INTRODUCTION

For many small homeotherms, daily torpor is an essential mechanism to cope with periods of food deprivation and/ or severe weather conditions that pose a challenge to their energetic balance. Torpor is known to occur in birds from at least six different orders (Procellariiformes, Columbiformes, Columbidae, Charadriiformes, Apodiformes, and Trochiliformes; see Richards 1983, Heller 1989, French 1993). Daily torpor has been extensively studied in hummingbirds, in which significant energetic savings are correlated with the use of daily torpor (Hansworth et al. 1977, 1981; Beuchat et al. 1976).

Hibert 1990). Most of the studies on hummingbirds suggest that daily torpor is a strategy employed in situations involving energetic stress. Thus, torpor has less often been reported in apparently well-fed individuals (Kluge et al. 1982, Carpenter and Hibert 1988, Hibert 1993a, 1993b). Because it is difficult to obtain physiological information from free-living hummingbirds, most studies have been of birds kept under laboratory conditions. Information about the use of torpor under natural conditions in hummingbirds is consequently scarce (Calder and Booser 1973, Carpenter 1974, Calder et al. 1990), as it is for other bird species entering torpor (Bingham 1992). The only study that has provided acceptable proof that hummingbirds need not be energetically stressed in order to resort to daily torpor is that of Carpenter and Hibert (1988), who
demonstrated torpor as a free-living, well-fed, Rufous Hummingbird Selasphorus rufus. In the same species, but under laboratory conditions, Hiebert (1993a, 1993b) reported increased inten-
sity of torpor during periods of food restriction, but when body mass nonetheless showed an in-
crease. In S. rufus the use of torpor was highest in the autumn, suggesting a function of torpor as a strictly energy saving mechanism, thereby minimizing the time required for premigratory fattening. In this case torpor is not correlated with inadequacy (ood intake) (Carpenter et al. 1993, Hiebert 1993a). However, it is still an open question whether hummingbirds normally need to be energy-stressed in order to enter tor-
por under natural conditions (Calder 1994).

We examined the use of torpor by three spe-
cies of Brazilian hummingbirds kept under semi-
natural conditions. We asked whether these spe-
cies would enter torpor under conditions as close to natural as possible. We also wanted to study the influence of short-term changes in their en-
ergetic status on the use of torpor. The energetic status of the hummingbirds was manipulated by experimentally depriving them of food from the time of capture until sunset.

**Methods**

The study was carried out at the Museu de Biol-
ogia, at Santa Teresa in the state of Espirito San-
to, Brazil (19’S 55’S, 40’S 6’W; about 700 m above sea level). We studied three species of hум-
mimgbirds, the Versicolored Emerald Amazilia versicolor (~ 4. 1 g), the Black Jacobin Melan-
othraxis fuscus (~ 7. 7 g), and the Swallow-
tailed Hummingbird Eugenides macrourus (~ 8. 6 g). We did not determine sexes in any of the three species, all of which are common breeding birds in the study area (Busch 1982).

We conducted the study from 2-20 December 1987. The length of the nights did not vary much, being approximately 11 h long. Sunset changed from 05:53 to 05:59 and sunrise from 19:10 to 19:19 during the study period. All times are given in Rio de Janeiro summertime.

The hummingbirds in the study area are ac-
customed to feeding at artificial feeders. Hence, individuals of all three species were easily caught at the feeders during the afternoon. After capture they were kept individually, at normal ambient temperature, in ca. 0.5 m³ cages and deprived of food for a variable time (range 0-
240 min) until sunset. The birds were weighed (Metler, accuracy 0. 01 g) and then placed indi-
vidually in smaller overnight cages (approxim-
ately 12 × 12 × 20 cm cardboard boxes) pro-
vided with a perch. Usually the birds roosted quietly on the perch during the night, although in some cases they apparently had spent the night sitting on the floor of the cage. The cages (up to six each night) were placed outdoors during the night. The walls and top of each cage were equipped with holes, to ensure that the hummingbirds were exposed to natural varia-
tions in both ambient temperature and photoperi-
iod.

