

SEASONAL DIFFERENCES IN THE RESPONSE OF RUFIOUS HUMMINGBIRDS TO FOOD RESTRICTION: BODY MASS AND THE USE OF TORPOR¹

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Abstract. Daily food consumption of captive Rufous Hummingbirds (*Selasphorus rufus*) was restricted during two different seasons to determine the effect of chronically reduced food intake on body mass and the role of nocturnal torpor in promoting changes in body mass. Daily food consumption was reduced to 70–90% of ad libitum levels for 15 days in spring and for 30 days in summer. In spring, all birds ($n = 4$) showed increases in both body mass and use of torpor during restriction, although energy saved by using torpor was sufficient to compensate for energy lost through food restriction in only two birds. As soon as ad libitum feeding was resumed, three of the four birds showed a decline in body mass and a reduction in the use of torpor. In summer, birds ($n = 9$) had higher body masses at the start of the experiment, reflecting normal seasonal fluctuations in body mass. During food restriction, birds spent less time torpid than during spring restriction, and in most birds body mass declined or showed no significant change. The initial response of all birds to the return of ad libitum feeding included decreased use of torpor and, in contrast to spring, a rapid increase in body mass. Seasonal differences in response to food restriction may reflect reduced stress response in these high-altitude, high-latitude breeders during the short breeding season, when the physiological and behavioral consequences of responding to environmental stress may interfere with breeding success.

Key words: Seasonal; body mass; torpor; food restriction; Rufous Hummingbird; *Selasphorus rufus*; body weight.

INTRODUCTION

Because of their extremely small size, hummingbirds are under especially strong selective pressure to manage their energy reserves effectively and to respond to external influences that reduce energy intake or increase energy expenditure. Nocturnal torpor, which results in dramatic energy savings (Lasiewski 1963; Lasiewski and Lasiewski 1967; Lasiewski et al. 1967; Hainsworth and Wolf 1970, 1978; Carpenter 1974; Krüger et al. 1982; Hiebert 1990), is an important means by which a hummingbird defends its energy reserves. During winter and early spring, for example, the morning prefeeding body masses of captive Rufous Hummingbirds (*Selasphorus rufus*) remain remarkably constant, and nocturnal torpor is an important means of achieving these constant body masses (Hiebert, in press).

In a study of nighttime metabolic rates in captive, non-molting Rufous Hummingbirds con-

ducted during the spring of 1985, food supply had to be restricted each day for several weeks to induce nighttime torpor (Hiebert 1990). Curiously, after 10–15 days of daily food restriction, all four of the birds in that study began to gain mass and enter torpor at higher and higher body masses. When these birds were again permitted to feed ad libitum, body mass declined and use of torpor ceased until body mass had returned to near its original level. These results suggested that body mass increased in response to food restriction but declined once the birds regained access to an unlimited food supply. These findings also suggested that Rufous Hummingbirds could use torpor not only to prevent energy supplies from being critically depleted (Hainsworth et al. 1977), but also to increase energy reserves in response to chronic energetic challenge. The observations reported here extend those preliminary findings.

METHODS

In August 1987, Rufous Hummingbirds of both sexes were captured as juveniles at Harts Pass, Whatcom County in the Cascade Mountains of Washington State. Birds were housed in individual $0.6 \times 0.6 \times 1.2$ m cages located in large

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controlled-environment chambers (5–8 cages per chamber). Air temperature was $20 \pm 1^\circ\text{C}$ during the day and $5 \pm 1^\circ\text{C}$ during the night. These two temperatures were selected because they lie within the range of air temperatures that occur in the habitats occupied by this migratory species throughout the year. Photoregime was adjusted seasonally to approximate the daylength experienced by Rufous Hummingbirds in nature. Daytime light was supplied by a "Daylight" fluorescent tube (15-watt 46 cm long) in each cage; at night a single 15-watt incandescent bulb provided diffuse light for the entire controlled-environment chamber.

Birds were maintained on an artificial hummingbird nectar consisting of approximately 11% sucrose equivalents (Nektar Plus, Nekton USA, Inc.) supplemented with live *Drosophila*. Food component analysis performed by the Institute of Food Science and Technology at the University of Washington showed that in dry form, Nektar Plus consists of 93.6% carbohydrates (mainly sugars) and 2.0% protein by mass. The remaining 4.4% consists of vitamins and minerals, a negligible amount of fat, and non-metabolizable components including water. Food bottles were weighed when filled in the morning and again when they were removed from the cage. Daily food consumption was computed as the difference between these two masses, corrected for dripping from the feeder.

Experiments were conducted in 1988 in two parts, one in spring at the conclusion of molt, and one in summer. Spring experiments were conducted at different times, from March to early May, according to each bird's molt schedule so that birds would be in similar seasonal physiological states during the experiment. Photoregime during spring experiments was LD 12:12. During summer, all birds were tested simultaneously from mid-July to the end of August. Photoregime during summer experiments was LD 16:8. In both spring and summer, the experiments described here followed other experiments that lasted 10 days, in which the bird experienced varying amounts of food restriction on alternate days, interspersed with days of ad libitum feeding.

