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Interruptions in nectar availability: responses of whitebellied sunbirds (*Cinnyris talatala*) and brown honeyeaters (*Lichmera indistincta*)

Angela Köhler^{†*}, Luke Verburgt[†], Patricia A. Fleming[‡], Todd J. McWhorter^{‡‡} and Susan W. Nicolson[†]

[†] Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

[‡] School of Veterinary and Biomedical Sciences, Murdoch University, Murdoch WA 6150, Australia

^{‡‡} School of Animal and Veterinary Sciences, University of Adelaide, Adelaide SA 5371, Australia

* Corresponding author, Tel: +27 12 420 4872

Fax: +27 12 362 5242

E-mail: akoehler@zoology.up.ac.za

Abstract

Limited food availability may disrupt the energy balance of animals, and small birds with high metabolic requirements and relatively low capacity for fuel storage may be particularly affected. The active lifestyle of nectar-feeding birds necessitates frequent feeding, and energy is accumulated throughout the day to sustain the birds during the night. To investigate how these birds cope with lost feeding time, we exposed captive whitebellied sunbirds (*Cinnyris talatala*) and brown honeyeaters (*Lichmera indistincta*) kept at 10°C to a 2 h fasting period during the day. Birds were fed a 0.63 M sucrose solution for the rest of the day. Food intake increased following the fast, relative to uninterrupted feeding. A comparison with the maximal food intake predicted by a digestive capacity model showed that both species fed at maximal levels in the hour following the fast. Although the short-term feeding pattern of honeyeaters was not investigated, sunbirds increased the duration of meals immediately after the fast, followed by a non-significant increase in meal frequency. In contrast to published data for hummingbirds, these two passerines accumulated energy at higher rates after the fast compared to a control day. However, food intake over the whole day was lower on the fasting day and birds weighed less in the evening compared to the control, indicating that the compensation of energy intake and accumulation was incomplete. Our study demonstrates that two phylogenetically distinct nectarivorous avian taxa show similarities in their response to fasting periods, possibly due to similar feeding behaviour and physiological constraints.

Additional keywords: body mass, digestive capacity modelling, fasting period, food intake, feeding duration, energy accumulation

Introduction

Food quality and availability fluctuate both in time and space in natural habitats, which greatly influences daily feeding patterns in small birds (Miles 1990; Rathcke 1992; Bednekoff and Houston 1994). Small nectar-feeding birds feed frequently to maintain their high metabolic rates, and accumulate energy at constant rates throughout the day to sustain them during the overnight fast (Wolf and Hainsworth 1977; Köhler *et al.* 2006). In foraging hummingbirds, recently ingested sugars are used to fuel up to 95% of metabolism (Welch and Suarez 2007). Consequently, interruptions to foraging are likely to influence energy balance of the birds. Short-term fasting periods occur during storms and heavy rains that prevent foraging (Carpenter and Hixon 1988) or after rain when nectar is diluted or washed away (Aizen 2003). Feeding may be interrupted by increased vigilance after the appearance of a predator (Glück 1987); or birds may need to compete for feeding opportunities because nectar availability varies within natural habitats (Collins *et al.* 1990). Reduced nectar availability when few flowers are blooming may even pose a longer-term energy challenge. Foraging may also be interrupted for long periods during reproduction (Williams 1993) and migration (McWilliams and Karasov 1998).

A loss of foraging time can lead to rapid depletion of energy stores of nectarivorous birds. Wild rufous (*Selasphorus rufus*) and broadtailed hummingbirds (*S. platycercus*) lose body mass when feeding is hindered by storms, and they may compensate for the energy deficit by going into torpor (Carpenter and Hixon 1988; Calder 1994). Honeyeaters that are deprived of food at the end of a day also drop their body temperature during the following night to conserve energy (Collins and Briffa 1984). Captive hummingbirds did not increase their food intake after a 2 h midday fast and lost mass (Tooze and Gass 1985); however, sunbirds compensated by increasing their nectar intake rate following a similar fasting period (Nicolson *et al.* 2005).

In order to compare two major families of avian nectarivores in their response to energetic challenges, we exposed whitebellied sunbirds (*Cinnyris talatala*, Nectariniidae) and brown honeyeaters (*Lichmera indistincta*, Meliphagidae), both

passerines and of similar size, to a 2 h midday fast. Are these avian nectarivores able to increase their feeding rates immediately after an imposed fasting period? Because the two species show similarities in feeding behaviour and energy accumulation throughout the day (Collins and Cary 1980; Collins *et al.* 1980; Köhler *et al.* 2006), we hypothesized that they will respond similarly to a fasting period by increasing their nectar intake. Do the birds feed at maximal capacity in an attempt to compensate for the loss in foraging time? We predicted the maximal food intake rate of each species using a mathematical model of digestive performance (McWhorter and Martínez del Rio 2000) and hypothesized that birds would feed at maximal rates following the fast. Are the birds able to avoid an energy deficit at the end of the day after a fasting period? We predicted that birds would increase their food intake following the fast sufficiently to maintain energy balance. Lastly, we determined the mechanism of short-term feeding adjustment for whitebellied sunbirds and hypothesized that they would have longer meals and feed more often following the fast.

