NECTAR INTAKE AND FORAGING EFFICIENCY: RESPONSES OF HONEYEATERS AND HUMMINGBIRDS TO VARIATIONS IN FLORAL ENVIRONMENTS

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ABSTRACT.—Costa Rican hummingbirds and Australian honeyeaters respond to an increase in the volume of nectar made available in tubular flowers by increasing the duration of foraging bouts, the rate at which nectar is ingested, and the energetic efficiency of that process. Enhanced intake is the result of increased nectar capture by the tongue during each lick rather than of any significant change in licking rate. All species react to an increase in floral length by spending more time foraging and reducing nectar intake, short-billed species being most affected. Decreased nectar capture per lick, rather than a change in licking rate, is responsible for this response. Honeyeater foraging times increase and nectar-intake rates decrease when the curvature of flowers is increased, though all but one of the short-billed hummingbird species were relatively insensitive to this change. Hummingbirds harvest nectar with equal proficiency whether foraging at erect or at pendulous flowers, whereas the bouts of honeyeaters are longer, and their nectar-uptake rates lower, when they visit pendulous flowers. Overall nectar-extraction rates of hummingbirds, as measured in the laboratory, were greater than those of honeyeaters; values for both groups were generally higher than rates recorded in the field. Hummingbird and honeyeater tongues are equally adept at extracting nectar from tubular flowers, though my results suggest that honeyeater tongues would be more effective in situations where nectar is thinly and widely dispersed. *Received 14 May 2007, accepted 3 November 2007.*

Key words: foraging efficiency, honeyeaters, hummingbirds, licking, nectar intake.

Consumo de Néctar y Eficiencia en el Forrajeo: Respuestas de Mieleros y Colibríes a Variaciones en los Ambientes Florales

RESUMEN.— Los colibríes de Costa Rica y los mieleros de Australia responden a un incremento en el volumen de néctar disponible en flores tubulares aumentando la duración de sus períodos de forrajeo, la tasa a la que ingieren néctar y la eficiencia energética de este proceso. El mejoramiento del consumo es el resultado de un incremento en la cantidad de néctar capturado por la lengua durante cada lamido, en lugar de cualquier otro cambio significativo en la tasa de lamido. Todas las especies reaccionan a un incremento en la longitud de las flores pasando más tiempo forrajeando y disminuyendo la toma de néctar, y las especies de pico corto son las más afectadas. Esta respuesta es causada por una disminución en la captura de néctar por lamido, no por un cambio en la tasa de lamido. Los tiempos de forrajeo de los mieleros aumentan y las tasas de ingestión de néctar disminuyen cuando se aumenta la curvatura de las flores, mientras que todas menos una de las especies de colibríes fueron relativamente insensibles a este cambio. Los colibríes obtienen néctar con igual habilidad en flores erectas y en flores péndulas, mientras que los mieleros exhiben períodos de forrajeo más largos y tasas de ingestión de néctar más bajas cuando visitan flores péndulas. En general, las tasas de extracción de néctar por parte de los colibríes, medidas en el laboratorio, son mayores que las de los mieleros; los valores para ambos grupos fueron generalmente mayores que los registrados en el campo. Las lenguas de los colibríes y los mieleros son igualmente efectivas para extraer néctar de flores tubulares, aunque mis resultados sugieren que las lenguas de los mieleros presentarían más efectividad en situaciones en las que el néctar está finamente y ampliamente disperso.

BIRDS THAT RELY, to some extent, on nectar as a source of food are found in various parts of the world. The Melaphagidae (honeyeaters) constitute one of the most diverse groups of such animals and occupy a wide range of habitats within the Australasian region (Collins and Paton 1989, Higgins et al. 2001). Equally widespread are the Trochiliidae (hummingbirds), whose species are conspicuous members of the avifauna in many parts of North, Central, and South America (Feinsinger 1976, Wolf et al. 1976, Gass and Montgomerie 1981).

Honeyeaters have body masses that range from 8 to 180 g (Collins and Paton 1989). Their bills, which vary in length, are decurved to some extent and attenuated toward the tip. Hummingbirds are

generally smaller, with body masses that vary from 2 to 20 g and bills that are mostly thinner and less tapered than those of honeyeaters (Paton and Collins 1989). Members of both groups have tongues that are capable of rapid extention and retraction and are structurally well suited for the uptake of nectar, though honeyeaters' tongues have brush-tips that differ markedly from the bifurcated tips found in hummingbirds (Hainsworth 1973, Paton and Collins 1989).

Nectar intake by hummingbirds and honeyeaters has been measured on several occasions under laboratory conditions. In some cases, special attention has been paid to the effects of tongue structure, licking rates, and floral characteristics such as nectar concentration and corolla length on nectar acquisition and foraging efficiency (Hainsworth 1973, Collins and Morellini 1979, Montgomerie 1984, Mitchell and Paton 1990, Temeles and Roberts 1993, Roberts 1995, Temeles 1996). Much less consideration has been given to the influence of such factors under field conditions (Wolf et al. 1972; Collins et al. 1984, 1990).

In their natural habitats, hummingbirds collect nectar principally from flowers that have tubular corollas. In at least some instances, there appears to be a close correlation between the length, curvature, or diameter of those flowers and the bill morphology of their principal visitors (Snow and Snow 1972, Stiles 1975, Feinsinger 1976, Hainsworth and Wolf 1976, Temeles et al. 2002). Although some honeyeaters visit similar-shaped flowers, much of the nectar that they acquire is obtained from sources such as eucalypts and banksias whose floral morphologies are much less restrictive, and there appears to be little correlation of the type mentioned above (Paton and Ford 1977, Collins and Rebelo 1987). Anecdotal evidence suggests that neither group has an overall preference for flowers that have particular orientations, with many species extracting nectar from erect, oblique, and pendulous flowers.

Virtually no attempt has yet been made to experimentally compare the efficiencies with which major avian groups are able to harvest nectar. Here, I attempt to redress this situation by presenting and interpreting evidence related to the effects of changes in nectar volume, floral morphology, and the spatial orientation of flowers on nectar intake in three species of Australian honeyeaters and four species of Costa Rican hummingbirds when foraging at tubular flowers under similar laboratory conditions. I also examine field data for the same or closely related species in an attempt to determine whether the performance of these birds equals that of birds tested in the laboratory and to identify situations that might favor birds with particular tongue or bill characteristics.

Methods

Experimental animals.—Male Violet Sabrewings (*Campylopterus hemileucurus*), Green-crowned Brilliants (*Heliodoxa jacula*), Purple-throated Mountaingems (*Lampornis calolaema*), and Green Hermits (*Phaethornis guy*) were maintained in aviaries at Monteverde, Costa Rica. Male New Holland Honeyeaters (*Phylidonyris novaehollandiae*), Brown Honeyeaters (*Lichmera indistincta*), and Western Spinebills (*Acanthorhynchus superciliosus*) were housed under similar conditions at Curtin University of Technology, western Australia. These species were chosen because of the diversity of body masses and bill attributes that they exhibited. With the exception of Green Hermits and Brown Honeyeaters, only

single individuals of which were available, sample sizes of four birds were used throughout. All birds were maintained between experimental periods on an ad-libitum supply of artificial nectar containing Complan health food, at a concentration equivalent to 16.0 mg sucrose per 100 µL water.

Body masses were measured for all birds on the morning of each day that experiments were conducted. Bill gape-tip lengths and curvature indices were also measured at the outset of the experimental period, using procedures outlined by Paton and Collins (1989). Depths to which bills could be inserted into the artificial flowers described below, and depths to which birds were able to reach nectar with their tongues, were measured in the manner outlined by Montgomerie (1984) and Temeles and Roberts (1993). The capacity of the birds to extend their tongues beyond the tips of their bills was then calculated as the difference between these two measures. Tongues were excised from the collection of museum specimens held at Curtin University and their lengths measured, though equivalent data were not obtained for hummingbirds. Single New Holland Honeyeater and Western Spinebill tongues were sputter-coated and examined by means of a Philips XL 30 scanning electron microscope. Other tongues were wax-embedded, and transverse sections cut at various levels, before being stained with haematoxylon and eosin.