The small size of hummingbirds makes the measurement of body temperature (Tb) a difficult task. We used a copper-constantan thermocouple (California Fine Wire Company, type 0.005) placed subcutaneously and laterally on the pec-
toral muscle for measurements of body temper-

ture. The thermocouple was fixed in place with small pieces of adhesive tape. During measure-
ments, the subcutaneously placed tip of the ther-

couple was covered by the wing. Flight studies of all three species indicated that such measure-
ments of pectoral temperature did not differ by more than 0.2-0.3°C from simultaneous mea-
surements of rectal temperature. A thermocouple was placed inside one of the cages to record the actual ambient temperature (Ta) to which the birds were exposed. All thermocouples were ex-
tended by using large-diameter copper-constantan 
thermocouples (Bicc Cables, U.K., 4-5 mm length) that went to a nearby house where the data-acquisition equipment was placed.

Body temperature was measured every 40 sec over several nights. The thermocouple wires were connected to a Data Translation (DT 2805) A/D converter, via a D1-757 terminal board, and processed by a computer using a Labtech Notebook data acquisition program. Each night, up to six individuals were studied simulta-

eously. We consistently used at least two different species, as well as variable fasting times, each night. After arousal of the birds, which usually occurred between 06:00 and 07:00, they were removed from their cages and re-
 leased again after removing the thermocouples and re-weighting.

The total time spent in torpor during a night was calculated as the time Tb was below 35°C during that particular night. Mean body tempera-

ture during torpor was only calculated if a sta-
tle value had been attained.
All statistics were carried out using SigmaStat software (ver. 1.0, Jandel Scientific). Results are given as the mean ± SD. Statistical significance was set at P < 0.05.

RESULTS
A total of 22 Amazilia versicolor, 29 Melanotrichia fuscus and 27 Eupetomena macroura were tested for one night. Of these, 16, 10 and 10 individuals, respectively, went into torpor.

There were marked variations in the pattern, as well as the likelihood, of entering torpor and the duration of torpor among individuals and species. In M. fuscus, those individuals entering torpor had a significantly lower body mass at evening time compared to those individuals that did not enter torpor (Table 1). Thus whether this species entered torpor during a particular night clearly depended upon the evening body mass, and hence their energy reserves. In contrast, evening body mass was not associated with torpor in A. versicolor and E. macroura (t-tests, P = 0.09 and P = 0.80, respectively; Table 1). In all three species the use of torpor resulted in a significant reduction in overnight mass loss compared to birds not in torpor (Table 1). There was a marked difference between M. fuscus and the other two species in the duration of torpor periods. Long torpor periods, lasting throughout the entire night, were regularly found in M. fuscus, whereas shorter torpor periods, sometimes less than 1 hr, were observed in the other two species (Fig. 1). In both A. versicolor and E. macroura, total torpor duration during a night varied between 2 and 11 hr, whereas in M. fuscus the torpor periods were always long (7.5–11 hr).

In all three species of hummingbirds we observed an unusual pattern of torpor with more than one torpor bout during a single night (Fig. 1). This pattern of torpor mostly was seen in A. versicolor, in which up to three distinct torpor bouts could be recorded during a single night (Fig. 1). Such a multiple torpor pattern was observed in 4 of the 16 torpid A. versicolor, in 1 of the 10 torpid M. fuscus, and in 1 of the 12 torpid E. macroura.

The mean nocturnal body temperatures of the hummingbirds when in a non-torpid state were 36.8 ± 1.3°C (n = 22) for A. versicolor, 37.3 ± 1.5°C (n = 25) for M. fuscus, and 37.1 ± 1.3°C (n = 27) for E. macroura. None of these means were different to our way ANOVA, F(2, 70) = 0.57, P > 0.5). During torpor the body temperature

