

Torpor in hummingbirds

by

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The phenomenon of precisely regulated metabolism in trochilids has been fairly well documented (e.g. Carpenter 1974, French & Hodges 1959, Hainsworth et al. 1977, Wolf & Hainsworth 1972). In these studies torpor, an extreme reduction of body temperature and metabolism, has often been observed experimentally when the bird (a) was exposed to cold and (b) could not gain its daily energy requirements. According to these previous investigations torpor should occur only in a state of emergency.

In this study, however, we demonstrate that torpor can be observed in all hummingbird species ($n = 18$) tested independent of any given ambient temperature (T_a : 5°, 10°, 15°, 20°, 25°C) and at a constant food supply with artificial nectar (see Schuchmann 1979). The species under observation varied in mean body mass from 2.7 g to 17.5 g. Gaseous metabolism was measured in a plastic chamber in an open flow system (flow rate 20 l/h) with a Hartmann & Braun paramagnetic O₂-analyser (Magnos 2T, accuracy ± 0.1 % O₂) and an infra-red CO₂-analyser (Uras 2T, accuracy ± 0.1 % CO₂) continuously over 5 days for each species and 24 h at each ambient temperature. All hummingbirds tested were collected in different climatical and altitudinal Central- and South-American habitats by K.-L.S. They had moulted while in captivity and were in excellent health condition. During the experiments (LD 12:12) artificial nectar was constantly available to all birds. Because of the delicate handling of these small sized birds, body temperature (T_b) during torpor was not measured cloacally but axillarily under the wing with a digital thermometer (Testotherm KG). For further methodical details see Krüger et al. (in print).

Our results reveal that all hummingbirds tested are capable of undergoing torpor regularly. They reduced their energy expenditure by lowering metabolism up to 95 % every night independent of ambient temperature (see Table 1). During torpor T_b varied from 18°C to 20°C. Recent comparative studies on torpid mousebirds (Coliidae) concluded that a T_b of 18°C must be maintained to secure proper endogenous physiological functions. A further decrease would be lethal (Prinzinger et al. 1981).

In Fig. 1 A and 1 B, daily rhythm of metabolism is shown for a Purple-throated Carib (*Eulampis jugularis*) and a White-bellied Woodstar (*Acestrura mulsant*). As expected O₂-consumption is greater during the day-time due to the bird's activity. Metabolism was drastically reduced at the beginning of the dark period. These observations imply that torpor is a normal part of daily

rhythm and is controlled by an endogenous mechanism rather than by external factors e.g. low ambient temperatures or shortage of food.

Torpor occurred mostly in the second part of the night and O₂-consumption was elevated again shortly before the following light period. In a previous stu-

Table 1: Metabolism during torpor in % of mean activity metabolism (measured in light, food ad libitum). Body mass and sex of species is given in parenthesis. Symbols signify: // = no measurements, — = no sign of torpor observed.

| Species | Ambient-Temperature | | | | |
|--|---------------------|-------|-------|-------|-------|
| | 5° C | 10° C | 15° C | 20° C | 25° C |
| <i>Ocreatus underwoodii</i> (2,7 g, ♀) | // | 8,4 | 6,0 | 7,3 | — |
| <i>Chlorostilbon mellisugus</i> (2,9 g, ♂) | 14,4 | 11,9 | 6,0 | 5,4 | 6,1 |
| <i>Orthorhyncus cristatus</i> (2,9 g, ♂) | 17,9 | 16,9 | 12,3 | 5,5 | 16,8 |
| <i>Orthorhyncus cristatus</i> 2,9 g, ♂) | // | 19,5 | — | 8,0 | 22,7 |
| <i>Archilochus alexandri</i> (2,9 g, ♂) | — | 10,2 | — | // | // |
| <i>Archilochus alexandri</i> (3,2 g, ♀) | // | 8,5 | — | — | — |
| <i>Acestrura mulsant</i> (3,3 g, ♀) | — | 6,2 | 9,8 | 6,2 | 8,1 |
| <i>Urosticte benjamini</i> (3,9 g, ♀) | — | — | — | 5,3 | — |
| <i>Trochilus scitulus</i> (4,0 g, ♀) | 21,1 | 12,4 | 5,7 | 6,6 | 19,9 |
| <i>Chrysuronia oenone</i> (5,0 g, ♂) | 13,1 | 9,4 | 11,2 | 8,4 | 22,5 |
| Hybrid <i>Trochilus scitulus</i> × <i>Thalurania furcata</i> (5,0 g, ♂) | 12,4 | 3,4 | 6,9 | — | — |
| <i>Florisuga mellivora</i> (6,0 g, ♂) | // | 14,9 | 4,9 | // | // |
| <i>Aglaeactis cupripennis</i> (7,2 g, ♀) | 2,8 | 2,6 | 3,3 | 17,9 | 26,3 |
| <i>Boissonneaua matthewsii</i> (7,2 g, ♀) | 10,5 | — | — | — | — |
| <i>Anthracothorax nigricollis</i> (7,7 g, ♀) | — | — | 12,9 | — | — |
| <i>Eugenes fulgens</i> (7,9 g, ♂) | 14,6 | 13,5 | 8,5 | 15,8 | 28,8 |