Experimental design.—Experiments undertaken at Monteverde and Curtin University were designed to test the hypothesis that changes in nectar volume, the length and curvature of flowers ("corollas") in which nectar was provided, and the spatial orientation of those flowers would significantly influence the ability of honeyeaters and hummingbirds to harvest nectar. They were also intended to determine whether members of the two groups responded in different ways or at different levels. Almost identical setups were employed at the two locations, using artificial flowers made from pieces of transparent polythene tubing with internal diameters of 4.6 mm (for hummingbirds) and 6.9 mm (for honeyeaters) mounted on the sealed tips of 1-mL syringes. Lengths of the flowers were varied (10, 20, 30, or 40 mm) depending on the experimental regime. In most cases, flowers were straight (i.e., had a curvature index of 0.0, as defined by Paton and Collins [1989], though in one series of experiments they were assigned a curvature index of 0.2). Artificial nectar with a sucrose concentration of 16.0 mg per 100 µL was added to each flower used, with an initial volume of 10, 20, 40, or 100 µL. Nectar volumes and flower lengths and curvatures were chosen to span the range of values that at least some honeyeaters and hummingbirds might reasonably be expected to encounter in their natural habitats (Wolf et al. 1972, Stiles 1975, Paton and Ford 1977, Feinsinger et al. 1986, Collins et al. 1990, Temeles et al. 2002).

I employed a repeated-measures design to test for the possible influence of nectar volume, corolla length, or both on nectar harvesting. This involved the application of four different treatments on successive days: (1) 10 µL of nectar was provided in a straight, erect corolla that was 10 mm long (µL10 mm10); (2) 10 µL of nectar was provided in a straight, erect corolla that was 40 mm long (µL10 mm40); (3) 100 µL of nectar was provided in a straight, erect corolla that was 10 mm long (µL100 mm10); and finally (4) 100 µL of nectar was provided in a straight, erect corolla that was 40 mm long (µL100 mm40). Each time that a bird was tested, access was given to only one flower, though the procedure was repeated with other flowers on four or five occasions.

In testing for possible effects of differences in corolla curvature on nectar intake by honeyeaters, birds were provided with (1) 10 µL of nectar in an erect corolla that had a curvature index of 0.0 (µL10 curv0.0), (2) 10 µL of nectar in an erect corolla that had a curvature index of 0.2 (µL10 curv0.2), (3) 100 µL of nectar in an erect corolla that had a curvature index of 0.0 (µL100 curv0.0), and (4) 100 µL of nectar in an erect corolla that had a curvature index of 0.2 (µL100 curv0.2). Sequential treatments applied when testing for the possible influence of changes in the spatial positioning of flowers involved the provision of (1) 10 µL of nectar in a straight corolla that was in an erect position (µL10 erect), (2) 10 µL of nectar in a straight corolla that was in a pendulous position (µL10 pend), (3) 100 µL of nectar in a straight corolla that was in an erect position (µL100 erect), and (4) 100 µL of nectar in a straight corolla that was in a pendulous position (µL100 pend). Identical treatments were used in studying hummingbirds, except that 40 rather than 100 µL of nectar was supplied to each flower. In all cases, the corollas used were 30 mm long.

Measurements.—Hummingbirds hovered while foraging at single flowers that had been attached temporarily to a wooden support in the aviary at Monteverde, whereas honeyeaters always perched adjacent to the flowers that they visited in the Curtin University aviary. The duration of each foraging bout (from the time of insertion of the bill into a flower to the time of its removal) and the volume of nectar extracted during that bout were recorded using Tag Heuer digital stopwatches and Drummond micro-pipettes, respectively. The rate at which nectar was extracted and the energetic efficiency of this process were then calculated for each bout. Foraging efficiency was computed as the difference between the amount of energy taken in and the cost of hovering or perching while foraging, assuming that the unit cost of hovering by hummingbirds was 900 J g^{-1} h^{-1}, the unit perching cost for honeyeaters at the prevailing aviary temperature of 20°C was 200 J g^{-1} h^{-1}, and the energy content of each milligram of nectar (sucrose) drunk was 16.74 J (Hainsworth et al. 1977, Collins and Briffa 1983, Collins and Newland 1986). Values obtained for individual birds during replicate foraging bouts associated with each treatment were averaged and the means used in the analyses outlined below. Licking rates were assessed by means of digital recording and frame-by-frame playback using a Canon MV30i camcorder during experiments involving New Holland Honeyeaters and

Western Spinebills. Similar data were not obtained for hummingbirds because suitable recording equipment was not available at Monteverde.

Statistical analyses.—Means and standard deviations of morphometric measurements were calculated for each species. Data generated using the repeated-measures protocols outlined above were analyzed using STATVIEW (SAS Institute 1998). For each group of species (honeyeaters or hummingbirds), multivariate analysis of variance (MANOVA) based on log-transformed data and using Wilks' lambda statistic was used to ascertain whether the parameters measured were significantly influenced by the treatments applied and whether responses differed between species. This approach avoided violations of the assumption that orthogonal components are uncorrelated and have equal variance that can occur when univariate analysis of variance (ANOVA) is used to analyze repeated-measures data (Zar 1999). In cases where overall treatment effects were detected, Scheffe pairwise comparisons were made for each species. In cases where honeyeaters and hummingbirds had been subjected to identical experimental conditions, comparisons of mean foraging times, percentage nectar extraction, rates of nectar intake, and foraging efficiencies for the constituent species were made using a repeated-measures ANOVA with "family" as an additional independent variable.

Results

Morphometric data.—Honeyeaters had mean body masses that ranged from 10.1 to 19.8 g, with bill gape-tip lengths of 18.3–22.8 mm and tongues whose lengths ranged from 20.2 to 28.9 mm. Hummingbirds were generally smaller, with body masses of 5.0–11.5 g, though the bill lengths of some species were much longer than those of the honeyeaters (Table 1). Bill curvatures were generally greater for honeyeaters than for hummingbirds other than Violet Sabrewings and Green Hermits, but values for all species were within the 0.0–0.2 range specified for corolla curvatures in one of the experimental protocols outlined above. Measured bill lengths, nectar extraction depths, and bill insertion depths were consistent for all species other than Green-crowned Brilliants, which have a shorter bill and insert it to a lesser distance into artificial flowers than Violet Sabrewings but have a slightly greater maximum nectar-extraction depth.

Table 1. Morphological characteristics (means ± SD) of birds used in the present study. Sample sizes were 4 in all cases, except for Brown Honeyeaters (*n* = 1) and Green Hermits (*n* = 1). Curvature indices (C.I.) were calculated as the ratios of the maximum distances between the chord joining the gape and tip of the bill and the lower surface of the culmen to the lengths of those chords (Paton and Collins 1989). Maximum nectar-extraction depths and insertion depths were measured for birds when foraging at erect, straight corollas, as indicated by Montgomerie (1984) and Temeles and Roberts (1993). An asterisk indicates that values are estimates based on data obtained during foraging experiments outlined in the text.

| Species	Mass (g)	Mean bill C.I.	Gape-tip (mm)	Extraction depth (mm)	Insertion depth (mm)	Tongue length (mm)
Western Spinebill	10.6 ± 0.3	0.131	22.8 ± 1.0	—	22.3 ± 0.9	28.9 ± 0.6
Brown Honeyeater	10.1	0.142	18.3	39.8*	19.3	23.2
New Holland Honeyeater	19.8 ± 2.7	0.085	21.7 ± 1.4	39.8*	20.3 ± 1.0	27.0 ± 0.9
Violet Sabrewing	11.5 ± 1.1	0.113	33.0 ± 1.3	62.5 ± 1.3	28.3 ± 0.4	—
Green-crowned Brilliant	9.2 ± 0.3	0.034	24.0 ± 1.5	62.9 ± 0.9	24.9 ± 0.0	—
Purple-throated Mountaingem	5.4 ± 0.1	0.007	20.0 ± 0.6	39.6 ± 0.4	22.0 ± 0.0	—
Green Hermit	6.8	0.087	44.0	81.2	38.2	—
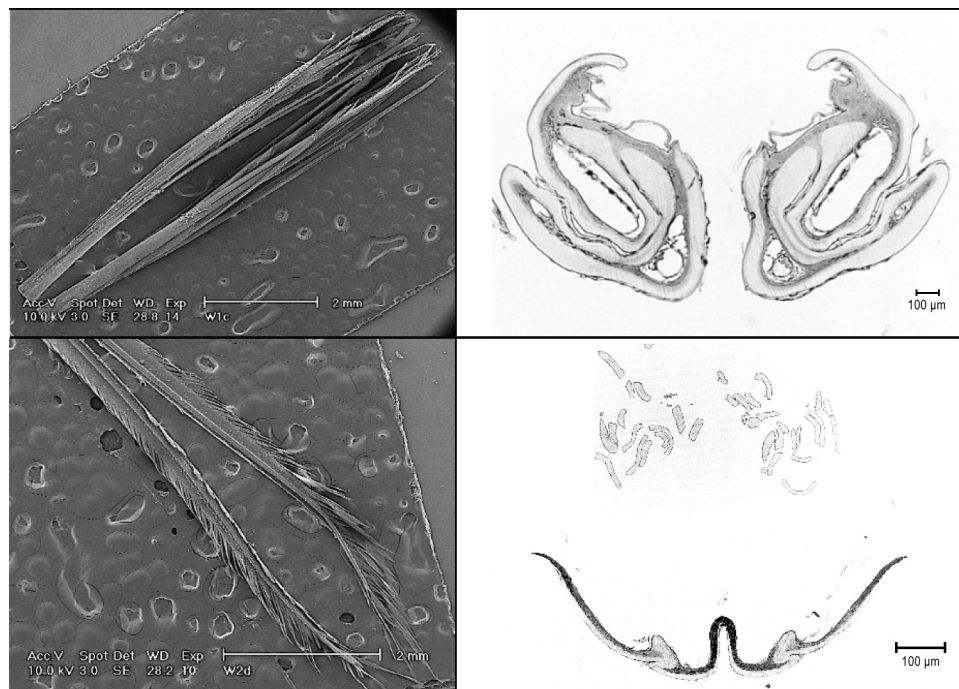
FIG. 1. Scanning electron microscope images of the brush-tipped tongues of a New Holland Honeyeater (upper left) and a Western Spinebill (lower left). Transverse sections cut through the tongues near regions where branching commences (upper right and lower right) show major grooves along which nectar is channeled by the two species, whereas the transverse section cut through the tip of the tongue of a New Holland Honeyeater (middle right) exhibits bristles with much finer and shallower grooves.

