BODY TEMPERATURE REGULATION IN RED-TAILED HAWKS AND GREAT HORNED OWLS: RESPONSES TO AIR TEMPERATURE AND FOOD DEPRIVATION

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ABSTRACT.—Core body temperatures of Red-tailed Hawks (*Buteo jamaicensis*) and Great Horned Owls (*Bubo virginianus*) were monitored by telemetry at intervals throughout the winter and summer. The mean body temperature of the hawks over a 24-h period was 41.1°C, compared to 39.5°C for the owls. Body temperature of both species fluctuated daily in association with periods of activity and rest. In the hawks, however, the difference between active and inactive body temperature increased in cold weather and in response to food deprivation because the birds maintained a lower nocturnal (inactive) body temperature. Hawks that were fasted in the winter kept their body temperatures 3.2°C lower at night than during the day, which may result in a substantial savings of energy for this species at night. Body temperatures of Great Horned Owls were not influenced by cold, but were lower during inactive periods in response to food deprivation. Thus, owls may also reduce metabolic expenses during periods of food shortage by physiological adjustments.

Most birds exhibit cyclical daily changes in body temperature (T_b), with highest temperatures occurring when they are active and lowest when they are inactive (see Dawson and Hudson 1970, Calder and King 1974 for reviews). A 1–3°C difference in T_b between the active and inactive phases of the daily cycle may be augmented by cold exposure or food deprivation, and is especially apparent in small species (<50 g), which are incapable of subsisting on their energy reserves for more than two to three days (Calder and King 1974, Chaplin 1976, Biebach 1977, Ketterson and King 1977, Bucher and Worthington 1982).

Birds of prey typically feed irregularly and may have to endure long periods of fasting during the winter when low temperatures and snow cover diminish or obscure the activity of their prey. Despite the energetic advantage gained by reducing T_b while inactive or fasting, daily fluctuations in T_b rarely exceed 1–2°C in several species of owls (Coulombe 1970, Siegfried et al. 1975, Gessaman 1978), even when they are fasted to 75% of their initial body mass (Ligon 1969). Daily cycles in T_b, specifically in response to cold and/or fasting, have been reported for only a few falconiforms, and the manner in which the birds respond is still unclear. For example, Heath (1962) and Hatch (1970) disagreed as to the stability of T_b of the Turkey Vulture (*Carthartes aura*) when it is fasted or cold-stressed. However, the T_b of the Black Vulture (*Coragyps atratus*) is very labile and highly dependent on air temperature (Larochelle et al. 1982). Is such lability characteristic of falconiforms, and are the metabolic adjustments of these birds to winter therefore different from those of owls, their nocturnal counterparts?

In this study, we compared the thermoregulatory responses of Red-tailed Hawks (*Buteo jamaicensis*) and Great Horned Owls (*Bubo virginianus*) to changes in air temperature and weight loss as a test of their metabolic adaptations to winter conditions. These two species are similar in size and in their utilization of habitat and prey (Craighead and Craighead 1956, Orians and Kuhlman 1956, Hagar 1957, Korshgen and Stuart 1972, McInvaille and Keith 1974, Petersen 1979, and Jaksic 1982). Their geographic ranges overlap throughout most of the United States year-round (Bent 1937, Robbins et al. 1983); even their home ranges overlap greatly in some localities (Craighead and Craighead 1956, Petersen 1979). In fact, the most notable ecological difference between them is the period of the day when they are active. Since these two species, representing different orders, are so similar ecologically, we wondered if their metabolic responses to such typical winter stresses as cold exposure and food limitation were also similar.

METHODS

Five Red-tailed Hawks and seven Great Horned Owls were kept in outdoor enclosures

(4 × 4 × 10 m) where they were exposed to natural temperature and photoperiod at the Charles W. Green Experimental and Research Wildlife Management Area in Boone Co., Missouri (38°N). Two of the hawks and one of the owls had been captured shortly after fledging in 1981 and were obtained from the Springfield, Missouri zoo in September of that year. Three other hawks were captured as juveniles in the winter of 1981–1982. Three adult owls were obtained from the Animal Psychology Laboratory at the University of Missouri and were kept outdoors for six weeks before we made any measurements of their T_b. We obtained three more owls in Boone Co. shortly after they fledged in April 1982 and used them, after they reached a stable body weight, for measurements of T_b in the summer. All birds were kept on falconer's jesses and a 1.5-m leash attached to a perch in the enclosures. They were weighed and fed once daily a weighed amount of white mice, rats, quail, or turkey poults adequate to maintain their body mass within ±1%.