Materials and methods

Study animals and their maintenance

Eight whitebellied sunbirds were mist-netted at Jan Cilliers Park, Pretoria, South Africa, and eight brown honeyeaters on the Murdoch University campus, Perth, Western Australia. Birds were housed in individual cages at $20 \pm 2^\circ\text{C}$ and a 12:12 h L:D photoperiod with lights-on at 07:00. The maintenance diet for sunbirds consisted of a 0.63 M sucrose solution (20% w/w) with a nutritional supplement (Ensure[®], Abbott Laboratories, Johannesburg, South Africa) to provide dietary nitrogen (Van Tets and Nicolson 2000). Brown honeyeaters were fed a maintenance diet consisting of commercially available honeyeater and lorikeet nectar (Wombaroo[®] Food products, Adelaide, South Australia), which contains sucrose as the main sugar type as well as protein; this diet was supplemented with additional sucrose for a total sugar content of 25% w/w. The maintenance diet and supplementary water were provided *ad libitum* in inverted, stoppered syringes. Body mass (mean \pm SE) of the four male and four female sunbirds was 8.4 ± 0.3 g (range: 7.2-9.5 g). The sexes of the honeyeaters could

not be distinguished; body mass of the eight individuals averaged 10.1 ± 0.4 g (range: 8.8-11.9 g).

Experimental procedure and data processing

Experiments were carried out in summer (sunbirds were tested in February and March; honeyeaters in December). Each bird was moved to an experimental cage and acclimated for one day to the experimental temperature of 10°C and a 0.63 M sucrose-only solution. This was followed by one control day with uninterrupted feeding and one day where feeding was interrupted for 2 h by turning off the lights. Switching off the lights ensured that all birds were exposed to the same length of fasting period, as they start feeding instantly when the light comes back on. If the feeder were removed instead (birds could not see the feeder, which was placed outside the Perspex cage), birds that returned to the feeding hole frequently would have started to feed earlier than others. The fast took place from 10:00-12:00 as the food intake rate of both study species is most stable in the morning (Collins and Briffa 1983; Köhler *et al.* 2006). For comparative purposes, our protocol was similar to those of Tooze and Gass (1985) and Nicolson *et al.* (2005). The order of control and fasting day was not randomized, as the fasting period may lead to an energy deficit, thus affecting the feeding behaviour of the birds on the following day.

Honeyeaters were tested in experimental Perspex cages (54 x 43 x 49 cm), where the only perch available was suspended from a balance (Scout Pro SP 402, 0.01 g, Ohaus Corp., Pine Brook, NJ USA), and body mass was recorded hourly (07:00-19:00). The feeder was attached outside the cage, allowing for hourly weighing with minimal disturbance to the honeyeaters. Food intake was corrected for dripping solution, which was collected in a tray with liquid paraffin. The sunbirds were tested sequentially in a Perspex cage (50 x 40 x 45 cm; Köhler *et al.* 2006) containing infrared photo-detectors next to the feeding aperture and two perches connected to electronic balances (Mettler Toledo PB-602S, 0.01 g, Microsep Ltd, Johannesburg, South Africa). The feeder and a container with liquid paraffin underneath were mounted on a third balance outside the cage. The photo-detection system and all balances were interfaced to a computer and time spent feeding (time from insertion of the bill into the feeder until its removal), number of feeding events, feeder mass and body mass of the bird were recorded every 0.5 s. Mean feeding duration and feeding

frequency were calculated for 0.5 h time intervals. Since the minute amount of solution consumed in a single feeding event could not be detected by our balance (0.01 g resolution), hourly food intake was calculated. Mean body mass of each sunbird was also calculated for each hour, using stable balance readings only. For both whitebellied sunbirds and brown honeyeaters, we calculated food intake rates ($\text{mg}\cdot\text{h}^{-1}\cdot\text{g body mass}^{-1}$) on the control and fasting day. We further calculated food intake ($\text{mg}\cdot\text{g body mass}^{-1}$) for the morning (07:00-10:00) and afternoon (12:00-19:00), and daily food intake (07:00-19:00).

