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Short-term energy regulation of whitebellied sunbirds (*Nectarinia talatala*): effects of food concentration on feeding frequency and duration

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Summary

Avian nectarivores show compensatory feeding by adjusting their volumetric intake in response to variation in nectar concentration. This study used an infrared photo-detection system to investigate the short-term feeding patterns of whitebellied sunbirds (*Nectarinia talatala*) consuming three different sucrose concentrations (10, 20 and 30% w/w). Sunbirds increased their feeding frequency on the most dilute diet, but there was no change in feeding duration. Thus, the increase in total time spent feeding on the dilute diet was due to the increased feeding frequency. No difference in short-term feeding patterns was found between the 20% and 30% diets. Total time spent feeding was extremely short on all diets (96–144 s in every hour). Birds maintained the same steady increase in body mass over the course of the day on all three diets. Daily rhythms in feeding patterns were evident, with longer feeding duration and lower feeding frequency in the early morning and evening than during the rest of the day. Because ingestion rates on a particular diet may vary through the day, caution must be exercised in using feeding duration as a surrogate for meal size. Individual birds varied greatly in their feeding patterns irrespective of diet concentration.

Key words: compensatory feeding, feeding duration, feeding frequency, sugar concentration, sunbird, *Nectarinia talatala*.

Introduction

Avian nectarivores are ideal subjects for investigating energy management in response to variation in food quality and quantity, since they are small, with a high energy turnover, and feed on a simple and easily digested diet. The nectar consumed by birds varies greatly in concentration among and within plant species (Nicolson and Fleming, 2003a), and avian nectarivores adjust the volume that they consume according to nectar concentration. The compensatory feeding hypothesis predicts that food intake is varied in order to maintain a constant energy intake, and this has been demonstrated in a variety of nectar-feeding birds (for a review, see Martínez del Rio et al., 2001). Whitebellied sunbirds (*Nectarinia talatala*), for instance, show perfect compensatory feeding over a tenfold range of nectar concentration. Their average daily intake of 0.31 g sugar g^{-1} body mass is maintained on diets from 0.25–2.5 mol l^{-1} sucrose by adjusting the volumetric intake from 30.3 to 3.3 ml per day, a ninefold difference (Nicolson and Fleming, 2003b).

These dramatic differences in volumetric intake require alterations in meal frequency and/or meal size as food concentration varies. Several hummingbird species increase the number of feeding bouts as sugar concentration decreases, but maintain a nearly constant feeding bout length (Wolf and Hainsworth, 1977). Other hummingbirds, and honeyeaters, have also been shown to increase their feeding frequency when sugar concentration is decreased (Gass, 1978; Collins and Clow, 1978; López-Calleja et al., 1997). Energy gained from the nectar is not only required for the time between feeding bouts but must also be accumulated for overnight requirements. In a more prolonged experiment using hummingbirds with depleted energy reserves due to food deprivation, *Eugenes fulgens* used increased meal frequency to increase their energy storage rates, whereas *Lampornis clemenciae* used increased meal size, and both species reduced energy expenditure between meals (Hainsworth et al., 1981). No comparable information is available for sunbirds.

In this study, the effect of various sugar concentrations on short-term feeding patterns of whitebellied sunbirds was determined. Sucrose solutions were used, since sucrose and hexoses are equally well assimilated by sunbirds (Lotz and Nicolson, 1996). Sucrose concentrations of 10, 20 and 30% w/w were fed to each bird and the effects on short-term feeding patterns were investigated by measuring the time and duration of each feeding event, and by recording body mass constantly throughout the day. We hypothesized that feeding frequency varies with the concentration of the food source in order to maintain constant energy intake on the different diets. Feeding duration, on the other hand, was not expected to increase with decreasing sucrose concentration because of volumetric constraints or increased metabolism resulting from the weight of the meal. We used feeding duration as an estimate of meal size, on the assumption that intake rates should be constant for birds feeding on a single sugar concentration in a high volume artificial feeder. In previous studies investigating feeding patterns of sunbirds (e.g. Nicolson and Fleming, 2003b; Fleming et al., 2004), the volumetric intake was recorded on a daily or hourly basis. With continuous recording of feeding events and their frequency, this study provides information on a much shorter time scale.

