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SEASONAL CHANGES IN BODY MASS AND USE OF TORPOR IN A MIGRATORY HUMMINGBIRD

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ABSTRACT.—In a study designed to determine seasonal patterns of body mass and torpor in Rufous Hummingbirds (*Selasphorus rufus*), birds were maintained for 12 months in the laboratory on a photoregime approximating that experienced by free-living birds. Ambient temperature cycled from 20°C during the day to 5°C at night. Body mass, torpor, and rates of nighttime oxygen consumption were measured under conditions of *ad libitum* feeding in LD 12:12 in autumn (when free-living birds are normally migrating south), LD 12:12 in spring (during molt), and LD 16:8 in summer. Both body mass and use of torpor were highest in autumn, suggesting that torpor is not reserved for immediate energy crises at this time, but may be important in maximizing energy savings and thus minimizing the time required for premigratory fattening. In spring, body mass was lowest; use of torpor, however, was significantly lower than in autumn, suggesting that torpor is used primarily for "energy emergencies" at this time of year. In summer, body mass was intermediate and use of torpor was also significantly lower than in autumn. Mass-specific rates of oxygen consumption during both normothermia and torpor were inversely related to body mass when data from all seasons were combined; large fat stores may contribute to lower metabolic rates by providing additional insulation, as well as by decreasing the proportion of highly metabolically active tissue in the body. Low fat stores also coincide with the molt, which itself may result in higher metabolic rates. Although the propensity for using torpor has a strong seasonal component that appears to reflect different energetic circumstances during such activities as migration and molt, Rufous Hummingbirds retain the ability to enter nocturnal torpor at all times of year, thus improving their chances of survival year-round. *Submitted 14 May 1992, accepted 12 November 1992.*

MIGRATORY HUMMINGBIRDS living in cool climates face potentially extreme threats to energy balance. Like other small homeotherms, they have high thermoregulatory costs resulting from high surface-to-volume ratios that increase rates of heat loss to the environment. Like other hummingbirds, they incur the additional cost of hovering, the most energetically demanding mode of flight. Unlike the many species of hummingbirds that are year-round residents in low-latitude habitats, however, the relatively few migratory species have an additional energetic requirement—they need to accumulate large fat stores to fuel long-distance flight.

Nocturnal torpor, during which energy expenditure is greatly reduced, is an important means by which hummingbirds offset large daytime energy expenditures and maintain energy balance. All species of hummingbirds that have been studied show this physiological adaptation. Most studies, however, have focused on instantaneous features of torpor (e.g. comparisons between rates of metabolism during steady-state torpor and steady-state normothermia), or on the effects of torpor on total nighttime energy balance (Hiebert 1990). Little consideration has been given to the fact that hummingbirds, particularly species residing at least part of the year in temperate zones, engage in activities that place very different energetic demands on the animal at different times of year. Therefore, one might expect there to be corresponding seasonal changes in the use of torpor. Yet, with the exception of Carpenter's (1974) study of the Andean Hillstar (*Oreotrochilus estella*), there have been no systematic comparisons of seasonal changes in the use of torpor. The seasonality of torpor has never been studied in a migratory species.

The Rufous Hummingbird (*Selasphorus rufus*) is one of the most highly migratory species of hummingbirds. It breeds at high latitudes, as far north as Alaska, but winters in Mexico. Yearly round-trip migratory flights may exceed 6,000 km (Phillips 1975, Calder 1987). Because of their

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small size (lean body mass ca. 3 g), Rufous Hummingbirds are unable to store sufficient fat to fuel an entire one-way flight between breeding and wintering grounds (Lasiewski 1962). Instead, these birds stop periodically along their migratory route to refatten. During these stopovers, birds establish and defend feeding territories for one to two weeks before long-distance flight is resumed (Gass et al. 1976, Gass 1979, Carpenter et al. 1983).

What is the role of torpor during migration? The "energy-emergency hypothesis" (Hainsworth et al. 1977) predicts that birds with sufficient energy reserves to maintain normothermia throughout the night should avoid the use of torpor. Because some laboratory studies have shown that hummingbirds appear to use torpor only when energy reserves are low (Hainsworth et al. 1977, Hiebert 1992), as yet undefined risks or costs are assumed to be associated with the torpid state. On the other hand, there may also be significant benefits to torpor at certain times of year. For example, might selective pressure to reduce time required for periodic refattening and to complete migration as quickly as possible result in an increased incidence of torpor during migration, even when stored energy reserves are abundant?

The annual molt in Rufous Hummingbirds, which occurs on the wintering ground before the vernal northward migration, involves a different set of energetic issues. A previous study (Hiebert 1992) suggests that use of torpor during the molt is consistent with the energy-emergency hypothesis. In this case, selective pressure to minimize the total time required for molt might result in reduced time spent in torpor during molt. In addition, birds may benefit energetically by maintaining a low body mass during a time when missing flight feathers reduce lift-generating capacity. Extraordinary means of saving energy for storage as fat might not be favored at this time.

