

Hyper-specialization for long-billed bird pollination in a guild of South African plants: the Malachite Sunbird pollination syndrome

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Received 30 March 2009; received in revised form 30 July 2009; accepted 3 August 2009

Abstract

A large diversity of floral morphological types exists within the bird pollination syndrome in the Cape Floral Region of South Africa. Here we focus on species with tubular flowers and ask: “Do differences in tube length among plant species correspond to differences in bill length among the birds that serve as pollinators?” To answer this question, we observed 1669 bird–plant interactions at thirteen bird-pollinated plant species across a spectrum of tube lengths. Only three nectar feeding bird species pollinated the focal plant species. The relatively short-billed species were the Southern Double-collared Sunbird (*Cinnyris chalybea*) and Orange-breasted Sunbird (*Anthobaphes violacea*); the only long-billed species was the Malachite Sunbird (*Nectarinia famosa*). We found that the groups of plant species pollinated by the long- and short-billed birds differed significantly in floral tube length. Short-billed sunbirds nevertheless often robbed long-tubed flowers by piercing the corolla, and there was a significant difference in floral tube length among those species that were robbed, and those that were pollinated by short-billed sunbirds. The presence of territorial Malachite Sunbirds depressed robbing rates by short-billed sunbirds at long-tubed flowers. In turn, the absence of Malachite Sunbirds from short-tubed plant species might be explained by the observed positive correlation between tube length and nectar volume. Together, these data suggest that there is a subset of the bird-pollinated plants at the Cape that are pollinated solely by the long-billed Malachite Sunbird, a pollination service irreplaceable by the more abundant, short-billed sunbird species. To extrapolate this finding to a greater subset of species in the Cape Floral Region, we measured flowers on herbarium specimens of all tubular putatively bird-pollinated plants. We find that floral tube length has a bimodal distribution with 37 Cape species potentially dependent on pollination by Malachite Sunbirds.

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Keywords: Floral tube length; Long-billed bird pollination; Malachite Sunbird; *Nectarinia famosa*; Nectar robbing; Nectar sugar

1. Introduction

The adaptations of organisms, in particular those of plants and their animal pollinators, are well known. Some of the clearest examples are displayed by flowers adapted to specialist nectar feeding birds. These are typically robust, reddish in colour, have large volumes of dilute nectar and lack scent (Van der Pijl, 1961). This set of traits – the bird pollination syndrome – has arisen independently in multiple plant lineages (Faegri and Van der Pijl, 1979). In the Cape Floral Region of South Africa, for example, the bird pollination syndrome occurs in families as diverse as the Apocynaceae, Orchidaceae, Penaeaceae and Retziaceae (Vogel, 1954; Rebelo, 1987).

Despite obvious similarities, plants that are pollinated by birds display a wide range of morphological types. Much of this diversity can be interpreted as adaptations for placing pollen on different parts of the foraging birds. Plant species are adapted for placing pollen on the tongue, bill, crown, throat, or feet of birds and each requires a different floral morphology to do so (Johnson, 1996; Pauw, 1998; Johnson and Brown, 2004; Wester and Claßen-Bockhoff, 2006; Botes et al., 2008). Amongst these, pollen placement on the head feathers (crown or throat) is numerically dominant.

Inflorescence architecture contributes an additional dimension to the diversity within the bird pollination syndrome. Rebelo (1987) classified bird-pollinated Cape plants as brushes (congested inflorescences of multiple small flowers) or tubes (lax inflorescences of single tubular flowers). The brush type is typical of the Proteaceae, while tubular flowers are typical in the Iridaceae and Amaryllidaceae, among others. Birds insert the

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entire bill into tubular type flowers and the pollen is most often deposited on the head feathers (Goldblatt and Manning, 2006).