Body temperature was measured with Model L Mini-mitter transmitters, accurate to 0.1°C (Mini-Mitter Co.). Each transmitter was soldered to two 1.5-V mercury batteries, placed in a plastic capsule, and then coated in Paraffin-Elvax®. The finished device measured 35 × 20 mm and weighed 14 g. These transmitters emitted pulsed radio signals at 27 mHz, the frequency of which was linearly related to temperature over a 30 to 45°C range. The signal was received on a modified CB transceiver (MacDonald Instruments).

On the day of a T_b trial, the transmitters were calibrated in a water bath and then force-fed to the birds. The birds were not disturbed again until the transmitters were cast (regurgitated as a pellet). If the transmitter was cast before the T_b trial had been completed we again force-fed it to the bird, and then waited 1 h before resuming T_b recording. Body temperature was recorded to the nearest 0.1°C every 15–30 min for 18–24 h.

To test the birds' thermoregulatory responses to a variety of average daily ambient temperatures (T_as) and day-night differences in T_a, we recorded T_bs of hawks during eight trials between October 1981 and May 1982, and those of owls during nine trials between October 1981 and August 1982. In order to test the effects of food deprivation on T_b, we withheld food from the birds for several days prior to a T_b trial, i.e., until they had lost approximately 5% of their initial body mass. This was done once in the winter and once in the summer. Results of these fasting trials were then compared with those obtained on the same birds one to four weeks earlier, when they had been fed normally.

Parametric statistical analysis was employed throughout this study, after initially determining that such tests were suitable by equality of variance (F-test) and normality of the data.

RESULTS

Several major differences in T_b regulation of Red-tailed Hawks and Great Horned Owls emerged in this study. First, the daily cycle of T_b in the winter was more marked in Red-tailed Hawks that were fed regularly than in the owls. Daytime T_b of 41.9°C fell at least 2°C after sunset, then leveled out at 39.9°C, and rose again well before sunrise to 41–42°C (Fig. 1 and Table 1). The amplitude of this cycle was less pronounced in the summer (0.8°C, $P < 0.001$). Owls fed regularly in the winter exhibited transient peaks of T_b (40°C) just before sunset and sunrise, which Kasparie (1983) found were associated with activity. This active-period T_b decreased again in 1–2 h (Fig. 2 and Table 2) and was relatively stable at 39.3°C between 11:00–15:00 and 22:00–03:00 (the inactive periods as established by Kasparie [1983]). Hence, the owls' winter T_b cycle varied only 0.8°C, much less than in the hawks. In the summer, the T_b of the inactive owls was 39.3°C at night, but rose to 40.7°C when the birds were active near sunrise. Thus, the T_b cycle in summer varied much more in the owls than in the hawks (see Tables 1 and 2).

During the winter, the T_b of active hawks was significantly higher ($P < 0.01$) than that of active owls; the birds showed no such significant difference in the summer. Despite nocturnal hypothermia, the T_b of inactive hawks was still 0.6°C higher in the winter (not significantly different) and 1.1°C higher in the summer ($P < 0.01$) than that of inactive owls (Tables 1 and 2). Thus, the mean daily T_b maintained by fed Red-tailed Hawks was 1.6°C higher than that of fed Great Horned Owls in the winter ($P < 0.005$) and 1.1°C higher than that of the owls in the summer ($P < 0.025$).

