Nectar intake and foraging efficiency: the responses of sunbirds to flower morphology

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Abstract

Floral traits vary greatly between plant species, and determine which pollinators are physically capable of accessing floral rewards and carrying out effective pollination. Research on the responses of nectarivorous birds to different flower morphologies has been largely restricted to hummingbirds, while other flower specialists, the sunbirds and honeyeaters, remain relatively unstudied. We investigated how flower morphology influences the foraging behaviour of White-bellied Sunbirds, *Cinnyris talatala*. Using artificial flowers made of clear PVC tubing and filled with 20% w/w sucrose solution, we measured maximum extraction depths of sunbirds foraging at 3 mm and 5 mm wide flowers at both upward and downward orientations. Flower width, but not orientation, strongly influenced maximum extraction depth, with the birds probing deeper at wider flowers. Foraging bout dynamics were tested at these two diameters and at two corolla lengths, 14 mm and 27 mm; birds fed faster at wider and at shorter flowers, when length and diameter were tested separately. In combination treatments, sunbirds fed fastest at the short and narrow flowers where the fixed volume of nectar was easier to reach. When given a choice between two floral lengths or two floral diameters, birds preferred short flowers, with diameter having no effect. Floral length appears to be more important than width in determining sunbird foraging behaviour, and White-bellied Sunbirds should be effective pollinators of short tubular flowers. The lack of effect of orientation is perhaps surprising when many sunbird-pollinated plants have downward-facing flowers.

Keywords: foraging choices; nectar; sunbird; flower morphology; corolla length; corolla width

Introduction

The mutualistic relationship between nectarivorous birds and plants depends on the birds providing pollination services while obtaining most of their energy requirements from nectar (Brown and Kodric-Brown 1979; Stiles 1978). Due to the relatively large size of their pollinators, bird-pollinated plants invest more energy into nectar production than do insect-pollinated plants, often producing large flowers and copious amounts of nectar (Stiles 1978; Cronk and Ojeda 2008; Johnson and Nicolson 2008). To ensure that the energy investments are repaid in terms of successful pollination, plants use floral traits such as size, shape, colour and nectar properties to screen out unwanted floral visitors and ineffective pollinators while at the same time increasing pollen transfer by effective pollinators (Campbell et al. 1996; Hargeaves et al. 2012; Santamaría and Rodríguez-Gironés 2015). Floral traits vary widely among species and these differences influence pollinator feeding behaviour and foraging efficiency (Hainsworth 1974; Smith et al. 1996; Lara and Ornelas 2001; Castellanos et al. 2004; Fenster et al 2004).

Tubular flowers are common in bird pollination systems (Stiles 1978; Nicolson 2002; Cronk and Ojeda 2008), thus floral length is the most obvious attribute when considering the morphological fit between pollinators and the flowers they pollinate. Long-billed birds are assumed to be the main pollinators of ornithophilous flowers with long corollas, while short-billed birds are associated with flowers with shorter corollas (Temeles 1996; Lara and Ornelas 2001; Geerts and Pauw 2009a). Long bills allow birds to reach deeper into floral tubes and shorten the handling times for taking up nectar (Montgomerie 1984; Temeles 1996). For both long- and short-billed birds, handling times increase with increasing corolla length because birds must extend their tongues to reach the nectar, thus increasing the time required for nectar uptake and decreasing feeding efficiency (Hainsworth 1973; Montgomerie 1984; Grant and Temeles 1992; Collins 2008). This suggests that both long- and short-billed birds feed more efficiently at flowers shorter than their bills. Thus, when given a choice between long and short flowers, with all other parameters being equal, birds should choose short flowers (Montgomerie 1984).

Bill length has been shown to correspond better with flower length when flower width is also taken into consideration (Temeles et al. 2002). Wider corollas allow more of the bird’s head to enter the corolla tube, increasing the maximum extraction depth and improving access to nectar for both long- and short-billed birds (Grant and Temeles 1992; Campbell et al.1996; Temeles et al. 2002). Deeper insertion of hummingbird bills into flowers of *Ipomopsis aggregata* leads to increased pollen export, making wide flowers more successful in terms of male fitness than narrow flowers (Campbell et al. 1996). Narrow corollas may also restrict access to nectar by causing birds to miss flower openings, as seen in ruby-throated hummingbirds (*Archilochus colubris*) which occasionally miss narrow artificial flowers or live flowers of *Monarda* sp. (Smith et al. 1996; Temeles 1996).

Another important morphological trait is floral orientation (Aizen 2003). Animal pollinated flowers may be erect (upward facing), horizontal or pendant (downward facing). Erect flowers can be easily seen by pollinators (Fenster et al. 2009), whereas the pendant orientation of many bird pollinated flowers is often thought to be an adaptation to protect nectar or pollen from rain and to hinder insect access (Fulton and Hodges 1999; Huang et al. 2002; Aizen 2003). Floral orientation has been shown to affect pollinator attraction, pollinator behaviour and pollen transfer (Ushimaru et al. 2009; Wang et al. 2014). In bee-pollinated *Corydalis sheareri*, which has a vertical raceme, manipulation of flowers showed that horizontal presentation resulted in the most efficient pollination (Wang et al. 2014), while for hummingbirds a change from a vertical to a horizontal orientation was found to change pollinator approach from random to directional (Fenster et al. 2009). Floral orientation changes during development of some *Aloe* species that are pollinated by sunbirds: the buds are upright, then the flower hangs downward at anthesis and finally tilts up after pollination (Botes et al 2008).

Observations on how flower morphology affects the feeding performance of hummingbirds may not apply to the main pollinators of African ornithophilous flowers, sunbirds (Cronk and Ojeda 2008; Nicolson and Fleming 2014; Skead 1967). Sunbirds (Nectariniidae) are larger than hummingbirds (Trochilidae), have lower mass-specific metabolic rates and typically perch rather than hover when they feed (Westerkamp 1990; Fleming and Muchhala 2008), although hovering during foraging has been reported (Geerts and Pauw 2009b**;** Padysakova and Jacenek 2016). Thus, sunbird preferences in terms of flower morphology may differ from those of hummingbirds.

Understanding the relationship between flower morphology and pollinator feeding behaviour has implications for understanding the success and evolution of both plants and their pollinators. Here we set out to investigate how the feeding behaviour of White-bellied Sunbirds is influenced by differences in flower morphology, specifically corolla length, width and orientation. First, we tested how maximum extraction depths vary with width and orientation, with the expectation that birds would probe deeper at wide, pendant flowers. We then examined how foraging bout dynamics and flower preferences of sunbirds change with varying length and width of artificial flowers, using flower colour as a cue for flower type. We expected birds to feed faster at wide and short flowers and to prefer short to long, and wide to narrow, flowers.

Materials and Methods

Bird capture and maintenance

Twelve White-bellied Sunbirds, seven females (7.46 ± 0.72 SD g) and five males (8.86 ± 0.98 SD g) were caught using mist nets in Jan Celliers Park in Pretoria, South Africa, during April and May 2015. Upon capture, birds were weighed and bill lengths were measured (from the point where the tips of the forehead feathers impinge upon the culmen to the tip of the culmen). We fitted each bird with colour rings for identification. Birds were housed in a large outdoor (9.0 x 5.5 m, 1.8 m high) aviary at the University of Pretoria experimental farm. The aviary is divided into five equal compartments by wire mesh walls. Except during testing, internal doors were left open so the birds had access to four of the five compartments, the sizeable roaming area preventing crowding and aggressive behaviour. During testing the focal bird was confined to one compartment, separated by gentle herding to avoid handling. The maintenance diet was 20% w/w sucrose solution with the addition of a nutritional supplement (Ensure®, Abbot Laboratories, Johannesburg, South Africa) for vitamins, minerals and protein. Feeders were inverted 20-mL syringes with the tip blocked and a feeding hole marked in red on the side. Food was replaced daily. Perching branches, water baths and water feeders were provided.