Materials and methods

Birds and their maintenance

Eight whitebellied sunbirds *Nectarinia talatala* (A. Smith) were captured by mist-netting in Jan Cilliers Park, Pretoria, South Africa in April 2004. Body mass of six males was 8.36±0.28 g (mean ± s.e.m.) and of two females 7.88 and 7.83 g. Birds were housed in individual cages measuring 45×45×32 cm in a climate-controlled room maintained at 20±2°C and 50% relative humidity on a 12 h:12 h L:D photoperiod with lights on at 07:00 h. Dawn and dusk were simulated with 0.5 h of dimmed light at the beginning and end of the photophase. The birds were fed a maintenance diet of 20% w/w sucrose solution (0.63 mol l^{-1}) with the addition of a nutritional supplement (Ensure®, Abbott Laboratories, Johannesburg, South Africa). Ensure was included in the diet to provide nitrogen that wild birds obtain from feeding on arthropods and pollen (van Tets and Nicolson, 2000). The diet and supplementary water were provided *ad libitum* in inverted, stoppered syringes attached to the cage sides.

Experimental design

The eight sunbirds were tested sequentially, since there was only one experimental cage, with each bird receiving three different sucrose concentrations, 10, 20 and 30% w/w sucrose (0.30, 0.63 and 0.99 mol l^{-1}), in random order for a period of 24 h each. To prevent mass loss on sucrose-only diets (e.g. Nicolson and Fleming, 2003b), the experimental diets were also supplemented with Ensure, with the amount adjusted to allow for compensatory feeding. The carbohydrate content of the added Ensure, even if completely digested, would increase the sugar concentration by only 0.58%.

For each bird the experimental procedure lasted 4 days. The sunbird was moved in the morning of the first day to the experimental cage (50×40×45 cm) and allowed an acclimation period with the maintenance diet for the remainder of the first day and the first night. Ambient temperature, humidity and light cycle were the same as before, but the dawn and dusk periods were omitted to synchronize start and end times of feeding. Measurements commenced at 07:00 h on the following day (day 2) and continued for 72 h, with the diets being changed every morning before lights on.

The experimental cage was constructed from Perspex, with ventilation holes, and contained a feeding perch and a resting perch (Fig. 1). The main perch, where the bird rested for most of the day, was suspended from an electronic balance (Mettler Toledo PB-602S, 0.01 g; Microsep Ltd, Johannesburg, South Africa). Throughout the duration of the experiment the body mass was recorded every 5 s if the bird was sitting on the main perch, using a computer interfaced with the balance. This main perch was connected to the ceiling of the cage by two slender metal rods to minimize swinging of the perch when the bird landed, which could disturb the measurements.

During a meal, the bird clung to the vertical feeding perch (Fig. 1). An infrared photo-detection system, consisting of an infrared diode light source and an array of four infrared photo-detectors interfaced to the same computer, allowed for the automated recording of the time spent feeding as well as the number of feeding events. The light source and detectors were mounted on either side of the feeder. Each time the bird inserted its bill into the sucrose solution the infrared photo-detection system recorded the feeding event, which lasted until the bird removed its bill. Prolonged resting on the feeding perch was discouraged by its smooth surface and pins inserted into the perch to reduce the space available. Since the cage was constructed from Perspex the bird was not able to cling to the sides. Furthermore, flexible plastic bristles discouraged the bird from resting on the bottom of the cage. Observation of the bird with minimal disturbance was

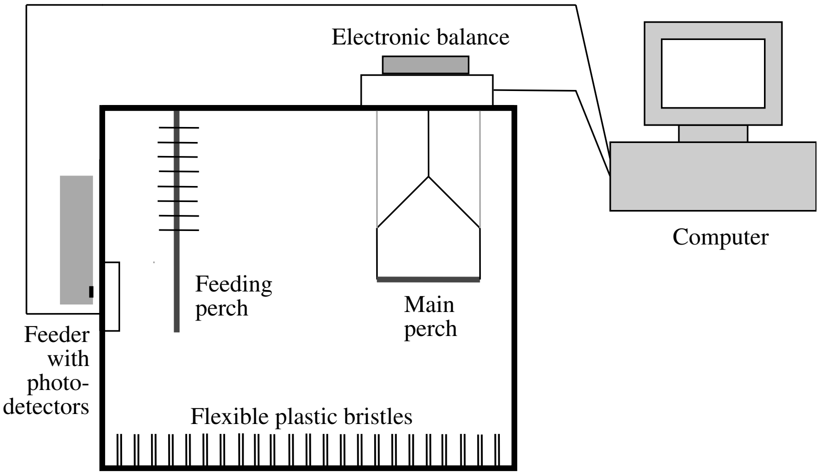

Fig. 1. The experimental equipment consisted of a cage constructed from Perspex with flexible plastic bristles at the bottom, a feeder with sucrose solution and two perches. The main perch was suspended from an electronic balance, interfaced to a computer. The vertical feeding perch had pins inserted to discourage prolonged resting. An infrared photo-detection system, interfaced to the same computer, was mounted on either side of the feeder in order to record feeding events. One-way mirrors on two sides of the cage allowed observation of the bird with minimal disturbance.

permitted by one-way mirrors on two sides of the cage. Each sunbird was observed for 1 h (09:00 h to 10:00 h) while feeding on each sucrose concentration, in order to confirm photo-detection records as well as natural behaviour of the birds.