FOOD RESTRICTION

Birds were fed at lights-on, but food ran out or was removed several hours before lights-out. The amount of food each bird received was adjusted

to induce the bird to enter torpor during the night. Individuals varied considerably in both pre-restriction ad libitum food consumption and in amount of daily food restriction required to induce torpor, in part because of differences in behavioral response to food restriction, e.g., time spent flying and searching for food. Food restriction by this method resulted in daily food intake ranging from 70–90% of the bird's pre-restriction ad libitum food consumption. Each bird's pre-restriction ad libitum food consumption was measured during the 10 consecutive days before the experiment preceding the present study began (see Table 1), i.e., a 10-day interval separated the beginning of the present study from the period of ad libitum food consumption used as a reference point. Live *Drosophila* were offered once per day in the morning. Except during molt, which was not occurring during the study described here, the birds show relatively little interest in live insects (pers. observation), probably because Nektar Plus is a complete, balanced hummingbird diet. *Drosophila* were assumed to contribute negligibly to energy balance (Hainsworth et al. 1981, Tooze and Gass 1985).

In spring experiments, the restriction period lasted 15 days. In summer, the restriction period was extended to 30 days because the expected response to food restriction, based on the spring experiments, had not occurred after 15 days.

The amount of energy lost due to food restriction was computed as follows: The mean daily food consumption during the restriction phase was subtracted from the mean daily food consumption during ad libitum feeding before the experiment began. Assimilable energy content of food was estimated as (wet mass of food) \times (0.106 g dry food g^{-1} wet food) \times (% carbohydrates plus proteins in dry food) \times (17.58 kJ g^{-1} dry carbohydrates). A single energy conversion factor (that for carbohydrates) was used because carbohydrates comprise 98% of metabolizable energy sources in the diet, and because of the very small difference in mass-specific energy content between proteins and carbohydrates (17.79 vs. 17.58 kJ g^{-1} , respectively). Hainsworth (1974) has shown that hummingbirds assimilate essentially 100% of dietary sugars.

Normally, the water contained in the artificial nectar is sufficient to supply the water needs of these birds (Calder 1979, Calder and Hiebert 1983). In the experiments described here, however, birds were also provided with a separate,

TABLE 1. Changes in morning body mass during food restriction.

Bird	Sex	% Res. ^a	Length of res. (day)	Beginning mass (g)	Net change mass (g)	% Nights torpid ^b	Nights torpid ^c		All nights	
							Slope mass	P	Slope mass	P
Spring										
1	M	89	15	3.50	+0.17	100	+	<0.0005	+	<0.0005
4	M	79	15	3.32	+0.56	100	+	<0.0001	+	<0.0001
9	M	87	15	3.25	+0.49	100	+	<0.01	+	<0.01
10	M	74	15	3.16	+0.88	91	+	<0.0001	+	<0.0001
Summer										
1 ^d	M	84	30	4.04	-0.07	93	-	<0.001	NS	>0.1
4 ^d	M	82	30	3.63	-0.43	93	-	<0.0001	-	<0.0001
9 ^d	M	86	30	3.23	-0.18	62	-	<0.01	NS	>0.1
3	M	76	30	3.37	+0.74	60	NS	>0.80	+	<0.001
5	F	77	30	3.83	-0.23	50	NS	>0.60	NS	>0.5
19	M	90	30	3.76	+0.46	92	+	<0.0001	+	<0.0001
20	M	79	30	3.39	-0.13	92	-	<0.0025	NS	>0.6
21	F	70	30	3.83	+0.04	75	NS	>0.05	+	<0.025
22	F	71	30	4.61	-0.30	62	+	<0.05	NS	>0.8

^a Average daily food consumption during food restriction, as percent of ad libitum food consumption before restriction.

^b The number of nights on which torpor occurred during food restriction, as a percentage of the total number of nights on which body temperature was measured.

^c Slopes and *P* values for the regression of morning body mass against day, using only those morning body masses obtained on mornings when the birds had entered torpor the night before.

^d Not included in statistical comparisons between seasons.

continuously available water supply to prevent dehydration when food was unavailable.

MEASUREMENT OF TORPOR

On nights when torpor was being monitored (approximately every two nights during the restriction and post-restriction ad libitum phases), food (if any still remained) and water were removed from the cage 45 min before lights-out. This is enough time for food to clear from the digestive tract (Hainsworth 1974, Diamond et al. 1986). Directly at lights-out, each bird was weighed and placed in a rectangular plastic box on a small (2 cm) perch fitted with a fine thermocouple wire. At rest, the hummingbird's abdomen contacted the perch near the thermocouple. Surface body temperatures obtained this way provide a clear indication of the beginning and end of torpor, as validated by comparing simultaneous measurements of surface body temperature and oxygen consumption. At lights-on, each bird was weighed and returned to its cage; unless otherwise specified, "body mass" refers to the pre-feeding mass at lights-on. The birds used in this study had had previous experience in this experimental apparatus and sat quietly on the perch during the night. Food was not available in the experimental apparatus, but birds did not feed at night in their home cages, either, even when food was present

and the cages were dimly illuminated at light levels sufficient for the birds to navigate in the cage.