Here we investigate floral diversity in response to birds with different bill lengths. This topic has received much attention in the New World, where three clear morphological subgroups have been identified: plants adapted for pollination by hermit hummingbirds (subfamily Phaethorninae), plants adapted for pollination by non-hermit hummingbirds (subfamily Trochilinae), and plants adapted for generalist perching birds. Hermit hummingbirds have comparatively long, decurved beaks; non-hermit hummingbirds have straight, short beaks; and generalist perching birds have very short broad beaks. Plants adapted for pollination by each of these functional groups of birds have floral tubes of appropriate length (Snow and Snow, 1972; Kress, 1985; Westerkamp, 1990). Recognition of these functionally different subgroups among bird-pollinated plants of the New World has proved important in addressing questions of coexistence (Snow and Snow, 1972; Feinsinger, 1978), diversification (Temeles and Kress, 2003; Nattero and Cocucci, 2007) and the conservation of New World bird-pollinated plants (Lindberg and Olesen, 2001).

Surprisingly similar studies have not been conducted in the Cape Floral Region of South Africa, where bird-pollinated plants constitute about 4% (or 318 species) of the flora. Congruence between sunbird bills and perianth tube length however has been mentioned before (Rebelo and Siegfried, 1985; Goldblatt and Manning, 2006). Bird-pollinated members of the Proteaceae and Ericaceae typically dominate late successional Fynbos vegetation (Van Wilgen, 1981; Le Maitre and Midgley, 1992), while bird-pollinated Iridaceae, Orchidaceae and Amaryllidaceae are sometimes prominent members of the ephemeral assemblage flowering after a fire (pers. obs.). Clear examples of floral adaptation in response to birds with different lengths of bills might be expected in the Cape Floral Region because there is a wide range of bill lengths among the specialist nectar feeders. There are three bill groups: (1) A long narrow curved billed group consisting of Cape Sugarbirds *Promerops cafer*, and Malachite Sunbirds *Nectarinia famosa* (29–36 mm); (2) A short narrow curved billed group consisting of Southern Double-collared Sunbirds *Cinnyris chalybea* (18–23 mm), and Orange-breasted Sunbirds *Anthobaphes violacea* (20–23 mm); (3) Generalist nectar feeders with broad uncurved beaks such as Cape Weavers *Ploceus capensis*, and Cape White-eyes *Zosterops virens* (12–15 mm) (Table 1). From an ornithophilous plant perspective each of these bird groups, determined by bill length, potentially represent unique clades that may in turn co-evolve with floral tube length.

To test our hypothesis that bird-pollinated plants show an evolutionary response to bill length diversity, we focus specifically on plants with tubular rather than brush-type blossoms, and ask firstly whether differences in tube length among plant species correspond to differences in bill length among the birds that serve as pollinators. Secondly, we examine the underlying mechanism resulting in observed patterns of bird-plant association by testing for a relationship between flower tube length and nectar volume, and by investigating the effect of competitive interactions (pecking order) on the structure of the

Table 1

Morphometrics of nectar feeding birds observed during this study according to Rebelo (1987).

Bird species	Culmen length (mm)	Total length of mouthparts (mm) ^a	Mass (g) (male)
Cape White-eye	12–15		10.9 (unsexed)
Southern Double-collared Sunbird	18–23	27–34.5	6–10
Orange-breasted Sunbird	20–23	30–34.5	9–11
Malachite Sunbird	29–34	43.5–51	15–21
Cape Sugarbird	30–36	45–54	34–40

The distance sunbirds can protrude their tongue has not been measured (Schlamowitz et al., 1976) but is about half the culmen length (pers. obs.).

^a Culmen plus length of exerted tongue.

nectar feeding bird community. Lastly, we expand the analysis of tube length variation by measuring tube lengths in herbarium specimens of a wide range of bird-pollinated species with tubular flowers.

2. Methods

2.1. Study sites and species

We conducted field studies during March to September 2006 at 18 different localities within the Western Cape, South Africa (Appendix A). At these sites, only species with tubular flowers were selected. The study species included: *Salvia africana-lutea* L., *Erica perspicua* J.C.Wendl., *Erica cruenta* Sol., *Erica speciosa* Andrews, *Chasmanthe aethiopica* (L.) N.E.Br., *Pelargonium fulgidum* (L.) L'Hér., *Brunsvigia josephinae* (Redouté) Ker Gawl., *Watsonia aletroides* (Burm.f.) Ker Gawl., *Chasmanthe floribunda* (Salisb.) N.E.Br., *Babiana thunbergii* Ker Gawl., *Watsonia meriana* (L.) Mill., *Babiana ringens* Ker Gawl. and *Watsonia fourcadei* J.W.Mathews & L. Bolus.