Re-diluted excreta samples were assayed for sucrose, glucose and fructose content, using Sigma-Aldrich (Munich, Germany) colorimetric/enzymatic kits and a spectrophotometer (Biowave S2100 UV/Vis, Biochrom Ltd., Cambridge, UK; UV mini 1240 UV-VIS, Shimadzu Scientific, Balcatta, Western Australia). The amount of sucrose, glucose and fructose excreted ($\text{mg}\cdot 24\text{ h}^{-1}$) by the birds as well as the sucrose assimilation coefficient were calculated (see Köhler *et al.* 2010 for detailed methods and calculations). Four additional whitebellied sunbirds (mean body mass \pm SE: 8.98 ± 0.70 g), caught at Jan Cilliers Park, Pretoria, and five of the brown honeyeaters used in the experiment (mean body mass \pm SE: 10.62 ± 0.51 g) were killed by a halothane overdose and data on gut morphology and total activity of the disaccharidase sucrase-isomaltase that hydrolyses sucrose to glucose and fructose were obtained (see Köhler *et al.* 2010 and references therein for detailed methods). Data on sucrose assimilation efficiency, gut morphometrics and sucrase activity of the two species (Table 1) were used to predict their maximal hourly food and sugar intake rates with a chemical reactor model of digestive capacity (McWhorter and Martínez del Rio 2000; Martínez del Rio *et al.* 2001), which assumes that sucrose hydrolysis is the limiting factor in sugar assimilation by nectar-feeding birds when they are feeding on sucrose-rich nectars.

Statistical analysis

Data were tested for normality and homogeneity of variance and were log transformed when heteroscedastic. Control and fasting days were compared in terms of food intake, afternoon food intake rate, mean feeding duration, feeding frequency, morning and evening body mass, and afternoon mass gain (slope of mass vs. time regression) using repeated-measures ANOVA, with species being categorical predictor. *Post-hoc*

comparisons were conducted with Tukey's HSD test. The observed food (and sugar) intake in the hour after the fast was compared to the predicted maximal intake using a *t*-test (single sample), followed by sequential Bonferroni correction (Rice 1989). All data are presented as mean \pm SE; level of significance was $\alpha \leq 0.05$ for all tests.

Results

Food intake

Sunbirds and honeyeaters showed similar food intake rates ($F_{1,14}=0.83$, $P=0.38$), which declined steadily over the control day (Fig. 1). An interesting response to the 2 h midday fast was a temporal shift in this feeding pattern: consequently, feeding rate on the fasting day was higher than on the control day for the same time points, but was not different if the comparison was carried out for an "equivalent" feeding time point (*i.e.* feeding rate at 14:00 on the fasting day was equivalent to that for 12:00 on the control day; Fig. 1). Food intake of both species differed between control and fasting days ($F_{1,14}=60.94$, $P<0.001$). Food intake was similar on both mornings ($P=0.99$), but was higher after the fast than on the control afternoon ($P<0.001$), with sunbirds consuming $19.2 \pm 2.9\%$ more and honeyeaters $13.4 \pm 3.1\%$ more. Afternoon feeding rates increased immediately following the fast and were higher than on the control day ($F_{1,14}=63.97$, $P<0.001$; Fig. 1). Despite this increased intake rate, lost feeding time led to lower overall daily food intake on the fasting day than on the control day ($F_{1,14}=49.93$, $P<0.001$), with sunbirds consuming $7.8 \pm 1.7\%$ less and honeyeaters $11.2 \pm 1.9\%$ less.

Predicted maximal food and sugar intake

The food, and thus sugar, intake of whitebellied sunbirds in the hour following the fasting period was higher than the maximal hourly food intake predicted by the chemical reactor model of digestive capacity ($t_7=3.27$, $P=0.01$; Table 2). The model accurately predicted maximal hourly food and sugar intake of brown honeyeaters, with birds feeding close to their maximal intake rates in the hour after the fast ($t_7=0.55$, $P=0.60$; Table 2).

Adjustment of feeding behaviour in sunbirds

Mean feeding duration and feeding frequency of whitebellied sunbirds did not differ between treatments overall ($F_{1,7} \leq 1.71$, $P \geq 0.23$), but differed between times of day ($F_{19,133} \geq 2.69$, $P < 0.001$). Sunbirds had longer meals immediately after the fast (12:00-12:30) than at the same time on the control day ($P = 0.01$; Fig. 2A). Feeding frequency appeared to be higher in the afternoon of the fasting day than in the control afternoon, but this was not statistically significant ($P \geq 0.95$; Fig. 2B).

