# Energy metabolism, respiration frequency and $O_2$-consumption per breathing act in 11 different sunbird species during day and night

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*Summary.* The mean metabolic rates of 11 sunbird species are in the expected range based on data from other birds. Nevertheless the difference between day and night levels is greater (58–69%) than normal. Breathing frequencies among these birds correspond more closely to the (higher) levels found in empirical data for mammals. $O_2$-consumption per breathing act remains nearly constant during day and night indicating that the diurnal cycle of $O_2$-consumption is regulated mainly by modulation of breathing frequencies, which correlate directly with gaseous metabolism.

*Key words.* Energy metabolism; $O_2$-consumption per breathing act; respiration frequency; sunbirds; tidal volume.

*Materials and methods.* The sunbird species examined are listed in the table. The metabolism of each species[1] was continuously recorded during a period of at least 5 consecutive days and nights at a constant ambient temperature of 25°C. The dark-light cycle was 12:12 h (dark-phase between 19.00 and 07.00 h); food and water were provided ad libitum.

During measurements the birds were kept in a plexiglas chamber (29 × 23 × 13 cm ≙ 8.7 l); the flow rate (open system) was 30 l/h.

Species, mean body mass and breathing parameters during day and night of the sunbirds examined: Metabolic rate (first number, in J/g · h); breathing frequencies (second number, in $\mathrm{min}^{-1}$); $O_2$-consumption per respiration act (third number, in µl); and tidal volume (in parenthesis, in µl, derived values, based on the following assumptions: $O_2$-extraction rate = 5%, $O_2$-concentration of air = 21%). All data are presented as mean values ± SD (except in those cases where only one measurement was available)

| Species (mean body mass in g) | | Breathing parameters during | | Differences between day- and night-time levels (%) |
|---|---|---|---|---|
| | | Day-time | Night-time | |
| 1. *Aethopyga siparaja* | (6.8)* | 177 ± 33 | 78 ± 8 | − 55.9 |
| Crimson Sunbird | | 148 | 94 | − 36.5 |
| | | 8.0 | 7.2 | − 10.0 |
| | | (160) | (148) | |
| 2. *Nectarinia venusta* | (7.1) | 242 ± 24 | 90 ± 5 | − 62.8 |
| Variable Sunbird | | 169 ± 24 | 85 ± 4 | − 49.7 |
| | | 9.7 ± 1.2 | 8.0 ± 1.0 | − 17.5 |
| | | (194 ± 20) | (160 ± 20) | |
| 3. *N. cuprea* | (7.4) | 182 ± 16 | 64 ± 4 | − 64.8 |
| Copper Sunbird | | 140 ± 20 | 64 ± 8 | − 54.3 |
| | | 8.3 ± 0.81 | 6.7 ± 0.4 | − 19.3 |
| | | (166 ± 16) | (134 ± 7) | |
| 4. *N. veroxii* | (8.4) | 200 ± 25 | 89 ± 5 | − 55.5 |
| Mouse-colored Sunbird | | 118 ± 16 | 59 | − 50.0 |
| | | 11.8 ± 1.76 | 12.0 | + 1.7 |
| | | (236 ± 35) | (240) | |
| 5. *Anthreptes collaris* | (8.5) | 200 ± 29 | 69 ± 6 | − 95.7 |
| Collared Sunbird | | 142 ± 16 | 60 | − 57.7 |
| | | 10.3 ± 3.86 | 9.0 | − 12.6 |
| | | (206 ± 78) | (180) | |
| 6. *N. adelberti* | (9.3)* | 202 ± 58 | 103 ± 35 | − 49.0 |
| Buff-throated Sunbird | | 132 ± 2 | 75.5 | − 42.8 |
| | | 12.2 ± 0.7 | 11.6 ± 0.9 | − 4.9 |
| | | (244 ± 14) | (233 ± 18) | |
| 7. *N. amethystina* | (10.0) | 240 ± 33 | 72 ± 5 | − 70.0 |
| Amethyst Sunbird | | 147 ± 42 | 68 | − 53.7 |
| | | 14.0 ± 3.12 | 10 | − 28.6 |
| | | (280 ± 60) | (200) | |
| 8. *Anthreptes orientalis* | (11.9)* | 125 ± 21 | 54 ± 12 | − 56.8 |
| Violet-backed Sunbird | | 131 | 77 | − 42.2 |
| | | 9.8 | 9.5 | − 3.1 |
| | | (196) | (190) | |
| 9. *N. senegalensis* | (12.6) | 215 ± 25 | 77 ± 10 | − 64.2 |
| Scarlet-chested Sunbird | | 116 ± 14 | 68 ± 4 | − 41.4 |
| | | 18.7 ± 2.53 | 14.0 ± 1.41 | − 25.1 |
| | | (374 ± 51) | (280 ± 28) | |
| 10. *N. tacazze* | (13.7) | 208 ± 18 | 54 ± 5 | − 74.0 |
| Tacazze Sunbird | | 127 ± 16 | 33 | − 74.0 |
| | | 18.9 ± 3.2 | 21 | + 11.1 |
| | | (378 ± 60) | (420) | |
| 11. *N. kilimensis* | (14.2) | 176 ± 33 | 50 ± 6 | − 71,6 |
| Broncy Sunbird | | 102 ± 32 | 34 ± 5 | − 66.7 |
| | | 22.8 ± 6.77 | 25.5 ± 2.10 | + 11.8 |
| | | (460 ± 14) | (510 ± 40) | |

*These birds were obtained from Dr K.-L. Schuchmann, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

All gas volumes were reduced to standard pressure and temperature conditions. Energy production was calculated as J/g · h from gaseous metabolism and the conversion factor of 1 ml $O_2 \hat{=} 20$ Joule.