2.2. Floral measurements

Flowers ($n=10$) were measured in the field using a steel ruler. Tube length was measured as distance between the top of the ovary (where the nectary is typically located) and where the petals separate. In some species there is a distinct thinner basal part of the tube, and a rapidly expanding distal part, these were measured separately and added.

2.3. Flower visitation

During observation, two positions were taken (a) close to the flowers (~4 m) for detailed observations of flower visitor's behaviour, and (b) further away (~10 m) to observe all flower visitors. A close focusing 8×40 pair of binoculars was used. Observations were recorded with a Dictaphone and later transcribed. Inclement weather was avoided and observations were done in the morning as peak of foraging generally occurs at dawn (Stiles, 1978). During observations all flower visitors and their contact with anthers and/or stigma were recorded.

When no contact occurred with the reproductive parts of the flower, i.e. nectar robbing or nectar theft, an illegitimate visit was recorded. A *t*-test was used to test for differences in floral tube length between species pollinated by long-billed and short-billed functional groups.

2.4. Nectar robbing

Robbers make characteristic holes in the base of the flower tube. Robbing rate was recorded as percentage of punctured flowers in a random sample of flowers at Malachite Sunbird absent and present sites (Appendix B). Sites where Malachite Sunbirds were recorded visiting flowers were referred to as "present sites" while sites where Malachite Sunbirds were not heard or seen were referred to as "absent sites".

2.5. Nectar volume and concentration

To test the prediction that the longer billed group has higher energy requirements, nectar standing crop was extracted in the field using either a 5 μ l or a 40 μ l capillary tube (Drummond Scientific Company, Broomall, Pennsylvania, USA). Nectar concentrations were determined with a 0–50% field handheld refractometer (Bellingham and Stanley, Tunbridge Wells, UK). Robbed and damaged flowers contain less nectar and were avoided. At least 10 flowers were sampled per species, except in small populations with high robbing rates. Amount of sugar per flower (in mg) was calculated from these measurements.

2.6. Herbarium measurements

In order to extrapolate the conclusions to a greater subset of species we measured all usable tubular putatively bird-pollinated plants of additional species (from the Cape Floral Region) in the Compton Herbarium, Kirstenbosch. Tube length distribution was tested for normality using Shapiro–Wilk's *W*-test and for bimodality using the methods outlined by Lafuma et al. (2003) where if the coefficient of bimodality (*b*) is greater than 0.55, frequency distributions are taken to be bimodal (Lafuma et al., 2003). All analyses were conducted using STATISTICA 8 (StatSoft, Inc. 2008, Tulsa, USA).

3. Results

3.1. Floral measurements and flower visitation

During 34.5 h of field observations a total of 1669 bird–plant interactions were observed. Malachite Sunbirds, Southern Double-collared Sunbirds, Orange-breasted Sunbirds and Cape White-eyes were observed visiting flowers. Although Sugarbirds were observed in the general area of some study sites, they did not visit the study species. This resulted in the Malachite Sunbird being the only representative of the long-billed functional group.

Floral tube length of the observed plant species varied from 14.2 mm to 48.3 mm. Seven species were observed to be

pollinated only by Malachite Sunbirds; four species were pollinated only by the short-billed functional group consisting of Southern Double-collared Sunbirds and Orange-breasted Sunbirds; and the remaining two species were pollinated by both Malachite Sunbirds and short-billed sunbirds. Tube length differed significantly between the long and short-billed pollinated plants (*t*-test, *df*=13 *t*=−4.8 *p*<0.005) (long-billed pollinated plants range, 6–34 mm; short-billed pollinated plants range 35–58 mm) (Fig. 1). During legitimate visits sunbirds grasp the stem below the flower and insert the entire bill into the tube. The stigma and anther touch the crown feathers (Fig. 6a,c,i), or in the case of the two *Babiana* species the feathers on the throat.

Non-bird visitors observed during the observation periods consisted only of *Apis mellifera*, which were observed at *W. fourcadei* (taking nectar but not touching the reproductive parts) and at *C. floribunda* (collecting pollen).