Body mass

Body mass of both species differed between control and fasting days ($F_{1,14} = 16.85$, $P < 0.01$), being similar in the mornings ($P \geq 0.11$), but lower in the evening following the fast than in the control evening ($P \leq 0.02$; Fig. 3). Birds accumulated body mass at a steady rate throughout the control day (Fig. 3): sunbirds increased their body mass by $7.9 \pm 0.8\%$, and honeyeaters by $5.8 \pm 1.4\%$. All birds lost body mass during the 2 h fasting period, and increased the rate of body mass gain in the afternoon following the fast compared to the control afternoon ($F_{1,14} = 38.60$, $P < 0.001$). However, this compensation was incomplete, as birds gained less mass over the entire fasting day than on the control day (sunbirds: $6.4 \pm 0.8\%$; honeyeaters: $4.7 \pm 0.9\%$).

Discussion

In this study, both whitebellied sunbirds and brown honeyeaters demonstrated an immediate feeding response following an imposed fasting period; they increased their food intake within the first hour and accelerated their rate of body mass increase. This confirms earlier findings for whitebellied sunbirds (Nicolson *et al.* 2005), and shows the same response to fasting in the brown honeyeater. Accumulating evidence suggests convergence in feeding behaviour of sunbirds and honeyeaters, two phylogenetically unrelated passerine families. Species of both families demonstrate similar daily feeding rhythms (Collins *et al.* 1980; Köhler *et al.* 2006), adjust their nectar intake according to its sugar concentration (Collins and Cary 1980; Lotz and Nicolson 1999), and have comparable sugar preferences, suggesting similar physiological constraints to digestion of nectar (Fleming *et al.* 2004, 2008). Our study demonstrates that sunbirds and honeyeaters show coevolved similarities in their

responses to the energetic challenge of a fasting period, possibly due to similarities in their feeding behaviour and physiological constraints.

Whitebellied sunbirds increased their food intake by increasing feeding duration immediately after the fast. Feeding duration is positively related to meal size in this species (Köhler *et al.* 2008a), *i.e.* the longer the birds feed the more they ingest during one feeding event. The increased meal size corresponds with an earlier study of whitebellied sunbirds: when birds were fed alternating dilute and moderate sucrose concentrations, meal size increased immediately after the return of the moderate diet (Köhler *et al.* 2008b). An increase in meal size has also been demonstrated for blue-throated hummingbirds with depleted energy reserves (Hainsworth *et al.* 1981). Birds might save energy immediately after the fast by ingesting fewer but larger meals, because this may reduce the number of visits to flowers / the feeder. The increase in body mass after a meal, however, is associated with higher flight costs (DeBenedictis *et al.* 1978), which did not affect our birds as they could remain perched next to the feeder. Higher energetic costs of flight following large meals would explain why avian nectarivores commonly regulate their intake by adjusting feeding frequency, rather than meal size (Collins and Clow 1978; López-Calleja *et al.* 1997; Köhler *et al.* 2006). Although the short-term feeding pattern of honeyeaters was not investigated in the present study due to experimental equipment constraints, they also increased their food intake immediately in response to food deprivation.

In contrast to passerines, hummingbirds are apparently unable to adjust their nectar intake according to changing energy reserves within one day (Hainsworth *et al.* 1981; Tooze and Gass 1985). Hainsworth *et al.* (1981) hypothesized that hummingbirds do not monitor their energy reserves constantly, but rather set the regulation of food intake by the extent of the energy deficit at the beginning of a day and then maintain constant energy accumulation rates. However, birds are known to closely monitor their energy stores via signals from peripheral tissues, transmitted to the brain where feeding adjustments are initiated (for a review see Denbow 1994). A negative energy balance results in a change in hormone levels, which stimulates food intake following food deprivation (Taouis *et al.* 2001). Thus, hummingbirds are likely to monitor their energy reserves constantly, but might not have the physiological capacity to compensate instantly, since they are very small and have extremely high

mass-specific metabolic rates. They adjust their food intake in the longer term, leading to a progressive increase in energy accumulation on successive fasting days (Hainsworth *et al.* 1981). The immediate adjustment of food intake after the fast that we found in our study demonstrates that both sunbirds and honeyeaters not only monitor their energy reserves continuously, but also have the capacity to increase their food intake in the short term.

Food intake of our birds was highest in the first hour after the fast and a comparison with the maximal intake predicted by the digestive model (McWhorter and Martínez del Rio 2000) indicates that the birds fed at maximum levels in an attempt to compensate for the loss in foraging time. Despite feeding at maximal capacity, whitebellied sunbirds and brown honeyeaters show a remarkably high digestive efficiency, always absorbing >99% of ingested sugar (Köhler *et al.* 2010; A. Köhler, unpubl. data). In the case of brown honeyeaters, the observed intake in the present study matched the predicted maximal intake, while sunbirds exceeded the predicted maximal intake rate in the hour after the fast. This discrepancy is possibly due to the use of different individuals for the feeding experiment and for the gut physiology measurements (see Köhler *et al.* 2010). Sunbirds were caught at slightly different times of the year, and exposure to different ambient temperatures or an exclusive sucrose maintenance diet could potentially influence gut morphometrics and other determinants of digestive performance (Starck 1999; Karasov and McWilliams 2005). The accuracy of the model has been shown for our honeyeaters, where individuals used in the experiment were killed for physiological measurements; and for hummingbirds in earlier studies (McWhorter and Martínez del Rio 2000; Martínez del Rio *et al.* 2001).