The purpose of my laboratory study was to examine seasonal changes in body mass and use of torpor under conditions of *ad libitum* food consumption and a daily temperature cycle that was maintained at the same levels throughout the year. Photoperiod was the only seasonal cue. Body mass, use of torpor, and rates of oxygen consumption during torpor were compared during three phases of this annual cycle: autumn (when free-living birds are migrating), spring (during molt), and summer.

MATERIALS AND METHODS

Rufous Hummingbirds were captured as juveniles during August of 1986 ($n = 12$) and 1987 ($n = 15$) in the Cascade Mountains, Skagit County, Washington. Experiments were carried out during the 12 months following capture. An additional four birds were captured on 24 May 1988 and were included in the summer measurements of 1988 (see below). Birds were housed individually in 0.6 × 0.6 × 1.2 m cages provided with an overhead light (46-cm "Daylight" fluorescent tube, 15 W). Five to eight cages were kept in a controlled-environment chamber in which the light cycle was adjusted seasonally (in increments of 15–30 min) to approximate the light cycle experienced by Rufous Hummingbirds in nature (lights-on at 0830 PST, lights-off variable). The only departure from a truly natural photoregime was that the periods of LD 12:12 were extended in autumn and spring to include the 30-day measurement periods (see seasonal comparisons below for further details), and to control for the effects of daylength per se on use of nocturnal torpor. During the artificial night, a single 15-W incandescent bulb provided low, diffuse light for the entire chamber. This bulb provided sufficient light for flying in the cage, but the birds did not fly or feed at night once they had found a suitable perch. Ambient temperature was 20°C during the day and 5°C at night; warming and cooling of the chamber took place at the beginning and end of the light period so that ambient temperature during the period of darkness was a constant 5°C. Eight of 12 birds studied during the annual cycle beginning in August 1986 were maintained on LD 12:12 from the autumn measurement period through January 1987, after which time all birds were maintained on a natural photoregime; otherwise, environmental conditions for these eight birds were the same as for other birds in this study.

Body mass and torpor.—Body mass at time of capture was measured to the nearest 0.1 g with a 5-g Pesola hand-held spring scale. All birds were captured in the morning and, except for a few birds captured at first light, undoubtedly had fed before they were weighed. Body mass at capture is therefore an overestimate of dawn body mass, which was used throughout this study as a point of comparison.

In the laboratory, body mass and torpor duration were measured at 1- to 10-day intervals throughout the year. All observations reported here are of unmanipulated body mass and spontaneous torpor. Birds fed *ad libitum* during the day, but food was removed 45 min before lights-out to allow the digestive tract to clear (Hainsworth 1974, Diamond et al. 1986). Birds were weighed at lights-out and again at lights-on on a Sartorius digital electronic balance accurate to 0.001 g. Unless otherwise noted, body mass reported in this study refers to prefeeding mass at lights-on and represents the mean of all days during a given period, whether or not the bird entered torpor on the night before.

During nights on which torpor was monitored, each bird was placed in a rectangular plastic container (18 × 28 cm) containing a small (2-cm) perch, on which a fine (40-g) thermocouple was mounted. When the bird was at rest, its abdomen contacted the thermocouple on the perch. Thermocouple temperature was recorded continually during the night on a Leeds and Northrup Speedomax 250 chart recorder. The duration of torpor, indicated by a drop in thermocouple temperature, was measured from the beginning of entry into torpor to the end of arousal. Simultaneous measurements of surface body temperature and oxygen consumption show that the occurrence and timing of torpor are accurately recorded by this method. The birds adjusted to this apparatus after a few days of experience and, thereafter, perched quietly throughout the night whenever placed on the perch.

Oxygen consumption.—I measured nighttime oxygen consumption at 5°C separately from torpor duration. To determine rates of oxygen consumption during torpor in some instances required the induction of torpor by food restriction, particularly during spring and summer when torpor tended to occur less often. On days of food restriction, food was removed up to 4 h before lights-out but a separate water supply was provided to prevent dehydration. Water and food, if any remained, were removed 45 min before lights-out. Birds were weighed at lights-out and lights-on, as for measurements of torpor duration. During the night, birds sat on a small perch (2-cm) fitted with a 40-g thermocouple in a cylindrical 1-L respirometry chamber. Excreta (usually 0.05 g or less and usually voided at the end of the night) were collected on filter paper that lined the base of the chamber. Dried air was passed into the chamber at a flow rate of 140 to 180 ml min^{-1}. Excurrent air was dried before passing through an Applied Electrochemistry S3A Oxygen Analyzer. The rate of oxygen consumption was computed according to Withers (1977: equation 3a) using an RQ of 0.85 since RQ was not measured directly. Mass-specific rates of oxygen consumption were computed for each hour of the night by dividing the mean rate of oxygen consumption by the computed mean body mass during that hour. Mean body mass at a particular time was computed as follows: the area under the oxygen consumption curve until that time was divided by the total area under the curve. This fraction was then multiplied by the total mass loss during the night (corrected for mass of excreta). Rates of oxygen consumption during torpor were computed as the mean of hourly rates from hours in which the birds were in steady-state torpor for the full hour.