Both Western Spinebills and New Holland Honeyeaters have brush-tipped tongues, though the spatial arrangement of branches and grooves on their dorsal surfaces were dissimilar (Fig. 1). In each case, multiple grooves at the tip join to form a single broad channel that runs to the proximal extremity of the tongue. I did not document tongue morphology for Brown Honeyeaters or any of the hummingbird species.

Influence of nectar volume and corolla length on nectar intake.—New Holland Honeyeaters and Western Spinebills responded to an increase in the volume of nectar provided by significantly increasing foraging time ($F = 18.4$, df = 1 and 6, $P < 0.01$), decreasing percentage nectar extraction ($F = 104.4$, df = 1 and 6, $P < 0.001$), and increasing both the rate of nectar intake ($F = 230.1$, df = 1 and 6, $P < 0.001$) and foraging efficiency ($F = 3,057.9$, df = 1 and 6, $P < 0.001$). Overall, foraging bouts were of similar duration for the two species, though New Holland Honeyeaters extracted a significantly greater percentage of the available nectar ($F = 26.9$, df = 1 and 6, $P < 0.01$), took in nectar faster ($F = 9.6$, df = 1 and 6, $P < 0.05$), and achieved greater foraging efficiency ($F = 21.3$, df = 1 and 6, $P < 0.01$) than Western Spinebills (Fig. 2). Licking rates for New Holland Honeyeaters were greater than those for Western Spinebills ($F = 6.6$, df = 1 and 6, $P < 0.01$), though a change in the volume of nectar provided did not significantly influence rates for either species (Table 2). The volume of nectar taken in per lick was similar for the two species and increased significantly when nectar volume was increased ($F = 106.5$, df = 1 and 95, $P < 0.001$).

Overall foraging time was marginally greater for New Holland Honeyeaters than for Brown Honeyeaters when they were subjected to treatments in which nectar volume and corolla length were varied, though times increased significantly for both species when both parameters were increased ($F = 18.0$, df = 3 and 9, $P < 0.001$; Fig. 3). The percentage extraction of available nectar by Brown Honeyeaters was similar to that by New Holland Honeyeaters and was unaffected by an increase in nectar volume, but values were markedly reduced when corolla length was increased ($F = 16.9$, df = 3 and 9, $P < 0.001$). New Holland Honeyeaters drank nectar at a slightly faster overall rate than Brown Honeyeaters, though rates for both species (1) increased when nectar volume was increased and (2) decreased when corolla length was changed from 10 to 40 mm ($F = 16.3$, df = 3 and 9, $P < 0.001$). Foraging efficiencies were similar for the two species, with values for both increasing significantly when more nectar was made available but decreasing to near zero when corolla length was extended to 40 mm ($F = 18.1$, df = 3 and 9, $P < 0.001$).

Foraging times were similar for three of the hummingbird species subjected to variations in nectar volume and corolla length, with only Green Hermits taking slightly longer when attempting to extract nectar ($F = 1.5$, df = 3 and 9, $P > 0.3$). Significant treatment effects were identified, with foraging times increasing for all species when nectar volume was increased and when corolla length was changed from 10 to 40 mm ($F = 45.4$, df = 3 and 7, $P < 0.001$; Fig. 4). Percentage extraction of nectar was significantly lower for Purple-throated Mountaingems than for other species ($F = 7.7$, df = 3 and 9, $P < 0.01$) and was significantly reduced when corolla length was increased ($F = 28.5$, df = 3 and 7, $P < 0.05$). The rate at which nectar was drunk varied among species, and values for

Violet Sabrewings and Green-crowned Brilliants were significantly greater than those for other hummingbirds ($F = 15.7$, df = 3 and 9, $P < 0.001$). Rates rose for all species when nectar volume was increased but dropped significantly when corollas were lengthened, especially in the case of Purple-throated Mountaingems ($F = 151.7$, df = 3 and 7, $P < 0.001$). Similar interspecific differences in foraging efficiency were detected, apart from the fact that Green Hermits proved the equal of Violet Sabrewings and Green-crowned Brilliants ($F = 22.7$, df = 3 and 9, $P < 0.001$). Purple-throated Mountaingem was the least energetically efficient of all species, particularly when obliged to drink from 40-mm corollas supplied with 100 μL of nectar ($F = 228.0$, df = 3 and 7, $P < 0.001$).

Regardless of nectar volume or corolla length, hummingbirds' foraging bouts were significantly shorter than those recorded for the honeyeaters ($F = 11.7$, df = 1 and 16, $P < 0.01$). By contrast, overall percentage nectar extraction ($F = 14.9$, df = 1 and 16, $P < 0.01$), rate of nectar intake ($F = 37.6$, df = 1 and 16, $P < 0.001$), and foraging efficiency ($F = 11.8$, df = 1 and 16, $P < 0.01$) were superior for hummingbirds.

Influence of corolla curvature on nectar intake.—New Holland Honeyeaters and Brown Honeyeaters both increased foraging times when corolla curvature was increased from 0.0 to 0.2 and more nectar was made available ($F = 40.5$, df = 3 and 9, $P < 0.001$), though the overall value was marginally lower for Brown Honeyeaters ($F = 7.7$, df = 1 and 3, $P < 0.07$; Fig. 5). Nectar extraction was least for Brown Honeyeaters ($F = 102.1$, df = 1 and 3, $P < 0.01$) but decreased for both species when they were obliged to forage at corollas with a curvature index of 0.2 ($F = 485.5$, df = 3 and 9, $P < 0.001$). Significant interaction between species and treatment was detected, with Brown Honeyeaters, but not New Holland Honeyeaters, increasing percentage extraction from curved corollas when larger volumes of nectar were provided ($F = 373.3$, df = 3 and 9, $P < 0.001$). The overall rate of nectar intake was greatest for Brown Honeyeaters ($F = 21.2$, df = 1 and 3, $P < 0.05$), despite the fact that this species experienced great difficulty when presented with small amounts of nectar in corollas with curvature indices of 0.2. Rates decreased for both species when corolla curvature was increased from 0.0 to 0.2 ($F = 348.1$, df = 3 and 9, $P < 0.001$). Foraging efficiency showed similar variations ($F = 16.5$, df = 1 and 3, $P < 0.05$; $F = 276.3$, df = 3 and 9, $P < 0.001$), Brown Honeyeaters being especially inefficient when obliged to forage at curved corollas containing 10 μL of nectar.