Both species fed at maximal capacity immediately after the fast. For the remainder of the afternoon, the birds appeared to have higher feeding rates (although not significantly) than on the control afternoon and accelerated their energy accumulation. However, feeding rates after the fast followed the daily rhythm observed on the control day and decreased throughout the afternoon (Fig. 1). Why did the birds not feed at maximal rates the entire afternoon and evening to compensate for the lost foraging time? Warming large amounts of ingested nectar to body temperature is energetically costly, and food warming costs increase with increasing difference

between body and nectar temperature (Lotz *et al.* 2003). Nectar temperature closely follows ambient temperature, so the nectar temperature of 10°C in our study may have resulted in high food warming costs. In addition, energy is expended during ingestion, digestion, absorption and assimilation of nectar meals. For honeycreepers (*Cyanerpes cyaneus*), it has been shown that oxygen consumption increases after ingestion of sucrose solution, compared to the fasted state (Mata 2010). Birds may therefore benefit from reducing their energy expenditure instead of feeding at maximal rates over longer time periods. This may be especially relevant under natural conditions, where foraging flights result in additional energetic costs.

Animals may exhibit various behavioural and physiological energy-saving mechanisms, such as reducing unessential activities and lowering body temperature (for a review see Wang *et al.* 2006; McCue 2010). Several avian nectarivores reduce their body temperature in response to energy stress (McKechnie and Lovegrove 2002). When exposed to a comparable 2 h fasting period, rufous hummingbirds became torpid to compensate for the energy deficit (Tooze and Gass 1985). Sunbirds and honeyeaters in our study did not become torpid during or after the fast, but a more subtle reduction in body temperature may have occurred. Future studies should record the body temperatures and metabolic rates of nectarivorous birds during fasting challenges to detect possible reductions in energy expenditure. Despite possible energy-saving mechanisms, evening body mass of our birds was lower on the fasting day than on the control day. This confirms the findings of an earlier study (Nicolson *et al.* 2005) where sunbirds tended to be lighter ($P=0.07$) on a day with interrupted feeding. The difference in statistical significance might be due to the different methods used to obtain body mass data, as feeding and excretion events may distort values when the bird is caught and weighed once, while more frequent recordings without disturbance are more accurate.

Birds are generally more susceptible to body mass loss during food deprivation than mammals, due to their higher body temperatures and mass-specific metabolic rates; and some small birds may tolerate only one day of starvation (McCue 2010). In our study, the rapid body mass loss caused by the 2 h fast could not be completely overcome by an accelerated energy intake and accumulation after the fast. Birds rested during the fasting period (darkness), while wild birds are likely to move

around to search for nectar sources. It may not seem optimal from an energetic point of view, but increased locomotor activity of food-deprived birds (Ketterson and King 1977), may increase foraging opportunities. Considering the additional energetic cost for flight and foraging of wild versus captive birds, wild sunbirds and honeyeaters may experience a higher body mass loss during food deprivation than measured in our experimental set up. Behavioural and physiological energy-saving mechanisms must therefore be involved when nectarivorous birds cope with prolonged interruptions to feeding, such as several days of rain.

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Tables

Table 1. Digestive parameters of four whitebellied sunbirds and five brown honeyeaters (mean \pm SE) that the chemical reactor model of digestive capacity was based on (McWhorter and Martínez del Rio 2000). Sucrose assimilation efficiency was determined for eight individuals per species.

Physiological parameter	Whitebellied sunbird	Brown honeyeater
Total intestine length (cm)	7.0 \pm 0.3	8.7 \pm 0.5
Total intestinal volume (μ l)	133.3 \pm 17.1	187.9 \pm 25.3
Maximal total intestinal sucrase activity (μ mol \cdot min ⁻¹)	8.3 \pm 1.1	11.5 \pm 4.0
Apparent Michaelis constant–K _m (mM)	15.4 \pm 2.2	37.8 \pm 6.2
pH optima for intestinal sucrase activity	5.5	6
Apparent sucrose assimilation efficiency (%)	99.8 \pm 0.1	99.8 \pm 0.02

Table 2. Observed food and sugar intake (mean \pm SE) of eight whitebellied sunbirds and eight brown honeyeaters in the first hour following a 2 h fasting period. Birds were fed a 0.63 M sucrose diet. Maximal hourly food and sugar intake on this diet was predicted for the two species by a chemical reactor model of digestive capacity (McWhorter and Martínez del Río 2000). Statistical results derive from *t*-tests (single sample) that were used to compare predicted and observed food (and sugar) intakes.