Seasonal comparisons.—I made seasonal comparisons of body mass and use of torpor using data collected during three 30-day periods in 1986–1987 and 1987–1988. For all birds, the autumn measurement period extended from 22 September to 21 October, and the summer measurement period extended from 1 June to 1 July. The spring measurement period, which was intended to include the period of molt, was different for each bird because the birds did not molt synchronously. For each bird, the spring period was the 30-day interval centered on the midpoint of its molt. One bird, 86-03, was still molting during the beginning of the summer measurement period; for this bird, only those data taken after the completion of molt are included in the summer measurement period. Photoregime was LD 12:12 during autumn and spring measurement periods and LD 16:8 during summer. Measurements of oxygen consumption for each season were made as close as possible to, but not necessarily within, the same 30-day periods as measurements of body mass and torpor because far fewer birds can be measured simultaneously in the apparatus for oxygen analysis.

Statistics.—Overall seasonal effects were calculated from the means of the variable for each bird using one-way analysis of variance (ANOVA). Data for each season represent pooled data from both years. Subsequent comparisons among pairs of seasons were made using the Tukey-Kramer method (Sokal and Rohlf 1981) because sample sizes were unequal. Unless otherwise noted, the Tukey-Kramer test was used. Data on incidence of torpor, expressed as the percentage of nights on which torpor occurred during each measurement period, were transformed using the arcsine transformation (Sokal and Rohlf 1981) before statistical testing. Other pairwise comparisons were made using the two-sample *t*-test. When Bartlett's test for homogeneity of variances showed that variances differed significantly between the two samples being compared, degrees of freedom were calculated using Satterthwaite's approximation and a test appropriate for unequal variances was used (Snedecor and Cochran 1980). Data are reported as $\bar{x}$ ± SD.

RESULTS

Body mass.—Birds captured in August typically underwent a dramatic increase in body mass after being brought into the laboratory (Fig. 1). Mean body mass at time of capture was 3.4 ± 0.3 g (Fig. 1b). Mean body mass during autumn was 4.49 ± 0.31 g (range 3.94–5.18 g), a significant increase over mass at time of capture (two-sample *t*-test, df = 51, $P < 0.0001$). The highest body mass measured at any time during this study was 5.77 g at lights-out in bird 15-86 on 6 October 1986. Body mass was significantly higher during autumn than at any other time of year ($P < 0.01$ for autumn vs. spring, and for autumn vs. summer; Fig. 2). Body mass remained high in most birds until some-

