

A NEW FUNCTION FOR TORPOR: FAT CONSERVATION IN A WILD MIGRANT HUMMINGBIRD¹

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Abstract. Laboratory studies of torpor in small endotherms suggest that body temperature is lowered periodically only when the animal is energetically stressed. Almost no data exist on the use and importance of torpor outside laboratory situations. We have monitored the daily energy state of hummingbirds in the field. A rare observation of a torpid individual whose energy state and ecological situation were well-documented showed that migrant hummingbirds may use torpor when they are very fat and not presently energetically stressed. In this case, torpor may be a mechanism to conserve the energy stored for later use on migration.

Key words: *Torpor; migration; fat; hummingbirds; energetics; energy conservation.*

Laboratory studies (e.g., Pearson 1950, 1954; Bartholomew et al. 1957; Lasiewski 1963; Lasiewski and Lasiewski 1967; Hainsworth and Wolf 1970) have shown that at night hummingbirds often become uncoordinated and insensitive to mild external stimuli. During these periods of torpor the birds allow their body temperature to approach ambient levels by greatly reducing their rate of metabolic heat production.

The use of hypothermia is widespread among small mammals and birds. For example, by using nocturnal hypothermia, wintering chickadees in New York deplete 70% of the food reserves accumulated during the previous day; without torpor, the birds would starve overnight (Chaplin 1974). Therefore, torpor has been interpreted as a crucially important mechanism for balancing the intense metabolic demands and relatively low energy reserves of small endotherms (Dawson and Hudson 1970, Calder and King 1974, Hainsworth and Wolf 1978a, Hudson 1978). Many authors have claimed on the basis of laboratory studies that torpor occurs only when the animal is energetically stressed (reviews in Dawson and Hudson 1970, Calder and King 1974, Hainsworth and Wolf 1978a, Hudson 1978). In fact, torpor is induced in small rodents (Tucker 1966, Hudson 1978) and in hummingbirds (Lasiewski

1963) by food deprivation in the laboratory and often seems to be associated with prior depletion of energy reserves (Dawson and Hudson 1970, Hainsworth et al. 1977, Hainsworth and Wolf 1978a). Furthermore, Hainsworth et al. (1977) showed that the duration of torpor was negatively related to body mass and therefore energy reserves in one of the two species of hummingbirds studied in the laboratory (although no such relation occurred in the other species). Because torpor renders the animal virtually helpless, it does seem reasonable that such a mechanism would be used only as an emergency measure under energetically stressful circumstances.

The relevance of such laboratory studies to animals in the field remains unclear: under what circumstances does torpor occur in nature? Dawson and Hudson (1970) bemoaned the fact that our understanding of torpor is "hindered by a paucity of quantitative observations of torpor in nature" and the situation has improved little since. Field studies of torpor in hummingbirds are exceedingly rare because these birds are almost impossible to locate in their nocturnal roosts. We are aware of only two field studies of torpid hummingbirds which collected data on the ecological conditions associated with use of torpor; both studies involved birds in roosts that could be easily located. Incubating female Broad-tailed Hummingbirds (*Selasphorus platycercus*) roosting on nests entered torpor only when bad weather prevented feeding (Calder and Booser 1973). Andean Hillstar Hummingbirds (*Oreotrochilus estella*) roosting in Peruvian caves used torpor more frequently and for longer durations

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FIGURE 1. Torpid immature male Rufous Hummingbird. This individual's body mass was 60% above lean body weight just before he roosted and entered torpor. He resumed migration at dawn the next day.

in the cold dry winter than in the warmer wet summer when more flowers and insects were available (Carpenter 1974). However, the energy state of the birds in these two studies was unknown.

We report a rare observation of torpor under field conditions that qualifies the "energy emergency hypothesis." We observed torpid behavior in the summer by an undisturbed, free-living hummingbird known to be healthy, normal, energetically unstressed, and fat. We present evidence that the function of torpor in this case was conservation of energy stored as fat for migratory flight. We also consider the alternative hypothesis that this bird's 24-hr energy balance would have been negative without the use of torpor.