Foraging arrays and artificial flowers

The foraging station consisted of a 36 × 36 cm sheet of mesh (Gecko Carpet Grip) attached to a wooden frame to make a feeding board. The feeding board was mounted on a 1.7 m high wooden stand with a frame (~46 × 46 cm) that enabled its removal and replacement with another already prepared feeding board: this reduced the ‘set-up’ time between bouts.

Artificial flowers were sections of straight, clear PVC tubing with an internal diameter of either 3 or 5 mm, with 0.5 cm of one end blocked with Marine clear silicone sealant (Bostik, Permoseal (Pty) Ltd, South Africa) to create a well. Clear tubes ensured easy measurement of sucrose solution residue. The diameters used are within the natural range of corolla widths for sunbird flowers (see Supplementary Table 1). Squares of coloured paper (2 cm × 2 cm) served as "petals", with a small cross cut at the centre for the corolla tubes to pass through.

During experiments, the artificial flowers (corolla tubes) were mounted through the mesh with 1 cm protruding at the open end, allowing the birds to perch in whatever position they chose relative to the flowers. When one flower was presented to the bird, it was mounted through the centre of the feeding board. When six flowers were presented simultaneously, they were arranged in two rows of three; each flower was 10 cm away from its horizontal and vertical neighbours, thereby forming a pattern of equilateral triangles.

Training and experimental protocol

Sunbirds were trained to feed from artificial flowers with pink paper surrounds (a "petal" colour that was only used for training and non-choice experiments, and not used at all in the choice experiments), filled to the brim with 20% w/w sucrose solution. We trained birds by mounting several (6 to 9) artificial flowers on the feeding board, which was then left in the aviary where all birds could access it until the following morning. On the day of the experiment, we presented the focal bird with one artificial flower on the feeding stand; when it drank from the artificial flower, the experiment could be started. Only three of the birds required that their normal feeder (inverted syringe) be mounted on the feeding board to guide them to the artificial flowers.

We filled flowers with the sucrose solution using a micropipette before mounting them on the foraging mesh to avoid formation of bubbles. The order of treatments differed across the birds, and each bird went through the complete set of treatments before we moved on to the next bird. When the flowers were mounted, the bird was left to feed while the experimenter observed from 3-4 m away outside the aviary. As soon as the bird began feeding, a stopwatch was started and ran for the duration of the treatment with the start and end times of each bout being noted in order to record bout durations and the intervals between bouts. A bout was measured from the time a bird started feeding until it flew off the foraging stand for more than five seconds, so if it returned within five seconds the bout continued.

Experiment 1: Maximum extraction depths

We measured the maximum extraction depth, i.e. how deeply a bird can feed from the flower (Montgomerie 1984), at different diameters and orientations. Each bird was provided with a 50 mm long flower, filled to the brim with 20% w/w sucrose solution. The corolla tubes were 50 mm deep to account for tongue extension and ensure that the sunbirds could not reach the bottom and fully empty them: bill lengths of *C. talatala* in this study ranged between 20.74 and 22.07 mm for females, and 21.63 and 22.12 mm for males (mean 21.34 ± 0.56 mm for all birds).

We presented sunbirds with nine treatments in total. These were the horizontal orientation i.e. 0^o, pendant (downward) orientations of -30^o, -60^o and -90^o and the erect (upward) orientations of 30^o and 60^o from the horizontal. For the 3 mm wide flowers, the birds were presented with all six orientations while for the wider 5 mm flowers birds were presented with only the upward and horizontal orientations (Fig. 1). Downward orientations for the wider flowers were omitted because gravitational forces moved the sucrose solution towards the tip of the corolla tube each time the bird drank.

To hold the flower at the desired orientation, the floral tube was attached using twist ties to a piece of cardboard cut at the desired angle, then the cardboard was tied to the feeding board. After each bout, we marked the position of the meniscus of the sucrose solution in the corolla tube using a black marker pen, until the position of the meniscus remained unchanged for three consecutive bouts (Montgomerie 1984). To calculate and record the volume of sucrose consumed per bout and the bird’s maximum extraction depth for that treatment, we measured the length shifted by the meniscus for each bout (length of tube between markings). The length obtained for each bout was then multiplied by the volume of sucrose per mm of each flower tube width, i.e. 8.6 µl/mm and 18.6 µl/mm for the 3 mm and 5 mm wide flowers, respectively.

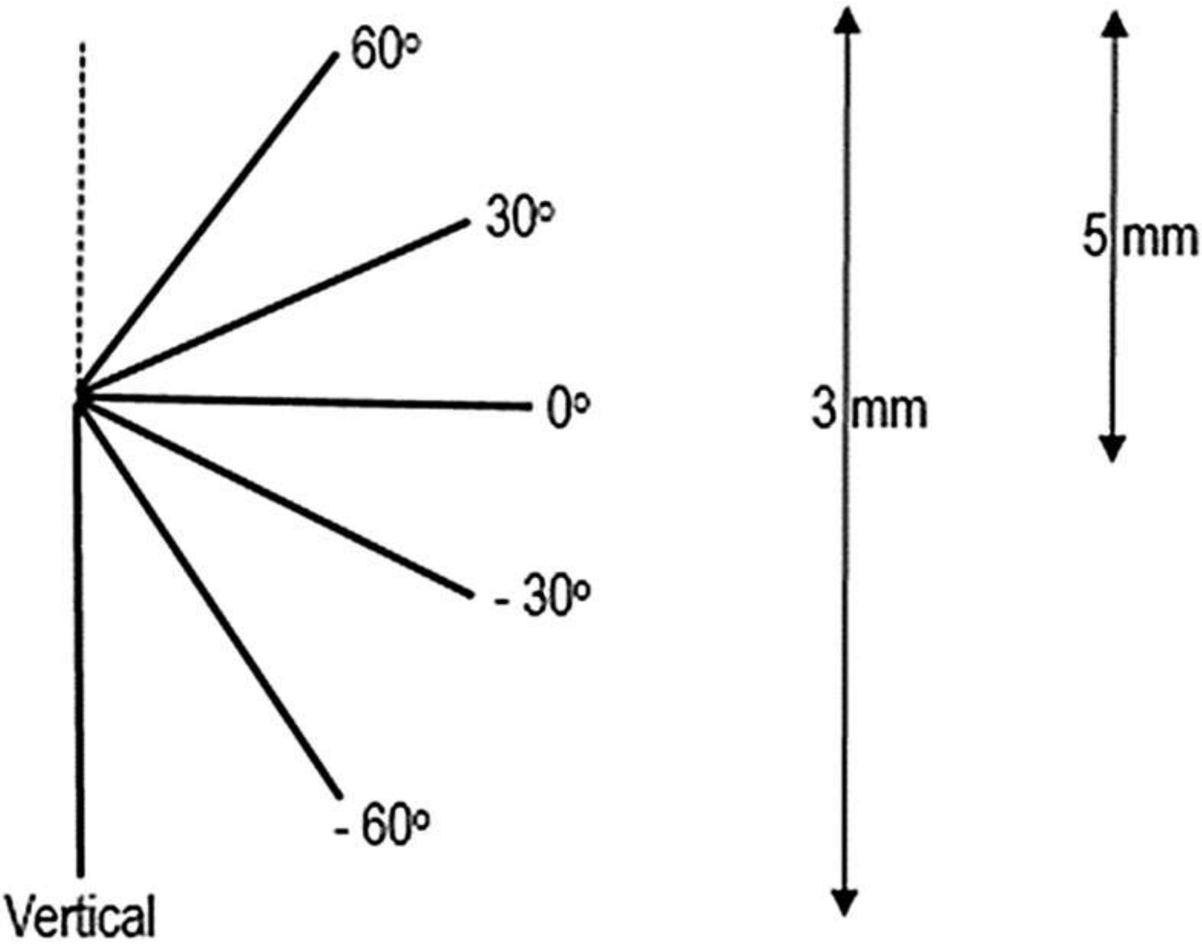

Fig. 1. Illustration of the orientation treatments and the diameters at which they were used