The measurements were repeated either partly or completely for four of the eight birds for two reasons: firstly, photo-detection malfunctions and therefore incorrect records of feeding events and secondly, insufficient use of the main perch and therefore too few mass measurements for analysis. Nevertheless, we were unable to successfully record body mass throughout the day for one of the birds since it avoided the main perch and we therefore excluded it from the analysis of mass data. Birds were released at the site of capture following termination of the study.

Definitions and analysis of feeding data

For each bird and each sucrose concentration we obtained start and end times of all feeding events, duration of feeding events in seconds (s) and time intervals between feeding events (s).

Separate feeding events could not be defined by return to the main perch after feeding, as occurs in hummingbirds that hover to feed. We defined a feeding event as beginning when the bill was inserted into the sucrose solution and ending when the bill was removed. The feeding event duration (hereafter referred to as FED) is defined as the time between inserting the bill into the sucrose solution and removing it. FED values of less than 0.05 s were excluded, since observations revealed that movements of the bird, particularly wing movement during flight near the feeder, caused such events. Separate feeding events were merged into a single feeding event if the interval between two consecutive feeding events was less than 0.25 s, since observation revealed that turns of the bill or its incomplete removal from the feeder were recorded as two feeding events. For three birds, larger merging intervals of 0.35, 0.50 and 0.75 s were used, owing to slight differences in the sensitivity of the photo-detectors.

The light period of the day was divided into 1 h intervals to allow for comparison with previous studies in which diet intake was recorded hourly. For each 1 h interval, mean FED and number of feeding events were calculated. Feeding event frequency (FEF) was taken as the number of feeding events per hour. Furthermore, total feeding duration during each hour was determined by summing the FED of every feeding event during the 1 h interval.

Analysis of mass data

The recording of body mass resulted in static mass values as well as dynamic values, the latter caused by swinging of the main perch during movements of the bird. Dynamic balance readings were filtered from static mass data. Because of few mass data for several birds, dynamic values were included in the analysis when the absolute difference between the focal dynamic record and the first static record prior to the focal dynamic record was less than 0.03 g.

The mass recordings were analyzed for each bird on each diet with the same 1 h intervals as for the feeding events. For each interval, the mean mass was determined. Body mass increase of each bird on each of the different diets was expressed as the percentage change from the mean body mass during the first 1 h interval, to eliminate individual differences.

Statistical procedures

Data are expressed as mean ± s.e.m. Mean FED, FEF and total feeding duration per 1 h interval as well as temporal changes in body mass were analyzed by repeated-measures ANOVA. Data were arranged according to hour of day and sucrose concentration, yielding 30 dependent variables. Sucrose concentration and hour of day were used as within-effects. *Post-hoc* comparisons were conducted with Tukey's Honest Significant Difference test for equal sample sizes. Relationships between FED, FEF and body mass were determined using Spearman rank correlations. Repeatability ± s.e.m. was calculated following the method of Becker (Becker, 1984). Mean daily FED and FEF for each individual were subjected to Grubb's test for outliers. For all tests the level of significance was $P \leqslant 0.05$.

Results

Interpretation of data

Whitebellied sunbirds varied in their start and end times of feeding irrespective of diet concentration. The times of the first and last feeding event of the day differed significantly between individuals (start times: $F_{7,16}=5.54$, $P=0.002$; end times: $F_{7,16}=9.50$, $P<0.001$). Both start and end times were highly repeatable within individuals (repeatability ± s.e.m. at start: 0.60±0.19; end: 0.74±0.14). After the lights went on, most individuals started feeding immediately (mean start time: 07:05±1.2 min). The greatest observed delay before feeding commenced after lights on was 20 min. The majority of the birds fed close to lights off (mean end time: 18:50±6 min); the bird with the shortest total feeding time had its last feeding event 59 min before the start of the dark period. Owing to these differences in start and end times of feeding, the first and last hour of the light period were omitted from analysis, resulting in 10 intervals. The daily feeding period ranged from 10.98 h to 11.98 h, with a mean of 11.74±0.10 h.