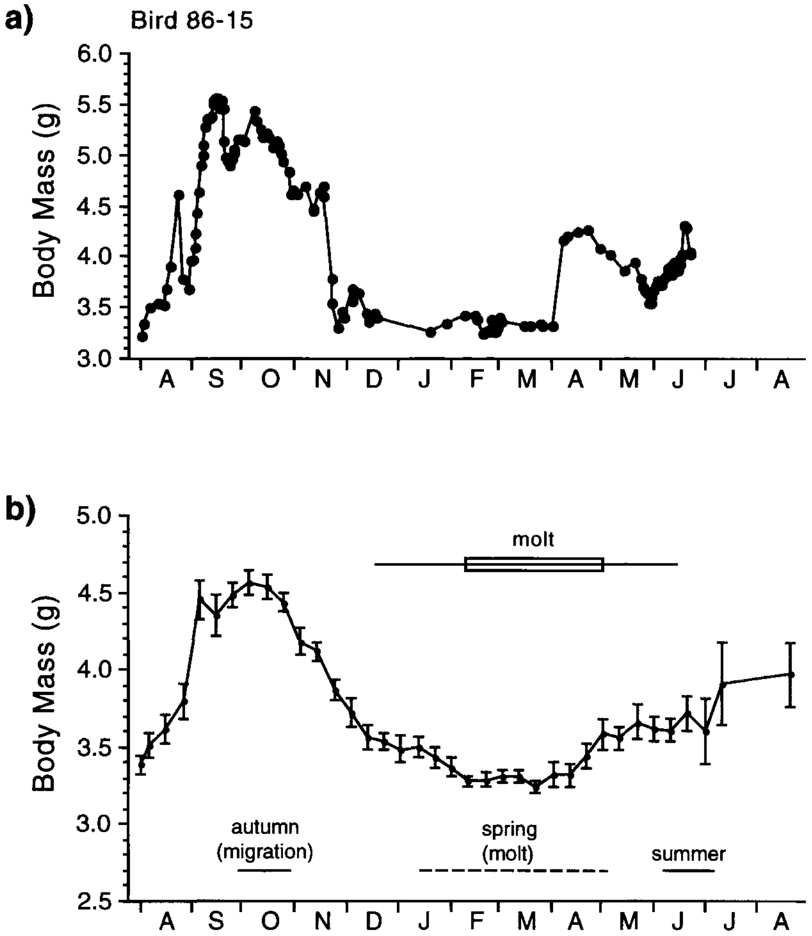

Fig. 1. Annual pattern of body mass, measured at lights-on before feeding, in captive Rufous Hummingbirds: (a) body mass of individual in captivity; (b) pooled data from all birds. For autumn and summer, 30-day measurement periods shown by solid horizontal bars below line. The 30-day measurement period for spring determined separately for each bird so that it fell in middle of molt; this period occurred sometime during period shown by dashed horizontal bar below line. Horizontal bar above line represents period from earliest starting date to latest ending date of molt; box in center of horizontal bar represents period from median starting date to median ending date of molt. Vertical bars represent ±1 SE.

time in November or December and then declined to a new, lower level (Fig. 1) in the absence of any change in the availability of food. In 1986–1987, the beginning of this postautumnal mass loss began significantly earlier in birds maintained on a natural photoregime (mean date = 17 December) than in birds maintained on LD 12:12 (mean date = 18 January; two-sample *t*-test; df = 6.8 [unequal variances]; $P < 0.05$, one-tailed).

Molt commenced on a median date of 8 February (range 18 January to 15 April) and ended on a median date of 22 April (range 6 March to 14 June). During the spring measurement period, mean body mass was 3.27 ± 0.13 g, significantly lower than in autumn ($P < 0.01$; Fig. 2). After completion of the molt, body mass typically began to rise (Fig. 1). During the summer measurement period, mean body mass was 3.65 ± 0.33 g, significantly lower than in autumn and significantly higher than in spring ($P < 0.01$ for both comparisons; Figs. 1 and 2).

Birds captured in May did not show the same pattern of mass gain as birds captured in August. Mean mass of May-caught birds was 3.39 ± 0.31 g at time of capture, not significantly different from the mass of August-caught birds at time of capture. During the summer mea-