Experiment 2: Foraging bout dynamics

We measured foraging bout dynamics i.e. flower visitation frequency per bout, the volume consumed per flower and the rate of sucrose consumption at different lengths and diameters, at a constant horizontal (0^0) orientation. We used the shortest mean extraction depth i.e. 27 mm (shorter than mean maximum extraction depths of horizontal flowers at both diameters) as our long flower length (maximum extraction depth) and about half of that (14 mm) as the short flower length (half maximum extraction depth). This ensured that all birds could reach the bottom of the flower.

In each treatment, each bird was presented with an array of six flowers identical in petal colour and dimensions. Abbreviations for the four treatments were derived from flower length (Max for maximum and Half-max for half maximum extraction depths) and the 3 mm and 5 mm diameters. The treatments were short and thin flowers (3|Half-max), short and wide flowers (5|Half-max), long and thin flowers (3|Max) and long and wide flowers

(5|Max). Each flower contained 40 µl of 20% w/w sucrose solution added using a Hamilton syringe (with a 22 gauge, 1.5 inch needle). As White-bellied Sunbirds drink an average of 80-120 µl per bout (Bailey and Nicolson 2016), providing 40 µl per tube allowed the birds to obtain a full meal from as little as 2-3 flowers unless they chose otherwise.

At the end of each bout, we measured the volume of sucrose solution consumed by collecting the sucrose solution residue in each flower using a 75 mm haematocrit tube (Hirschmann Laborgeräte GmbH & Co. KG, Germany) and measured it against graph paper with 1 mm graduations, where 1 mm of liquid in the capillary tube equals 1 µl. Each flower was then refilled with 40 µl sucrose solution before the next bout. This was done for 20 bouts per bird per treatment. For each bout we recorded the volume consumed, bout duration, the number of flowers visited and which flowers were visited. We also recorded the intervals between bouts.

Experiment 3: Flower choice

To investigate how flower morphology affects sunbird choices of where to feed, we provided each bird with six flowers of two morphologies (three of each) for two treatments, length and diameter, tested separately. For the length treatment the birds had to choose between long (27 mm) and short (14 mm) flowers at a constant width (3 mm) while for the diameter treatment they chose between narrow (3 mm) and wide (5 mm) flowers at a constant length (14 mm). Flower type was cued by colour. Flower colours were selected pseudo-randomly ensuring that no two birds had the same colours for the same treatment. Each flower was filled with 40 µl of 20% w/w sucrose solution.

Flower positions were allocated numbers 1-6 starting from the left, such that row 1 had positions 1-3 and row 2 had positions 4-6. To ensure that birds did not use spatial cues (Whitfield et al. 2014; Kaczorowski et al. 2014), we changed flower positions after every five bouts. Positions of flowers were chosen pseudo-randomly with no sequence used more than once in a treatment. To ensure that side bias did not become an issue in choice of flower positions, the position of the feeding stand was changed after every six or seven bouts by moving it 50 cm forward/backward and/or turning to one side by 45°.

For each of the 20 bouts per treatment, we recorded the volume consumed (measured as in Experiment 2), bout duration, the number of flowers visited and which flowers were visited. We also recorded the intervals between bouts. All but one of the birds completed the length and diameter treatments on consecutive days, due to rainy weather conditions.

A summary of the experimental design is shown in Supplementary Table 2.

Data analyses

Data were analysed in IBM SPSS Statistics 23. Data were non-parametric, thus we used the Friedman ANOVA test to test for differences in maximum extraction depths, foraging bout dynamics and sunbird flower type preferences. The Wilcoxon Signed Ranks test was used to test for differences between diameter and length in the floral choice experiment. Post-hoc tests were Wilcoxon Signed Ranks tests with a Bonferroni correction. Regression analysis was used to relate the volume of sucrose to bout duration. Unless stated otherwise, results are presented as means ± SD.

Results

Sunbirds fed for an average 15.86 ± 15.49 sec per bout in the maximum extraction depth tests, 16.51 ± 13.17 sec in the foraging bout dynamics tests and 12.33 ± 8.38 sec in the choice experiments. Intervals between bouts were longer in the foraging bout dynamics tests (5.98 min) and the choice experiments (5.22 min) when birds were presented with six flowers simultaneously than they were in the maximum extraction tests with the single flower (3.50 min). In all experiments, there was a positive correlation between bout duration and the volume of sucrose solution consumed per bout, i.e. when the birds spent longer on the feeding board, they consumed greater volumes of sucrose solution (Experiment 1; $y = 3.5806x + 4.9958$, $R^2 = 0.434$, Experiment 2; $y = 2.7562x + 31.821$, $R^2 = 0.5388$ and Experiment 3; $y = 4.0551x + 33.753$, $R^2 = 0.5932$).

Maximum extraction depths

Mean maximum extraction depths for 11 birds at all nine treatments are shown in Fig. 2. The shortest maximum extraction depth was 27.0 ± 0.98 mm on the 3 mm wide flowers at the vertical orientation while the longest was 32.75 ± 1.17 mm on the 5 mm wide flowers at the horizontal orientation.