The two species also responded differently to changes in T_a. We tested the influence of T_a on T_b in both species by determining the degree of correlation between several measures of their T_b (mean daily T_b, active T_b, inactive T_b, and daily change in T_b, ΔT_b [=active T_b − inactive T_b]) and T_a (mean T_a, minimum T_a, maximum T_a, and daily change in T_a, ΔT_a [=maximum T_a − minimum T_a]; Table 3). In five T_b trials on two to five hawks (October 1981 through May 1982), in which mean daily T_as ranged from −15.0 to 19.7°C, the measure of T_b that was most highly correlated with the various measures of T_a was ΔT_b, and it was most sig-
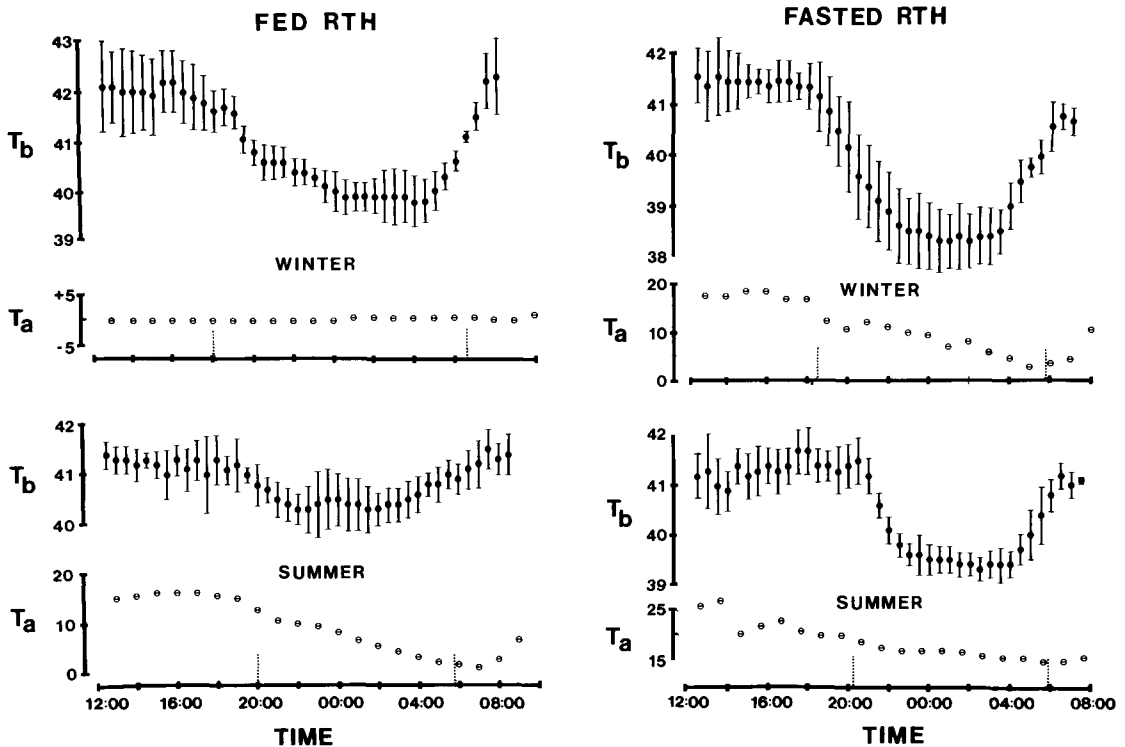
FIGURE 1.   Daily cycle of core T_b, ($\bar{x} \pm$ SD, in °C) of five Red-tailed Hawks fed regularly to maintain body mass constant within $\pm 1\%$ (left) and after being fasted two to four days to achieve a mean loss of body mass of 5% (right). Data are presented for birds tested in late winter (March 1982) and early summer (May 1982). Air temperatures (open circles) were obtained from a meteorological station 1.6 km from the hawk enclosures. Times (CST) of sunset and sunrise are indicated by the dotted lines on the abscissa.
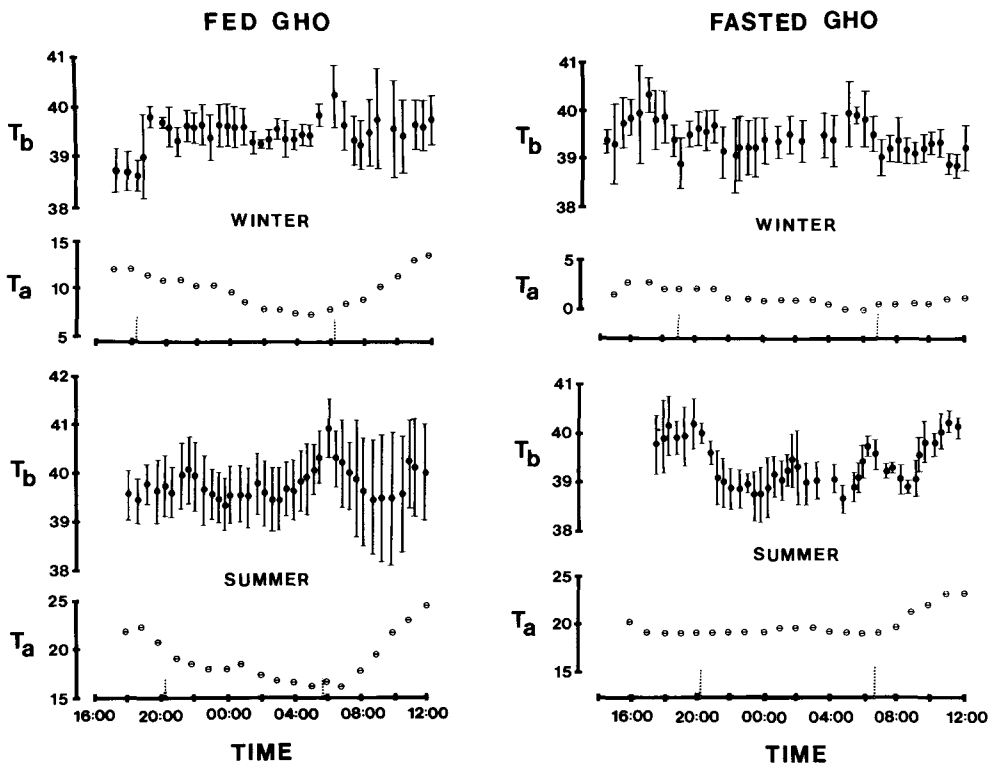