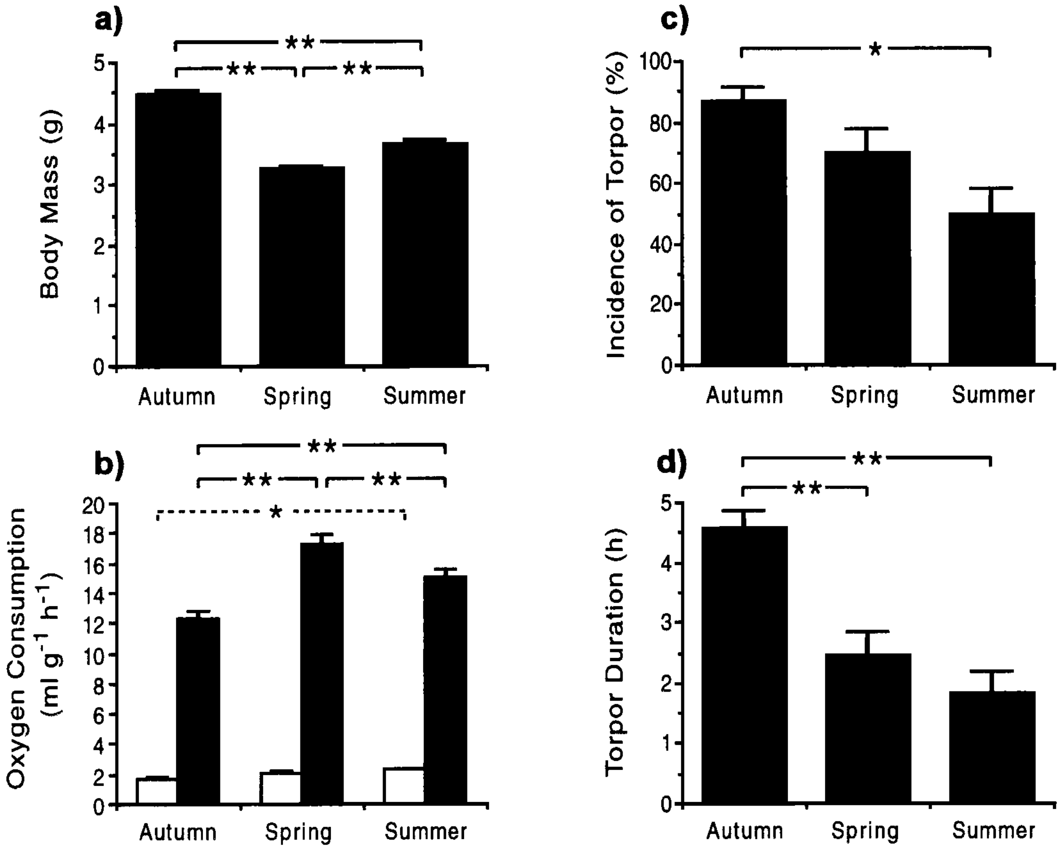

Fig. 2. Seasonal comparisons of (a) body mass; (b) mass-specific rates of oxygen consumption during nighttime normothermic rest (black bars) and during steady-state torpor (white bars) at ambient temperature of 5°C; (c) incidence of torpor, as percent of nights on which torpor occurred; and (d) torpor duration. Vertical bars represent ±1 SE. Horizontal brackets and asterisks indicate significant differences in pairwise comparisons: *, $P < 0.05$; **, $P < 0.01$. For rates of oxygen consumption, dashed bracket is for pairwise comparison of rates during torpor and solid brackets are for pairwise comparisons during normothermia.

surement period, the body mass of May-caught birds did not differ significantly from the body mass of birds that had been captured in August (two-sample t-test, df = 23, $P > 0.15$); therefore, measurements from birds captured in both August and May are included in the summer measurement period. Comparison of mass gain patterns (Fig. 3) shows that, after approximately 20 days in captivity, birds captured in August gained mass more rapidly than birds captured in May, resulting in significantly higher body masses in the August-captured birds by the time the birds had been in captivity approximately one month (two-sample t-test, $P < 0.05$ for each 10-day period after first 20 days in captivity; see Fig. 3).

Incidence and duration of torpor.—The percentage of nights on which torpor occurred varied significantly with season (one-way ANOVA, $P = 0.0009$; Fig. 2). Whereas incidence of torpor was significantly greater in autumn than in summer ($P < 0.05$), the mean incidence during spring was intermediate between the means for autumn and summer, but was not significantly different from either ($P > 0.05$ for both spring vs. autumn and spring vs. summer).

Torpor duration also varied significantly with season (one-way ANOVA, $P < 0.0001$; Fig. 2). Mean torpor duration was greatest in autumn and lowest in summer. Torpor duration was significantly greater in autumn than in either spring or summer ($P < 0.01$ in both cases), but did not differ significantly between spring and summer ($P > 0.05$).

Oxygen consumption.—Mass-specific oxygen consumption during steady-state torpor at 5°C

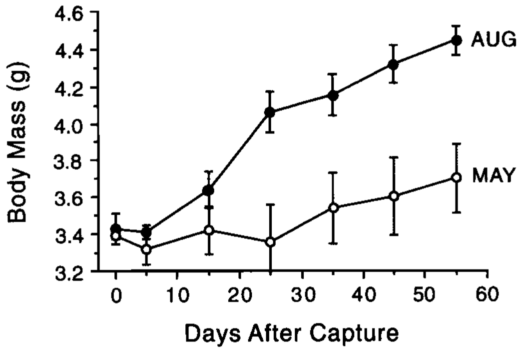

Fig. 3. Comparison of mass gain in birds captured in August (filled circles) and May (open circles). Day 0 is day of capture; each point represents mean prefeeding mass at lights-on for 10-day period in which it is centered. Each vertical bar represents ±1 SE (n for each point in upper line varies from 19 to 26; n for each point in lower line is 4). For a two-sample t-test comparing masses of birds captured in August and those captured in May, P-values were: at capture, $P = 0.79$; days 1-9, $P = 0.44$; days 10-19, $P = 0.40$; days 20-29, $P = 0.018$; days 30-39, $P = 0.027$; days 40-49, $P = 0.012$; days 50-59, $P = 0.0023$.

varied significantly with season (one-way ANOVA, $P = 0.0006$; Fig. 2). Mean mass-specific oxygen consumption during torpor was highest in summer (2.30 ml O_2 g^{-1} h^{-1}), lowest in autumn (1.72 ml O_2 g^{-1} h^{-1}), and intermediate in spring (2.12 ml O_2 g^{-1} h^{-1}). However, only the differences between autumn and spring ($P < 0.05$), and between autumn and summer ($P < 0.01$) were significant (spring vs. summer, $P > 0.05$).

Mass-specific oxygen consumption during normothermic nocturnal rest at an ambient temperature of 5°C also varied significantly with season (one-way ANOVA, $P < 0.0001$; Fig. 2). Mean mass-specific oxygen consumption during normothermia was highest in spring (17.09 ml O_2 g^{-1} h^{-1}), lowest in autumn (12.27 ml O_2 g^{-1} h^{-1}), and intermediate in summer (15.05 ml O_2 g^{-1} h^{-1}); all paired comparisons between seasons showed significant differences ($P < 0.01$).