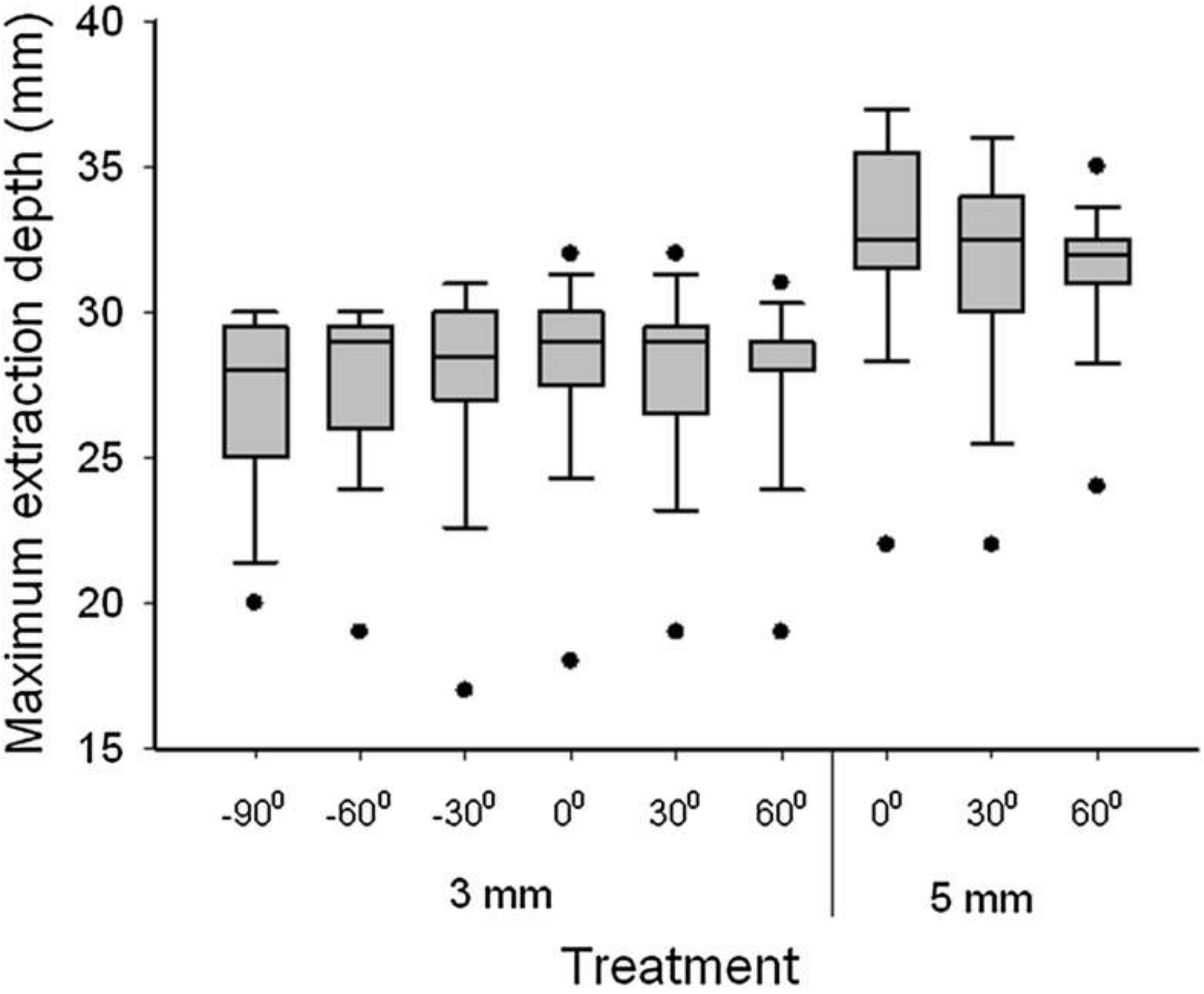

Fig. 2. Birds probed deeper at the 5 mm wide flowers than at the 3 mm wide flowers while maximum extraction depths were similar among orientations at the same diameters. For each treatment there was at least one outlier (black dots); maximum extraction depths above or below the data included in the boxplot

When the two floral diameters were compared for the upward oriented flowers, a significant difference was observed in the maximum extraction depths (Friedman ANOVA test: $X^2 = 42.03$, N = 11, df = 5, $p < 0.001$) with the birds probing deeper at the 5 mm wide flowers than at the 3 mm wide flowers. There were no significant differences in maximum extraction depths among the orientations at 3 mm wide flowers (Friedman ANOVA test: $X^2 = 8.19$, N = 11, df = 5, $p > 0.050$) or at 5 mm wide flowers (Friedman ANOVA test: $X^2 = 42.03$, N = 11, df = 2, $p > 0.050$). Orientation was therefore omitted from the subsequent experiments i.e. all flowers in subsequent experiments had the same horizontal (0^0) orientation.

Foraging bout dynamics

Birds consumed the sucrose solution at significantly different rates from flowers of the two diameters (Friedman ANOVA test: $X^2 = 116.57$, $N = 880$, $df = 1$, $p < 0.001$; Fig. 3A), feeding faster from the wider flowers. Their rates of consumption also differed significantly between the two lengths (Friedman ANOVA test: $X^2 = 868.04$, $N = 880$, $df = 1$, $p < 0.001$; Fig. 3B), with the birds feeding faster at the shorter flowers.

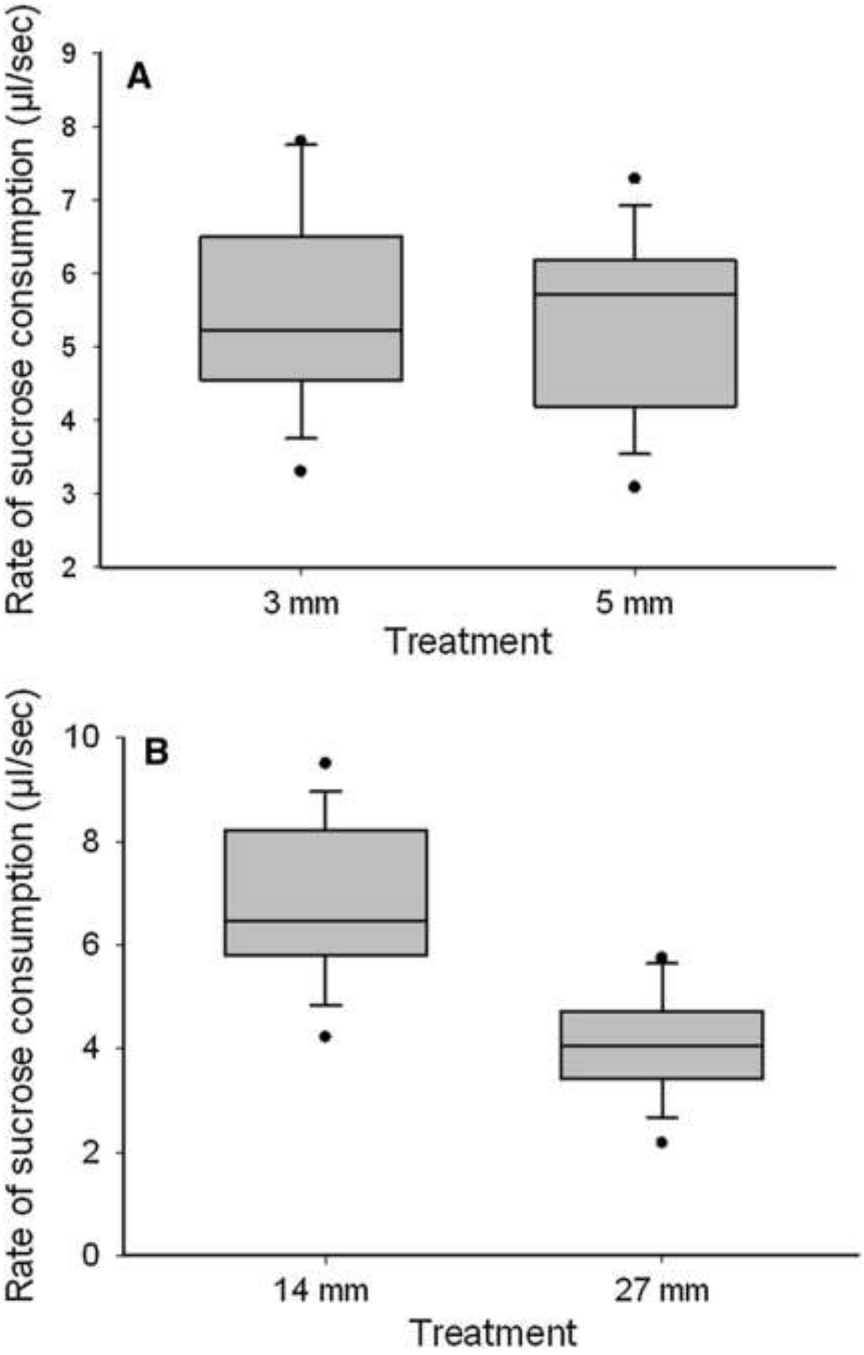

Fig. 3. Birds fed faster (µl/sec) at the 5 mm wide than at the 3 mm wide flowers (**a**) and at the 14 mm long than at the 27 mm long flowers (**b**)