Table 1 (cont'd)

| Species | Ambient-Temperature | | | | |
|--|---------------------|-------|-------|-------|-------|
| | 5° C | 10° C | 15° C | 20° C | 25° C |
| <i>Lampornis clemenciae</i> (8,0 g, ♂) | // | // | 2,1 | 13,5 | 7,1 |
| <i>Lampornis clemenciae</i> (8,3 g, ♂) | 10,7 | — | — | 18,9 | 29,1 |
| <i>Oreotrochilus estella</i> (8,5 g, ♂) | 9,1 | 2,6 | 5,5 | 11,6 | 27,6 |
| <i>Oreotrochilus estella</i> (8,9 g, ♂) | 7,1 | 7,9 | 5,3 | 16,9 | 28,6 |
| <i>Eulampis jugularis</i> (9,5 g, ♂) | 20,2 | 8,1 | 3,5 | — | 39,7 |
| <i>Patagona gigas</i> (17,5 g, ♀) | 21,7 | 7,0 | — | 18,8 | 41,6 |

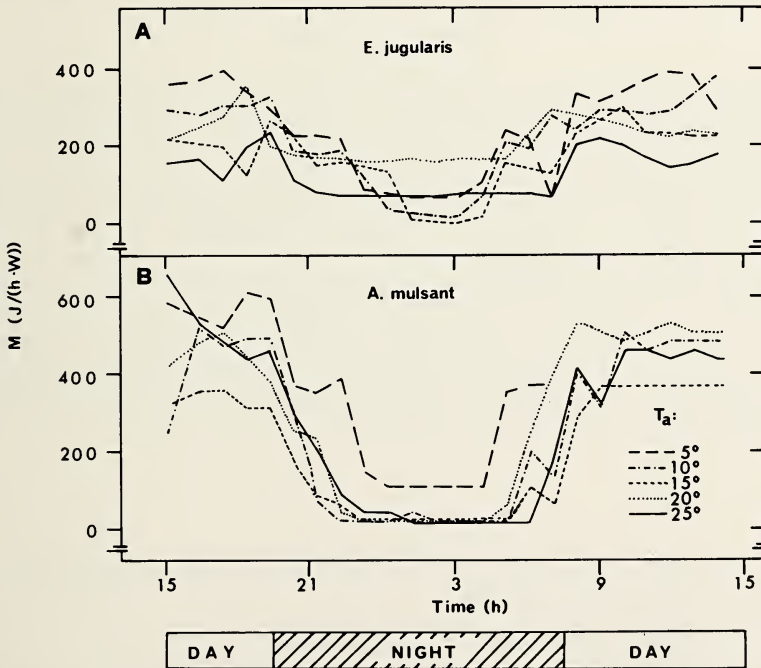


Fig. 1: Metabolism $M [J/(h \times W)]$ as a function of time at 5 different ambient temperatures (T_a). A. Purple-throated Carib (*Eulampis jugularis*, body mass 9.5 g), B. White-bellied Woodstar (*Acestrura mulsant*, body mass 3.3 g).

dy Carpenter (1976) observed torpor frequently in free living and captive Andean Hillstars (*Oreotrochilus estella*) at all ambient temperatures from 0° C to 30° C. This observation corresponds to our findings with 18 species of hummingbirds from tropical and subtropical regions. All showed the physiological capability of torpor at any given ambient temperature.

Calculations based on measurements of the caloric intake of hummingbirds under laboratory conditions revealed that the net energy gain for the night varies from 4000 to 8000 J depending on species-specific body mass (Schuchmann et al. 1979, Schuchmann & Jakob 1981). These energetical estimates are very close to the critical value of energetic requirements needed during the night when no food is consumed. This is true, however, only for the assumption that a constant body temperature of about 39° C is maintained. In the light of our findings the energy savings in torpor exceed 40 % of the total energy storage by simply reducing body temperature and metabolism. An even less positive energy balance could be largely compensated by such a physiological regulation pattern. We therefore assume that torpor as a means of energy saving has a much broader ecological significance for the energy balance of hummingbirds and does not occur only in a state of emergency.

Zusammenfassung

Stoffwechseluntersuchungen an 18 Kolibriarten aus unterschiedlichsten Klimaten und Lebensräumen Mittel- und Südamerikas ergaben, daß alle Versuchstiere, unabhängig von der getesteten Umgebungstemperatur (5° C, 10° C, 15° C, 20° C, 25° C), torpide wurden. Exemplarisch wurden die Tagesgänge des Stoffwechsels bei *Eulampis jugularis* und *Acestrura mulsant* bei verschiedenen Umgebungstemperaturen vorgestellt. Während der Nacht sank die Stoffwechselrate extrem gegenüber den Tageswerten ab (bis 95 %). Die Körpertemperatur im Torpor schwankte zwischen 18° C und 20° C. Da Torpor jede Nacht auftrat, wird bei diesen Vögeln ein endogener Stoffwechsel-Rhythmus vermutet. Während des starreähnlichen Zustandes wurden die Körpertemperatur und der Stoffwechsel aktiv an einer unteren Grenze geregelt. Dadurch war es den Trochiliden möglich, während der Nacht ihren Energieverbrauch erheblich zu reduzieren, um so diese lange Hungerphase zu überstehen. Nach diesen Untersuchungen muß davon ausgegangen werden, daß Torpor eine weitreichendere energetische und ökologische Funktion hat, als bisher angenommen wurde.

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