Species	Food intake (mg·h ⁻¹)		Sugar intake (mg·h ⁻¹)		Observed vs. Predicted
	Observed (mean \pm SE)	Predicted	Observed (mean \pm SE)	Predicted	
Whitebellied sunbird	1438.8 \pm 59.9	1242.9	287.8 \pm 12.0	248.6	<i>P</i> =0.01
Brown honeyeater	1533.0 \pm 59.5	1500.4	306.6 \pm 11.9	300.1	<i>P</i> =0.60

Figure legends

Fig. 1. Mass-specific food intake rate ($\text{mg}\cdot\text{h}^{-1}\cdot\text{g body mass}^{-1}$; mean \pm SE; SE partly omitted for clarity) of eight whitebellied sunbirds (above) and eight brown honeyeaters (below). Birds fed continuously on the control day, whereas feeding was interrupted for 2 h (10:00-12:00) on the fasting day. Statistical significance derives from the Tukey's Honest Significant Difference *post-hoc* test that followed comparison of the mass-specific food intake rate of both species between control and fasting day by RM-ANOVA (** $P\leq 0.01$; *** $P\leq 0.001$).

Fig. 2. Feeding duration (s) of eight whitebellied sunbirds (A) and the number of feeding events (B) (mean \pm SE; SE partly omitted for clarity). Birds fed continuously on the control day, whereas feeding was interrupted for 2 h (10:00-12:00) on the fasting day. Statistical significance derives from the Tukey's Honest Significant Difference *post-hoc* test that followed comparison of the feeding duration between control and fasting day by RM-ANOVA (* $P\leq 0.05$).

Fig. 3. Body mass (g) throughout the day for eight whitebellied sunbirds (above) and eight brown honeyeaters (below) (mean \pm SE; SE partly omitted for clarity). Birds fed continuously on the control day, whereas feeding was interrupted for 2 h (10:00-12:00) on the fasting day. The slopes of the regression lines (body mass vs. time) are given as m . Slopes of body mass vs. time regressions for the afternoon (12:00-19:00) were significantly steeper on the fasting day than on the control day in both species ($F_{1,14}=38.60$, $P<0.001$).