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean mass (g)</th>
<th>Mean torpor duration (hr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. versicolor</td>
<td>3.57 ± 0.23</td>
<td>3.41 ± 0.18</td>
</tr>
<tr>
<td>M. fuscus</td>
<td>6.98 ± 1.19</td>
<td>6.56 ± 0.44</td>
</tr>
<tr>
<td>E. macroura</td>
<td>6.45 ± 1.15</td>
<td>6.91 ± 0.37</td>
</tr>
</tbody>
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*Note: Significant differences (P < 0.05) are indicated by **.
was regulated at a level close to the ambient temperature, with mean values of 23.8 ± 1.4°C (n = 13), 24.7 ± 1.7°C (n = 12), and 23.2 ± 1.4°C (n = 11) for A. versicolor, M. fuscus and E. macuana, respectively. These values correspond to body-to-ambient temperature differences of 2.4 ± 0.8°C, 3.2 ± 0.8°C, and 2.4 ± 1.2°C, respectively. The mean body temperatures during torpor and the body-to-ambient temperature differences between the three species approached significance (F1,26 = 2.98, P = 0.06; and F1,26 = 3.05, P = 0.06, respectively), suggesting that M. fuscus kept a slightly higher body temperature during torpor. The overall mean body-to-ambient temperature difference was 2.6 ± 1.0°C (n = 36, Fig. 2). The relative constancy of this difference is best illustrated by those individuals experiencing sudden temperature changes crying the recording. During one particular night there was a heavy rainstorm that lowered the ambient temperature by about 2°C. This caused the body temperatures of the torpid birds to change in parallel (Fig. 3).

As an index of overnight energy expenditure, we calculated the mean overnight body-mass loss (BML). The overnight BML (expressed as a percentage of the initial body mass lost per hour during the night) decreased in all three species with the use of torpor (Fig. 4 and Table 1). In A. versicolor there also was a decrease in nocturnal energy expenditure with increasing fasting time (FT) before sunset. This relationship is described by the equation: BML = 0.779 − 0.039FT (r = 0.79, n = 5, P < 0.05, Fig. 4). Interestingly, even those individuals that did not enter torpor but remained normothermic throughout the night, showed a decrease in noc-
tural energy expenditure with increasing fast-
ing time. This relationship was statistically sig-
nificant for M. fascus (BML = 0.934 - 0.003FT, r = 0.78, n = 19, P < 0.001) and E. macroura (BML = 0.675 - 0.001FT, r = 0.57, n = 15, P < 0.05; Fig. 4). A similar relationship could not be demonstrated for A. vernicolor, probably be-
cause too few individuals failed to enter into tor-
por (Fig. 4). Because of this relationship be-
 tween BML and fasting time in non-torpid E. macroura and M. fascus, there may be a rela-
tionship between non-torpid body temperatures
and BML. This was in fact the case for E. ma-
croura, in which there was a significant positive relationship between nocturnal non-torpid body temperature and overnight body-mass loss (BML = 0.627 + 0.022T, r = 0.48, one-tailed t-test; t0.05,0.08 = 1.86, P = 0.05). In M. fascus there was, however, no such relationship.

In the smallest species (A. vernicolor), torpor occurred even in one individual that was al-
lowed to feed up to the time of onset (Fig. 4). It seems that A. vernicolor is less tolerant of fast-
ing stress than the other two larger hummingbird species, which could remain normothermic throughout the night even after fasting for al-
most three hours (Fig. 4). However, for all three species, the saving of energy achieved by entry into torpor is reflected in lower overnight body-mass loss compared to those which did not enter torpor. This also is manifested in Figure 5, which shows that the overnight mass loss was correlated, negatively and significantly, with the total time spent in torpor during the night.

As BML is an indirect measure of energy ex-
penditure, the energy saved by entry into torpor can be calculated using the regression lines re-
lating overnight mass loss to torpor duration (Fig. 5). Using these regression lines, we cal-
culated the decrease in overnight body-mass loss (assumed to correspond to the change in energy expenditure) associated with a torpor period of 10 hours out of a total night of 11 hours. The results indicated a mean nightly energy savings of 40% for A. vernicolor, 61% for M. fascus, and 80% for E. macroura.

DISCUSSION

The present results indicate that, at the prevail-
ing ambient temperatures, a noneregulated torpor

**FIGURE 3.** Ambient and body temperatures of two Melanocharis fascus throughout a single night. The sudden drop in ambient temperature at 01:31 is due to heavy rain.