Rate of mass-specific oxygen consumption during torpor was inversely related to dawn body mass when data from all seasons were combined ($R = -0.4920$, $n = 44$, $P < 0.0001$), but body mass accounted for only 24% of the variance in mass-specific oxygen consumption. In this analysis, only those body masses measured on mornings following nights when the bird had entered torpor were included. The rate of mass-specific oxygen consumption during normothermic nighttime rest also was inversely related to body mass when data from all seasons were combined ($R = -0.6486$, $n = 49$, $P < 0.0001$), with body mass accounting for 42% of the variance.

DISCUSSION

PERSISTENCE OF ANNUAL CYCLE IN CAPTIVITY

Patterns of body mass and molt in captive Rufous Hummingbirds approximate the annual sequence in nature as far as it is known. In the laboratory, body mass rose to its highest level in autumn (when free-living birds are migrating south), decreased in early winter and remained low during the molt, and increased to intermediate levels after completion of the molt. However, the timing of events in captivity was somewhat delayed with respect to the annual cycle in free-living birds.

Autumn.—For several reasons, the rise in body mass appears to be a consequence of the seasonal physiological state of the birds rather than the transition to captivity. First, birds captured in May did not show the rapid increase in body mass characteristic of birds captured in August. This effect is particularly striking in view of the fact that day length (and, thus, time available for feeding) was decreasing to 12 h during the first 60 days of captivity for birds captured in August, but was increasing from 12 to 15 h during the 60 days after birds were captured in May. The fact that body mass and patterns of torpor use during summer in May-caught birds were similar to those of August-caught birds in summer is further evidence that the difference in mass-gain patterns was due to season, not to the amount of time in captivity.

Second, the average dawn mass of birds in autumn (4.49 g) matched closely the normal body mass for wild Rufous Hummingbirds on the day before they migrate (4.6 g) (Carpenter and Hixon 1988). Higher body masses (up to 5.2 g) have been measured in free-living birds; in captivity, the maximum dawn body mass was 5.18 g. Of course, the pattern of body mass in captive Rufous Hummingbirds during the migratory period differs from that in wild conspecifics. Whereas body mass remains constantly high during autumn in captive birds, body mass in free-living migrants undergoes short periods of rapid mass loss, corresponding to long-distance migratory flight, alternating with one- to two-week periods of mass gain as the birds refatten in preparation for the next migratory flight.

Third, body mass declined spontaneously in November and December, around the time when migration normally ends. Although adult males may reach wintering grounds as early as August or September, adult females and juveniles of both sexes may be as much as six weeks behind the adult males in their autumnal migratory movements (Phillips 1975). The birds in this study were adult females or juveniles and, therefore, would be expected to reach wintering grounds as late as mid-November. The gradual decline in body mass depicted in Figure 1b represents pooled data from all the birds in the study. In fact, many individuals showed a much more abrupt decline in body mass at this time of year (Fig. 1a). Although not all individuals showed as abrupt a decline as the bird shown in Figure 1a, this pattern was not unusual. The fact that many individuals showed such a striking pattern, seasonally synchronized in two groups of birds studied in different years, supports the interpretation that the decline is a marker for a change in the seasonal physiological state of the birds.

Spring.—In my study, molt occurred in late winter to spring, varying widely among individuals and in many cases lasting into April, by which time free-living birds of both sexes have already reached the border between the United States and Canada. The reason for the delayed molt in the captive birds is not known, nor are there sufficient records from birds captured or collected in the field to determine accurately the duration of molt in free-living birds.

Summer.—Following the molt, body mass in the captive birds increased but generally not to the level observed in autumn during the time of the southward migration. The exact physiological condition of these birds was difficult to assess. Zugunruhe (migratory restlessness), regarded as a definitive indicator of migratory condition in captive nocturnal migrants, cannot be used as an index of migratory condition in captive Rufous Hummingbirds. No bird in this study was active at night at any time of year, even though dim light was provided; this observation is consistent with field observations that suggest these birds migrate during the day (Carpenter et al. 1983). Thus, although Rufous Hummingbirds migrate north in spring, presumably after the completion of the molt, it was difficult to determine if the birds in my study were in migratory condition after the completion of molt. However, behavioral changes during late winter and spring suggested that the birds were undergoing physiological changes associated with reproduction. During this time, the birds began using a vocalization that in nature is used in squabbles with other hummingbirds over territory boundaries or food sources (pers. obs.). Although the ventriloqual nature of this vocalization often made identification of the bird producing the sound difficult, the vocalization appeared to be produced primarily by males during aggressive interactions with birds in nearby cages. This vocalization was often accompanied by gorget flaring, another aggressive behavior. These behaviors were never observed in autumn.