During the period before the experiment began, birds often remained normothermic during the night when they had had access to food ad libitum during the previous day. Energy saved by using torpor during food restriction was therefore determined by subtracting the energy cost on nights when torpor was used from the energy cost for remaining normothermic all night. All $\dot{V}O_2$ and total VO_2 values used for calculations of nighttime energy expenditure were obtained for Rufous Hummingbirds in our laboratory (Hiebert 1990). The cost of remaining normothermic was computed as follows: (nightlength) \times (mass-specific $\dot{V}O_2$ at 5°C) \times (body mass), where nightlength was 12 or 8 hr (spring or summer, respectively), mass specific $\dot{V}O_2$ at 5°C was 17.42 ml g⁻¹ hr⁻¹, and body mass was the mean body mass during the restriction phase. For all calculations of nighttime energy expenditure, mean body mass is the mean of daily averages of morning and evening body masses.

Torpor bouts are comprised of three phases: entry, steady-state torpor, and arousal. Entry and arousal are fixed in duration and energy cost at a given ambient temperature, whereas steady-state torpor is variable in duration (Hiebert 1990).

TABLE 2. Effects of increased food intake and reduced duration of torpor on energy balance during first five days ad libitum feeding, relative to restriction period.

Bird	Mean add'l food consumed ^a (g day ⁻¹)	Mean energy gained ^b (kJ day ⁻¹)	Mean reduction in torpor (hr day ⁻¹)	Energy saved by using torpor (kJ day ⁻¹)	Predicted change body mass (g day ⁻¹)	Actual change body mass (g day ⁻¹)
Spring						
1	5.7	10.16	2.4	2.58	+0.15	+0.02
4	3.1	5.52	1.5	1.36	+0.12	-0.01
9	-1.2	-2.14	5.9	6.22	-0.17	-0.09
10	4.0	7.13	2.9	2.60	+0.14	-0.03
Summer						
1 ^c	3.8	6.77	1.6	0.63	+0.12	+0.18
4 ^c	4.2	7.48	3.2	2.25	+0.04	+0.05
9 ^c	1.0	1.78	2.8	1.97	-0.02	+0.02
3	3.5	6.24	2.5	0.51	+0.10	+0.10
5	2.9	5.17	1.9	1.24	+0.09	+0.02
19	3.1	5.52	1.8	-0.71	+0.15	+0.05
20	2.8	4.99	0.9	0.85	+0.08	+0.04
21	5.9	10.51	3.2	2.05	+0.16	+0.21
22	8.4	14.97	3.7	2.88	+0.22	+0.19

^a Wet mass of diluted Nektar Plus, expressed as [(mean daily food intake during ad libitum feeding) - (mean daily food intake during restriction)].

^b Values in column 2 multiplied by energy conversion factor (see Methods).

^c Not included in statistical comparisons between seasons.

The cost of a night on which torpor occurred was therefore computed as [(total time spent torpid - duration of entry - duration of arousal) × (\dot{V}_{O_2} during steady-state torpor at 5°C) + (total \dot{V}_{O_2} consumed during entry into torpor) + (total \dot{V}_{O_2} consumed during arousal from torpor) + (time spent normothermic) × (\dot{V}_{O_2} during normothermy at 5°C)] × (body mass), where time spent torpid was the mean torpor bout duration measured during the restriction phase, duration of entry was 0.3 hr, duration of arousal at 5°C was 0.9 hr, \dot{V}_{O_2} during steady-state torpor at 5°C was 2.48 ml g⁻¹ hr⁻¹, body mass was the mean body mass (see above) during the restriction phase, \dot{V}_{O_2} during entry was 1.93 ml g⁻¹, and \dot{V}_{O_2} during arousal was 11.03 ml g⁻¹. Although individual torpor bouts were always longer than 1.1 hr (the time required for entry + arousal), mean torpor bout length was sometimes less than 1.1 hr. For this reason, total nighttime O₂ consumption was computed first for each night, then averaged over the phase of the experiment in question. The difference in total O₂ consumption of hummingbirds between torpid and normothermic nights was converted to its energy equivalent by assuming an RQ of 0.7 (fat metabolism) (Hainsworth et al. 1977, Suarez et al. 1990).

Predicted daily changes in body mass during restriction, based on the balance between energy losses due to food restriction and energy "gains"

due to energy-saving torpor, were computed by the following formula: [(mean energy saved, kJ day⁻¹) - ((mean energy lost, kJ day⁻¹) × (efficiency of converting dietary sugar to fat))]/(39.36 kJ g⁻¹ fat), where energy saved by entering torpor was computed as described above, energy lost was computed as the difference between daily food consumption during pre-restriction ad libitum feeding and that during restriction, and efficiency of conversion was 0.8 (Milligan 1971). Thus predicted daily changes in body mass during restriction are based on the assumption that birds feeding ad libitum and remaining normothermic at night exhibit stable masses. This is a conservative assumption because in both spring and summer, birds feeding ad libitum before the experiment began occasionally used torpor; i.e., this calculation tends to overestimate the additional savings due to torpor and therefore tends to overestimate gains (and underestimate losses) in body mass. For all calculations of predicted changes in body mass, I assumed that all energy ingested (98% of which was carbohydrate) is stored as fat, as supported by the findings of Tooze and Gass (1985), and that nocturnal energy expenditures are fueled by fat (Hainsworth et al. 1977, Suarez et al. 1990).