FIGURE 2.   Daily cycle of core T_b ($\bar{x} \pm$ SD, in °C) of four Great Horned Owls fed regularly to maintain body mass constant within $\pm 1\%$ (left) and after being fasted three to four days to achieve a mean loss of body mass of 5% (right). Data are presented for birds tested in late winter (March 1982) and late summer (August 1982). See Figure 1 for explanation of other symbols.

TABLE 1. Body temperatures of fed and fasted Red-tailed Hawks ($n = 5$) during winter (March) and summer (May). Numbers are means and SD (in parentheses) for active (08:00–16:00) and inactive (22:00–02:00) periods.

| | Body temperature (°C) | |
	Fed	Fasted
Winter		
Date of measurement	3 Mar. 1982	31 Mar. 1982
Active period	41.9 (0.7)	41.6 (0.3)
Inactive period	39.9 (0.4)	38.4 (0.6)
24-h mean	41.1 (0.4)	40.4 (0.4)
ΔT_b*	2.0 (0.3)	3.2 (0.5)
Summer		
Date of measurement	9 May 1982	17 May 1982
Active period	41.2 (0.3)	41.3 (0.4)
Inactive period	40.4 (0.4)	39.5 (0.2)
24-h mean	40.9 (0.3)	40.7 (0.3)
ΔT_b*	0.8 (0.3)	1.8 (0.4)

* ΔT_b = (T_b when active) − (T_b when inactive).

TABLE 2. Body temperatures of fed and fasted Great Horned Owls ($n = 4$) during winter and summer. Numbers are means and SD (in parentheses) of all birds during active (± 2 h of sunset and sunrise) and inactive (11:00–15:00 and 22:00–03:00) periods.

| | Body temperature (°C) | |
	Fed	Fasted
Winter		
Date of measurement	18 Mar. 1982	25 Mar. 1982
Active period		
Sunrise	40.0 (0.4)	39.9 (0.2)
Sunset	39.9 (0.2)	40.1 (0.5)
Inactive period		
Day	39.2 (0.4)	39.0 (0.2)
Night	39.3 (0.1)	39.0 (0.2)
24-h mean	39.5 (0.3)	39.6 (0.2)
ΔT_b*	0.8 (0.4)	1.1 (0.4)
Summer		
Date of measurement	7 Aug. 1982	26 Aug. 1982
Active period		
Sunrise	40.7 (0.4)	39.8 (0.3)
Sunset	40.1 (0.3)	40.4 (0.3)
Inactive period		
Day	40.0 (0.3)	39.6 (0.2)
Night	39.3 (0.5)	38.9 (0.4)
24-h mean	39.8 (0.5)	39.5 (0.2)
ΔT_b*	1.4 (0.5)	1.5 (0.3)