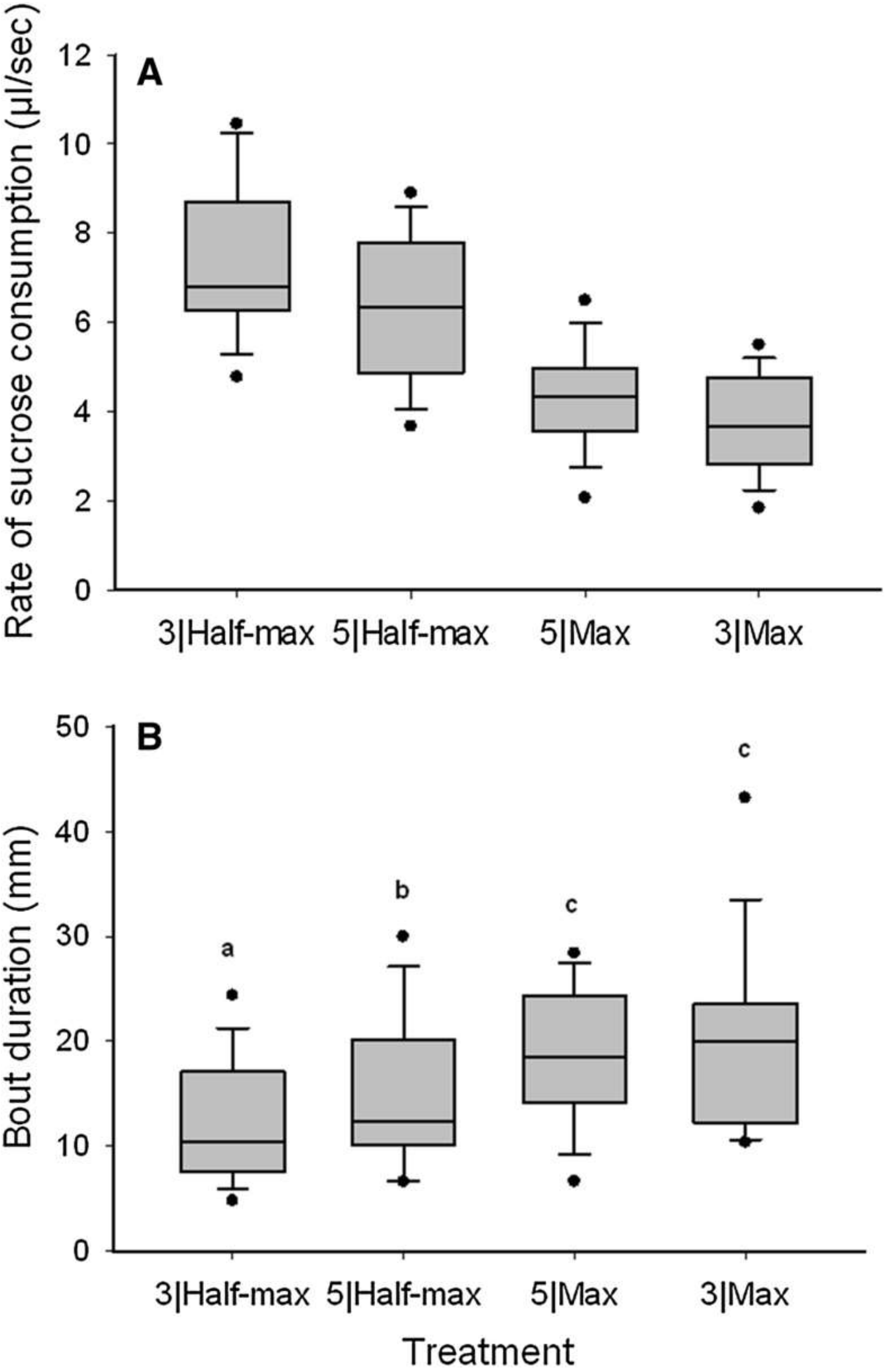

Fig. 4. Birds fed at significantly different rates (µl/sec) among the four treatments (**a**), feeding fastest at the thin and short flowers and slowest at the thin and long flowers. Birds showed significantly different bout durations among the four treatments (**b**), spending the longest time at the short and wide flowers and similar durations at the two long treatments

There were no significant differences in the number of flowers visited per bout among the four treatments (Friedman ANOVA test; $X^2 = 1.909$, N = 880, df = 1, $p > 0.100$). However, significant differences were observed in the rate of consumption (µl/sec) (Friedman ANOVA test; $X^2 = 546.94$, N = 880, df = 1, $p < 0.001$; Fig. 4A) among the four treatments, with the birds feeding fastest at the short and narrow flowers. Post-hoc analysis revealed significant differences between all treatment pairs.

There were also significant differences in bout duration (sec) (Friedman ANOVA test; $X^2 = 815.38$, N = 880, df = 1, $p < 0.001$; Fig. 4B), with the birds taking longer to feed from the long and narrow flowers. Post-hoc analysis revealed no significant differences between 3|Max and 5|Max ($p > 0.008$), so bout durations were similar between the two long treatments. There was a significant difference between the two short treatments (3|Half-max and 5|Half-max) although the p-value ($p = 0.006$) was close to the significance value of 0.008 for the post-hoc test, while differences in bout duration were highly significant between the long flower treatments 3|Max and 5|Max ($p < 0.001$).

The volume of sucrose consumed per bout (µl) differed significantly (Friedman ANOVA test; $X^2 = 854.16$, N = 880, df = 1, $p < 0.\ 001$) among the treatments. Post-hoc analysis revealed significant differences ($p < 0.001$) only when the long and thin (3|Max; $\bar{x} = 69.5 \pm 50.69$ µl) flowers were tested against the short flowers (3|Half-max; $\bar{x} = 80.77 \pm 46.34$ µl and 5|Half-max; $\bar{x} = 81.71 \pm 47.77$ µl).

Flower choice

Birds consumed greater volumes of sucrose solution when they visited a larger number of flowers per bout than when they visited fewer flowers (Friedman ANOVA; $X^2 = 356.01$, N = 360, df = 1, $p < 0.001$).

The rate of sucrose consumption (µl/sec) was faster when flower diameter was variable and flower length was constant at 14 mm (diameter treatment) than when the length was variable and the diameter was constant at 3 mm (length treatment) (Wilcoxon Signed Rank Test; N = 360, $z = -16.440$, $p < 0.001$; Fig. 5). The birds visited a significantly larger number of flowers per bout when flower length was variable than when length was constant (Wilcoxon Signed Rank Test; N = 360, $z = -11.807$, $p < 0.001$).