3.2. Nectar robbing

Visits by Malachite Sunbirds to all species were legitimate except to *Watsonia fourcadei*, where in 49% of the visits, holes made by Cape White-eyes (Fig. 6f) were utilized in what is known as secondary robbing (Inouye, 1980) (Fig. 6h). All visits to the focal species by Cape White-eyes were illegitimate (Appendix B). Among the 11 plant species visited by the short-billed sunbirds (Southern Double-collared and Orange-breasted Sunbirds), five were legitimate (Fig. 6j) and six were illegitimate (Fig. 6b,d). In five of these cases the birds robbed nectar by piercing a small hole in the base of the corolla at the level of the nectar (Fig. 6e,g). In the remaining species, the relatively short-tubed *Salvia africana-lutea*, the birds occasionally thieved nectar (*sensu* Inouye, 1980) by entering the flower tube at an angle and circumventing the overarching anthers and stigma. There were clear differences in floral tube length among those species that were robbed, and those that were pollinated

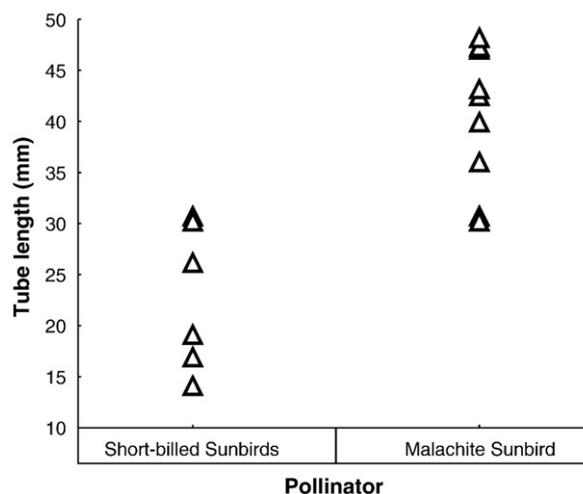


Fig. 1. Legitimate visits by short-billed sunbirds and the long-billed sunbird (Malachite Sunbird) to the range of tube lengths.

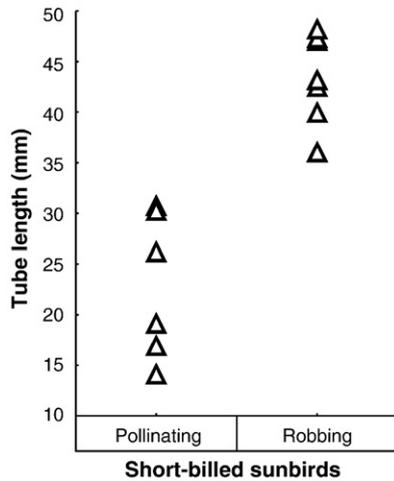


Fig. 2. Legitimate and illegitimate (robbing) visits by short-billed sunbirds at the range of flower tube lengths.

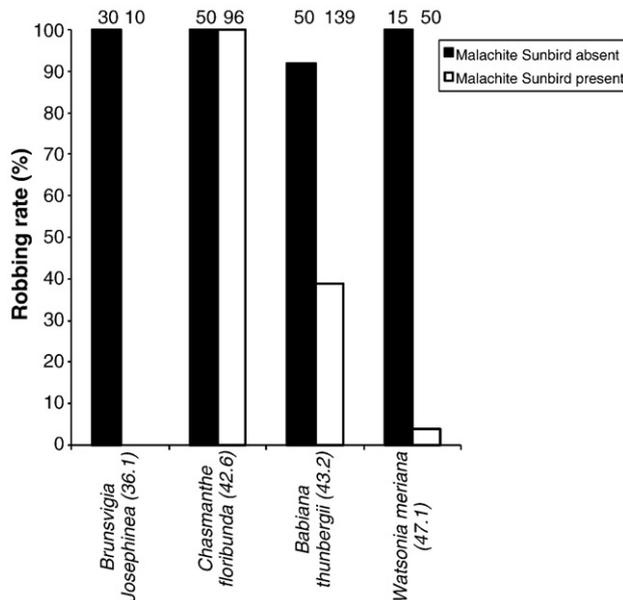


Fig. 3. Percentage (%) of flowers in population with damage to the corolla tube indicating robbing by smaller sunbirds or/and Cape White-eyes (*Zosterops virens*) in the absence (closed bars) and presence (open bars) of Malachite Sunbirds (*N. famosa*) (sites in Appendix A). Present sites involved Malachite Sunbirds were observed visiting flowers, while absent involved no visual or auditory Malachite Sunbird records. Numbers above bars indicate number of flowers checked for robbing. Tube lengths (mm) in brackets.