* ΔT_b = (highest active T_b) − (lowest inactive T_b).

nificantly influenced by mean T_a($r = -0.65$, $P < 0.002$; Table 3). Nocturnal inactive T_b was the only other measure of T_b that correlated significantly with any measure of T_a (Table 3). In seven trials on three or four Great Horned Owls between October 1981 and August 1982, when mean daily T_as ranged from 1.3 to 25°C, the highest correlation was between mean daily T_b and mean T_a ($r = 0.53$, $P < 0.05$). This correlation was promoted by the higher mean T_b that the owls maintained during the summer when daytime T_a was high; in fact, the only other significant correlations obtained were of maximum T_a and ΔT_b ($r = 0.46$, $P < 0.05$) and of maximum T_a and daytime inactive T_b ($r = 0.48$, $P < 0.05$). To summarize, the daily cycle of T_b of both species was influenced significantly by T_a, but for different reasons. In the hawks, variations in ΔT_b were due primarily to the influence of low T_as on nocturnal (inactive) T_b, whereas in the owls, variations in ΔT_b were dependent on the influence of high T_as on daytime T_b.

A third difference between the two species concerned their thermoregulatory response to a moderate degree of fasting. In both summer and winter, the amplitude of the daily T_b cycle, the nocturnal T_b, and the mean daily T_b of Red-tailed Hawks were all significantly affected by food deprivation (Table 1 and Fig. 1). In the winter, fasted hawks maintained a significantly lower mean daily T_b (paired t-test, $P < 0.01$) and dropped their nocturnal T_b 1.2°C more than when they were fed (paired t-test, $P < 0.005$). In the summer, the hawks maintained similar mean daily T_bs when fasted or fed, but when fasted had nocturnal T_bs that were 1.0°C lower (paired t-test, $P < 0.01$). In both winter and summer, they maintained the

same T_b when active, whether fasted or fed regularly.

Body temperatures of Great Horned Owls were affected to a lesser degree by fasting. The amplitude of the daily T_b cycle of fasted and fed owls was not significantly different (1.1 vs. 0.8°C, respectively, in the winter; and 1.5 vs. 1.4°C, respectively, in the summer; Table 2 and Fig. 2). The T_b differed between active and inactive owls mostly in the summer when they were fasted, but this difference was still much less than that of hawks fasted in the winter. As was true of the hawks, food deprivation resulted in significant decreases in the T_b of the owls during periods of inactivity, compared to the T_b of fed birds under similar conditions (paired t-test, $P < 0.05$ in both winter and summer). Body temperatures did not differ, however, between fed and fasted owls when they were active.

Low T_a and change in body mass had an interactive effect on the nocturnal T_b maintained by the hawks. Nocturnal T_bs were highest in fed birds at warm T_as and decreased as a function of both cold exposure and fasting (Table 1). To determine which of these variables had the greater influence on T_b, we compared the contributions of the four measures of T_a listed above and change in body mass to the total variance in nocturnal T_b, using step-

TABLE 3. Correlations between various measures of the T_b of Red-tailed Hawks and T_a. NT_b = nocturnal (inactive) T_b; ΔT_b = difference between active and inactive T_b; ΔT_a = difference between the daily maximum and minimum T_a. Values in the table are correlation coefficients (r). Those followed by asterisks are significant at the 0.05(*), 0.01(**), 0.005(***), and 0.001(****) levels; others are not statistically significant. Daytime (active) T_b and mean daily T_b were not significantly affected by T_a, and correlation coefficients for them have been omitted from the table.