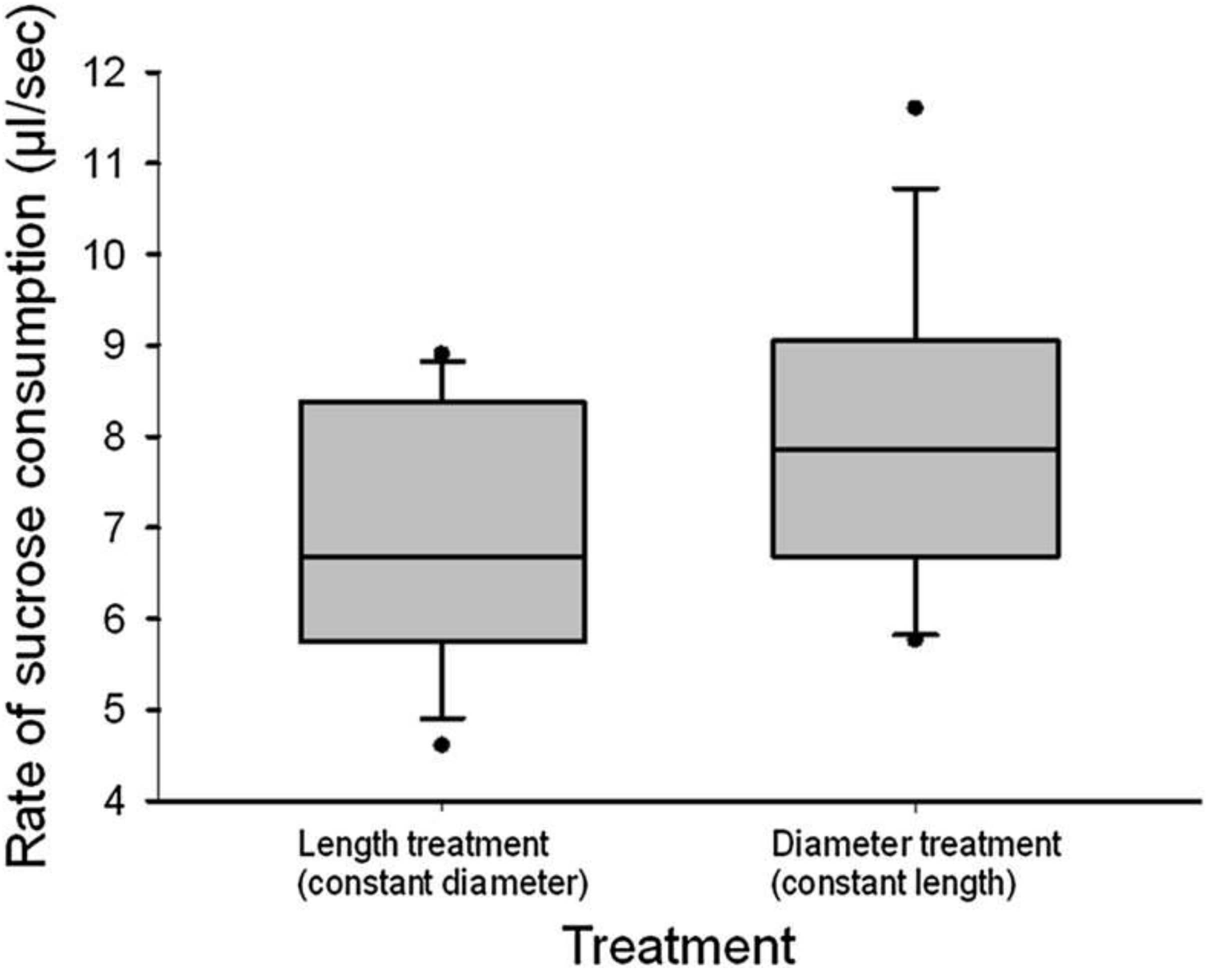

Fig. 5. Birds fed significantly faster when flower diameter was variable and flower length was constant (14 mm) than when flower length was variable and flower diameter was constant (3 mm)

There was no significant difference in preference between the two diameters: the birds visited a similar number of flowers per bout for the 3 mm wide flowers and 5 mm wide flowers (Friedman ANOVA Test; $X^2 = 1.485$, $N = 180$, $df = 1$, $p > 0.100$; Fig. 6A). There was however, a significant difference in the number of flowers visited per bout between the two lengths (Friedman ANOVA Test; $X^2 = 103.041$, $N = 180$, $df = 1$, $p < 0.001$; Fig. 6B). The birds preferred the short (14 mm) flowers to the long (27 mm) flowers.

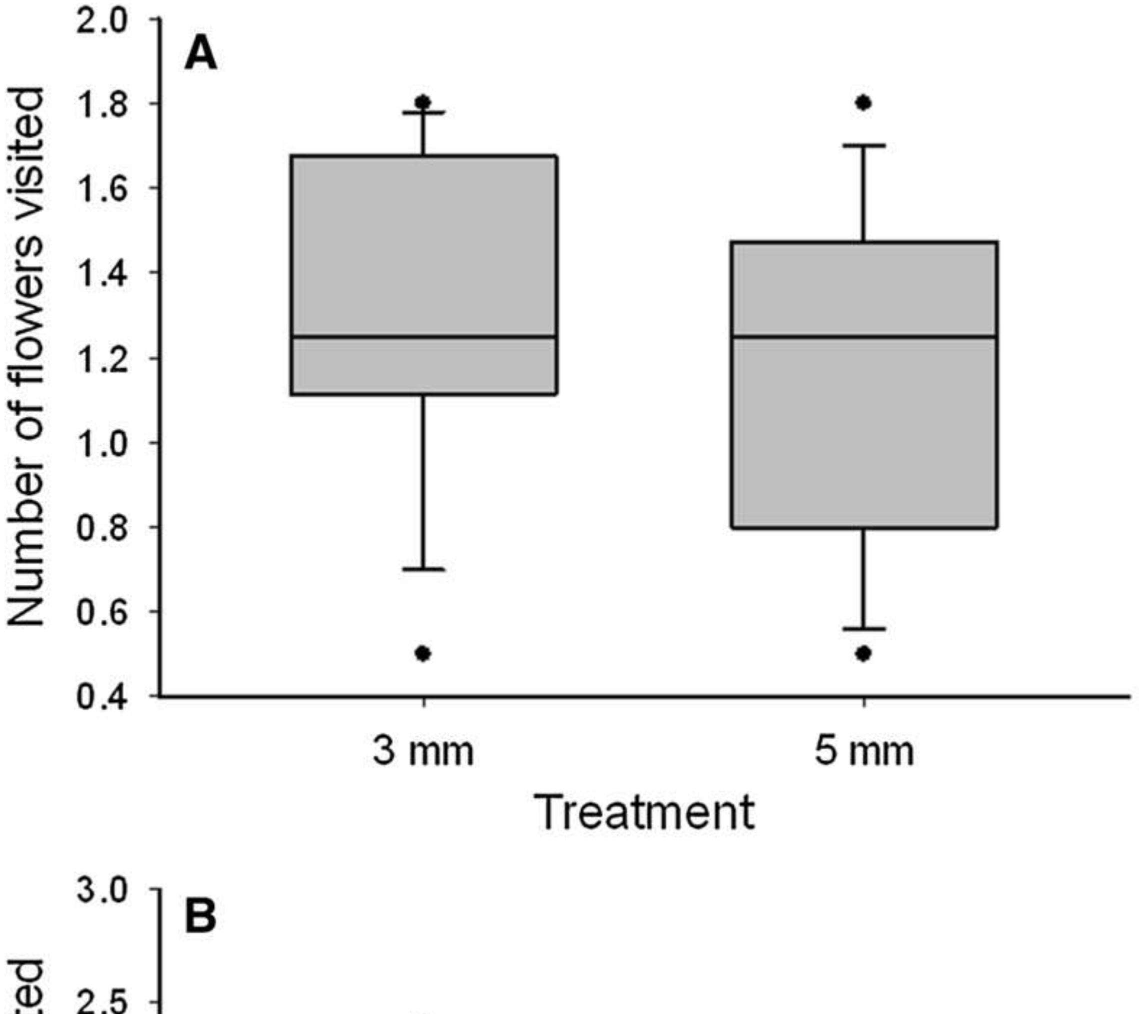

Fig. 6. Sunbirds visited a similar number of flowers of both diameters in the diameter treatment (**a**) and visited more short flowers than long flowers in the length treatment (**b**)

Discussion

Floral morphology clearly influenced the feeding behaviour and feeding efficiency of White-bellied Sunbirds. Flower length had a clear effect on the feeding parameters measured; when flowers were longer the birds fed more slowly, had longer bout durations and selected these flowers less frequently than shorter flowers. Flower diameter had significant effects on how deeply the birds probed flowers and the rate of consumption, with sunbirds probing deeper and feeding faster at wider flowers, but surprisingly sunbirds did not prefer wider to narrower flowers, at least at the widths we tested. Flower orientation, however, had no effect on how deeply the birds probed the flowers and was therefore omitted from the subsequent experiments.

