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THE RELATIONSHIP OF ENERGETICS OF FALCONIFORM BIRDS TO BODY MASS AND CLIMATE[1]

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Abstract. I measured body temperature and resting metabolic rate as a function of ambient temperature in eleven species of falconiforms. Body temperatures range from 37.1°C to 41.3°C and are independent of body size and climate. Resting metabolic rates correlate with variations in body size and climate. Falconiforms from hot habitats have lower resting metabolic rates than those from temperate habitats. The relationship between the mass-specific metabolic rate (mW g^{-1}) and mass (g) for birds in this order may be expressed as $\dot{H}_m = 34.62W^{-0.36}$. The relationship between the minimal thermal conductance (mW $[g°C]^{-1}$) and mass (g) for falconiforms may be expressed as $C = 2.96W^{-0.45}$.

Key words: Energetics; falconiforms; metabolic rate; temperature regulation; climate; hawk; falcon; eagle; allometry.

INTRODUCTION

Allometric equations are commonly used to predict energetic variables from body mass in studies of falconiform energy budgets. The data used to generate the most commonly used predictive equations for metabolic rate and thermal conductance (Aschoff and Pohl 1970a, Aschoff 1981), however, include measurements from only a few falconiforms. I believe more accurate predictive equations could be generated by increasing the number of falconiforms used in the allometric analysis. I therefore examined the relationships between body mass and resting metabolic rate and mean minimal thermal conductance in eleven falconiforms and considered data from the literature for eleven others. This larger data base and more potent predictive equations also allowed me to examine in falconiforms some of the relationships between climate and resting metabolic rate and minimal thermal conductance, which are critical to an understanding of an animal's physiological response to its environment.

MATERIALS AND METHODS

BIRDS

I made measurements on the following falconiforms: American Kestrel (*Falco sparverius*), three females; Prairie Falcon (*F. mexicanus*), one immature male; Yellow-throated Caracara (*Daptrius ater*), two males; Sharp-shinned Hawk (*Accipiter striatus*), one male; Cooper's Hawk (*A. cooperii*), one immature female; Red-shouldered Hawk (*Buteo lineatus*), two females, one sex undetermined (probably a male); Red-tailed Hawk (*B. jamaicensis*), two females; Harris' Hawk (*Parabuteo unicinctus*), one male; Tawny Eagle (*Aquila rapax*), one male; Mississippi Kite (*Ictinia mississippiensis*), one immature, sex undetermined; and Osprey (*Pandion haliaetus*), three sex undetermined. These birds were all long-term captives. The American Kestrels, Yellow-throated Caracaras, Red-shouldered Hawks, Red-tailed Hawks, Sharp-shinned Hawk, Harris' Hawk, Tawny Eagle, and Ospreys were from the collection of the Santa Fe Community College Teaching Zoo, Gainesville, Florida, where they were maintained outdoors under natural conditions of temperature and photoperiod. A Gainesville falconer loaned the Mississippi Kite to me. I obtained the Cooper's Hawk and the Prairie Falcon from the University of Minnesota Raptor Rehabilitation Program, St. Paul, Minnesota. I was unable to determine the sex of some of the immature birds and the Ospreys, and I could not obtain permission to sex the birds by laparotomy. I was also unable to determine the geographic origins of any of these birds other than the Mississippi Kite and the Ospreys, which were from Florida.

I kept all of the birds that I studied in an indoor aviary at approximately 25°C with an approximate 12L:12D photoperiod for one to two months during which time I made the metabolic rate measurements. I fed the falconiforms rats, mice, and an artificial raptor diet. I conducted my experiments throughout the year but do not believe that the seasonal variation in resting metabolic rate reported by Weathers and Caccamise (1978) for small (<100 g) birds significantly affected my analyses; almost all of the species that I studied had masses over 100 g, and these authors reported only small seasonal variations in birds

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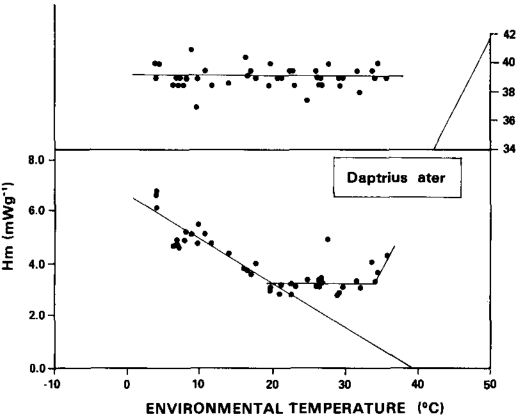

FIGURE 1. Relation of body temperature and rate of metabolism to environmental temperature in *Daptrius ater.* Each point represents the value from a single steady-state experimental measurement. Data from two individuals are presented.

of this size. Furthermore, my analysis of the energetic variables of falconiforms is for the most part restricted to species from tropical or desert regions. Unlike cold-climate forms, these species presumably show no significant seasonal variations in resting metabolic rate (Weathers 1979).