Measuring instruments: Hartmann & Braun Caldos 4T ($CO_2$-analyzer: 0–5%) and Magnos 2T (oxygen-analyzer: 0–2%). Respiration frequency was recorded simultaneously in undisturbed birds during day and night by a highly sensitive (0–35 mbar) pressure transducer (Bell & Howell, type BHL 4104) which was inserted into the respiratory chamber. This allowed the monitoring of pressure oscillations caused by lung ventilation under standardized conditions without handling the bird. These data allowed the determination of $O_2$-consumption per breathing and the calculation of tidal volume (based on the assumption of a mean $O_2$-extraction rate of about 5% and an air-oxygen concentration of 21%).

*Results and discussion.* All data are summarized in the table.

*Metabolic rate:* The mean metabolism-weight regression line of the day-time values follows the equation $M = 266 \cdot W^{0.862}$ ($r = +0.79$; M = metabolism in J/h and W = b.wt in g); that of the night-time values is $M = 244 \cdot W^{0.456}$ ($r = +0.55$). These correlations are not based on measurements in the thermoneutral zone (TNZ) of the birds. Corresponding values at an ambient temperature of 30 °C (TNZ) result in the following regression line: $M = 102 \cdot W^{0.716}$ (night-time) (Lübben and Prinzinger in prep.); the resulting values are in the same range as those reported for the mean basal metabolism of most passerine and nonpasserine birds: $(127 \pm 34.4) \cdot W^{0.723 \pm 0.006}$ (combined data from previous measurements by Dawson and Hudson[1], Aschoff and Pohl[2], Lasiewski and Dawson[3], Prinzinger and Hänssler[4]). Hummingbirds, which are physiologically analogous to sunbirds, show night-time values of energy metabolism which are approximately 100% (and more) above these levels (Prinzinger, Krüger and Schuchmann[5]). Diurnal increases in metabolism in sunbirds during periods of activity are between 58–69% (mean values, range: 30–77%). These are relatively large differences between day- and night-time levels (in comparison to other birds: mean difference 25%, Aschoff and Pohl[2]), indicating an energy-saving strategy through a severe reduction in metabolism during the resting phase.

*Breathing frequencies* (F, $min^{-1}$) during activity (day-time) correlate inversely with b.wt (g) using the equation $F = 314 \cdot W^{-0.38}$; during the night $F = 457 \cdot W^{-0.88}$. The resulting values clearly correspond more closely with the empirical equations for mammals (higher frequencies) than those normally obtained for birds (see Calder[6], Adolph[7]). Our results on unrestrained birds therefore do not support the opinion that birds breathe at lower frequencies than do mammals of similar body mass. It seems possible that this observed difference may result in part from differences in the conditions under which the data were collected (only very few data are from unrestrained animals).

The day/night differences in the exponents of the allometric equations are based on the fact that heavier sunbirds show a greater reduction of breathing frequency (and metabolism) during resting time than lighter species do. Breathing frequency correlates directly ($\sim M^1$) with gaseous metabolism. The equations (linear regression) are $F = 93 + 0.21 \cdot M$ for the day-time and $F = 0.97 + 0.87 \cdot M$ for the night-time (F in $min^{-1}$, M in J/g · h). These linear correlations lead to the assumption that the $O_2$-extraction rate is the same for all birds tested (that is, independent of body weight, or proportional to $W^0$) and that tidal volumes are directly related to b.wt (proportional to $W^1$). Nevertheless the lack of detailed experiments on $O_2$-extraction rates in birds and the paucity and variability of data on tidal volumes in birds which has been directly determined and not derived from other parameters prohibits a useful regression analysis. Therefore, the statement that the tidal volumes of birds are more than twice those of mammals of the same weight range must be viewed with a certain scepticism because of the fact that many other breathing parameters are closely correlated in these two homoeothermic groups.

Regarding the mean $O_2$-consumption per breathing act we could not find great differences between day and night. Consequently the diurnal cycle of $O_2$-consumption (high activity levels, low resting levels) seems to be primarily regulated by the observed modulations in breathing frequencies while the other respiratory parameters ($O_2$-consumption per breathing act, oxygen-extraction rate and tidal volume) remain relatively constant.

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## Acquired protein appetite in rats: Dependence on a protein-specific need state[1]

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*Summary.* Rats are shown to acquire a preference for protein-predictive olfactory cues which depends on a state of mild deficit in protein intake – i. e. a learned protein-specific appetite.

*Key words.* Protein appetite; nutrient self-selection; need cue learning; protein-conditioned preference; odour conditioning.

When faced with diets varying in nutrient content, animals can choose sufficient protein to sustain growth [2–5]. Rats adapt their dietary selection patterns successfully in the face of changing protein requirements and availability[6–9].

Yet, no reliable natural cues to the protein content of a diet are known that might allow protein selection via innate preferences or aversions. Therefore, protein-specific dietary selection behaviour must depend on learning which dietary cues predict protein content, by associating those sensory characteristics with the protein-specific after-effects of eating[10–12]. However, such learned preferences for protein-predictive dietary cues would only produce selection behaviour sufficient to satisfy metabolic demands if the preferences were activated by incipient or current protein need. Protein-conditioned preferences have been demonstrated in mildly hungry rats, but there was no evidence that the preferences depended on a protein-specific deficit rather than, e. g., an energy deficit[13]. The experiment reported here provides the first evidence for an acquired protein appetite – that is, a preference for protein-predictive cues that depends on current lack of protein intake.

The rats were associatively conditioned to prefer a flavour by pairing it with the effects of ingested protein on mild food depri-