Sunbirds fed faster at and preferred the short flowers, which is consistent with results from similar studies on members of the other two families of flower specialists, the Trochilidae (hummingbirds) and Meliphagidae (honeyeaters). In both hummingbirds and honeyeaters, handling times are shortest when flower lengths are shorter than bill lengths (Montgomerie 1984; Temeles 1996; Collins 2008). At longer corollas the birds must extend their tongues well beyond their bill tips in order to reach the nectar source (Hainsworth 1973; Montgomerie 1984; Collins 2008). Rufous hummingbirds (*Selasphorus rufus*) are capable of extending their tongues by almost the bill length when feeding on artificial flowers (Grant and Temeles 1992). The 27 mm flowers that we used were longer than the bills of the White-bellied Sunbirds, which averaged 21.3 mm. When flowers are short, more of the surface area of the tongue comes into contact with the nectar, ensuring that larger amounts of nectar adhere to the tongue (Hainsworth 1973; Schlamowitz et al. 1976). When given a choice between flowers of different lengths with the same corolla width and volume of sucrose solution, sunbirds showed a preference for the shorter flowers. In choice experiments using artificial flowers, Maglianesi et al. (2015) found three species of hummingbird to prefer short flowers over long flowers. Similarly, in studies on nectar quality and feeding efficiency of another three hummingbird species, birds showed a preference for the feeders with shorter artificial corollas (Hainsworth 1973; Hainsworth and Wolf 1976).

The reduced rate of nectar uptake with increasing corolla length is due to a decrease in the volume of nectar obtained per lick, rather than reduced licking rates (Hainsworth 1973; Schlamowitz et al. 1976). When investigating rates of nectar consumption in White-bellied Sunbirds as a response to viscosity and concentration, Köhler et al. (2010) also found that variations in nectar uptake depend more on tongue loads than on licking frequencies. The decreased rate of consumption that we observed at 27 mm long artificial flowers is perhaps surprising since sunbirds commonly visit flowers with corolla tubes that are approximately 30 mm in length (Frost and Frost 1980; Vos et al. 1994; Hargreaves et al. 2012; see also Supplementary Table 1). However, variable nectar volumes also affect the rate of consumption: in tubular corollas the volume of nectar determines its height and whether immersion of bird tongues is partial or complete. Moreover, the volume of nectar in a flower decreases during a drinking bout (Kim et al., 2012). In hummingbirds and honeyeaters feeding from tubular artificial flowers, the amount of nectar loaded per lick increases with shorter flowers or higher nectar volumes, both of which increase the contact between tongue and nectar (Collins 2008). The most efficient feeding occurs when each lick fills the tongue to capacity, which will happen at high nectar volumes (Montgomerie 1984; Collins 2008).

Maximum extraction depths of foraging White-bellied Sunbirds were significantly affected by flower width, and the birds fed faster at the wider flowers. However, they did not show any preference between the 3 and 5 mm wide flowers. The floral diameters used in this study (see also Supplementary Table 1) are within the range of corolla widths of sunbird flowers: *Aloe* species 3.7 – 4.3 mm (Hargreaves et al. 2012), *Kniphofia laxiflora* 4.5 – 4.8 mm (Brown et al. 2010), *Leonotis leonurus* mean 5.3 mm (Vos et al. 1994). When Temeles (1996) tested diameters ranging from 1.6 – 6.5 mm, a range that corresponds with corolla lengths of plants visited by short-billed hummingbirds (Grant and Temeles 1992), he found no significant differences between 3 and 5 mm wide flowers in the maximum extraction depths of Ruby-throated Hummingbirds (*Archilochus colubris*). For hummingbirds, narrow artificial flowers may result in bill insertion errors, which impose time and energy costs during foraging (Smith et al. 1996; Temeles (1996). Insertion errors were not observed in our study. Hummingbirds feeding at narrow floral tubes typically have longer handling times than at wider tubes (Temeles 1996). However, floral widths of *Ipomopsis* and *Penstemon* flowers did not affect handling times of hummingbirds in studies carried out by Campbell et al. (1996) and Castellanos et al. (2004) respectively. When investigating the effect of *Burmeistera* floral width on the feeding behaviour of bats and hummingbirds, Muchhala (2007) found that pollen deposition by hummingbirds decreased with increasing corolla width, corresponding to reduced precision and accuracy of bill insertion. However, the same study found no effect of flower width on handling time (visit duration) for either bats or hummingbirds (Muchhala 2007). Collins (2008) examined the effects of several floral traits on foraging performance of honeyeaters, but these did not include width.

That sunbirds fed fastest at the short and narrow flowers is not surprising because in narrow flowers a fixed volume of nectar extends further up the flower and is easier to reach. Similarly, in the length treatment when diameter was constant and length variable, half the flowers were too long for birds to feed from easily so birds had to search for short flowers: they therefore visited more flowers and fed more slowly. While many ornithophilous flowers produce copious volumes of dilute nectar, there is a dichotomy between the flowers of generalist bird pollinators and those of specialist bird pollinators such as sunbirds and hummingbirds (Johnson and Nicolson 2008). For the specialists, volumes are in the range 10–30 µl. For experiments on foraging dynamics and flower choice we used 40 µl, so that a full meal of 80-120 µl could be obtained from 2-3 flowers. Nectar volumes are important in preference experiments: for example, Mitchell and Paton (1990) found for honeyeaters that optimal nectar concentrations differed between equal volume presentation (with varying concentration) and equal sugar presentation (with volume and concentration varied inversely to keep sugar rewards equal). Because of this, Roberts (1996) tested the sugar concentration preferences of hummingbirds at realistically low nectar volumes. Similarly, the use of unnaturally large reward volumes affects assessment of flower constancy in honey bees (Grüter et al. 2011). Large nectar volumes can make long corollas less effective as filters (Lázaro et al 2015). Maglianesi et al. (2015) found that three Costa Rican hummingbird species differing in bill morphology all preferred short artificial flowers attached to high-volume feeders, but under natural conditions, with limited nectar resources, they chose flowers with floral traits (length and curvature) corresponding to their bill morphology.

Orientation of flowers relative to the vertical varies considerably between species, and this may influence pollinator behaviour and pollen transfer (Fulton and Hodges 1999; Ushimaru et al. 2009). Contrary to our prediction, the maximum extraction depths of White-bellied Sunbirds were unaffected by flower orientation. In other studies, researchers have examined whether floral orientation affects handling times of bird pollinators, using manipulated real flowers or artificial flowers. Montgomerie (1984) found no effect of floral orientation on the handling times of hummingbirds, but his sample size was very small. Collins (2008) confirmed this with four hummingbird species. In *Penstemon* flowers, the pendant orientation results in increased handling times for both bees and hummingbirds (Castellanos et al. 2004). In Brown Honeyeaters (*Lichmera indistincta*) and New Holland

Honeyeaters (*Phylidonyris novaehollandiae),* which like sunbirds sometimes perch when foraging, handling times are longer at pendant than at erect artificial flowers (Collins 2008).