Rufous Hummingbirds (*Selasphorus rufus*) migrate from July to September through the western U.S. mountains from their breeding grounds in the Pacific Northwest to their wintering grounds in Mexico (Phillips 1975). They stop en route periodically, defend territories around flowers in meadows (Gass et al. 1976), and replenish their migratory fat stores by feeding on nectar (Carpenter et al. 1983). By weighing birds undisturbed on their territories with artificial perch-balances, we have monitored mass changes (Carpenter et al. 1983, Hixon and Carpenter 1988). On average, Rufous Hummingbirds stop to refuel at a body mass of 3.3 g (fat-free mass is about 2.8 g; birds die below this mass in captivity; Carpenter, unpubl. data), and gain 1.2 to 2.3 g over about a week while on territory. Then they resume migration early in the morning at 4.5 to 5.6 g. As the birds gain

mass, a smooth layer of subcutaneous fat accumulates over their backs and breasts, and a conspicuous cluster of yellow fat accumulates at the base of the neck anterior to the furculum. Fat accounts for almost 100% of the gain in mass above 3.5 g (C. A. Beuchat, unpubl. data).

Every summer since 1979 we have selected individuals to study intensively. We color-mark individuals soon after they arrive at our 1,700-m elevation site in the eastern Sierra Nevada, monitor their mass changes, measure their time budgets daily, and measure territory sizes and nectar production. Usually the birds disappear into the trees at dusk, typically just after our last daily time-budget observation. In 1983 we saw for the first time where a study bird roosted one night. This individual, an immature male, had disappeared into the trees the evenings of 17 to 22 August. However, at 19:15 on 23 August, he flew to the top of an exposed 5-m tall willow tree near his territory and roosted. His feather fluffing, posture, and declining responsiveness to external stimuli indicated that he began entering torpor before 20:00 and was completely torpid by 20:45. He did not respond to the gusts of wind that shook his branch nor to flashlights, electronic flashes, and noise as we photographed him. His posture was typical of that assumed by hummingbirds in torpor (Carpenter 1976) (Fig. 1). When touched lightly, he did not change posture and emitted a long, slow cry, behaviors typical of hummingbirds only when they are torpid.

The disturbances necessary to document that the bird was in fact torpid did not cause early arousal. We did not measure body temperature because this necessitates removing the bird from the perch, which invariably causes them to arouse (Carpenter, unpubl. observ.). We wanted to know how long the bird naturally remained torpid to calculate its energy savings over the night, so we could not risk such extreme disturbance. Laboratory measurements show that the body temperatures of torpid hummingbirds generally fall to within 1°C of ambient temperature (Bartholomew et al. 1957). However, regulation of torpid body temperature above ambient may occur when ambient temperature falls below 12 to 14°C (Hainsworth and Wolf 1978b). In the case of our observed Rufous Hummingbird, ambient temperature at the roost fell linearly from 17°C at 20:00 to 14°C at 05:15, then dropped quickly to its minimum of 12°C at 05:45. The bird was still torpid at 05:30 as dawn approached. He appar-

ently was arousing at this time, because he stirred and stretched at 05:45. At 05:50 he flew in the direction toward which these birds resume migration (south) and was not seen again.

We propose that the function of torpor in this individual was conservation of energy reserves for migratory flight, reserves which were more than enough to balance the overnight energy cost. We can discount the possibility that this individual was energetically stressed or abnormal. He established his territory on 17 August by displacing a Costa Hummingbird (*Calypte costae*) from a prime flowering site in our meadow (Hixon and Carpenter, in press). Using a perch-balance on the territory, we determined that he gained mass at an average rate of 0.23 g or 0.30 g per day for the last 5 days (Fig. 2), the value depending on whether the extremely rapid gain on the morning of 19 August is included. The 0.23 g value equalled the average rate of mass gain of birds measured previously (Carpenter et al. 1983; Hixon and Carpenter, in press). On the night of observed torpor the bird was 1.8 g above lean mass, and migrated the morning after it reached 4.6 g, which is the normal mass the evening before migration in this species (Carpenter et al. 1983). His behavior as measured by time budgets during the last 5 days on territory was entirely typical of other birds preparing to resume migration (Table 1). The ambient temperature the night of torpor was mild (most of it spent at greater than 15°C), characteristic of summer evenings in the desert, and at no time approached levels at which temperate-zone hummingbirds fail to arouse from torpor spontaneously. Although Lasiewski (1963) did not obtain spontaneous arousal at 12°C or below, Beuchat et al. (1979) obtained normal behavior down to -1°C, and Hainsworth and Wolf's (1978b) birds remained healthy at their minimum test temperature of 5°C. They suggested that Lasiewski's (1963) problems were caused by