Continuous measurements of feeding events and body mass resulted in detailed information about short-term feeding patterns and body mass over the course of the day. Fig. 2 shows feeding duration and body mass of one bird (individual 7) feeding on the 10% w/w sucrose diet. From this figure, it can be seen that feeding events lead to an increase in body mass. Between feeding events, birds lose mass as a result of evaporative water loss and excretion of cloacal fluid. Large amounts of data necessitated the use of mean values of FED, FEF and body mass over hourly intervals for statistical analysis and graphical representation.

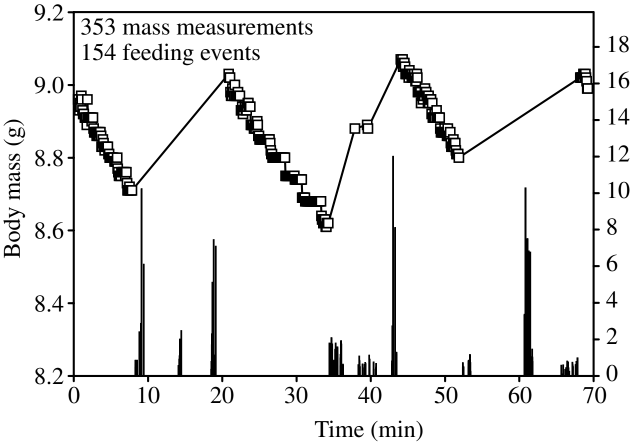

Fig. 2. Body mass (g; top) and feeding duration (s; bottom) of one bird (individual 7) feeding on the 10% w/w sucrose diet. The *x*-axis shows a time period of 70 min during the morning of the experimental day. The bird steadily lost body mass as a result of evaporation and excretions, and feeding events led to increases in body mass. Note that multiple overlapping symbols appear filled.

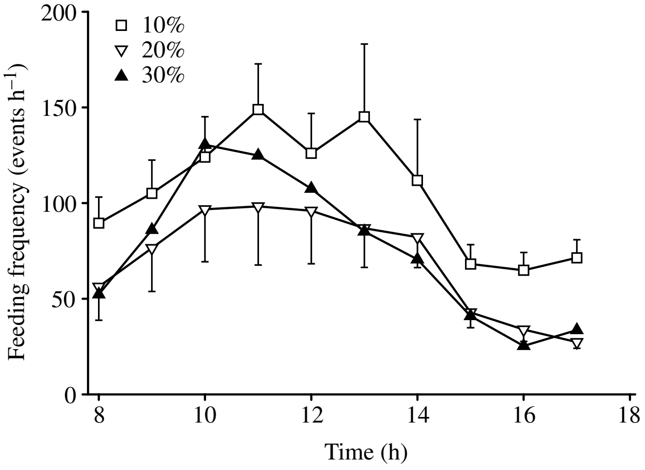

Fig. 4. Feeding frequency (events h^{-1}) of the eight sunbirds each fed three sucrose concentrations (10, 20 and 30%). The *x*-axis shows the start time of each 1 h interval (mean ± s.e.m.; error bars were partly omitted for clarity as there were large individual differences).

Short-term feeding patterns

Sunbirds varied their intake according to the diet concentration. The mean FED and FEF for each hour of the eight sunbirds consuming three different sucrose concentrations are shown in Figs 3 and 4, respectively. The mean FED ranged from 1.03 to 4.55 s (mean: 1.88±0.14 s). Large differences in FED and FEF between individuals (see below) made it necessary for partial omission of standard errors in graphical presentations of FEF and total feeding duration (Figs 4 and 5). FED did not differ between the diet concentrations ($F_{2,12}$=2.19, P=0.15). Repeated-measures ANOVA revealed a significant difference in FEF between the diets ($F_{2,14}$=20.93, P<0.001). *Post-hoc* analysis confirmed that there were significantly more feeding events on the dilute diet of 10% sucrose than on the diets of 20% and 30% (10% and 20%: P<0.001; 10% and 30%: P<0.001). FEF did not differ between the 20 and 30% sucrose solutions (P=0.58).

Total feeding duration, i.e. the total time that birds spent feeding per hour, differed significantly between diets ($F_{2,14}$=46.60, P<0.001; Fig. 5). Birds had a higher total feeding duration on the dilute diet than on the other two diets, due to the demonstrated increase in FEF on the 10% diet (P<0.001). Total feeding durations on the 20% and 30% sucrose concentrations did not differ (P=0.89). The total time that the birds spent feeding was very short, approximately 144 s h^{-1} on the dilute diet and 96 s h^{-1} on the other diets.