BODY MASS AND TORPOR

Autumn.—During autumn, when free-living conspecifics were migrating south, body mass of captives was maintained at an average of approximately 1.5 g above lean body mass. Although body mass was significantly higher during autumn than any other season, both the mean duration and incidence of torpor were highest at this time of year. The heaviest bird (86-15) entered torpor every night during the autumn measurement period.

These results are consistent with the prediction that energy balance during migration should be geared toward minimizing energy expenditure in favor of accumulating fat stores to fuel migratory flight, and suggest that torpor is used during periodic refueling to reduce nocturnal energy expenditures. A fortuitous field observation supports this interpretation. Carpenter and Hixon (1988) observed a migratory male Rufous Hummingbird on its nocturnal roost the night before the bird left its territory for its next southward migratory flight. The body mass of this bird, measured repeatedly as it foraged on and defended its feeding territory, indicated that the bird had gained 1.5 g in the preceding five days and that, on the night of observation, the bird had more than sufficient energy reserves to maintain normothermia. Yet, this bird entered torpor at dusk and remained torpid throughout the night. Comparison of dawn and dusk body masses of other migratory Rufous Hummingbirds at the same study site provide circumstantial evidence that these birds use nocturnal torpor regularly during migratory refueling to save energy (Carpenter et al. 1983, Carpenter and Hixon 1988).

If, as the energy-emergency hypothesis assumes, there are costs associated with entering torpor (Hainsworth et al. 1977), these costs appear to be outweighed by the benefits of reducing nighttime energy expenditure and increasing the rate of premigratory fattening. Such benefits might include reduction of risks inherent in migration (exposure to uncertain weather conditions at high altitudes in late summer [Gass and Lertzman 1980], short-term residence in unfamiliar surroundings) and augmentation of time available for other activities in the annual time budget (e.g. reproduction).

Spring.—Although body mass was lower during the spring molt than at any other time of year, mean torpor duration was significantly lower during spring than during autumn. Differences could not be attributed to differences in the availability of food or availability of time for feeding because the birds were feeding *ad libitum* in all cases and because photoregime (LD 12:12) was the same in both autumn and spring. Rather, physiological differences in the birds had to be responsible.

Reduced use of torpor during molt may be related to a variety of factors. I have suggested (Hiebert 1992) that ecological constraints result in selection for minimizing the total time required for molt, the duration of which may be determined by the total area under the curve of metabolic rate and/or body temperature during molt. Torpor thus may be disadvantageous during molt simply because it prolongs the duration of molt. In particular, the need for efficient flight during migration may be incompatible with the reduced ability to generate lift when remiges are missing during molt; thus, onset of the vernal northward migration that directly follows molt may be constrained by the length of the molt itself. It is also possible that periodic reduction of feather growth during torpor somehow weakens the structure of the developing feather. In other birds, fault bars in the feathers may result from periods of undernutrition and may represent points at which the feather is more likely to break when exposed to mechanical stress (see Grubb 1989).

Reduced use of torpor during molt may also be a consequence of hormonal changes during molt (see Payne 1972). Increases in plasma levels of thyroxine that normally accompany molt may result in increased metabolic rate in normothermic molting birds. It is possible that these high levels of thyroxine inhibit entry into or are in some other way incompatible with nocturnal torpor.

Because body mass decreases and reaches molting levels well before the onset of molt (Fig. 1), the low body mass during molt is not a consequence of molt, although it may be a consequence of hormonal changes that initiate the molt (e.g. increases in thyroxine secretion). A similar pattern of mass loss prior to the beginning of molt has been observed in other birds (e.g. King 1968). For hummingbirds, low body mass during molt may be beneficial because these birds rely almost completely on flight for foraging and, therefore, must minimize wing loading at a time when missing flight feathers reduce the lift produced by each wing stroke.

After the molt, body mass rises, but not to levels observed in the autumn, even though the northward migration normally follows molt. Although this pattern may be an artifact of prolonged captivity, it also may reflect differences between the vernal and autumnal migrations in nature. During the autumn migration, Rufous Hummingbirds are found primarily at high altitudes, where hummingbird food flowers bloom later in the season than at lower altitudes. However, montane habitats are risky, particularly in late summer, because of unpredictable and often severe storms (Gass and Lertzman 1980, Hixon et al. 1983). Thus, Rufous Hummingbirds may be under selective pressure to fatten rapidly so that southward movement to safer climates can proceed as quickly as possible. In spring, the northward migration occurs at low altitudes along the west coast of North America (Phillips 1975, Calder 1987). At this time there may well be less selective pressure to fatten rapidly, which may be reflected in the lower body masses after the molt. Data from birds held in captivity for more than 12 months, from birds captured at different times of year, and from free-living birds on the spring migration are needed to address this hypothesis more fully.