Similarly, predicted *relative* daily changes in body mass during post-restriction ad libitum feeding, based on the energy gained due to in-

TABLE 3. Changes in morning body mass during ad libitum feeding following food restriction.

Bird	% Inc. ^c	First five days of ad libitum ^a				Peak mass ^b		
		Beginning mass (g)	Net change mass (g)	Slope mass (g day ⁻¹)	<i>P</i>	% Nights torpid	Net change in mass to peak (g)	Days to peak mass
Spring								
1	118	3.66	+0.10	+	<0.01	100	—	—
4	112	3.90	-0.08	-	<0.001	100	—	—
9	94	3.70	-0.45	-	<0.01	25	—	—
10	123	4.07	-0.15	-	<0.05	80	—	—
Summer								
1 ^d	116	3.83	+0.90	+	<0.05	25	+1.00	7
4 ^d	127	3.16	+0.24	+	<0.01	50	+0.31	8
9 ^d	106	3.04	+0.09	NS	>0.70	0	+0.37	1
3	116	3.84	+0.50	+	<0.025	75	+0.50	5
5	118	3.23	+0.10	NS	>0.80	0	+0.38	2
19	116	4.12	+0.37	+	<0.005	50	+0.43	4
20	120	3.20	+0.19	+	<0.005	100	+0.19	5
21	128	3.60	+1.06	+	<0.001	25	+1.06	5
22	148	4.03	+0.93	+	<0.001	25	+0.93	5

^a Slopes and *P* values for the regression of morning body mass against day, using all morning body mass values obtained during the time period indicated.

^b In summer, body mass first increased and then decreased during ad libitum feeding following food restriction.

^c Average food consumption during the ad libitum phase, as percent of food consumption during the restriction phase.

^d Not included in statistical comparisons between seasons.

crease in food intake over restriction levels and on energy "lost" due to reduction in the use of torpor relative to restriction levels, were computed as follows: [(mean energy gained from food intake, kJ day⁻¹) - ((mean reduction in energy saved by using torpor, kJ day⁻¹) × (efficiency of converting dietary sugar to fat))]/(39.36 kJ g⁻¹ fat). The predicted daily changes in body mass shown in Table 2 represent the sum of the calculated relative values and the actual rates of change in body mass during restriction. Thus, predicted daily changes in body mass during post-restriction ad libitum feeding are based on the assumption that differences in rates of change in body mass between the restriction and ad libitum phases are due solely to changes in the balance of food intake and use of torpor.

STATISTICS

Paired *t*-tests were used to compare effects between phases of the experiment within a season; all individuals tested in that season were included. Two-sample *t*-tests were used to compare effects between seasons. 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 samples with unequal variances was used (Snedecor and Cochran 1980).

Although tables show data from all birds, the three birds that were tested in both spring and summer (birds 1, 4, and 9) were omitted from the summer sample in statistical comparisons between seasons so that conditions of independence would be met.

PERMITS

Capture, maintenance and laboratory study of Rufous Hummingbirds were authorized by permits to the author from the Washington State Department of Game and from the United States Fish and Wildlife Service.

RESULTS

SPRING

All birds showed a significant gain in body mass during the 15-day restriction period (Table 1, Fig. 1). Average mass at the start of the restriction phase was 3.31 g (range 3.16 to 3.50 g). Mean net gain in body mass during this period was 0.52 g (range 0.17 to 0.88 g). During the post-restriction ad libitum phase, three of four birds showed a significant decline in body mass (Table 3, Fig. 1), in two cases resulting in body masses near those at the beginning of the experiment (Fig. 1).

Most birds entered torpor every night during the restriction phase of the experiment (Table 1).