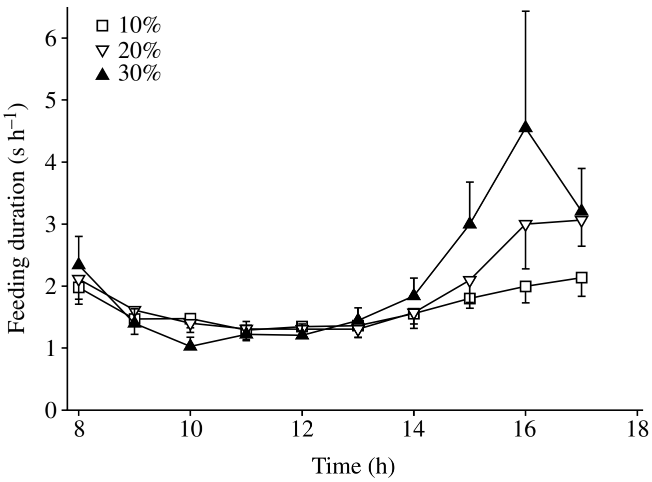

Fig. 3. Feeding duration (s h^{-1}) (mean ± s.e.m.) of eight sunbirds each fed three sucrose concentrations (10, 20 and 30%). The *x*-axis shows the start time of each 1 h interval.

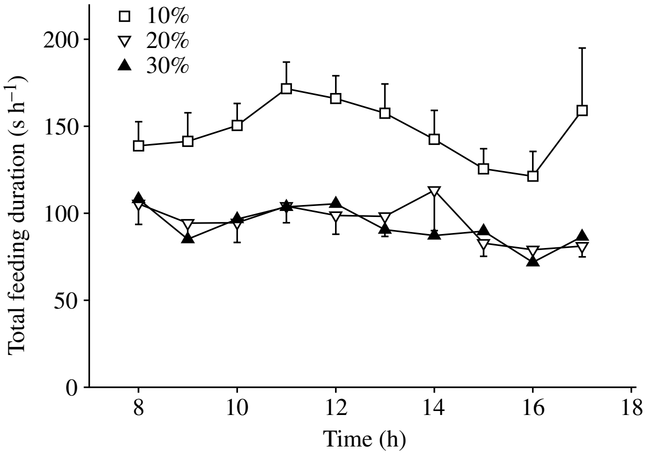

Fig. 5. Total feeding duration (s h^{-1}) of the birds on the three different diets. The *x*-axis shows the start time of each 1 h interval (mean ± s.e.m.; error bars were partly omitted for clarity as there were large individual differences).

Body mass gains on the different diets

The body mass increase during the light period for seven of the birds is presented in Fig. 6. There was a trend for body mass increase to be positively correlated with diet concentration, but this was not significant ($F_{2,12}$=1.47, P=0.27). Mass gains were similar on all three diets. Birds showed a linear increase in their body mass over the day on all sucrose concentrations (linear regressions: 10%: R^2=0.96; 20%: R^2=0.95; 30%: R^2=0.85). All birds maintained their body mass during the four experimental days ($F_{2,12}$=0.32, P=0.73).

Daily rhythms in feeding patterns

From Figs 3 and 4 it is clear that birds showed daily rhythms in their feeding patterns, irrespective of the concentration of the sucrose solution. Both FED and FEF varied significantly over the course of the day (FED: $F_{9,54}$=3.86, P<0.001; FEF: $F_{9,63}$=5.61, P<0.001). FED was generally higher in the morning and the evening than during the rest of the day (Fig. 3). FEF showed the opposite pattern (Fig. 4), with a peak in the late morning and early afternoon and fewer feeding events in the early morning and evening. Total FED also varied over the light period of the day ($F_{9,63}$=6.25, P<0.001; Fig. 5) with higher total FED in the late morning than in the late afternoon.

Individual differences in feeding patterns

Irrespective of diet concentration and time of day, large between-individual differences in feeding patterns were observed in terms of FED and FEF. Fig. 7 demonstrates these differences for the 20% diet, which is equivalent to the bird's maintenance diet. Individual birds employed different feeding strategies. Whereas most birds had long FED combined with a low FEF, others showed short FED and fed more often. One female bird in particular showed a much higher FEF and lower FED than all other birds (Fig. 7A,B, individual 3). We calculated the repeatability of individual feeding behaviour on the 20% diet over four half-hour intervals between 9:00–11:00, where feeding was not influenced by morning deficits or energy savings in the evening (see below). Both FED and FEF were highly repeatable (repeatability ± s.e.m. for FED: 0.75±0.13; FEF: 0.91±0.05). Individual differences in FEF and FED were not related to body mass (Spearman R: FED: R_7=0.54, P=0.22; FEF: R_6=0.26, P=0.62) but this might be due to our small sample size. One bird had to be excluded from both of the above analyses because of insufficient mass data. Individual 3 was shown to be a statistical outlier (Grubb's T=2.22, P<0.05) and was excluded from the correlation between FEF and body mass.