OXYGEN CONSUMPTION

Rates of oxygen consumption during normothermic nighttime rest at 5°C were highest in spring and lowest in autumn. In autumn, the low mass-specific rates of oxygen consumption probably reflect an increase in tissue that is less metabolically active (fat), an increase in insulation due to new feathers and fat deposits around the torso, and the absence of energy-requiring feather replacement. For the whole animal, the result of the lowered mass-specific metabolic rate is to offset the effect of increased body mass on total oxygen consumption; that is, total oxygen consumption of a normothermic bird of average autumn mass during a 12-h night in autumn (661 ml O_2) is roughly equivalent to that of a normothermic bird of average spring mass during a 12-h night in spring (676 ml O_2). In summer, the shorter night results in a lower total oxygen consumption during a night of normothermia (438 ml O_2). Of course, energy expenditures of free-living birds at different times of year will also be affected by differences in both meteorological conditions and the microhabitats in which the birds roost at night.

The typical increase in metabolic rate during molt (Wallgren 1954, West 1960, Blackmore 1969, Payne 1972) can be attributed to several factors, including an increase in plasma levels of thyroxine. Feather growth itself contributes to the increase in energy expenditure (King and Farner 1961, Irving 1964), but increased conductance due primarily to the increased vascularization of the skin around each growing feather also increases metabolic requirements of thermoregulation in cool environments (Lustick 1970).

Although I cannot rule out the possibility that the metabolic activities involved in feather replacement are temperature compensated and can occur even at the very low body temperatures during torpor (as low as 13°C; Hiebert 1990), it is likely that these processes are slowed, if not suspended, during torpor. When oxygen consumption is measured at 5°C during nocturnal normothermia, spring values are significantly higher than both autumn and summer values, but rates of oxygen consumption during torpor at the same temperature were not significantly different in spring and summer. One explanation for this is that during normothermia, metabolic consequences of molt may account for much of the difference between mass-specific rates of oxygen consumption in summer and spring. During torpor, on the other hand, mass-specific rates of oxygen consumption may be indistinguishable among seasons because molt-specific processes are no longer occurring, or are occurring so slowly as to have negligible impact on the mass-specific rate of oxygen consumption.

SEASONALITY OF TORPOR

In the Rufous Hummingbird, seasonal changes in the tendency to use torpor, expressed as variation in duration or incidence of torpor or both, are superimposed on a year-round capacity to use torpor as a means of conserving energy at night. Various studies have shown that hummingbirds can be induced to enter torpor in the laboratory at any time of year by manipulation of environmental variables that affect energy balance, such as food supply (Hiebert 1991, 1992), ambient temperature (Beuchat et al. 1979), or photoperiod (Hainsworth et al. 1977, Krüger et al. 1982, Schuchmann et al. 1983). Like the birds in this study, however, a wild population of Andean Hillstars showed seasonal fluctuations in the incidence and duration of torpor, possibly in response to photoperiodic cues (Carpenter 1974). Thus, the actual use of torpor is a function both of the bird's immediate energetic situation and its seasonal physiological state. The ultimate energetic decision to enter torpor may depend on a suite of factors. These include costs inherent in the torpid state, such as increased risk of predation, physiological imbalance, or lack of sleep (Hainsworth et al. 1977, Hiebert 1990, Daan et al. 1991, Trachsel et al. 1991), as well as the energetic circumstances surrounding the particular seasonal activity in which the bird is engaged. During migration, the overriding energetic goal appears to be the rapid accumulation of fat; torpor is one of the means by which this goal can be achieved. During molt, even though body mass is low, torpor is used less, possibly because of the impact of torpor on the duration of molt.

Although the seasonality of daily torpor has received almost no attention in other groups of birds that exhibit daily torpor (swifts, caprimulgids, colies, and possibly doves and swallows; Reinertsen 1983), the phenomenon is well-known in a variety of small mammals. Some species, such as the kangaroo mouse *Microdipodops pallidus* (Bartholomew and MacMillen 1961, Brown and Bartholomew 1969) and the pocket mouse *Perognathus californicus* (Tucker 1965), can be induced to enter torpor at any time of year by restricting the food supply. Others, such as the white-footed mouse (*Peromyscus leucopus*) and the Siberian hamster (*Phodopus sungorus*), do not normally express torpor in the absence of environmental cues associated with winter (Gaertner et al. 1973, Tannenbaum and Pivorun 1984, Heldmaier and Steinlechner 1981, Elliott et al. 1987, Ruf et al. 1989). At least in Siberian hamsters, the inhibitory effect of the reproductive hormones testosterone and prolactin on torpor may explain why spontaneous torpor occurs only in winter, when gonads are regressed and the animals are not reproductive (Ruby et al. 1993). The greater flexibility in the occurrence of torpor in hummingbirds, especially when compared with other small homeotherms in which spontaneous torpor is completely absent at some times of year, may be associated with the extremely small body size and extraordinarily high energy demands on these birds. By continually maintaining the option to enter torpor at night, hummingbirds improve their chances of surviving environmental conditions that result in negative energy balance.

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