Violet Sabrewings and Green-crowned Brilliants spent significantly less time than other hummingbird species while foraging for nectar at flowers whose curvature indices were either 0.0 or 0.2, whereas Purple-throated Mountaingems spent more ($F = 15.2$, df = 3 and 9, $P < 0.001$; Fig. 6). All species increased foraging times when presented with more nectar, but only Purple-throated Mountaingems and, to a lesser extent, Green Hermits did so when corolla curvature was increased ($F = 50.2$, df = 3 and 7, $P < 0.001$). Percentage nectar extraction did not vary significantly between species, nor was it influenced to any marked extent by an increase in curvature of the corolla or the volume of nectar supplied. The rate of nectar intake was greatest for Violet Sabrewings and Green-crowned Brilliants ($F = 32.6$, df = 3 and 9, $P < 0.001$) and increased for all species when nectar volume changed from 10 to 40 μL, though only Purple-throated Mountaingems appeared to suffer, and Violet Sabrewings to benefit, from an increase in corolla
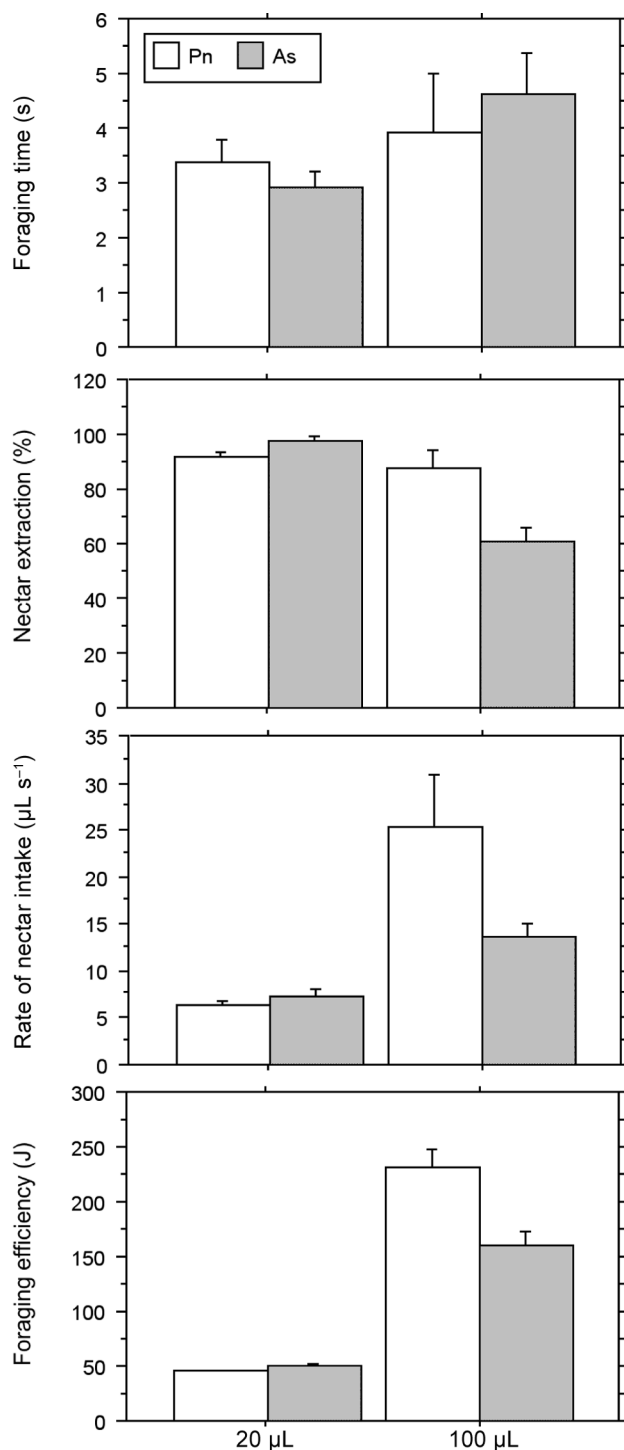

Fig. 2. Mean foraging time, percentage nectar extraction, rate of nectar uptake, and foraging efficiency for Western Spinebills (As) and New Holland Honeyeaters (Pn) when presented with either 20 or 100 μL of nectar in erect corollas that were 20 mm long. Numbers of foraging bouts observed per treatment for each Western Spinebill and New Holland Honeyeater were 18–19 and 19–20, respectively. Vertical lines represent ± 1 SD.

Table 2. Nectar extraction (means ± SD) during visits by Western Spinebills and New Holland Honeyeaters to artificial tubular flowers (internal diameter 6.9 mm, depth 20 mm) when 20 or 100 μL of nectar was available. Numbers of foraging bouts are indicated in parentheses.

Honeyeater species	Nectar availability (μL)	Foraging time (s)	Nectar intake rate (μLs⁻¹)	Licking rate (licks s⁻¹)	Licking nectar uptake (μL lick⁻¹)
Western Spinebill	20	2.7 ± 0.9 (239)	7.7 ± 2.3 (239)	7.5 ± 1.4 (36)	0.9 ± 1.0 (36)
	100	4.6 ± 2.1 (74)	13.6 ± 2.5 (74)	7.6 ± 4.8 (28)	2.5 ± 1.2 (28)
New Holland Honeyeater	20	3.2 ± 1.5 (135)	7.0 ± 3.2 (135)	8.9 ± 0.8 (25)	0.9 ± 0.3 (25)
	100	4.0 ± 1.6 (105)	24.9 ± 7.9 (105)	9.3 ± 0.9 (10)	2.7 ± 1.0 (10)

curvature ($F = 305.0$, df = 3 and 7, $P < 0.001$). Foraging efficiency was similar for all species and increased when nectar availability rose ($F = 1{,}373.5$, df = 3 and 7, $P < 0.001$) but was not influenced by a change in corolla curvature.

Statistical comparisons of the responses of hummingbirds and honeyeaters to changes in corolla curvature have been restricted to instances where all birds had been supplied with the same amounts (10 μL) of nectar. Under these conditions, an increase in corolla curvature tended to increase honeyeater foraging time ($F = 60.5$, df = 1 and 16, $P < 0.001$) while decreasing the percentage nectar extraction ($F = 31.5$, df = 1 and 16, $P < 0.001$), rate of nectar intake ($F = 63.1$, df = 1 and 16, $P < 0.001$), and foraging efficiency ($F = 82.7$, df = 1 and 16, $P < 0.001$), whereas equivalent measures for hummingbirds were not significantly affected.

Influence of spatial position of corolla on nectar intake.—The time taken by Brown Honeyeaters in foraging for nectar was, again, marginally greater than that taken by New Holland Honeyeaters, with values for both species increasing when the corolla position was changed from erect to pendulous ($F = 7.4$, df = 3 and 9, $P < 0.01$; Fig. 7). Nectar extraction was similar for the two species, though New Holland Honeyeaters, in particular, experienced some difficulty when foraging at pendulous flowers ($F = 3.2$, df = 3 and 9, $P < 0.05$). New Holland Honeyeaters harvested nectar at a slightly faster rate than Brown Honeyeaters, with rates for both species decreasing when birds were obliged to forage at pendulous flowers ($F = 520.2$, df = 3 and 9, $P < 0.05$). Foraging efficiencies of the two species were similar, with birds reducing their net energy intake when extracting nectar from pendulous corollas that contained relatively large volumes of nectar ($F = 232.3$, df = 3 and 9, $P < 0.001$).

The duration of foraging bouts was least for Violet Sabrewings and Green-crowned Brilliants when birds were presented with nectar in erect or pendulous corollas ($F = 3.6$, df = 3 and 9, $P < 0.05$; Fig. 8). Times increased significantly for all species when they were provided with larger volumes of nectar but seemed to be only slightly affected by changes in the spatial orientation of the corolla. Overall percentage nectar extraction was lowest for Purple-throated Mountaingems ($F = 5.6$, df = 3 and 9, $P < 0.05$), though no species' values varied significantly in response to a change in position of the corolla. Rates at which nectar was extracted were greatest for Violet Sabrewings and Green-crowned Brilliants ($F = 4.0$, df = 3 and 9, $P < 0.05$) but were essentially independent of corolla position. Foraging efficiencies were similar for the four species, regardless of whether corollas were erect or pendulous.

Statistical comparisons of the responses of hummingbirds and honeyeaters to changes in corolla position have been restricted to instances where all birds had been supplied with the same amount (10 μL) of nectar. Under these conditions, a switch in corolla position from erect to pendulous tended to increase honeyeater foraging time ($F = 32.4$, df = 1 and 16, $P < 0.001$) while decreasing the percentage nectar extraction ($F = 7.5$, df = 1 and 16, $P < 0.01$), rate of nectar intake ($F = 39.0$, df = 1 and 16, $P < 0.001$), and foraging efficiency ($F = 18.0$, df = 1 and 16, $P < 0.001$), whereas equivalent measures for hummingbirds were not significantly affected.

Discussion

Efficiency of nectar extraction under controlled laboratory conditions.—Data presented above clearly indicate that the duration of foraging bouts increased significantly for all seven hummingbird and honeyeater species when the volume of available nectar was increased, extraction presumably ceasing when drinking was no longer profitable or when birds were temporarily unable to swallow more fluid, or both (Collins and Cary 1981). This suggests that enhanced rates of nectar intake were at least partly attributable to a reduction in the distance each bird had to insert its bill and protrude its tongue into a flower before contacting the nectar (Table 3; Ewald and Williams 1982, Temeles and Roberts 1993). In this situation, the amount of time spent inserting the bill would have become a smaller proportion of total foraging time, with a higher proportion devoted to licking (Paton and Collins 1989).

