. hallackii*, is typical of hawkmoth-adapted flowers as well as many flowers pollinated by long-tongued bees (Kevan & Baker, 1983).

## Ecotypes and systematics

Ecotypes are morphologically and genetically distinctive forms adapted to local environments (Turreson, 1922). Among systematists, pollination ecotypes are usually treated as geographical races (cf. Grant & Grant, 1965), or, more formally, as subspecies or closely related species. There has been a tendency to regard ecotypes and geographical races as incipient species which do not yet have the isolating mechanisms required for full speciation (cf. Grant & Grant, 1965; Pellmyr, 1986). However, the notion that species are formed by the evolution of isolating mechanisms is losing favour, and decisions about the taxonomic status of ecotypes and geographical races are increasingly being based solely on the criterion of diagnosibility (Cracraft, 1989; Baum, 1992).

The degree of differentiation required for full species status of taxa may, ultimately, be a question of taxonomic preference, rather than biological reality. The two forms of *Satyrium hallackii* could be regarded either as full species (as they were earlier this century) or as subspecies (current taxonomy). Clearly, however, diagnosable taxa may result when adaptation to different pollinators leads to the differentiation of plant characters.

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