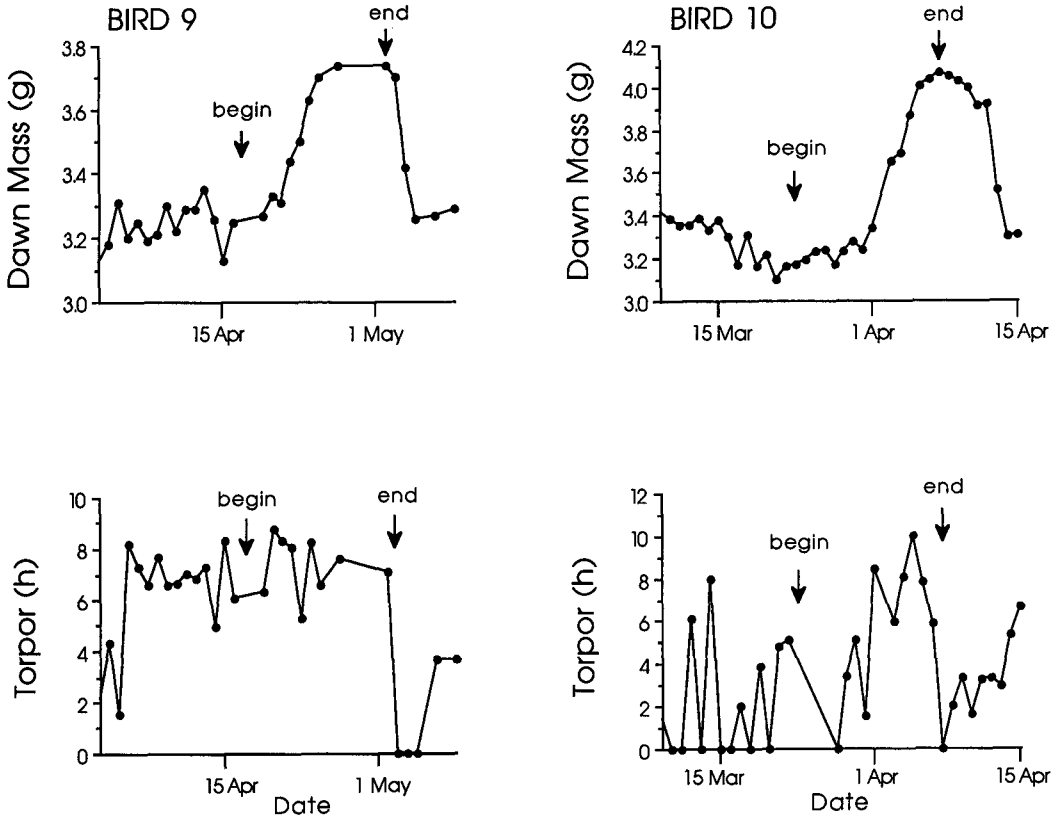


FIGURE 1. Morning body mass and time spent in torpor for two birds tested in spring (bird 9, left column; bird 10, right column). Arrows show (1) the beginning of food restriction and (2) the end of food restriction (= beginning of ad libitum feeding).

In all birds, mean torpor bout duration during the post-restriction ad libitum phase was less than that during restriction (paired *t*-test, *df* = 3; *P* < 0.05) (Table 4). In all birds, torpor bout duration decreased markedly on the first night following the resumption of ad libitum feeding; in two cases (birds 9 and 10), the birds did not enter torpor at all on the first night of the ad libitum feeding; on subsequent nights these two individuals resumed use of torpor, but for shorter periods than during the restriction phase.

When the reduction in energy intake during food restriction was compared with the amount of energy saved by entering torpor during this period, torpor could compensate for the lost energy in only two individuals (birds 1 and 9) (Table 5). For the other two birds (4 and 10), the energy savings achieved by using nocturnal torpor were not sufficient to make up for the energy deficit due to food restriction, even though these

birds also gained body mass during restriction. By contrast, three of four birds lost mass at higher rates than predicted during the post-restriction ad libitum phase (Table 2).

SUMMER

In contrast to spring, most birds showed a net decrease in body mass during food restriction in summer (Table 1). Average mass at the start of restriction was 3.74 g (range 3.23 to 4.61) for all birds and 3.80 g (range 3.37 to 4.61) for the six birds tested only in summer; this value was significantly higher than in spring [two-sample *t*-test; *df* = 6.4 (unequal variances); *P* < 0.05] (Table 1). Mean net change in body mass during restriction was -0.01 g (range -0.43 to +0.74 g), and linear regression of body mass against day during restriction demonstrated a decline or no significant change in body mass in six of nine birds (Table 1, columns 10 and 11). If, to make

TABLE 4. Mean duration of torpor (hr) and nighttime normothermy (hr) during food restriction and the first five days of post-restriction ad libitum feeding.

Bird	Spring				Summer			
	Restriction		Ad libitum		Restriction		Ad libitum	
	Torpid	Normo	Torpid	Normo	Torpid	Normo	Torpid	Normo
1	5.9	6.1	3.5	8.5	2.7	5.3	1.1	6.9
3	—	—	—	—	3.4	4.6	1.0	7.0
4	6.5	5.5	5.0	7.0	3.8	4.2	0.6	7.4
5	—	—	—	—	1.9	6.1	0.0	8.0
9	7.4	4.6	1.5	10.5	2.8	5.2	0.0	8.0
10	5.6	6.4	2.7	9.3	—	—	—	—
19	—	—	—	—	2.9	5.1	1.2	6.8
20	—	—	—	—	3.4	4.6	2.6	5.4
21	—	—	—	—	3.5	4.5	0.3	7.7
22	—	—	—	—	4.0	4.0	0.4	7.6
Mean	6.3	5.7	3.2	8.8	3.2	4.8	0.8	7.2

the comparison between spring and summer as close as possible, I considered only 15 days of the restriction period beginning with the first occurrence of torpor, the results are similar: seven of nine birds showed a decrease or no significant trend in body mass. When linear regression was performed on only those body masses that followed a night during which torpor occurred, there was a decline or no significant change in body mass in seven of nine birds (Table 1, columns 8 and 9).