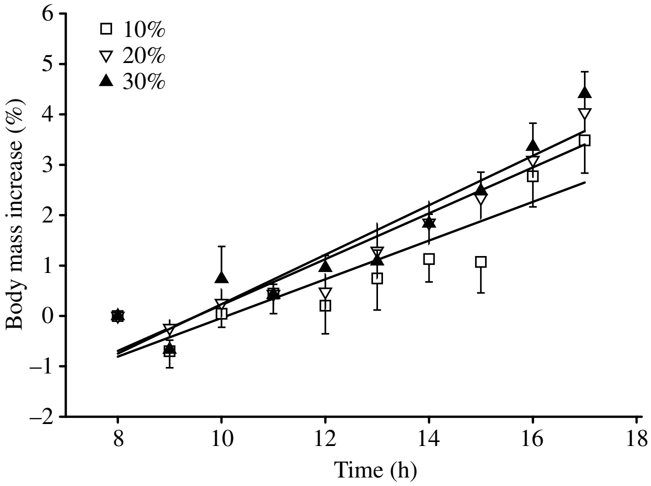

Fig. 6. Increase in body mass throughout the day, as a percentage of the mean mass of the first hour, for seven birds on the three different diets (mean ± s.e.m.). The x-axis shows the start time of each 1 h interval.

Discussion

Short-term feeding patterns

The increased food intake on the dilute diet was caused by an increase in FEF rather than FED: thus short-term adjustment of food intake in sunbirds, as in other avian nectarivores, takes place through regulation of feeding frequency. On the assumption that FED is an estimate of meal size (but see

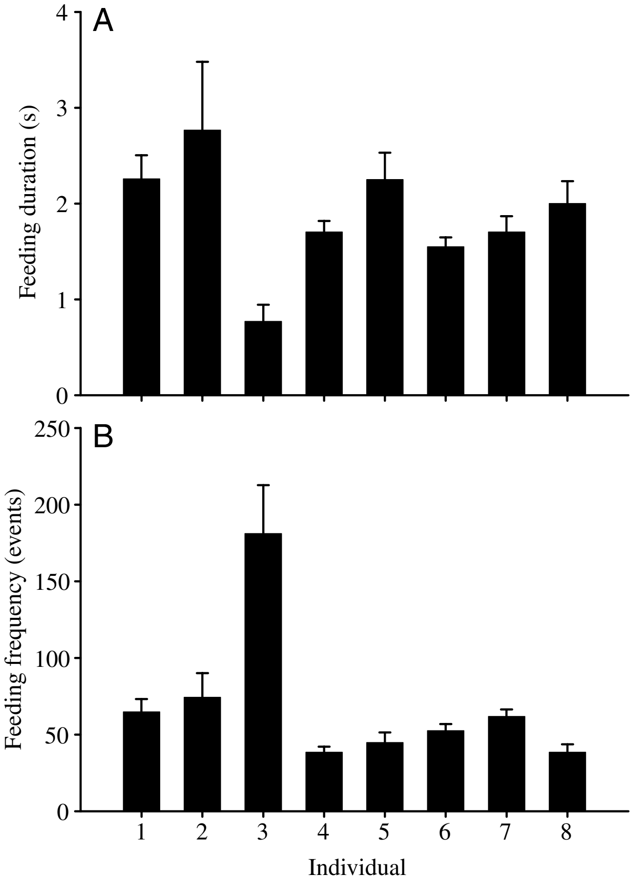

Fig. 7. (A) Feeding duration (s) and (B) feeding frequency (number of events) of individual sunbirds over the whole day on a diet of 20% sucrose (mean ± s.e.m.).

below), we consider the possible roles of some constraints which may limit meal size rather than meal frequency.

Volumetric intake during a meal could be limited by crop size. Diamond et al. (Diamond et al., 1986) proposed that crop-emptying time limits feeding frequency in hummingbirds, thus explaining the large amount of time spent perching. However, hummingbirds usually fill their crops to only 10–30% of capacity (Carpenter et al., 1991), and neither honeyeaters nor sunbirds possess crops (Collins et al., 1980; Mbatha et al., 2002). Hummingbirds are also capable of processing food much faster than indicated by their rates of *ad libitum* intake (Tiebout, 1989).