The reduction in distance between nectar surface and corolla opening that is associated with an increase in nectar volume should have resulted in increased contact between tongue and nectar, with more nectar moving by capillarity into grooves on the tongue during each lick (Kingsolver and Daniel 1983). This proposition is supported by data obtained for Western Spinebills and New Holland Honeyeaters in the present study (Table 2) and for a range of other honeyeater species whose tongues collected
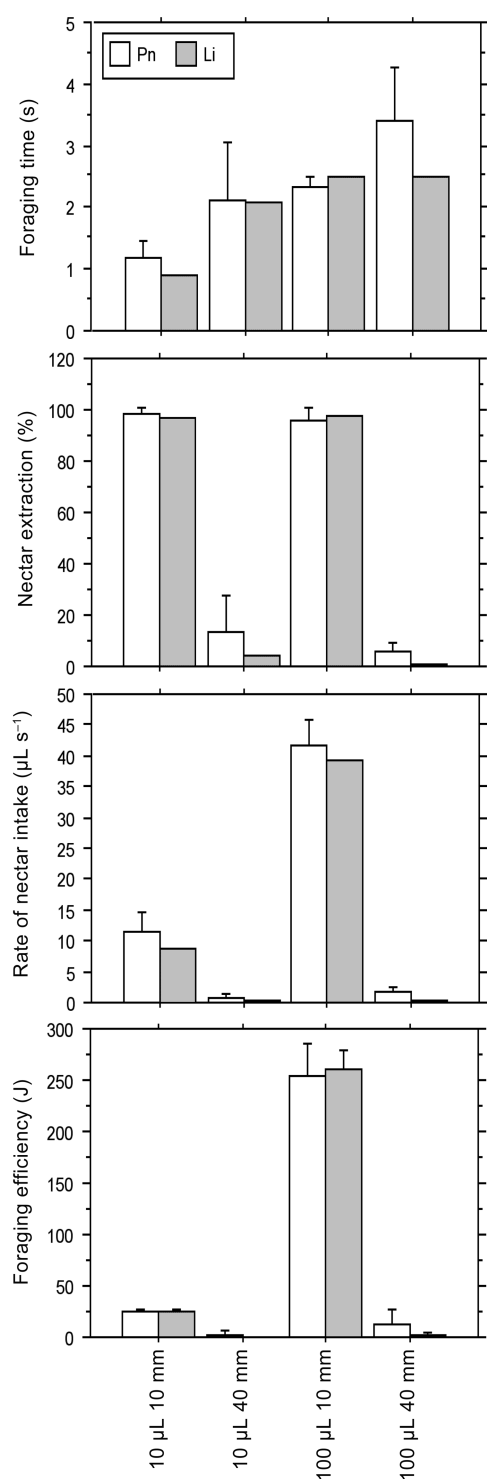
FIG. 3. Mean foraging time, percentage nectar extraction, rate of nectar uptake, and foraging efficiency for Brown Honeyeaters (Li) and New Holland Honeyeaters (Pn) when presented with either 10 or 100 μL of nectar in erect corollas that were either 10 or 40 mm long. Twenty foraging bouts were observed per treatment for each bird. Vertical lines represent ± 1 SD.

FIG. 4. Mean foraging time, percentage nectar extraction, rate of nectar uptake, and foraging efficiency for Violet Sabrewings (Ch), Green-crowned Brilliants (Hj), Purple-throated Mountaingems (Lc), and Green Hermits (Pg) when presented with either 10 or 100 μL of nectar in erect corollas that were either 10 or 40 mm long. Between 3 and 5 foraging bouts were observed per treatment for each bird. Vertical lines represent ± 1 SD.