**FIGURE 4.** Overnight body mass loss (% decrease in body mass to* *) in three species of hummingbirds as a function of fasting time before sunset. Open cir-
cles indicate birds that were normothermic (T > 35°C) throughout the night, and filled circles signify hummingbirds that entered torpor for a period of vari-
able duration. Lines signify significant relationships (for equations; see text). For two individuals (one A. vernicolor and one M. fascus) we did not record the accurate time of food deprivation prior to sunset, and the number of individuals consequently do not corre-
spond to the number of individuals from which body mass recordings were obtained (Fig. 5).
 occurred in all three hummingbird species. Thus, $T_0$ was not regulated at the lowest level. Our unpublished data, based on metabolic studies at ambient temperatures experimentally lowered below that of the outside conditions, indicate that $M. fuscus$ regulates its $T_0$ at 18–22°C, and $E. macroura$ regulates its $T_0$ at 13–16°C during torpor. We have no equivalent data for $A. versicolor$, but for five other species of hummingbirds ($Lophornis magnificus$, Callipetes amethystina, Ctenosaura rubricauda, Lencochochis albicollis, and Phaethornis previsi) from the same area in Brazil, the regulated body temperatures recorded during torpor range between 12 and 18°C (unpublished data). Thus, at ambient temperatures of between 19 and 23°C, as encountered in the present study, the hummingbirds apparently were not exposed to temperatures low enough to elicit a regulation of $T_0$ (Fig. 2). The nightly energy savings (49–61% of potential nightly energy expenditure) resulting from using torpor at these ambient temperatures fall within the same range as previously reported for other hummingbirds (Kriger et al. 1982, Wang 1988).

Entry into torpor clearly depended upon the hummingbirds' energetic state (the duration of fasting time before sunset), and supports the general view that torpor in hummingbirds is a mechanism normally evolved as a response to energy stress (Hainsworth et al. 1977). This also accords with findings in many other species of birds in which a nightly hypothermia has been described as a response to energy stress (Bierbach 1977, Reinertsen and Haftorn 1984, Graf et al. 1989). Interestingly, the present study has revealed that, in $M. fuscus$ and $E. macroura$, those individuals that did not resume a torpid state during the night, but suffered from a long fasting period before dusk, could decrease their overnight energy expenditure (Fig. 4). In $E. macroura$ this was paralleled by a decrease in $T_0$, as well. Thus, even before hummingbirds reach the body mass threshold for torpor initiation they may enter a low metabolic flow $T_0$ state, which may qualitatively be similar to the nightly hypothermia seen in other groups of birds. The body temperatures (36.8–37.3°C) observed when hummingbirds were resting at night in a non-torpor state are within the range of nightly body temperatures previously reported in hummingbirds (35.3–39.5°C; Prinzinger et al. 1991).

In addition to the use of torpor as a defense mechanism against energy stress, some studies have indicated that hummingbirds also may enter into torpor during presumably normal non-stressed periods (Kriger et al. 1982, Carpenter and Horn 1988) showed that the Rufous Hummingbird ($M. calliphorus$) may become torpid during the premigratory period, apparently in order to enable a more rapid build-up of fat reserves. This recently has been supported by further studies (Carpenter et al. 1993, Hiebert 1993a, 1993b). Carpenter (1974) reported torpor in the Andean Hillstar Hummingbird ($Oreotrochilus estrella$) during natural resting conditions, and found a clear seasonal difference in the use of torpor, both the number of instances and the duration of the torpor periods were greater during the winter. Carpenter (1974) concluded that neither the ambient temperature nor low food availability could explain the use of torpor by this species.
In the Poorwill (Phalaenoptilus nuttallii), daily torpor also may occur in free-ranging individuals independent of their energetic state (Brigham 1992). The results of the present study complement the above observations with the Versicolored Emerald Hummingbird A. versicolor, which may undergo nightly torpor during periods of apparently high food availability, as was indicated by the use of torpor in an individual caught at normal roosting time (Fig. 4). For the other two species studied, a fasting period seemed to be necessary for the induction of torpor. The shortest time of food deprivation necessary to induce torpor in M. fasciatus and E. macroura was 100 and 20 min, respectively (Fig. 4). Thus, our data suggest that E. macroura also has the ability to enter torpor under normal, non-stressed circumstances. M. fasciatus, on the other hand, seems to be less prone to enter torpor, since torpor was not recorded even after fasting periods of up to 100 min duration before dusk (Fig. 4). Heavy rain or cold weather probably could hinder hummingbirds in feeding for a period before dusk, and it is conceivable that periods of food-deprivation of up to 100 minutes could indeed occur under normal circumstances in the study area. There are no apparent interspecific differences in the biology of the three species which could explain the observed differences in torpor pattern.