The metabolic rates of birds held in aviaries for up to a year are comparable to those of wild birds exposed to the same temperature and photoperiod (Weathers et al. 1983). In fact, my metabolic rate data for captive American Kestrels and Red-tailed Hawks compares favorably with data for individuals trapped in the wild by Hayes and Gessaman (1980). I believe my use of long-term captive birds is therefore reasonable, and for the most part unavoidable, since permission to trap wild raptors for physiological studies is difficult to obtain. I therefore restricted this study to species available in captivity, and this restriction prevented my measuring any arctic or subarctic species.

METABOLIC RATES

I measured oxygen consumption ($\dot{V}_{O_2}$) in an open-circuit system using either Beckman Paramagnetic Oxygen Analyzers (Models G2 and F3) or an Applied Electrochemistry Oxygen Analyzer (Model S3A). Before measuring

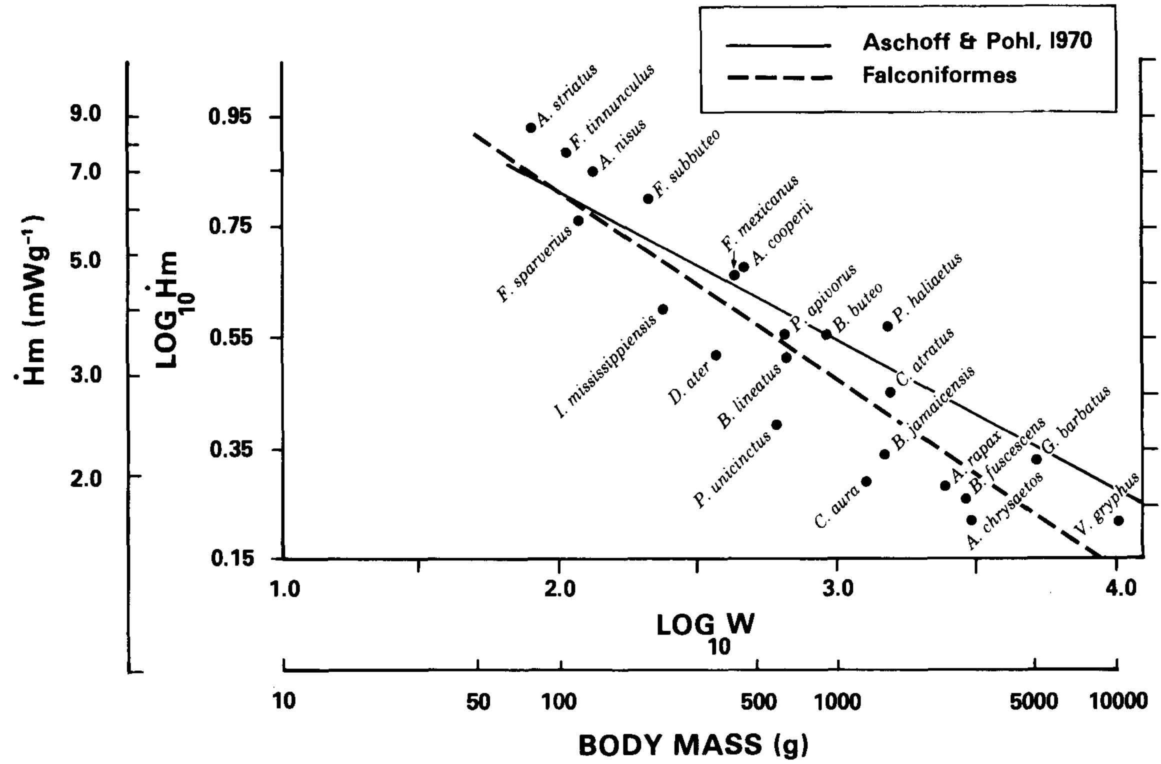

FIGURE 2. The relationship of the resting rate of metabolism to body mass in falconiforms. Each point represents the mean value for metabolic rate within the thermoneutral zone. Mean curves for non-passerine birds during their resting phase (Aschoff and Pohl 1970*a*) and falconiforms (this study) are indicated. Sources for data not from this study are: Eurasian Kestral (*Falco tinnunculus*) and Golden Eagle (*Aquila chrysaetos*), Giaja and Males 1928; Northern Hobby (*Falco subbuteo*), European Sparrow Hawk (*Accipiter nisus*), Gray Eagle Buzzard (*Buteo fuscescens*), Lammergeier (*Gypaetus barbatus*) and Honey Buzzard (*Pernis apivorus*), Kendeigh et al. 1977; Common Buzzard (*Buteo buteo*), Jud and Kulzer 1975; Andean Condor (*Vultur gryphus*), Benedict and Fox 1927; Turkey Vulture (*Cathartes aura*) and Black Vulture (*Coragyps atratus*), Enger 1957.

TABLE 1. Parameters of energetics for selected falconiforms.

