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Food quality, fasting periods and temperature stress: effects of energy challenges on the feeding patterns of avian nectarivores

by

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The whitebellied sunbird (*Cinnyris talatala*)

The amethyst sunbird (*Chalcomitra amethystina*)

The brown honeyeater (*Lichmera indistincta*)

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Declaration

The experimental work described in this thesis was carried out in the Department of Zoology and Entomology, University of Pretoria, South Africa, and in the School of Veterinary and Biomedical Sciences, Murdoch University, Western Australia, from 2006 to 2008. I, Angela Köhler, declare that the thesis, which I hereby submit for the degree Doctor of Philosophy (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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Angela Köhler Date

Disclaimer

This PhD thesis consists of chapters that have been prepared as stand-alone manuscripts. These manuscripts have either been published or are being prepared for future submission. As a consequence, there may be some repetition between chapters.

Publications and manuscripts in preparation

In the course of this research, several manuscripts were published or are currently in preparation. A list of these manuscripts follows in chronological order:

Journal publications

Köhler A., Verburgt L. and Nicolson S.W. 2008. Nectar intake of whitebellied sunbirds (*Cinnyris talatala*): can meal size be inferred from feeding duration? Physiological and Biochemical Zoology 81: 682–687.

Köhler A., Verburgt L., Fleming P.A. and Nicolson S.W. 2008. Changes in nectar concentration: how quickly do whitebellied sunbirds (*Cinnyris talatala*) adjust feeding patterns and food intake? Journal of Comparative Physiology B 178: 785–793.

Journal articles in preparation

Köhler A., Verburgt L., Fleming P.A., McWhorter T.J. and Nicolson S.W. The responses of two avian nectarivores to interruptions in food availability.

Köhler A., Verburgt L., McWhorter T.J. and Nicolson S.W. Low temperature challenges in sunbirds: effects on food intake, feeding patterns and body mass of *Cinnyris talatala* and *Chalcomitra amethystina*.

McWhorter T.J., Fleming P.A., Köhler A. and Nicolson S.W. Does digestive spare capacity in honeyeaters vary with body size? An experimental test and a model.

Köhler A., Verburgt L. and Nicolson S.W. Nectar extraction by sunbirds: does licking behaviour depend on nectar concentration or viscosity?

SUMMARY

The small size of nectarivorous birds is associated with high mass-specific metabolic rates and energetic lifestyles. Their energy balance is likely to be strongly influenced by environmental factors. Firstly, nectar varies in sugar concentration between different food plants and birds must adjust their consumption to maintain a constant energy intake. Secondly, unfavourable weather conditions, such as storms and heavy rains, may prevent birds from feeding, and they must increase their energy intake to compensate for the loss in foraging time. Low ambient temperature, as a third energetic challenge, results in higher energy demands for thermoregulation, which leads to increased food intake. However, these compensatory feeding responses may be constrained by physiological limitations to nectar ingestion, digestion and osmoregulatory processes.

My research focused on the behavioural and physiological responses of captive sunbirds (Nectariniidae) and honeyeaters (Meliphagidae) to energetic challenges, namely variations in nectar quality and availability and in ambient temperature. For sunbirds, I also investigated on a novel short-term scale how feeding patterns are adjusted in order to compensate for alterations in energy intake or requirements. Feeding events were recorded using a photodetection system, and body mass was monitored continuously by connecting the perches to electronic balances, interfaced to a computer.

Whitebellied sunbirds (*Cinnyris talatala*) were fed various nectar sugar concentrations. Their feeding durations were found to provide an estimate of meal size on all food concentrations. When exposed to a decrease in sugar concentration, birds generally demonstrated an increased feeding frequency and food intake within 10 min. The number and duration of meals increased in the first few minutes after return of a more concentrated diet. When whitebellied sunbirds and brown honeyeaters (*Lichmera indistincta*) were exposed to a 2 h fasting period during the day, they increased their nectar intake and energy accumulation after the fast. Sunbirds achieved this by increasing

meal size but not meal frequency. However, both species weighed less in the evening following the fast than the previous evening, indicating that the compensation for lost foraging time was incomplete. During acute cold exposure, whitebellied sunbirds, amethyst sunbirds (*Chalcomitra amethystina*) and brown honeyeaters increased their nectar intake, but lost body mass irrespective of nectar sugar concentration. Honeyeaters ingested more food at subsequent cold exposure, suggesting physiological adaptation to high feeding rates. A chemical reactor model of digestive capacity, which assumes sucrose hydrolysis to be the limiting step in nectar digestion, accurately predicted maximal food intake in honeyeaters, but mostly underestimated it in sunbirds. Sugar assimilation efficiency was higher than 99% in whitebellied sunbirds and brown honeyeaters. Lastly, licking frequencies and tongue loads of whitebellied and amethyst sunbirds were investigated. In both species, tongue lick duration increased, and licking frequency and consumption per lick decreased, with increasing nectar concentration. Birds did not adjust their licking behaviour after a fasting period.

In conclusion, the response to varied energy challenges is shaped by both compensatory feeding and physiological constraints. Although unrelated, sunbirds and honeyeaters showed convergence in their responses, probably due to their similar nectar-feeding lifestyle.