	ΔT_b	NT_b
Fed hawks (n = 20 observations during 5 trials)		
Maximum daily T_a	−0.35	0.44*
Minimum daily T_a	−0.58**	0.51**
Mean daily T_a	−0.65***	0.49*
ΔT_a	−0.62**	0.15
Fasted hawks (n = 12 observations during 3 trials)		
Maximum daily T_a	−0.73**	0.79***
Minimum daily T_a	−0.82****	0.82****
Mean daily T_a	−0.79***	0.84****
ΔT_a	−0.30	−0.11

FIGURE 3. The relationship between percent reduction of metabolic rate per °C reduction in T_b and body mass for 10 species in which hypothermia was induced by cold stress and/or food deprivation. Species are indicated by number on the figure: 1 = Black-capped Chickadee (Chaplin 1976); 2 = Red-capped Manakin (*Pipra mentalis*; Bucher and Worthington 1982); 3 = Golden-collared Manakin (*Manacus vitellinus*; ibid); 4 = White-crowned Sparrow (*Zonotrichia leucophrys gambelii*; Ketterson and King 1977); 5 = Inca Dove (*Columbina inca*; MacMillen and Trost 1967); 6 = Speckled Mousebird (*Colius striatus*; Bartholomew and Trost 1970); 7 = Monk Parakeet (*Myiopsitta monachus*; Weathers and Caccamise 1978); 8 = Burrowing Owl (Coulombe 1970); 9 = Roadrunner (*Geococcyx californianus*; Ohmart and Lasiewski 1970); 10 = Red-tailed Hawk (Diesel 1983).

wise multiple regression. For eight T_b trials with fed or fasted hawks, we found that change in body mass explained 44% of the variance in nocturnal T_b ($P < 0.0002$) and was the first variable entered in the regression. Minimum daily T_a was the next variable entered and explained an additional 14% of the variance in T_b. None of the other variables that we tested contributed significantly to the regression. Thus, the most important factor that affected the T_b of inactive hawks at night was the change in their body mass induced by fasting.

DISCUSSION

Red-tailed Hawks and Great Horned Owls both exhibited the typical daily rhythm in body temperature associated with the activity-rest cycle of endotherms. However, as we demonstrated in this study, the T_bs maintained by these species were influenced by factors other than just activity. Daily variation in T_b and the nocturnal T_b of the hawks also depended on their feeding activity and low T_a. Daily variation in T_b and level of daytime T_b of the owls depended on feeding activity and on high T_a. We expected some of these responses because they have been reported in other species. The hypothermic response of Red-tailed Hawks to cold stress and food deprivation was, however, surprising.

Elevation of daytime T_b following exposure to heat is a common response in birds, especially owls (Ligon 1969, Coulombe 1970). Hyperthermia facilitates passive heat loss, allows conservation of water, and reduces the metabolic expenses incurred in cooling (Calder and King 1974, Bartholomew 1982). This phys-
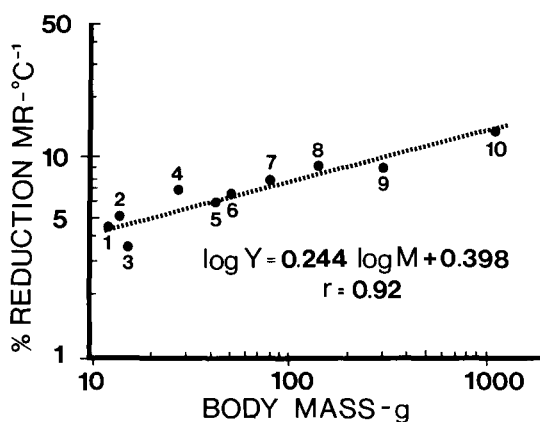
iological response is particularly important to owls during periods when T_as are high and food intake is limited, since these birds obtain their water from their food (Duke et al. 1973). In addition, it probably explains why the daytime inactive T_b and mean daily T_b of fasted Great Horned Owls was higher in the summer than in the winter.

Lowering of T_b following exposure to cold, however, has generally been noted only in small insectivorous or frugivorous passerines (Serventy 1970, Chaplin 1976, Bucher and Worthington 1982), swifts, and hummingbirds (see Calder and King 1974, Hainsworth and Wolf 1978 for reviews). Large-bodied birds such as Red-tailed Hawks should be comparatively resistant to cooling. In addition, the hawks possess excellent insulation against winter cold, rivalling that of the Great Horned Owls (Chaplin and Diesel, unpubl.). Since the two species exhibit similar insulative and thermogenic capacities at low T_as, we were surprised that the T_b maintained by the hawks was influenced by low T_a while that of the owls was not.