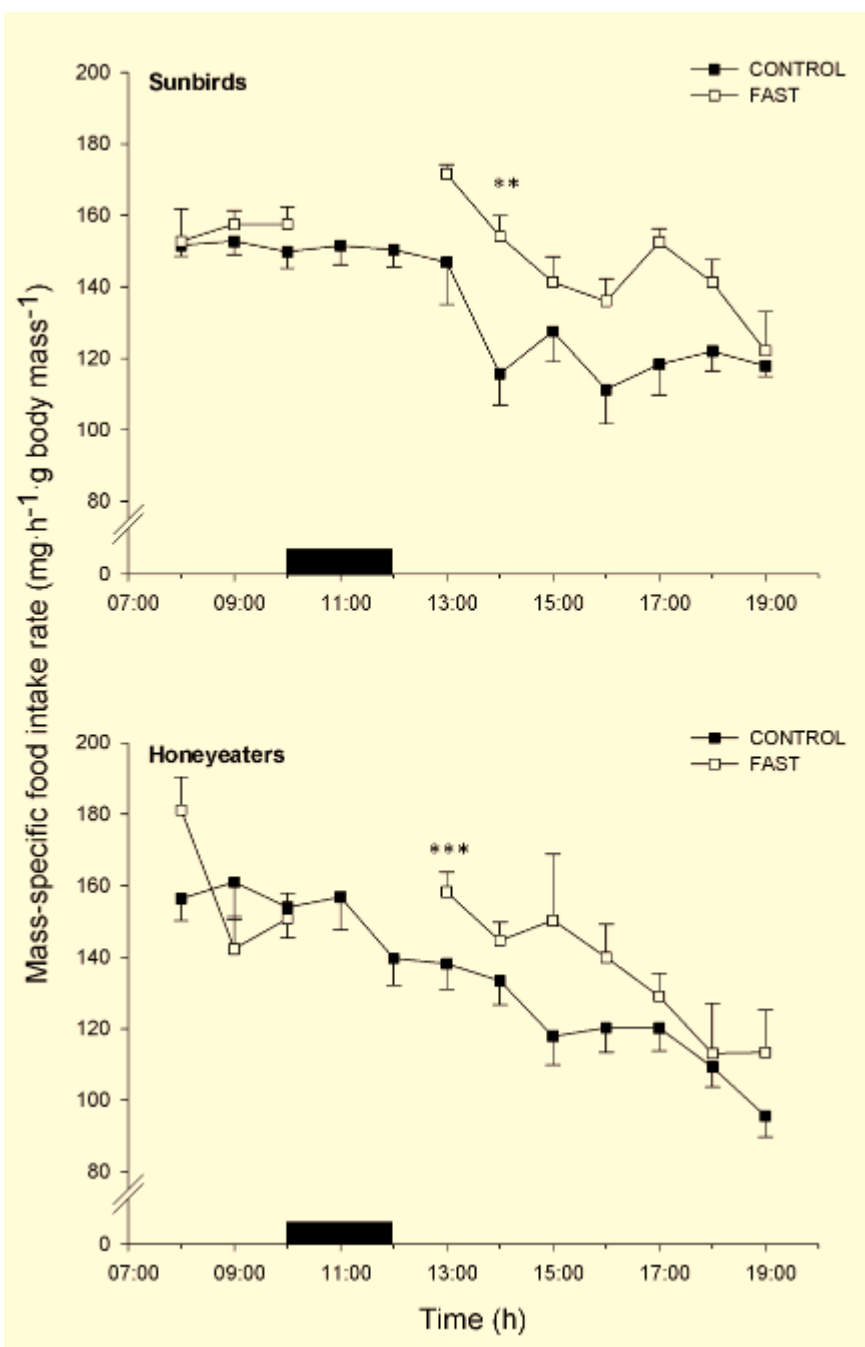


Figure 1.