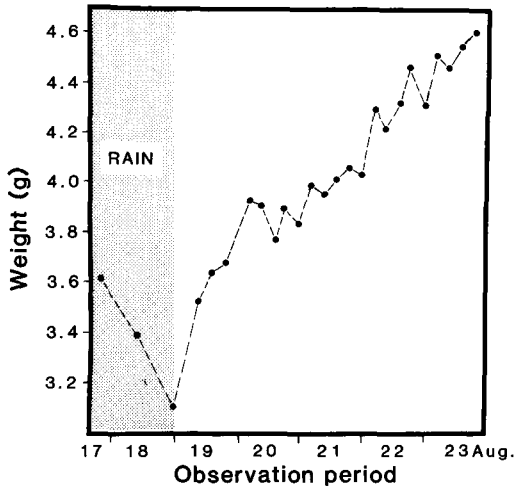


FIGURE 2. Daily mass change during the week before migration in the individual illustrated in Figure 1. Masses were recorded every few minutes during five 1-hr periods per day when the bird perched on an electronic balance fitted with a dowel rod for an artificial perch. The artificial perch was substituted for the bird's natural perch on its territory (Carpenter et al. 1983). During the first 2 days that this bird occupied its territory, periodic heavy rain prevented feeding and the bird lost mass. When the rain stopped on 19 August, the bird gained mass at normal rates and resumed migration on 24 August. The data point for each hour in the graph was the most stable value achieved during the hour; when values fluctuated greatly during the hour, all values for the hour were averaged.

restraining jackets which prevented ptiloerection at ambient temperatures low enough to elicit increased metabolism.

Based on laboratory measurements of metabolic rates in Rufous Hummingbirds and other similar-sized North American hummingbirds during normothermia, torpor, and transitional periods at similar ambient temperatures (Pearson 1954, Lasiewski 1963), applying appropriate engineering calculations (Holman 1981), and attributing overnight mass changes to changes in

TABLE 1. Comparison of Rufous Hummingbird found torpid (Bird 1) with two other immature male Rufous Hummingbirds studied in 1983. Only data from the final 5 days on territory (Fig. 2) were used in computing the statistics for Bird 1 because of loss of weight during rainy weather over the first 2 days on territory. Means ± 1 SD are given.

Bird	% Time spent		No. 0.5-hr samples	Territory size No. flowers	Daily mass gain	
	Nectar-feeding	Chasing			g/24 hr	No. days
1	34 ± 2	3 ± 2	49	3,100-3,900	0.30 ± 0.19	5
2	28 ± 3	4 ± 1	30	4,000-4,100	0.37 ± 0.09	3
3	27 ± 8	2 ± 2	9	2,500	0.23 —	1

fat, we calculated how much fat this bird would have lost by spending the night normothermic rather than torpid in its exposed roost or in a sheltered roost protected from radiation to the night sky and from wind chill (Appendix). This bird would have used about 0.24 g of fat if normothermic in a sheltered roost or 0.37 g of fat if normothermic in the exposed roost. In contrast, he would have lost only 0.03 g of fat if torpid in a sheltered roost and 0.04 g in the exposed roost.

We cannot reject but we can cast doubt on the alternative hypothesis that this bird would have experienced a negative 24-hr energy balance without torpor. This bird chose an exposed roost, which made little difference in overnight energy expenditure because it was torpid, but which would have greatly increased expenditure if it had remained normothermic. If this bird had remained normothermic, we assume it would not have chosen the most exposed roost site possible in our area, but rather, a protected site as do other roosting and nesting hummingbirds (e.g., Calder 1973, Carpenter 1974). Many sites protected from wind and radiation to the night sky exist in our study area, and consist of dense willow, locust, and pine trees. In such a roost, we calculate that fat lost overnight (0.24 g) would not have matched the mass gain over the previous day (0.50 g), and it would have barely balanced this bird's average daily fat gain (0.23 to 0.30 g). Furthermore, this bird began descending into torpor as soon as it roosted. Even in the exposed roost, it could have attained energy balance overnight by spending only part of the night torpid, as occurs frequently in laboratory studies (e.g., Pearson 1950, 1954; Lasiewski 1963; Beuchat et al. 1979). Yet this bird spent the maximum time possible in torpor.