The processing of nectar meals requires hydrolysis of the sucrose component to glucose and fructose, then absorption of the latter. Birds must also deal with large volumes of preformed water. Gut transit time decreases with increasing volume of a sucrose meal (Tiebout, 1989) and with increasing concentration (López-Calleja et al., 1997; Markman et al., 2006). The decrease in transit time on dilute diets accounts for the increased meal frequency that we measured. It has also been suggested that delivery of nectar meals to the intestine should be faster for sucrose than hexose nectars of equivalent energy content, because of the lower osmotic concentration (Beuchat et al., 1990). Sucrose hydrolysis rates may be limiting in birds feeding on low nectar concentrations (McWhorter and Martínez del Rio, 2000), and the passive component of hexose absorption may also be affected, because it depends on contact time with the absorptive surfaces (McWhorter et al., 2005). However, if water is absorbed rapidly down the length of the intestine, dilute meals will not remain dilute. This especially applies to hummingbirds which, unlike sunbirds, do not modulate their intestinal water absorption in response to food dilution (McWhorter and Martínez del Rio, 1999; McWhorter et al., 2003). In the latter study, Palestine sunbirds (*N. osea*) decreased the fraction of absorbed water by 60% on a diet of 0.29 mol l^{-1} sucrose: under these conditions, the load on the kidneys is correspondingly reduced but nutrients may have to be extracted from low luminal concentrations. Unfortunately we have no information on the gradients of sugar concentration along the intestine in nectar-feeding birds.

Energetic considerations may explain why FED did not increase on the dilute diet. For hummingbirds with access to unlimited food supplies, a model of optimal meal size (DeBenedictis et al., 1978) suggests constraints due to the weight of the meal (although the water in dilute meals is eliminated quickly). Large meal sizes would lead to increased body mass and increased energy expenditure between meals. European starlings (*Sturnus vulgaris*), when exposed to different amounts of work required to obtain food, save energy during a hard treatment by reducing body mass (Bautista et al., 1998). This is expected to reduce flight costs, although the implications of body mass for flight performance of hummingbirds remain mechanistically unclear (Altshuler and Dudley, 2002). Ruby-throated hummingbirds (*Archilochus colubris*) on restricted diets showed effects of body mass on hovering ability in low-density air, but not on maximum flight speed in a wind tunnel (Chai et al., 1999). When the metabolic costs of flight are measured directly, the short flights of sunbirds have been shown to be relatively inexpensive compared to those of starlings (Hambly et al., 2004).

Concentration effects

The increase in total feeding duration of sunbirds on the dilute diet of 10% sucrose can be attributed to compensatory feeding (Martínez del Rio et al., 2001). Adjustment of food intake according to diet concentration is exhibited by many nectar-feeding birds, including honeyeaters (Collins and Clow, 1978; Collins et al., 1980), several hummingbird species (López-Calleja et al., 1997; McWhorter and Martínez del Rio, 1999; Fernández et al., 2002), and three sunbird species (Lotz and Nicolson, 1999; McWhorter et al., 2003; Nicolson and Fleming, 2003b).

Unexpectedly, there was no difference in total feeding duration between the 20% and 30% sucrose diets. The inverse exponential relationship between volumetric intake of whitebellied sunbirds and diet concentration provides a proximate explanation. For sucrose concentrations between 0.25 and 2.5 mol l^{-1}, this relationship is described by the function:

$$V = \mathrm{a}C^{-\mathrm{b}} = 8.0052C^{-0.9768},\ r^2 = 0.9668,$$

where V = volumetric intake (ml), C = sucrose concentration (mol l^{-1}) and a and b are empirically derived constants (Nicolson and Fleming, 2003b). Applied to the sucrose concentrations used in the present study (10%=0.30 mol l^{-1}, 20%=0.63 mol l^{-1}, 30%=0.99 mol l^{-1}), this function shows that, over a 12 h light period, birds have to consume 25.70 ml of the most dilute diet of 10%, 12.53 ml of the 20% diet and 8.10 ml of the 30% diet. Hence, the volume consumed daily differs far more between the 10 and 20% diets than between 20 and 30%, explaining the increase in total feeding duration on the most dilute diet. The small expected difference between the 20% and 30% diets will be obscured by large between-individual differences. With larger sample sizes and more concentrated diets, it might be possible to demonstrate decreases in total feeding duration with increasing sugar concentration. Support for our findings also comes from a study on lesser double-collared sunbirds (*N. chalybea*) (Lotz and Nicolson, 1996), which preferred 20% over 10% sucrose solutions, but were indifferent to 20% and 30% sucrose. Feeding frequencies of hummingbirds have been measured on sucrose concentrations similar to those in the present study: in *Archilochus colubris* and *Lampornis clemenciae*, feeding frequencies were similar on 0.5 and 1.0 mol l^{-1} sucrose solutions, but much higher on 0.25 mol l^{-1} sucrose (Wolf and Hainsworth, 1977), again showing effects only on the most dilute diets. Studies of feeding behaviour in small honeyeaters also show significant changes in feeding frequency only on dilute solutions such as 0.2 mol l^{-1} sucrose (Collins and Clow, 1978; Collins et al., 1980).