Although all birds entered torpor on the majority of nights for which measurements were made during the restriction phase, each remained normothermic on one or more nights during restriction (Table 1). Neither mean percent food restriction nor daily reduction in energy intake due to food restriction was significantly different in summer and spring (two-sample *t*-test; *df* = 8; *P* > 0.3 in both cases). Nevertheless, the percent of nights on which the birds entered torpor was significantly lower in summer than in spring [two-sample *t*-test; *df* = 5.9 (unequal variances); *P* < 0.02]. Mean torpor bout duration during restriction was also significantly lower in summer than in spring (two-sample *t*-test; *df* = 8; *P* < 0.0005) (Table 4). However, mean time spent normothermic was not significantly different in summer and spring (two-sample *t*-test; *df* = 8; *P* > 0.1) (Table 4).

During the post-restriction ad libitum phase, the body mass of all birds increased when unlimited food was first returned. Once body mass had peaked, body mass again declined. Although each bird showed a distinct peak in body mass, the

time required to reach the peak after food restriction had ended varied from 1 to 8 days (mean 4.7 days) (Table 3). As in spring, torpor bouts were significantly shorter during ad libitum feeding than during the preceding period of food restriction (paired *t*-test; *df* = 8; *P* < 0.0005) (Table 4).

In all birds tested during the summer, the amount of energy lost because of food restriction exceeded the amount of energy saved by using torpor during that period (Table 5). Although most birds underwent a net decrease in body mass during restriction, none lost as much mass as predicted based on food intake and torpor bout duration alone; i.e., if losses are considered to be negative gains, actual gains exceeded predicted gains (paired *t*-test; *df* = 8; *P* < 0.001) (Table 5). Conversely, during post-restriction ad libitum feeding, predicted rates of mass gain equaled or exceeded actual rates in five of nine birds (Table 2); however, the difference was not statistically significant (paired *t*-test; *df* = 8; *P* > 0.3).

DISCUSSION

In spring, body mass increased and torpor duration was relatively high during moderate food restriction; when ad libitum feeding was subsequently resumed, both body mass and the use of torpor declined. In summer, however, body mass of most birds declined or showed no significant trend during restriction; torpor bouts were moderately long but not as long as during restriction in spring. During the subsequent ad libitum phase in summer, body mass increased rapidly and the

TABLE 5. Effect of reduced food intake and increased use of torpor on energy balance during food restriction.

Bird	Mean amount restricted ^a (g day ⁻¹)	Mean energy lost ^b (kJ day ⁻¹)	Mean duration torpor (hr day ⁻¹)	Energy saved by using torpor (kJ day ⁻¹)	Predicted change body mass (g day ⁻¹)	Actual change body mass (g day ⁻¹)
Spring						
1	2.4	4.28	5.9	5.77	+0.06	+0.01
4	5.1	9.09	6.5	6.40	-0.02	+0.04
9	2.9	5.17	7.4	7.04	+0.07	+0.03
10	6.2	11.05	5.6	5.11	-0.09	+0.06
Summer						
1 ^c	4.6	8.20	2.7	2.39	-0.11	-0.002
4 ^c	3.5	6.24	3.8	3.10	-0.05	-0.01
9 ^c	2.9	5.17	2.8	1.98	-0.05	-0.01
3	7.0	12.47	3.4	3.05	-0.17	+0.02
5	4.6	8.20	1.9	1.24	-0.14	-0.01
19	2.2	3.92	2.9	2.69	-0.07	+0.02
20	3.8	6.77	3.4	2.74	-0.07	-0.004
21	9.1	16.22	3.5	3.07	-0.03	-0.001
22	7.0	12.47	4.0	4.06	-0.15	-0.01

^a Wet mass of diluted Nektar Plus.

^b Values in column 2 multiplied by energy conversion factor (see Methods).

^c Not included in statistical comparisons between seasons.

use of torpor declined to levels significantly lower than those during summertime restriction and significantly lower than those during the post-restriction ad libitum phase in spring.

The general pattern of response is similar in the two seasons in that the use of torpor increases during food restriction but declines when an unlimited food supply is returned. This result is consistent with the important energy-conserving function of torpor. Implicit in several models that attempt to explain the incidence of daily torpor in hummingbirds is the assumption that torpor is initiated in response to the balance of energy intake and expenditure, which, ultimately, is manifested as a net change in the energy stores of the bird (Hainsworth et al. 1977, Hiebert, in press). These models propose that when energy stores, estimated in the laboratory by whole body mass, fall below a certain value or "threshold," torpor is initiated. The present study was not designed to examine the physiological cues that trigger changes in the use of torpor during and after food restriction, but several results suggest that a simplistic threshold model is insufficient to explain the pattern of torpor observed here. In spring, the post-restriction ad libitum phase was characterized not only by reduced use of nocturnal torpor, but also by falling body mass. This result indicates that the body mass at which torpor is initiated may change markedly depending on the availability of food.

In addition, the behavior of bird 9 in spring suggests that energy stores alone may be insufficient for predicting whether or not torpor will occur. This bird showed a dramatic rise in body mass during restriction and a corresponding decline in body mass, as well as a complete absence of torpor, during the first three days of the subsequent ad libitum phase (Fig. 1). Yet, this bird failed to increase its food consumption during ad libitum feeding, despite the fact that food restriction had ended and an unlimited food supply was now available (Table 3). Although a complete 24-hr energy budget is needed for a full understanding of this bird's response, its behavior suggests that the perceived availability of food, independent of the amount of food actually consumed, is enough to trigger changes in energy economy. Similarly, studies by Harvey et al. (1983) on chickens have shown that perceived availability of food, regardless of the amount consumed or its nutritional content, is sufficient to reverse at least temporarily some of the physiological consequences of food restriction.