by short-billed sunbirds (t -test, $df=13$ $t=-6.1$ $p<0.005$) (Fig. 2). Species that were robbed by shorter-billed sunbirds were often also robbed by Cape White-eyes.

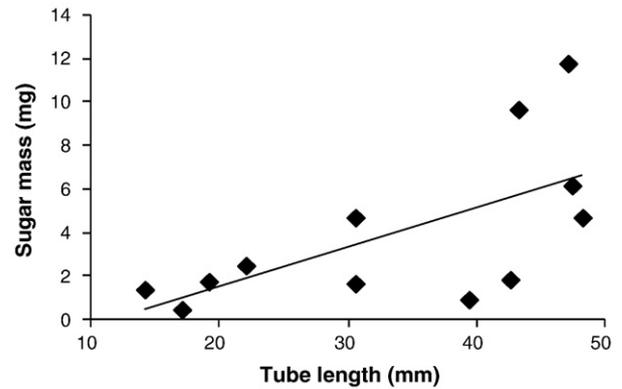


Fig. 4. Correlation between tube length and energy available (mg sugar) in bird-pollinated plants in the Cape Floristic Region ($r^2=0.41$ $F_{(1, 10)}=6.95$ $p<0.025$) (no data for *B. josephinae*).

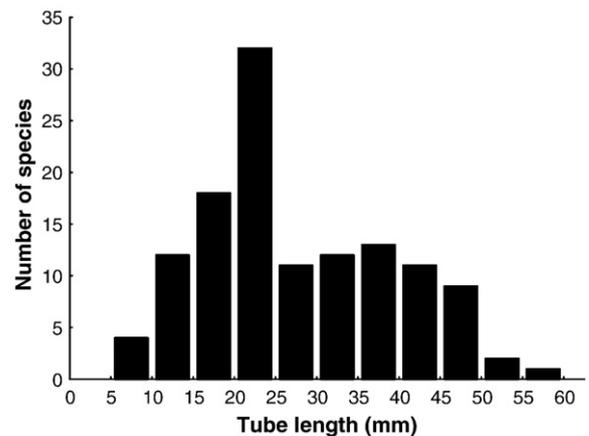


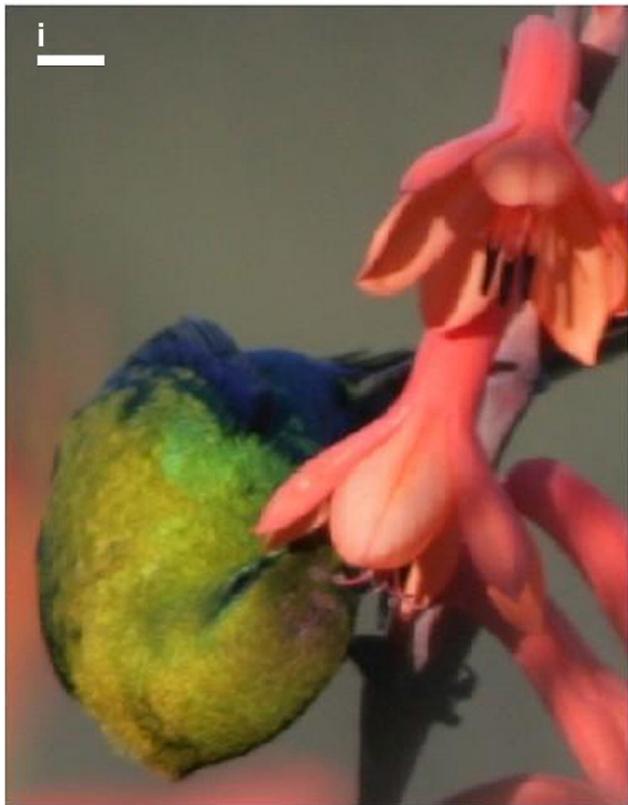
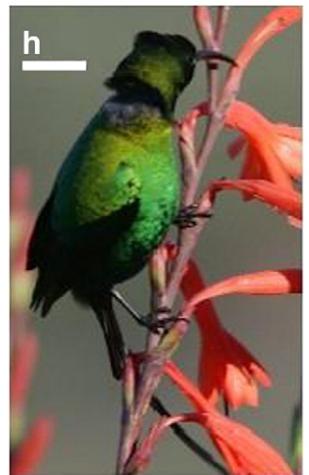
Fig. 5. A bimodal distribution of tube lengths (field and herbarium specimens included) of tubular bird-pollinated plants in the Cape Floristic Region ($n=125$).