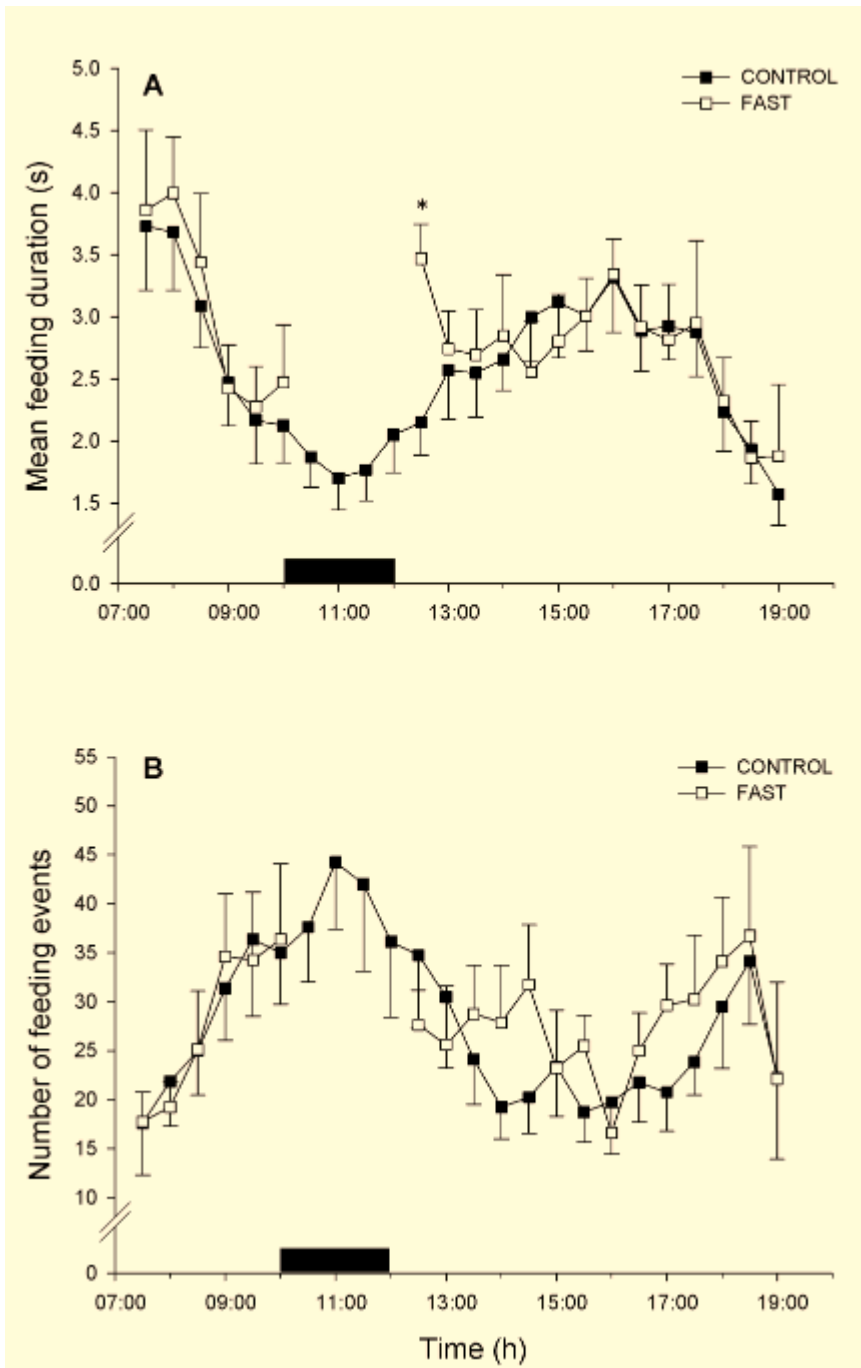


Figure 2.

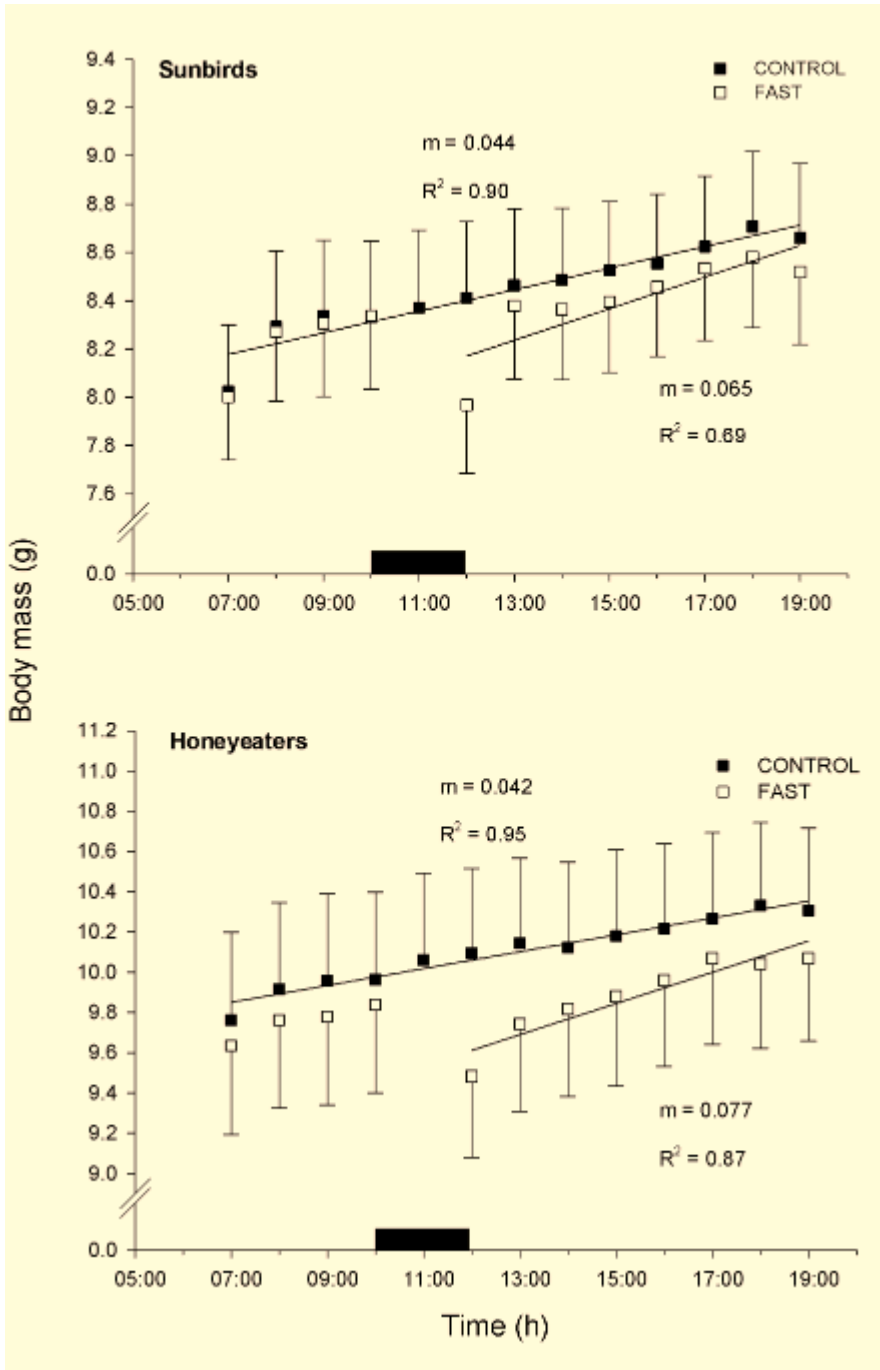


Figure 3.