FIG. 5. Mean foraging time, percentage nectar uptake, rate of nectar uptake, and foraging efficiency for Brown Honeyeaters (Li) and New Holland Honeyeaters (Pn) when presented with either 10 or 100 µL of nectar in erect 30-mm corollas that had curvature indices of either 0.0 or 0.2. Twenty-one foraging bouts were observed per treatment for each New Holland Honeyeater and 10 for each Brown Honeyeater. Vertical lines represent ± 1 SD.
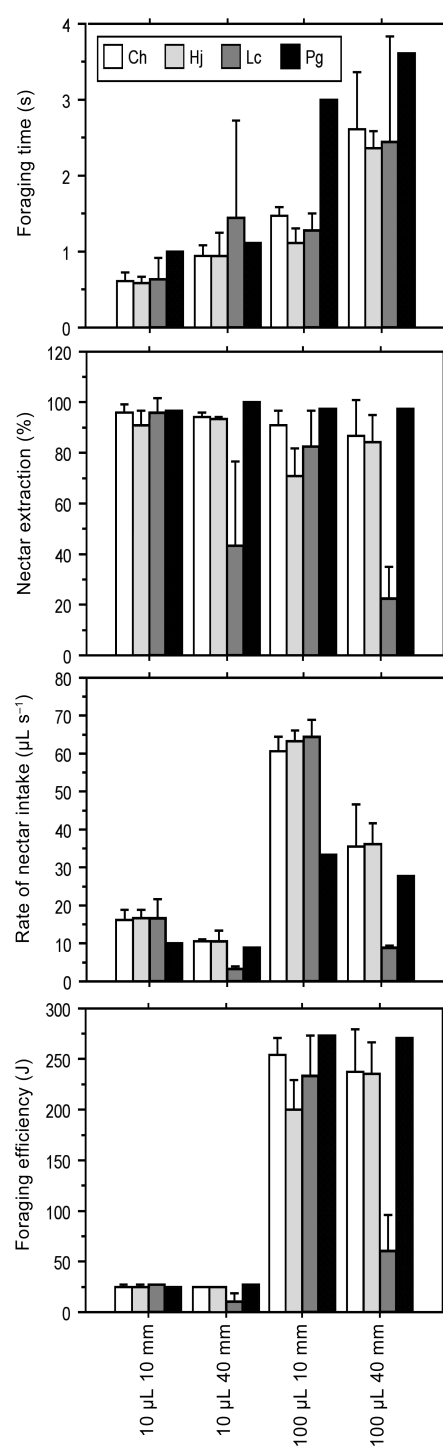
FIG. 6. Mean foraging time, percentage nectar extraction, rate of nectar uptake, and foraging efficiency for Violet Sabrewings (Ch), Green-crowned Brilliants (Hj), Purple-throated Mountaingems (Lc), and Green Hermits (Pg) when presented with either 10 or 40 µL of nectar in erect 30-mm corollas that had curvature indices of either 0.0 or 0.2. Four or five foraging bouts were observed per treatment for each species. Vertical lines represent ± 1 SD.
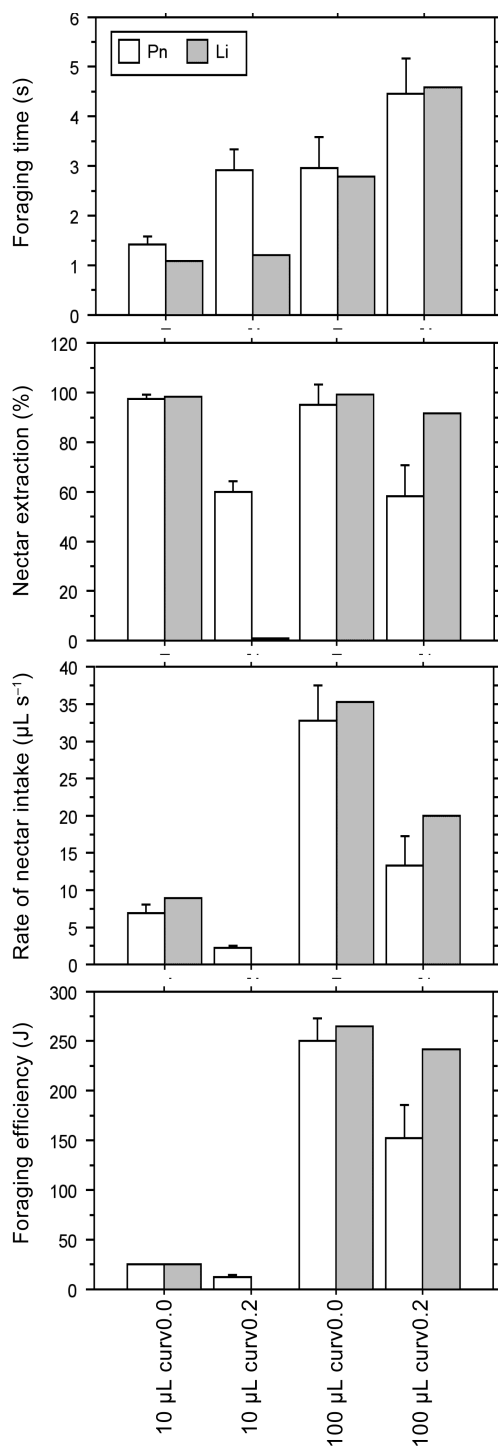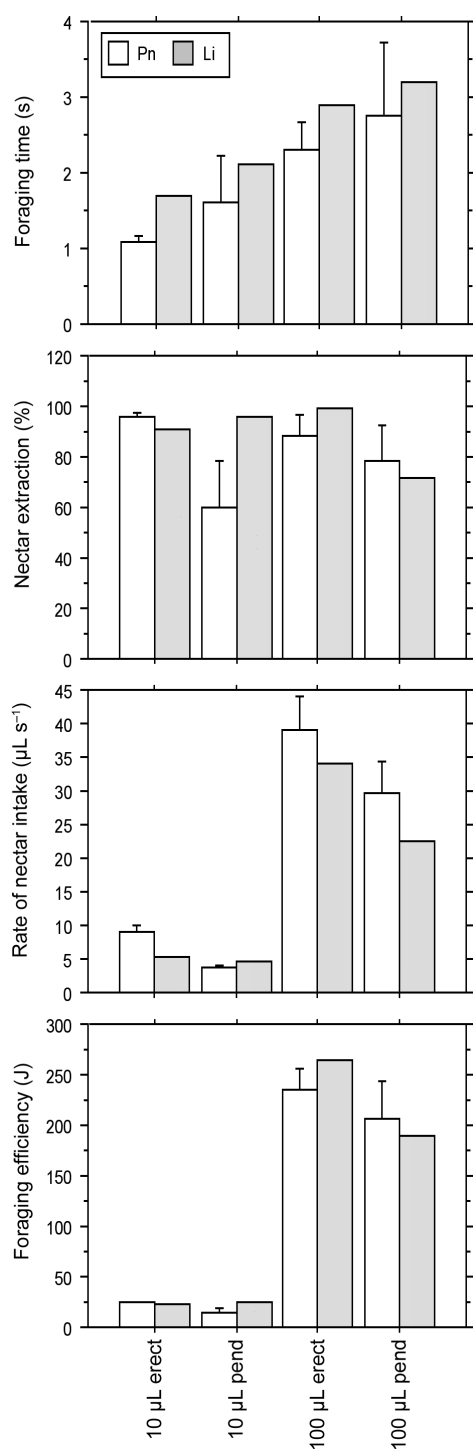
FIG. 7. Mean foraging time, percentage nectar extraction, rate of nectar uptake, and foraging efficiency for Brown Honeyeaters (Li) and New Holland Honeyeaters (Pn) when presented with either 10 or 100 µL of nectar in 30-mm corollas whose spatial orientation was either erect or pendulous. Ten foraging bouts were observed per treatment for each New Holland Honeyeater and 20 for each Brown Honeyeater. Vertical lines represent ± 1 SD.
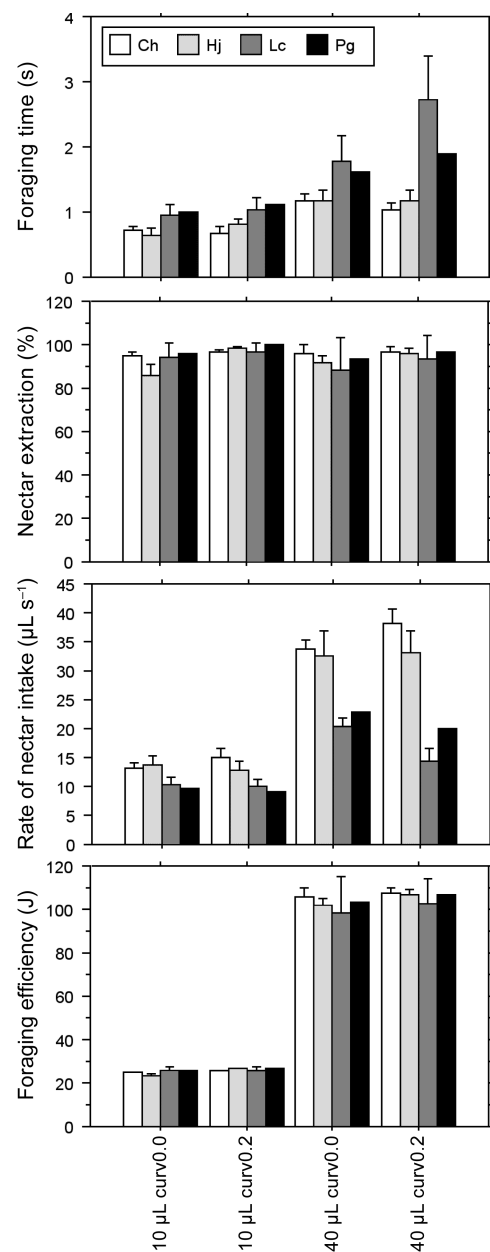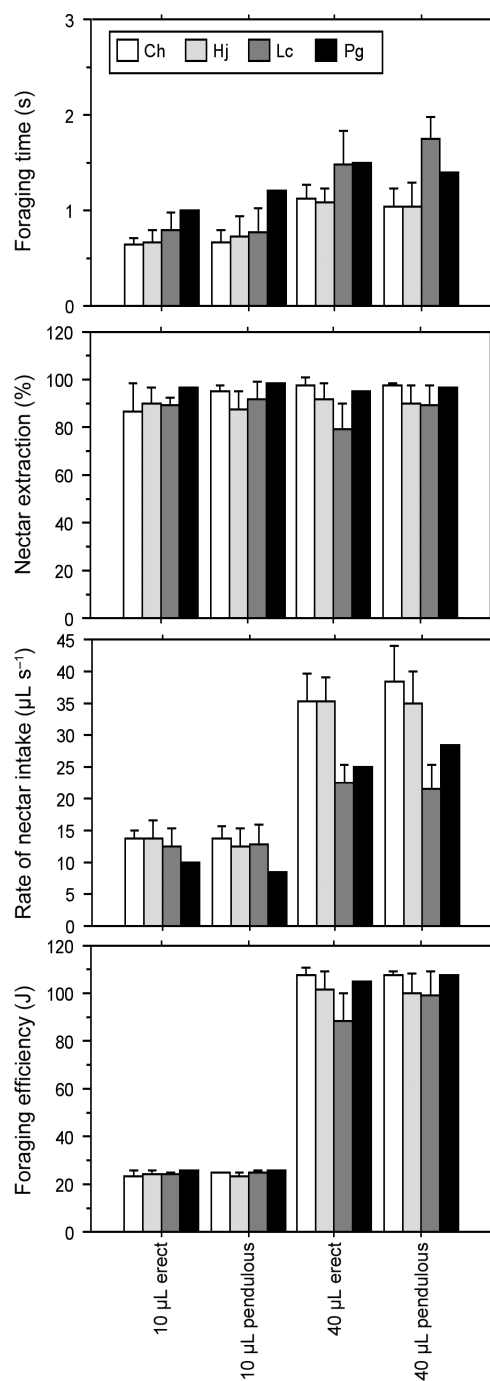
FIG. 8. Mean foraging time, percentage nectar extraction, rate of nectar uptake, and foraging efficiency for Violet Sabrewings (Ch), Green-crowned Brilliants (Hj), Purple-throated Mountaingems (Lc), and Green Hermits (Pg) when presented with either 10 or 100 µL of nectar in 30-mm corollas whose spatial orientation was either erect or pendulous. Four foraging bouts were observed per treatment for each species. Vertical lines represent ± 1 SD.

Table 3. Maximum depth of drinking, tongue extension, and accessibility of nectar for hummingbirds and honeyeaters that visited artificial flowers. Internal diameters of corollas visited by these birds were 4.6 and 6.9 mm, respectively. Nectar accessibility has been calculated as the distance from the opening of the corolla to the surface of the nectar supplied.

Nectarivorous species	Depth of drinking (mm)	Insertion depth (mm)	Tongue extension (mm)	Corolla length (mm)	Accessibility of nectar (mm)		
					10 µL supplied	40 µL supplied	100 µL supplied
Western Spinebill	—	22.3	—	10	9.7	—	7.3
				40	39.7	—	37.3
Brown Honeyeater	39.8	19.8	20.0	10	9.7	—	7.3
				40	39.7	—	37.3
New Holland Honeyeater	39.8	20.3	19.5	10	9.7	—	7.3
				40	39.7	—	37.3
Violet Sabrewing	62.5	28.3	34.2	10	9.4	7.6	—
				40	39.4	37.6	—
Green-crowned Brilliant	62.9	24.9	38.0	10	9.4	7.6	—
				40	39.4	37.6	—
Purple-throated Mountaingem	39.6	22.0	17.6	10	9.4	7.6	—
				40	39.4	37.6	—
Green Hermit	81.2	38.2	43.0	10	9.4	7.6	—
				40	39.4	37.6	—

additional nectar when immersed more deeply into the fluid (Table 4; Paton and Collins 1989). There is no suggestion that licking rates changed appreciably. Nevertheless, New Holland Honeyeaters, which are larger than Western Spinebills, lick at a slightly faster rate, are capable of taking in more nectar per lick, and have a higher overall rate of nectar intake. Similar evidence is not available in relation to Brown Honeyeaters or any of the hummingbirds observed in the present study, though Roberts (1995) has shown that the average nectar intake per lick by Rufous Hummingbirds (*Selasphorus rufus*) increased when they were provided with larger volumes of nectar.