Thus, torpor saved about 10% of this bird's total reserve of 1.8 g of fat. Because ambient temperatures and the rate of mass gain in this bird were average values for this system, the calculation of energy balance for this individual represents the average situation for this species at this site. Fat conservation via use of torpor may be common in Rufous Hummingbirds preparing for resumption of migration, since field measurement (0.05 g accuracy) showed no detectable overnight mass loss in 13 bird-nights; 16 bird-nights showed a loss of almost exactly 0.2 g overnight (Carpenter et al. 1983). Although water flux

could confound these field data, a laboratory study (Beuchat et al. 1979) showed that torpid Rufous Hummingbirds frequently lost 0.2 g overnight, almost all of which was water, and replenished this loss within the first hour of feeding at daybreak. Lasiewski's (1963) measurements on torpid Costa Hummingbirds (3.3 g) suggest mass loss due to evaporation would be 0.10 to 0.15 g, similar to the observations on Rufous Hummingbirds. Combined with our field data (Carpenter et al. 1983), these laboratory data suggest that almost all of our migrant birds may have entered torpor.

Without torpor, these birds would fatten for migration more slowly. This conclusion is supported by a detailed study (Hixon and Carpenter, in press) on mass gain patterns on the same territory occupied first by a Costa Hummingbird, then by this same Rufous Hummingbird individual. The data were more intermittent for the Costa Hummingbird, but suggested that overnight losses nearly balanced daytime gains, so that the bird only increased 0.38 g over 6 days. In contrast, the Rufous Hummingbird made about the same daytime mass gains as the Costa Hummingbird, but lost substantially less mass over each night. As a result, it increased 1.17 g over 5 days and resumed migration with a substantial fat store.

Therefore, torpor is used in a nonemergency situation by apparently healthy, normal, nonstressed Rufous Hummingbird individuals. Although migrants might be considered energetically stressed because they might not be able to complete the migration without using torpor, this is a future prospective rather than an immediate stress. The bird in this study went torpid when its current energy state was excellent, and therefore could not have used low blood sugar, fat, or glycogen levels as cues to go torpid. This finding therefore has important ramifications for the elusive search for the physiological mechanisms of torpor (Lyman et al. 1982). Specifically, torpor is not necessarily triggered by depleted energy reserves but may involve other physiological factors.

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APPENDIX

The bird was entering torpor by 20:00 and we assumed 1 hr for entry at an ambient temperature (T_a) of 17°C (body temperature dropping from 40 to 18°C, Lasiewski and Lasiewski 1967). We calculated from Heinrich and Bartholomew (1971) that the bird required 24 min to arouse at $T_a = 12^\circ\text{C}$, arousal being completed by 05:45. We used Pearson's (1954) values for costs of entry [mean of 7 cc O₂/(g hr) interpolated for $T_a = 17^\circ\text{C}$] and arousal [mean of 13 cc O₂/(g hr) measured at $T_a = 12^\circ\text{C}$]. We multiplied these values by the mass of the bird (4.6 g) measured at 19:10, 0.5 hr before it roosted, thus avoiding the rapid increase in mass these birds occasionally exhibit during the last 10 min or so before retiring. We divided the torpid period into five intervals, applying the appropriate T_a for each interval. For calculation of costs in a sheltered roost, we applied Lasiewski's (1963) metabolic measurements at 15.5°C for torpid Rufous Hummingbirds [his fig. 3, 0.17 cc O₂/(g hr)] and for nontorpid Rufous Hummingbirds

TABLE 2. Assumptions and constants for calculation of radiation and wind chill effects.

Heat transfer coefficient of air, $K = 0.025$
Stephan-Boltzman constant, $b = 5.67e - 8$
Emissivity of bird, $e = 0.80$
Kinematic viscosity of air, $\nu = 0.015$
Reybolds number, $Re = (u \cdot \text{length})/\nu$
Nusselt number, $N_u = 0.65Re^{0.5}$
Heat transfer coefficient, $hc = (N_u \cdot K)/\text{length}$
Bird's body length, $\text{length} = 0.038 \text{ m}$
Resting normothermic body temperature of bird = 40°C
Wind speed = 4.47 m/sec
1 g fat = 9 Kcal
1 cc $O_2 = 4.69 \text{ cal}$ (Lasiewski 1962)
1 cal = 0.239 J

[his fig. 1, 10 cc O_2 /(g hr)]. For calculation of costs in the exposed roost, we accounted for radiation and wind chill by applying standard techniques (Holman 1981) in the same manner as Kingsolver (1983). Assumptions and constants are in Table 2. The value for wind speed is probably excessive, since it is based on gusts, but gives a conservative bias to the test of our hypothesis.