In populations of long-tubed plants a high percentage of robbing by small sunbirds was common, but varied greatly among populations and apparently depended on whether Malachite Sunbirds were present. Malachite Sunbirds were often observed to actively defend territories of long-tubed nectar plants against entry by smaller sunbird species. In three of the four plant species examined (with Malachite Sunbird absent and present populations) Malachite Sunbirds depressed robbing rates. The exception being the very extensive *C. floribunda* population (Fig. 3).

3.3. Nectar sugar amount and concentration

Long-tubed flowered species have significantly more sugar (mg) per flower than short-tubed species ($r^2=0.41$, $F_{(1, 10)}=6.95$,

Fig. 6. Long-tubed flowers are pollinated solely by the only long-billed sunbird, the Malachite Sunbird (*Nectarinia famosa*) and robbed by short-billed sunbirds. (a) The sole pollinator of *Brunsvigia josephinae* the Malachite Sunbird. Scale bar=1.5 cm; (b) A small sunbird, the Southern Double-collared Sunbird (*Cinnyris chalybea*) robbing the long-tubed *B. josephinae*. Scale bar=2 cm; (c) The long-tubed *Chasmanthe floribunda* (tube length=43 mm) is pollinated by Malachite Sunbird. Scale bar=1 cm; (d) Southern Double-collared Sunbird piercing a long-tubed *C. floribunda* flower. Scale bar=1 cm; (e) Small sunbirds rob these flowers by making a small slit. Scale bar=0.25 cm; (f) Cape White-eyes rob these flowers by making a hole and after a few visits the flower is destroyed. Scale bar=0.5 cm; (g) A hole in a *B. josephinae* flower made by Southern Double-collared Sunbird. Scale bar=1 cm; (h) Malachite Sunbird using the hole made by robbing Cape White-eyes in a *Watsonia fourcadei* flower. Scale bar=2 cm; (i) Malachite Sunbird touching the anthers with the feathers on top of the head. Scale bar=1 cm; (j) Southern Double-collared Sunbird pollinating *Erica versicolor*. Scale bar=1 cm. Photos S. Geerts.



$p < 0.05$) (Fig. 4), with no difference in nectar concentration ($r^2 = 0.007$, $F_{(1, 10)} = 0.068$, $p = 0.80$).

3.4. Herbarium measurements

To extrapolate our findings to a greater subset of species within the Cape Floristic Region we measured floral tube lengths in the herbarium ($n = 107$ species) and also included additional field measurements ($n = 18$ species). In our sample, 46 of the 88 short-tubed species belonged to the genus *Erica*. A non-normal distribution pattern is obtained (Shapiro–Wilk's W -test $W = 0.96$, $p < 0.01$.) which is almost bimodal ($b = 0.51$) (Fig. 5). The putatively Malachite Sunbird-pollinated group contained 37 species.

4. Discussion

Based on the data presented here, a large group of Cape plants with long, tubular flowers are apparently adapted for pollination only by the Malachite Sunbird *Nectarinia famosa* (Figs. 1 and 5). Short-billed birds can access the nectar of these species only by piercing a hole in the base of the corolla tube (Figs. 2 and 6b,d). Southern Double-collared Sunbirds are known to regularly pierce gladioli and other South African plants with long corollas (Skead, 1967; Fry, 2000), a behaviour similar to many shorter-billed hummingbirds (Lara and Ornelas, 2001).