It has been suggested that hummingbirds and honeyeaters are roughly similar in terms of their capacity to remove nectar from artificial tubular flowers, six species of hummingbird being

Table 4. Morphology and fluid-collecting capacity of honeyeater tongues whose distal extremities were immersed to varying degrees in artificial nectar (Paton and Collins 1989).

Species	Brush length (mm)	Tongue width (mm)	Mean mass (mg) of fluid collected by	
			Entire brush	Tip
Eastern Spinebill	5.7	0.7	1.80	0.50
Red Wattlebird (*Anthochaera carunculata*)	16.3	2.7	20.02	6.20
Yellow-faced Honeyeater (*Lichenostomus chrysops*)	6.4	1.4	2.60	1.32
Yellow-throated Miner (*Manorina flavigula*)	10.2	1.5	4.84	1.80
Brown-headed Honeyeater (*Melithreptus brevirostris*)	5.4	1.4	2.10	0.64
New Holland Honeyeater	12.9	1.1	6.14	1.37

known to drink from an *ad-libitum* supply of 0.5–1.0 M nectar at 10–72 µL s^{-1} (Hainsworth 1973, Wolf and Hainsworth 1977, Ewald and Williams 1982), whereas three species of honeyeater drank 0.8 M sucrose at 20–74 µL s^{-1} (Collins and Clow 1978, Collins and Morellini 1979, Collins et al. 1980). Nevertheless, data generated in the present study when all birds were subjected to essentially identical treatments and the availability of nectar was limited indicate that significant differences occur. For instance, Brown Honeyeaters and New Holland Honeyeaters extracted 97–98% of the available nectar at rates of approximately 9–11 and 40–42 µL s^{-1}, respectively, when supplied with 10 or 100 µL of nectar. By contrast, hummingbirds had generally higher nectar-intake rates of 10–17 and 33–65 µL s^{-1}, even though most of these birds were smaller than the honeyeaters in the study. This does not necessarily mean that hummingbirds' tongues are more capable of capturing nectar than those of honeyeaters; it may be a consequence of hummingbirds licking slightly faster.

Licking rates were not recorded for hummingbirds during the present study, but Ewald and Williams (1982) and Roberts (1995) have demonstrated that Anna's Hummingbirds (*Calypte anna*) and Rufous Hummingbirds averaged mean rates of 13.8 and 9.4 licks s^{-1}, respectively, when drinking small volumes of dilute nectar. These values exceed rates reported here for Western Spinebills and New Holland Honeyeaters. Regardless of whether or not hummingbirds maximize their rate of net energy gain during individual foraging bouts, it would be advantageous for these birds, which usually hover while foraging, if they reduced foraging times and increased the rate at which they acquired nectar (Hainsworth 1991). Three of the hummingbird species involved in the present study appeared to be particularly adept at doing this, having intake rates that were >35% greater than those of the larger Brown Honeyeater or New Holland Honeyeater but foraging times that were similar or shorter, while still achieving comparable or greater foraging efficiencies (Table 5). Responses such as these may also have the added advantage of reducing the risk of predation while foraging (Newman et al. 1988).

Table 5. Nectar intake from erect tubular flowers with a depth of 10 or 40 mm during individual foraging bouts by Brown Honeyeaters (Li), New Holland Honeyeaters (Pn), Violet Sabrewings (Ch), Green-crowned Brilliants (Hj), Purple-throated Mountaingems (Lc), and Green Hermits (Pg). Values used are means extracted from Figures 3 and 4 and Table 1.

| Parameter | Species | Bill length (mm) | Nectar availability / corolla length | | | |
			10 µL / 10 mm	100 µL / 10 mm	10 µL / 40 mm	100 µL / 40 mm
Foraging time (s)	Li	18.3	0.9	2.5	2.1	2.5
	Pn	21.7	1.2	2.4	2.1	3.4
	Ch	33.0	0.6	1.5	0.9	2.6
	Hj	24.0	0.6	1.1	0.9	2.4
	Lc	20.0	0.7	1.3	1.0	2.2
	Pg	44.0	1.0	3.0	1.1	3.6
Rate of nectar intake (µL s–1)	Li	18.3	10.7	39.9	0.1	0.3
	Pn	21.7	8.6	41.9	0.7	2.0
	Ch	33.0	16.0	60.9	10.4	35.7
	Hj	24.0	16.7	63.2	10.9	36.6
	Lc	20.0	16.3	64.7	3.3	8.4
	Pg	44.0	10.0	33.3	9.0	27.6
Foraging efficiency (J)	Li	21.7	25.5	260.3	0.0	1.4
	Pn	33.0	24.9	254.7	2.5	19.9
	Ch	24.0	25.5	252.2	24.1	237.0
	Hj	20.0	24.8	197.3	24.3	240.4
	Lc	44.0	26.5	236.2	8.1	54.1
	Pg	18.3	25.9	272.5	26.6	271.5

Investigations conducted by Hainsworth (1973) and Montgomerie (1984) have shown that an increase in the length of artificial corollas visited by hummingbirds such as the Black-chinned Hummingbird (*Archilocus alexandri*), Blue-throated Hummingbird (*Lampornis clemenciae*), Cinnamon Hummingbird (*Amazilia rutila*), and Broad-billed Hummingbird (*Cyanthus latirostris*) resulted in an initial moderate increase in foraging time and drop in the rate of nectar intake, with more pronounced changes occurring once corolla length exceeded bill length. It has been suggested by Hainsworth (1973) and Montgomerie (1984) that the initial change in nectar intake was accompanied by a significant increase in licking rate and a marked drop in the volume of nectar taken during each lick, though subsequent changes were attributable almost entirely to further reductions in nectar uptake per lick. Reported changes in licking rates for these birds are at variance with what might be expected on theoretical grounds, where an increase in corolla length would be expected to result in birds taking longer to protrude and retract their tongues, thus licking at a slower rate.

All hummingbirds and honeyeaters observed during the present study responded in superficially similar fashion to an increase in corolla length, with the duration of foraging bouts increasing and the percentage nectar extraction, rate of nectar intake, and foraging efficiency decreasing. New Holland Honeyeaters, Brown Honeyeaters, and Purple-throated Mountaingems experienced particular difficulty in extracting nectar from corollas that were 40 mm long, exhibiting a marked drop in foraging efficiency (Figs. 3 and 4). They appeared to be constrained by their relatively short bills and tongues, even when larger volumes of nectar were provided (Table 3). Limited information obtained for two of the honeyeater species involved in this project suggest that licking rates may not have changed as corolla length was increased, though the

volume of nectar taken in per lick decreased, most likely as a consequence of reduced contact between tongue and nectar (Table 2; B. G. Collins unpubl. data).

Bills of New Holland Honeyeaters and Brown Honeyeaters, in particular, and of Violet Sabrewings and Green Hermits were moderately decurved, whereas those of Green-crowned Brilliants and Purple-throated Mountaingems were essentially straight (Table 1). As expected, given that it has a straight bill, the Purple-throated Mountaingem increased the rate at which it drank nectar from curved flowers. However, the straight-billed Green-crowned Brilliant and the curved-billed Violet Sabrewing and Green Hermit remained largely unaffected by an increase in curvature (Fig. 6). By contrast, both honeyeater species increased the duration of their foraging bouts and reduced the percentage nectar extraction, rate of nectar intake, and foraging efficiency when probing corollas with a curvature index of 0.2. Overall differences between the responses of honeyeaters and and those of hummingbirds suggest that factors such as bill width and depth, which are generally greater in honeyeaters, may have influenced the capacity of these birds to maneuver their bills when foraging for nectar in curved flowers. Further experimental work will be required to establish whether species such as Green Hermits and Violet Sabrewings would be better suited than other hummingbirds for foraging at curved flowers that were longer than those used in the present study, or whether the responses of any species would be affected by a reduction in the diameter of these flowers.