The three species of hummingbirds used in the present study were able to enter torpor more than once during a single night (Fig. 1; see also Bech et al. 1994). This implies that some of the single torpor periods were short duration, lasting for only a few hours. Hainsworth et al. (1977) also reported torpor periods of only 2.5 hr in Rivoli’s Hummingbird Eugenes fulgens and 3.5 hr in the Black-chinned Hummingbird Archilochus alexandri, whereas Hiebert (1990) showed that torpor bouts of 2.5–3.0 hr could occur late in the night in Rufous Hummingbirds. Thus, most hummingbirds may have the ability to enter torpor for short periods at a time. However, the present description of multiple periods of torpor in hummingbirds would seem to be the first report of such cases. We cannot offer any explanation as to the cause of such a pattern, which seems to conflict with the assumption that there is a minimum body mass (set-point) below which the hummingbird is obliged to enter torpor (Hainsworth et al. 1977). However, in contrast to most other (laboratory) studies on torpor in hummingbirds, the birds in the present study were exposed to natural photoperiod, temperature and winds. Thus, it is likely that the multiple torpor bouts could be related to the environmental conditions. Any external sound stimulus from the tropical night could have initiated arousal. However, we never detected any obvious external stimuli that occurred during the nights on which we observed multiple bouts of torpor. In addition, often only one of the individuals studied during a single night would exhibit multiple torpor bouts, while the others had either one long period, or did not enter torpor at all. This obviously could stem from differences in energetic state and different levels of susceptibility to external stimuli. Regardless of the reason for multiple nightly torpor bouts, further studies employing hummingbirds in their natural habitat are needed to establish how widespread this pattern is. Most earlier studies were conducted on hummingbirds with lower body temperatures during torpor. Assuming a gradual loss of response with body temperature, the relative high Td during torpor in the tropical hummingbird species of the present study might cause a higher degree of susceptibility to external stimuli, in contrast to hummingbirds from temperate and montane areas, which often have lower levels of torpor body temperatures (5–10°C; Calder and Boosee 1973, Calder 1974, Carpenter 1974).

When hummingbirds experienced these interrupted torpor periods, they would invariably enter torpor again after having reached the nonthermic right Td level (Fig. 1). This still lends credit to the theory that a threshold-value of body mass is operating (Hainsworth et al. 1977, Hiebert 1992). The observation of multiple torpor bouts, on the other hand, raises a fundamental question about the energetics of torpor, namely whether the individuals will still have an energetic advantage from such very short torpor bouts. Our results indicate that some individuals may not even utilize the full time required to enter torpor, but may actually arousal from torpor before their body temperature has reached its lowest level. Thus, Td, only was lowered to a value between the nonthermic and normal torpid values (A. versicolor, Fig. 2). However, our data do not allow us to test whether such very short periods of torpor are of thermoregulatory significance to the birds. The hummingbirds would benefit from these torpor bouts if the cost
of arousal would not counteract the, even short-term, reduction in body temperature and metabolic rate; recall the effects of arousal from both hummingbirds (Hiebert 1990) and mammals (Ruf and Heldmaier 1992) seem to indicate that homeotherms will in fact benefit energetically from any torpor bout regardless of its length.

In summary, we have shown that there are large interspecific differences in the use of torpor between the three Brazilian hummingbird species studied. Whereas A. versicolor and E. macroura seem to enter torpor very readily without any previous energy stress, M. fuscus apparently only enter torpor when energetically stressed (low body mass). The reason for these differences is unknown. All three species will at times have multiple torpor bouts during the night. We suggest that this is caused by interruption of the normal torpor period by external stimuli.

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LITERATURE CITED


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