A lack of response to changes in orientation may be due to the adaptability and opportunistic feeding behaviour of bird pollinators (Stiles 1978). White-bellied Sunbirds can change their angle and direction of approach with changes in flower orientation, and they can feed while perching upside down (as observed in this study). Sunbirds are also capable of hovering if there is a need (Geerts and Pauw 2009b; Kaczorowski and Markman 2016). Flower orientation may affect the angle at which sunbirds approach flowers but not their ability to probe flowers. It is unfortunate that we could not test the effect of downward orientations on sunbird foraging behaviour. Many sunbird-pollinated plants, like those of hummingbirds (Fulton and Hodges 1999; Tadey and Aizen 2001), have downward-facing flowers: *Aloe, Kniphofia,* and *Erica* are obvious examples (Botes et al. 2008; Brown et al. 2010; van der Niet et al. 2014). One consequence of a downward orientation is that the dilute nectar consumed by birds may drip out of flowers (as we found when trying wider flowers at downward orientation). However, spillage from naturally pendant flowers may be prevented by exserted anthers blocking the corolla entrance as in *Aloe* species (Botes et al 2008), by hairy partitions inside the corolla as in *Leonotis* (Frost and Frost, 1980; Vos et al. 1994), or by surface properties of the corolla (Tadey and Aizen 2001). Tests of sunbird responses to flower orientation should be carried out with real flowers. Another floral character affecting mechanical fit is curvature. Many specialist nectar-feeding birds of all main lineages have curved bills (Paton and Collins 1989). The responses of birds to varying corolla curvature have been examined in honeyeaters and hummingbirds (Collins 2008; Maglianesi et al. 2015).

White-bellied Sunbirds fed more efficiently at short and wide flowers, but does this make them efficient pollinators of such flowers? Despite the fact that birds can visit and feed from flowers whose corolla tubes are longer or shorter than their bill lengths (Temeles et al. 2002), the flower-pollinator morphology mismatch often prevents effective pollination (Van der Niet et al. 2014; Geerts 2016). In a study of pollination ecotypes in the shrub *Erica plukenetii*, van der Niet et al. (2014) showed that flowers with intermediate corolla length are pollinated by short-billed Orange-breasted Sunbirds (*Anthobaphes violacea*), while northern populations with longer corollas are pollinated by long-billed Malachite Sunbirds (*Nectarinia famosa*). The Cape Floristic region is rich in bird-pollinated plants, many with tubular flowers, and Geerts and Pauw (2009a) investigated whether different corolla lengths correspond to different bill lengths among the pollinators. They found about 40 plant species with long corollas to be reliant on long-billed Malachite Sunbirds for pollination. Two short-billed sunbird species, *A. violacea* and the Southern Double collared Sunbird (*Cinnyris chalybeus*), were found to be efficient pollinators of short to medium length flowers, while frequently robbing the long-tubed flowers. *Anthobaphes violacea* is also an efficient pollinator of a relatively short-tubed *Erica* species, *E. halicacaba* (Turner et al. 2012). The long tubed flowers of *Chasmanthe floribunda* (Iridaceae) are pollinated by *N. famosa* but, when this sunbird is absent in transformed landscapes, nectar thieving *A. violacea* and *C. chalybeus* do not provide efficient pollinator services (Geerts 2016). Since White-bellied Sunbirds have bill length ranges similar to those of these two short-billed sunbirds (Geerts and Pauw 2009a), it can be assumed that they would also be efficient pollinators of relatively short tubular flowers. However, further research is required to confirm this. Predicting patterns of flower use from bill and corolla morphologies is complicated by other factors, such as energetic costs and benefits, the availability of other flowers, and the presence of nectar competitors (Temeles et al. 2002; Geerts and Pauw 2009a).

In summary, the results of this study confirm that sunbirds, like hummingbirds and honeyeaters, feed more efficiently from flowers where nectar is more readily accessible. For the range of diameters and lengths we tested, reduced foraging efficiency at longer flowers resulted in sunbirds developing a preference for shorter flowers. However, although the sunbirds foraged more efficiently from wider than from narrower flowers this difference was insufficient to translate into a preference for wider flowers. It may be that in the wild, under conditions of food limitation and competition, such slight differences in foraging efficiency between flower widths may be sufficient to elicit a preference. To more completely understand the attributes of flowers that contribute to variation in flower choice and pollination efficiency will require considerably more research into a wider range of bird pollinators and their natural floral resources, particularly under natural conditions where preferences may be more pronounced.

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Supplementary material

Table S1 Corolla width, length and curvature of sunbird flowers (mean ± SE, n=10).

Plant species	**Corolla width (mm)**	**Corolla length (mm)**	**Corolla curvature (degrees)**
Aloe arborescens	3.4 ± 0.16	40.5 ± 0.52	10.1 ± 0.30
Aloe cryptopoda	4.1 ± 0.23	36.0 ± 1.07	13.9 ± 0.75
Aloe greatheadii var. davyana	3.8 ± 0.13	25.1 ± 0.60	20.7 ± 1.19
Clivia caulescens	4.6 ± 0.22	37.7 ± 0.67	28.9 ± 1.32
Leonotis leonurus	3.2 ± 0.13	31.4 ± 0.50	19.4 ± 0.92
Tecomaria capensis	4.1 ± 0.23	33.0 ± 0.63	24.6 ± 0.71

To ensure that the artificial flowers had corolla parameters similar to those encountered by white-bellied sunbirds in nature, we measured corolla widths, lengths and curvatures of flowers visited by sunbirds. Flowers (10 per species) were plucked from two or three plants of the same population growing at the National Botanical Gardens in Pretoria or the Hatfield campus of the University of Pretoria. The internal diameter of the corolla tube at the aperture was measured to the nearest 0.1 mm using vernier calipers. Corolla length was measured to the nearest 1 mm from the distal end of the corolla to the flower opening. To measure corolla curvature, we photographed flowers on graph paper and calculated the angle of deflection using simple trigonometry as described in Maglianesi et al. (2015).

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Table S2 A summary of the methods and materials

Experiment	Treatment	Orientation	Tube width	Tube length	Petal colour	Repetition	Parameters measured
1. Maximum extraction depth (single flower presented at a time)		-90^0 (vertical),-60^0, -30^0, 0^0 (horizontal), 30^0,60^0	3 mm, 5 mm	50 mm	Identical (Pink)		Volume of sucrose consumed per bout, bout durations, interval between bouts, maximum extraction depth
2. Foraging bout dynamics (six identical flowers presented simultaneously - Each flower containing 40 µl sucrose solution).	3|Max	Horizontal	3 mm	27 mm	Identical (Pink)	× 20	Volume of sucrose consumed per flower per bout, bout durations, intervals between bouts, number of flowers visited
	5|Max		5 mm	27 mm			
	3|Half-max		3 mm	14 mm			
	5|Half-max		5 mm	14 mm			
3. Flower choice (six flowers of two flower types presented simultaneously – each flower containing 40 µl sucrose solution)	Length treatment	Horizontal	3 mm	14 mm vs. 27 mm	Varying (not including pink)	× 20	Volume of sucrose consumed per flower per bout, bout durations, intervals between bouts, number of flowers visited
	Diameter treatment		3 mm vs. 5 mm	14 mm			