Gravity would be expected to influence the capillary movement of nectar into grooves on hummingbird and honeyeater tongues, with greater uptake when birds are obliged to forage at pendulous flowers (Kingsolver and Daniel 1983). However, Montgomerie (1984) found no consistent variations in the rates of nectar

uptake for two hummingbird species when the spatial positioning of artifical flowers that they visited was altered. This finding has been confirmed for all four hummingbird species considered here, with foraging time, nectar extraction, rate of nectar intake, and foraging efficiency unaffected by a change in corolla position from erect to pendulous. Although New Holland Honeyeaters and Brown Honeyeaters were able to forage effectively at pendulous flowers, individual foraging bouts were longer and less rewarding than when flowers were erect. These differences are not unexpected, because honeyeaters perch while foraging, often having to lean over before being able to insert their curved and relatively broad bills into flowers before extracting nectar. Under these conditions, the proportion of foraging time devoted to licking might have been less than that when birds were visiting erect flowers.

Efficiency and rate of nectar extraction in the field.—Hummingbirds and honeyeaters are clearly capable of adjusting their nectar intake in response to changes in floral traits. Nevertheless, it is conceivable that they may be unable to extract nectar from real flowers with the efficiency achieved in the laboratory because their performance is closely related to the manner in which nectar is packaged and presented.

Data that might allow us to address questions relating to nectar extraction in the field are sparse and, in many cases, little more than anecdotal. Nevertheless, hummingbirds for which quantitative field data are available clearly manage to remove 70–100% of the nectar present in flowers they visit (Wolf et al. 1976, Hainsworth 1977, Gass and Montgomerie 1981, Feinsinger et al. 1985). Divergent bill and floral traits are undoubtedly responsible for the seeming inefficiency that sometimes occurs, and the presence of complex internal partitions or other structures that impede the entry of bills and tongues into flowers of plants such as *Heliconia* spp. and *Salvia* spp. would certainly be expected to hamper nectar intake (E. Temeles pers. comm.).

Field data for honeyeaters suggest that these birds remove closer to 90–100% of the available nectar, apart from instances where they visit plants such as banksias and dryandras, and forage for nectar that is often widely dispersed between, rather than confined within, their closely packed flowers (Paton and Ford 1977, Collins and Briffa 1982, Collins and Newland 1986, Collins et al. 1990; Table 6). The perceived failure of honeyeaters (or hummingbirds) to remove all available nectar is not necessarily an indication of inefficiency, given that birds may benefit energetically by moving to flowers where greater or faster acquisition of nectar is possible (Collins and Paton 1989).

Rates of nectar intake have been measured for a small number of hummingbirds under field conditions at Finca La Selva and Villa Mills in Costa Rica, with values ranging from 3 to 21 μL s^{-1}, depending on the bird and plant species involved (Wolf et al. 1972, 1976). Rates for some honeyeaters are similar but can be considerably higher when birds forage at plants such as banksias and dryandras, which have high-nectar standing crops, and can vary substantially throughout the day (Table 7). As a general rule, intake rates for both honeyeaters and hummingbirds in the field are lower than those recorded for similar-sized birds in the laboratory. This is not surprising, given that flowers with higher nectar concentrations, smaller nectar standing crops, and narrower or partially obstructed corollas are often found in natural habitats (Feinsinger et al. 1986, Collins and Rebelo 1987, Mitchell and Paton 1990).

Anecdotal evidence suggests that some hummingbirds forage preferentially at flowers that exhibit particular attributes, with a correlation between bill shape–length–curvature and the morphology of those flowers. For example, Wolf et al. (1976) demonstrated that Magnificent Hummingbirds (*Eugenes fulgens*), which have relatively straight bills 30–35 mm long, often visit flowers of *Centropogon talamancensis*, which has long, straight corollas. By

TABLE 6. Floral morphology, mean nectar availability, and nectar extraction by honeyeaters visiting a range of plant species at various times of day in southern and western Australia (Paton and Ford 1977, Hopper and Burbidge 1978, Collins and Briffa 1982, Collins et al. 1990, B. G. Collins unpubl. data). One asterisk indicates that inflorescences of *Dryandra sessilis* and the *Banksia* spp. listed comprise multiple, closely packed gullet-shaped flowers; nectar availability and removal data for these species refer to entire inflorescences rather than individual flowers. A double asterisk indicates that corollas of these flowers are lost by the time foraging for nectar commences. Where known, sample sizes are indicated in parentheses.

Plant species	Flower shape	Corolla length/ diameter (mm)	Nectar availability (μL)	Nectar removal (%)
Adenanthos barbigera (30)	Gullet	15/5	9	95
Anigozanthos humilis (??)	Gullet	23/5	30	—
Anigozanthos manglesii (??)	Gullet	31/7	12	—
Astroloma conostephioides	Tube	21/—	25	88
Banksia attenuata* (15)	Gullet	18/2	200	—
Banksia prionotes* (15)	Gullet	13/–	68	—
Callistemon macropunctatus** (??)	Shallow open cup	0/0	13	96
Calothamnus quadrifidus (40)	Semi-fused tube	27/—	15	87
Calothamnus rupestris (30)	Semi-fused tube	32/10	5	94
Dryandra sessilis* (30)	Gullet	14/2	7	71
Epacris impressa (??)	Tube	14/—	2	99
Eucalyptus leucoxylon** (??)	Shallow open cup	0/0	5	99
Eucalyptus rhodantha** (20)	Shallow open cup	0/0	89	—
Grevillea wilsonii (30)	Gullet	15/7	30	—
Lambertia inermis (20)	Tube	17/5	—	—

Table 7. Nectar-extraction and mean foraging efficiencies of Brown Honeyeaters and New Holland Honeyeaters when visiting flowers (*) or inflorescences (**) in Western Australia at different times of day: (A) the first two hours after dawn, (B) the two hours after noon, and (C) the two hours before dusk (Collins et al. 1984, 1990; Collins and Newland 1986; B. G. Collins unpubl. data). Numbers of honeyeater visits to flowers are indicated in parentheses after foraging times; other parameters were measured or calculated using the same sample sizes.

Parameter	Time of day	Brown Honeyeater			New Holland Honeyeater	
		*Calothmnus quadrifidus**	*Dryandra carduacea***	*Dryandra sessilis***	*Calothamnus rupestris**	*Dryandra sessilis***
Foraging time (s)	A	0.6 (40)	9.3 (28)	14.4 (33)	1.4 (16)	10.3 (25)
	B	0.6 (20)	10.6 (17)	9.0 (21)	—	—
	C	0.6 (20)	7.0 (10)	13.0 (11)	1.2 (11)	15.2 (10)
Nectar intake (µL flower^{-1})	A	12.2	71.4	140.6	31.6	64.8
	B	1.0	1.0	21.4	—	—
	C	0.6	4.6	12.0	4.5	4.8
Rate of intake (µL s^{-1})	A	20.3	7.7	9.8	22.6	6.3
	B	1.7	0.1	2.4	—	—
	C	1.0	0.7	0.9	3.8	0.3
Foraging efficiency (J)	A	43.9	257.7	509.6	115.8	234.6
	B	3.3	−2.3	73.7	—	—
	C	1.9	13.0	36.8	16.1	11.6

contrast, the shorter, curved flowers of *Centropogon valerii* are usually visited by Green Violet-ears (*Colibri thalassinus*), a species that has a slightly decurved 21-mm bill. Tight correlations of this type are rarely found in habitats occupied by honeyeaters. For instance, the Western Spinebill, which has a thin and moderately curved bill, visits the narrow, slightly curved, gullet-shaped flowers of *Adenanthos barbigera* but is an even more frequent visitor to flowers that do not offer the same restrictions (Collins and Newland 1986). The closely related and morphologically similar Eastern Spinebill (*Acanthorhynchus tenuirostris*) often visits straight, tubular flowers of *Correa*, *Epacris*, and *Astroloma* in other habitats but is not restricted to flowers with curved corollas (Paton and Ford 1977). Within Australian ecosystems, where eucalypts and banksias are common sources of easily accessible nectar, most honeyeaters are quite catholic in their search for food, generally foraging at the most rewarding flowers or inflorescences rather than being constrained by floral dimensions or spatial arrangements (Collins et al. 1990).

Nectar consumed by hummingbirds is commonly offered in tubular flowers, on which they undoubtedly forage effectively in natural and artificial situations. Results of the present and other studies have shown that honeyeaters, too, are adept at extracting nectar from tubular flowers. Nevertheless, nectar is generally packaged and presented quite differently in habitats occupied by honeyeaters, with nectar often thinly and widely dispersed among the flowers. Supporting data are not yet available, but I suggest that the fimbricated tongues possessed by honeyeaters would be much better suited for nectar harvesting than bifurcated hummingbird tongues under these conditions.

Acknowledgments

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