The Cape Sugarbird *Promerops cafer* has a bill as long as that of the Malachite Sunbird. Its apparent absence during our observation periods might be partly explained by the difference in habitat preference between Malachite Sunbirds and Cape Sugarbirds (Rebelo, 1987). Cape Sugarbirds are very closely tied to dense stands of large Proteaceae shrubs that dominate the plant community in late stages of post-fire succession (Rebelo et al., 1984). Malachite sunbirds often visit Proteaceae (Rebelo, 1987; Hargreaves et al., 2004), but also move into more open vegetation tracking abundant nectar sources (Geerts and Pauw, 2009), this includes recently burnt areas with few or no flowering Proteaceae (pers. obs.). It is precisely in these more open habitats that the long-tubed bird-pollinated monocots (Iridaceae and Amaryllidaceae) flower most prolifically. It is likely that larger body size and hence energy requirements of the Cape Sugarbird necessitates a closer link with the brush-type, nectar rich Proteaceae inflorescences. Anecdotal sightings of sugarbirds on Iridaceae however do exist but were not observed in this study (Skead, 1967).

The small Southern Double-collared Sunbirds are more abundant than Malachite Sunbirds (pers. obs.), and the two species overlap almost entirely in habitat choice in the Cape Region (Hockey et al., 2005). Why then, have a large number of tubular plants specialized towards a less abundant sunbird species? Competitive interactions among nectarivores are part of the explanation for this pattern. Malachite Sunbirds set up fiercely defended territories at dense stands of long-tubed nectar plants (Skead, 1967). Their ability to competitively exclude smaller sunbirds is clearly illustrated by a

decline in robbing rate (the fraction of flowers damaged by short-billed sunbirds) that occurs when Malachite Sunbirds are present (Fig. 3). It is likely that morphological specialization for pollination by Malachite Sunbirds will be selected for if other sunbirds are normally excluded from flowering populations by competitive interactions. With different pollinators varying in effectiveness, specialization for one often implies exclusion of others (Faegri and Van der Pijl, 1979).

The inverse of this pattern is detected in short-tube flowers. Apparently the long bills of Malachite Sunbirds allow access to nectar in short-tubed flowers. However, in accordance with Goldblatt et al. (1999) and similar to hummingbird systems (Kaczorowski et al., 2005), short-tubed flowers in our sample contained on average less nectar than long-tubed flowers (Fig. 4). For this simple reason we propose that short-tubed flowers are unattractive to the relatively large-bodied Malachite Sunbird, while being sufficient for smaller sunbirds. In comparison the long-billed and generally larger Hermit hummingbirds of the New World also visit the long-tubed flowers containing higher nectar volumes (Stiles, 1975).

The demonstration of fine level specialization among bird-pollinated plants of the Cape has both ecological and evolutionary implications. Although in the South-Western Cape there is a discontinuous pattern between long and short-billed birds (Table 1), further eastward more of a continuum may be observed as various other sunbird species are present. Malachite Sunbirds apparently fulfil an important ecological role as the sole pollinators of several Cape plants, including many showy and rare species such as *Brunsvigia litoralis* and *Cyrtanthus carneus*. Many of these species, including some of the ornithophilous gladioli (Goldblatt et al., 2001), are self-incompatible and therefore completely reproductively reliant on Malachite Sunbirds for pollen transfer. Malachite Sunbirds are more sensitive to landscape transformation and fragmentation than the ubiquitous short-billed Southern Double-collared Sunbird (Pauw, 2004). However, this study shows that smaller species are unable to replace the lost pollination services provided by Malachite Sunbirds.

Repeated shifts from insect to bird pollination are thought to be one of the drivers of plant speciation at the Cape (Goldblatt et al., 1999). From an evolutionary perspective, the results of this study suggest that finer resolution shifts between different bird species might generate additional diversity within bird-pollinated lineages. Occurrence of both short- and long-tubed bird flowers in genera such as *Brunsvigia* and *Chasmanthe* supports this view.

Acknowledgements

We are grateful to Ruan Veldtman for assistance with statistics, Rosanne Stanway and two anonymous reviewers for comments, Dawid Woodton for locating *B. josephinae* and the Lategan's for allowing fieldwork on their farm. This work was funded by Stellenbosch University and the NRF (South Africa).