Body mass gains on the different diets

The increase in body mass over the course of the day is necessary to provide energy for the night, when birds do not feed. Similar increase in body mass during the day on all three diets confirms the occurrence of compensatory feeding by the sunbirds. Lesser double-collared sunbirds also achieve the same daily mass gain irrespective of diet concentration (Lotz and Nicolson, 1996). In a variety of nectar-feeding birds the pattern of energy accumulation is commonly linear through the day, sometimes slowing in the afternoon (Wolf and Hainsworth, 1977; Collins and Morellini, 1979; Nicolson et al., 2005).

In previous studies, whitebellied sunbirds fed sucrose-only diets at 20°C lost approximately 3% of body mass per day, since sucrose solutions can not meet all their dietary requirements (Nicolson and Fleming, 2003b). Experimental diets in the present study were supplemented with Ensure and birds maintained their body mass throughout the experimental procedure.

Daily rhythms in feeding patterns

Whitebellied sunbirds feed steadily during the morning and early afternoon, followed by reduced intake during mid-afternoon and then an increase at the end of the day to provide energy stores for the night (Fleming et al., 2004). The high rate of feeding in the early morning compensates for overnight mass loss and rehydrates the birds after the overnight fast. A rather different pattern is evident when feeding is examined on a short-term basis. FED and FEF were found to vary greatly during the course of the day on all diet concentrations. In the early morning and in the evening, birds fed less often and therefore had longer FED. During the rest of the day, birds showed a higher FEF coupled with a shorter FED. This observed daily pattern in feeding behaviour is unlikely to be related to ambient temperature normally experienced by wild birds since birds used in our study were kept under constant temperature for 11 months prior to the experiment. Despite the inverse relationship between FEF and FED, total feeding duration also showed a daily rhythm, being higher in the late morning than during the afternoon.

However, this reduction in feeding rate in mid-afternoon was much less obvious than in previous studies where food intake of whitebellied sunbirds was measured on an hourly basis (Fleming et al., 2004; Nicolson et al., 2005). The different pattern may be due to disturbance of the birds during hourly weighing of feeders, or may reflect the fact that intake rates and total feeding duration are not directly comparable. Collins and Clow (Collins and Clow, 1978) also recorded varying ingestion rates in honeyeaters, with nectar extraction being least efficient in the early morning. The relationship between meal size and meal duration in nectar-feeding birds needs further investigation.

Individual differences in feeding patterns

We have examined sunbird feeding patterns in much more detail than previous studies. Measurements over a short time scale have highlighted unexpectedly large between-individual variation in feeding patterns. Individual birds differed greatly in terms of their FED and FEF, irrespective of diet concentration and time of day. Recently, sex-specific differences in transit time were demonstrated in Palestine sunbirds, which might affect their foraging behaviour (Markman et al., 2006). However, only two females were used in our study and we were unable to test whether the sexes differ in their feeding patterns. Observations on another group of whitebellied sunbirds feeding in an outdoor aviary (A. Köhler, unpublished data) showed similar high variation between individuals in both feeding frequency and feeding duration.

Although they have received limited attention, inter-individual differences are also apparent in the responses of hummingbirds and starlings to imposed energetic constraints (Tooze and Gass, 1985; Bautista et al., 1998), and in the sugar preferences of sugarbirds and sunbirds (Jackson et al., 1998). In whitebellied sunbirds fed diets ranging from 0.25–2.5 mol l^{-1} sucrose, greater variation in sucrose intake was found between individuals on a particular diet than between diets (Nicolson and Fleming, 2003b). The variation in physiology and behaviour seen under constant laboratory conditions is likely to be accentuated as circumstances vary in the natural environment. Perhaps individual differences in feeding behaviour of sunbirds may translate into varying proficiencies in handling flowers of different morphology and nectar characteristics.

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