A second similarity in the results from the two seasons is that in many individuals, predicted gains in body mass during post-restriction ad libitum feeding exceeded actual gains. Because predicted changes in body mass during the ad libitum phase are based on observed patterns of energy use and mass change during restriction, the differences between predicted and actual val-

ues suggest a higher "energy efficiency" during restriction than during post-restriction *ad libitum* feeding in these birds. In summer, the reverse relation of predicted and actual changes in body mass during restriction (when actual gains exceeded predicted gains in all birds) further supports this interpretation. Whole-animal energy efficiency can be defined as energy stored per unit mass of food ingested; for our purposes it includes any means of increasing energy gains or reducing expenditures other than increased torpor or food intake, which are already taken into account by the calculation. For example, overall energy efficiency might be affected by changes in the efficiency of food assimilation. However, because assimilation of sugars in the mostly carbohydrate diet of hummingbirds is normally assumed to be 100% (Hainsworth 1974; Hainsworth et al. 1981), assimilation efficiency is unlikely to have improved during restriction. Theoretically, a temporary decline in efficiency of assimilation during post-restriction *ad libitum* feeding could have contributed to the relatively higher energy efficiency during restriction, but there is no empirical evidence to support or refute such a possibility. Reducing energy expenditure during the day by curtailing certain kinds of activities is probably more important for increasing overall energy efficiency during restriction (e.g., Hainsworth et al. 1981). The birds in this study quickly habituated to the experimental protocol; after several days' experience with food removal, they spent less time flying and searching for food once it had been removed. The energy saved by reducing flight time could presumably have been reallocated to storage. In the field, birds may be able to reduce certain energy-demanding behaviors such as courtship flights and chasing intruders from a territory (Ewald and Carpenter 1978), but survival may dictate against reducing other activities such as avoiding predators or searching for new sources of food in the event of local shortage. Thus, whereas the general nature of shifts in energy economy demonstrated by captive birds may well parallel those of free-living birds confronted by a reduced energy supply, the amount of energy actually saved is likely to depend on the available avenues for conserving energy.

In addition to certain similarities in responses to food restriction across seasons, there are striking differences. The most salient of these is the response of body mass. In summer, body mass

declined or showed no significant linear trend during restriction; upon resumption of *ad libitum* feeding, body mass quickly rose. In spring, however, a paradoxical effect was observed: birds tended to gain mass during restriction and lose mass when an unlimited food supply was returned. The three birds tested in both spring and summer illustrate this seasonal difference—whereas all three showed a significant increase in body mass during restriction in spring, none showed a significant increase in summer. What might be responsible for seasonal changes in the response to food restriction?

One possibility is that nightlength is the determining factor. In summer, nights are shorter than in spring (8 hr vs. 12 hr). Because torpor usually occurs only during the dark, inactive period, there is less time available for energy-saving torpor during summer nights than during spring nights. In this study, torpor bouts were significantly shorter in summer than in spring, even though there is no significant difference in the amount of energy lost to food restriction between the two seasons. Note, however, that in both seasons, torpor bouts are much shorter than the dark period. In spring and summer, birds were normothermic for an average of 5.7 hr and 4.8 hr per night during food restriction, respectively. Why didn't birds increase torpor bout duration to fill the inactive period, especially in summer when energy lost during food restriction always exceeded energy saved by using torpor?

Various factors may set limits on torpor bout duration. For example, postulated costs of entering torpor, including increased risk of predation, unspecified physiological imbalances resulting from low body temperatures (Hainsworth et al. 1977), and the incompatibility of sleep and torpor (Hiebert 1990) may counterbalance the energy-saving benefits of entering torpor. Thus, a simple hypothesis to explain the observed patterns of torpor might be that the birds require approximately 5–6 hr per night for functions, such as sleep, that are incompatible with torpor. This hypothesis proposes that the same physiological rules for determining torpor bout duration apply in both spring and summer, but that differences in nightlength result in differences in torpor duration, which in turn influences energy balance and hence body mass. This view invites us to focus not on torpor bout duration, but on its inverse, the amount of time spent normothermic each night. In fact, there is no significant

seasonal difference in duration of nighttime non-mothermy. Far from conclusive support for this hypothesis, this preliminary evidence merely points out the need for experiments that assess the relative influence of factors other than energy economy in determining when, and for how long, torpor is used. At present, such information is not available.

An alternate interpretation is that seasonal differences in the response to food restriction reflect seasonal shifts in the underlying physiology. Like other kinds of stress, food restriction triggers a neuroendocrine response that includes elevation of plasma glucocorticoids (in birds, primarily corticosterone). Observations in other species of birds have suggested that the intensity of this neuroendocrine response may vary seasonally. In white-crowned sparrows (*Zonotrichia leucophrys*), for example, there is evidence that the stress response is reduced during the breeding season (Lorenzen and Farner 1964, Wingfield et al. 1983). Wingfield (1988) has suggested that the reduced response to stress is adaptive for birds with short breeding seasons because physiological and behavioral consequences of responding to stress may interfere with breeding. Similar ecological pressures could have led to selection for seasonal shifts in the neuroendocrine response to stress in Rufous Hummingbirds, which are faced with a long migratory flight and a restricted breeding season (Phillips 1975, Calder 1987).