Appendix A. Study species and localities

Study species	Locality	GPS location
<i>Salvia africana-lutea</i> L.	Rondevlei Nature reserve	S33 13.061 E18 08.114
<i>Erica perspicua</i> J.C.Wendl.	Between Kleinmond and Betty's bay	S34 20.503 E18 58.880
<i>Erica cruenta</i> Sol.	Kirstenbosch Botanical garden	
<i>Erica speciosa</i> Andrews	Harold Porter Botanical garden	
<i>Chasmanthe aethiopica</i> (L.) N.E.Br.	Red-Hill	S34 12.113 E18 24.233
	Wolwegat nature reserve	S34 04.269 E18 37.992
<i>Pelargonium fulgidum</i> (L.) L'Hér.	West-Coast National Park	S33 10.416 E18 03.525
<i>Brunsvigia josephinae</i> (Redouté) Ker Gawl	Worcester Botanical garden	
	Worcester Audenberg Ridge	S33 34.629 E19 27.493
<i>Watsonia aletroides</i> (Burm.f.) Ker Gawl.	Two sites along R316	S34 21.424 E19 40.009
<i>Chasmanthe floribunda</i> (Salisb.) N.E.Br.	Red-Hill	S34 12.113 E18 24.233
	Kirstenbosch Botanical garden	
<i>Babiana thunbergii</i> Ker Gawl.	Two sites along shore line at Elands Bay	S32 18.973 E18 19.918
	Muiskerm	
<i>Watsonia meriana</i> (L.) Mill.	Opposite Spier wine farm	S33 59.095 E18 46.442
	Rondevlei nature reserve	
<i>Babiana ringens</i> Ker Gawl.	Fields along Mamre road	S33 32.490 E18 24.693
<i>Watsonia fourcadei</i> J.W.Mathews & L.Bolus	Romansrivier	S33 28.241 E19 13.405

Appendix B. Observation time, tube length and percentage of legitimate visits by floral visitors

Study species	Tube length (mm)	Observed (min)	Flower visitors	Legitimate visits	Illegitimate visits	% Legitimate visits
<i>Salvia africana-lutea</i>	14.2	60	<i>C. chalybea</i>	11	18	38
<i>Erica perspicua</i>	17.0	20	<i>A. violacea</i>	30	0	100
<i>Erica cruenta</i>	19.2	60	<i>C. chalybea</i>	11	0	100
<i>Erica speciosa</i>	26.3	110	<i>C. chalybea</i>	16	0	100
<i>Chasmanthe aethiopica</i>	30.6	30	<i>N. famosa</i>	23	0	100
		10	<i>C. chalybea</i>	41	0	100
<i>Pelargonium fulgidum</i>	30.6	30	<i>N. famosa</i>	0	7	0
			<i>C. chalybea</i>	12	0	100
<i>Brunsvigia josephinae</i>	36.1	160	<i>N. famosa</i>	24	0	100
			<i>C. chalybea</i>	0	192	0
<i>Watsonia aletroides</i>	39.4	24	<i>N. famosa</i>	2	0	100
			<i>C. chalybea</i>	0	125	0
<i>Chasmanthe floribunda</i>	42.6	756	<i>N. famosa</i>	77	0	100
			<i>A. violacea</i>	33	111	23
			<i>Z. virens</i>	0	66	0
			<i>C. chalybea</i>	0	415	0
<i>Babiana thunbergii</i>	43.2	305	<i>N. famosa</i>	40	0	100
			<i>C. chalybea</i>	0	140	0
<i>Watsonia meriana</i>	47.1	240	<i>N. famosa</i>	32	0	100
			<i>Z. virens</i>	0	32	0
			<i>C. chalybea</i>	0	36	0
<i>Babiana ringens</i> ^a	47.4	56 h	<i>N. famosa</i>	59	0	100
<i>Watsonia fourcadei</i>	48.3	265	<i>N. famosa</i>	53	50	51
			<i>Z. virens</i>	0	13	0

^a Observational data on *B. ringens* was provided by B. Anderson.

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