All endotherms typically respond to food deprivation by decreasing their T_bs, both during daylight hours and at night. Reduced T_b has been reported in fasting studies of a wide

range of birds, including those with large and small mass, passerines and nonpasserines, insectivores and granivores (reviewed by Ketterson and King 1977), and a few falconiforms (Hatch 1970, Shapiro and Weathers 1981, Larochelle et al. 1982). However, thermoregulation of Red-tailed Hawks was influenced not just by fasting per se, but also by the degree of fasting, i.e., the amount of mass lost during food deprivation. The latter did not affect the thermoregulatory responses of the owls in this study, but does reportedly affect those of American Kestrels (*Falco sparverius*; Shapiro and Weathers 1981). Lowering of body temperature and consequently, metabolism, would be expected to accompany fasting in such a small raptor but not in the Red-tailed Hawk. The energy stored by a bird is proportional to mass$^{1.003}$, but the energy used is proportional to mass$^{0.42}$ (Calder 1975). Consequently, large birds expend less of their stores daily and can therefore tolerate longer periods of fasting by virtue of their size alone.

Why should Red-tailed Hawks respond so to thermal stress and food shortage in the winter? In other studies, we have found that the daily existence costs (i.e., total daily energy expenditure minus that for flight) of Red-tailed Hawks was 21% higher than that of Great Horned Owls (Diesel 1983, Kasparie 1983). This means that hawks would have to consume more prey than owls and would therefore be at an energetic disadvantage compared to owls in the winter, unless they possessed some means of saving energy during periods of high energy demand. Becoming hypothermic at night, and thereby decreasing the metabolic cost of thermoregulation, is one such method of saving energy. How much energy is conserved depends upon body size and the degree of hypothermia that the birds attain, as illustrated in Figure 3. The percent reduction in metabolic rate, per °C reduction in T_b below normal, increases as a function of body size in 10 species from 4.5% °C^{-1} in 12-g Black-capped Chickadees (*Parus atricapillus*; calculated from Chaplin 1976) to 12.6% °C^{-1} in 1,100-g Red-tailed Hawks (Diesel 1983). If the van't Hoff (Q_{10}) effect is solely responsible for this decrease in metabolism and if metabolism decreases linearly with decreases in T_b, the 3.0°C drop in the nocturnal T_b of the hawks represents a substantial 35.5% reduction in their metabolism at night. Thus, small daily variations in the T_b of large species such as Red-tailed Hawks may indicate rather significant changes in their metabolic intensity and should not be considered simply as normal variations related to the birds' activity schedules.

Hypothermia in Red-tailed Hawks in re-

sponse to extreme cold or food deprivation illustrates one way of dealing with the energetically demanding conditions of winter. Great Horned Owls do not use this method, yet conserve some energy by maintaining a comparatively low T_b throughout most of the day and the night. Assuming that reductions in metabolic rate per °C reduction in T_b are the same for hawks and owls of similar size, 1-kg owls expend approximately 20% less energy per day than hawks because their mean T_b is 1.6°C lower. Other researchers have found that owls of several species tolerated extensive mass loss (up to 24% of their initial weight) and extreme low temperatures without changing their T_b or metabolic rate (Ligon 1969, Gessaman 1978). Nevertheless, we suggest that Great Horned Owls *do* attempt to conserve energy during periods of cold stress and food shortage by both physiological and behavioral means. They respond physiologically by lowering their body temperature during inactive periods, and behaviorally by decreasing their activity (Kasparie 1983), thereby prolonging the daily period of the lower (inactive) T_b. Limiting activity, and thus daily energy expenditures, may be a viable option for Great Horned Owls (but not Red-tailed Hawks) because they are a more generalized predator than the hawks, taking a greater variety of prey species and sizes while hunting during both day and night. The extent and priority of adjustments in the physiology (metabolism) and behavior (activity) of owls in response to thermal stress and food deprivation deserve closer scrutiny.

ACKNOWLEDGMENTS

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