Such a hypothesis is consistent with the results of the present study if we assume that summer birds were in fact in breeding condition. In the Cascade Mountains of Washington, where I obtained the birds used in this study, breeding lasts until late July. The dates of the summer testing period (mid-July through late August) thus coincide with the beginning of the post-breeding southward migration of Rufous Hummingbirds in the wild. However, the annual cycle of captive birds appears to be delayed one to two months with respect to that of their free-living counterparts. In our laboratory, for example, the median completion date for molt was in early May (Hiebert, unpubl. data), whereas observations on wild birds in Mexico suggest that the molt should be completed by March (W. A. Calder, pers. comm.). Therefore, it is likely that results from summer testing reflect the breeding condition rather than the autumn migratory condition. This interpretation is supported by the observation that these

birds had not yet undergone the dramatic mass gain typical of captive Rufous Hummingbirds during autumn (Hiebert 1989).

Seasonal physiological changes in the response to food restriction may also explain differences in the intensity of the body mass response in the four birds tested in spring. For example, in spring bird 1 had the highest body mass at the start of food restriction, showed the smallest gain in body mass, and failed to show a significant decrease in body mass during post-restriction ad libitum feeding. Body mass typically increases sometime after the completion of the molt (Hiebert 1989). Thus, this bird may already have initiated seasonal physiological shifts that altered its response to food restriction.

Is the rise in body mass during springtime food restriction a phenomenon likely to be observed in the field, or is it a response limited to captivity? I have already discussed why captive birds may be able to save more energy than free-living birds by such means as reducing flight time. There is, however, a further question: even if free-living birds could make as much energy available for allocation to storage as the birds in this study did, would they do so? Changes in energy economy influence body mass, but the reverse is also true; of particular importance is the correlation between body mass and the energy cost of flight (e.g., Pennycuik 1975, Epting 1980). In a recent study, Calder et al. (1990) showed that free-living male hummingbirds defending a territory tend to maintain low body mass during the day; most of the daily gain in body mass occurs during the peak in feeding just before nightfall and the onset of inactivity. He suggests that this temporal pattern of energy accumulation is favored because keeping body mass low during the day reduces the energy cost of flight and improves aerial performance. Individually housed captive birds have greatly reduced needs for feeding flights and essentially no use for territorial chasing or display and are likely to benefit far less from keeping body mass low. If, as Calder et al. (1990) suggest, aerial performance itself feeds back on the systems that control body mass, captive birds might be expected to allow daytime body mass to reach higher levels than free-living birds. Consistent with this hypothesis are the results of several studies on feeding rates of captive hummingbirds, in which body mass increases were distributed much more evenly over the course of the day (Wolf and Hainsworth 1977, Gass 1978,

Schuchmann et al. 1979, Tooze and Gass 1985). As before, the application of laboratory results to the field must be tempered by considering the ecological constraints faced by free-living birds.

Various studies on the use of torpor by temperate-zone hummingbirds suggest that torpor may serve different energetic functions in different circumstances. Observations by Hainsworth et al. (1977) suggest that these birds use torpor to conserve energy only when it is needed in an "energy emergency" (Hainsworth et al. 1977), i.e., to prevent critical depletion of energy reserves. Observations of Rufous Hummingbirds, both in the field (Carpenter and Hixon 1988) and in the laboratory (Hiebert 1989), suggest that there may also be a strong seasonal component in the use of torpor by this long-distance migrant. For the Rufous Hummingbird, torpor appears to play an important role in shifting energy balance so that fat can be accumulated rapidly before migration. A third role for torpor is suggested by the present study, in which Rufous Hummingbirds responded to moderate food restriction during spring by increasing both their body mass and their use of torpor. Like the use of torpor during migratory fattening, the response to food restriction has a seasonal component. However, unlike the increased use of torpor during the migration season, which persists for a period of several months and declines at the end of the migration season in the absence of changes in food supply (Hiebert 1989), the food restriction response is more immediately dependent on the availability of food. Indeed, the mere perception of increased availability may be sufficient to terminate the food restriction response.

Rufous Hummingbirds that increase body mass and the use of torpor in response to food restriction survive adequately on lower levels of energy reserves both before and after the period of restriction. Therefore, these birds do not need the extra energy reserves they accumulate during the restriction response to survive immediate circumstances. The continued use of torpor during the rise in body mass might therefore be interpreted as evidence against the energy emergency hypothesis (Hainsworth et al. 1977). An alternate interpretation is that the birds in this study were in fact experiencing an energy emergency, not in the immediate physiological sense, but in the ecological sense, and that torpor was an important line of defense in preparing to face that emergency. The birds may interpret food restriction

as a predictor of prolonged reduction in food availability; the increase in energy stores is used not to meet an immediate crisis but to provide energy for surviving future energy shortage.

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