Species	n[a]	Sex[b]	Mass (g)	$\dot{H}_m$ (mW g^{-1})	% of regression[c]	C (mW[g°C]$^{-1}$)	% of regression[d]	T_b (°C)	T_l (°C)
Falco sparverius	3	F	116.0	5.706	91.2	0.346	99.2	40.2	23.0
F. mexicanus	1	M	430.0	4.518	115.8	0.290	150.0	40.8	25.4
Daptrius ater	2	M	362.0	3.313	79.8	0.173	82.8	39.1	19.5
Accipiter striatus	1	M	83.0	8.428	119.5	0.424	104.6	39.5	23.7
A. cooperii	1	F	452.0	4.708	122.8	—	—	41.3	—
Buteo lineatus	3	2F/1?	658.0	3.207	95.8	0.095	59.4	40.3	11.5
B. jamaicensis	2	F	1,475.0	2.153	86.0	0.084	75.4	39.6	14.5
Parabuteo unicinctus	1	M	572.0	2.460	69.9	0.123	72.2	39.0	18.0
Aquila rapax	1	M	2,398.0	1.885	89.7	0.073	81.3	38.2	9.5
Ictinia mississippiensis	1	—	232.0	3.938	80.8	0.290	113.6	37.1	23.7
Pandion haliaetus	3	—	1,495.0	3.693	148.2	0.190	171.9	39.0	22.6

[a] Sample size.
[b] M = male; F = female; see Methods.
[c] Calculated from the relation mW g^{-1} = $34.62W^{-0.36}$ from this study.
[d] Calculated from the relation mW (g°C)$^{-1}$ = $2.96W^{-0.45}$ from this study.

the flow rate, I removed carbon dioxide and water from the air stream by using soda lime and silica gel after the air exited the animal chamber. For each experiment I selected a flow rate between 0.200 and 5.000 l min^{-1} (STPD) according to animal size and metabolic chamber size. I calculated the rate of oxygen consumption from the equation

$$\dot{V}_{O_2} = \dot{V}_E(F_{IO_2} - F_{EO_2}/1 - F_{IO_2}),$$

(derived from Hill 1972) and calculated metabolic heat production ($\dot{H}_m$) from $\dot{V}_{O_2}$ by assuming 20.08 kJ of heat produced per liter of O_2 consumed (Hayworth and Weathers 1984). I confined birds weighing less than 600 g in a chamber of approximately five liters volume that was submerged in a thermoregulated water bath. I held larger birds in a 44-liter aluminum chamber with an insulated water jacket through which water of the desired temperature circulated. I measured temperatures within the chambers with either a mercury thermometer

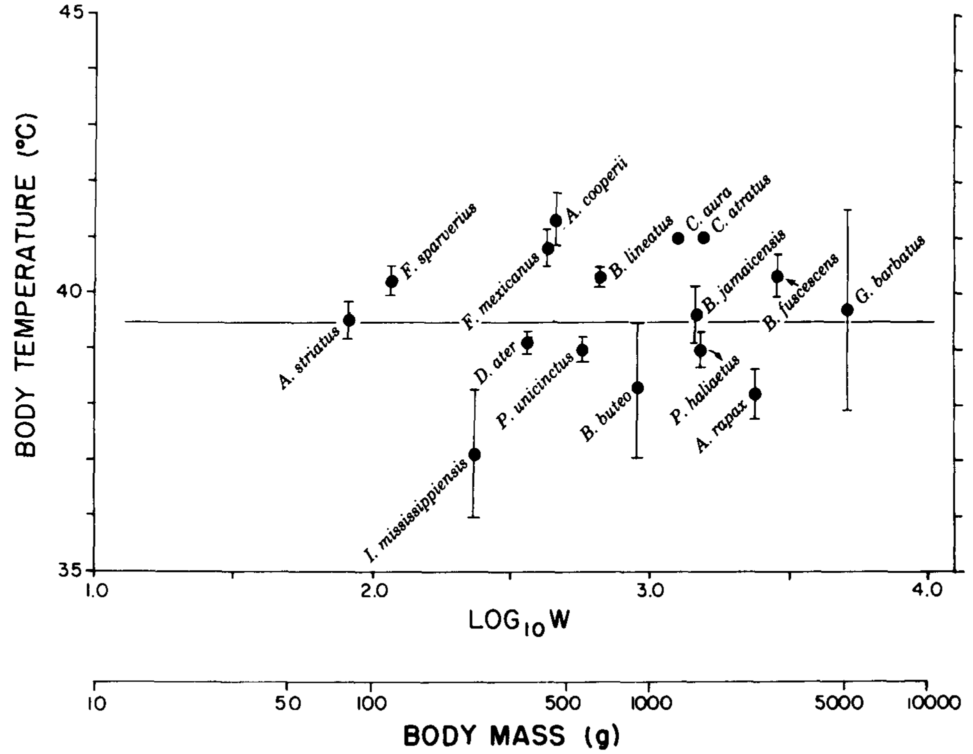

FIGURE 3. The relationship of body temperature to body mass in falconiforms. Each point represents the mean value for body temperature measured within the thermoneutral zone. Vertical lines indicate ±2 SE where available. Sources as in Figure 2.

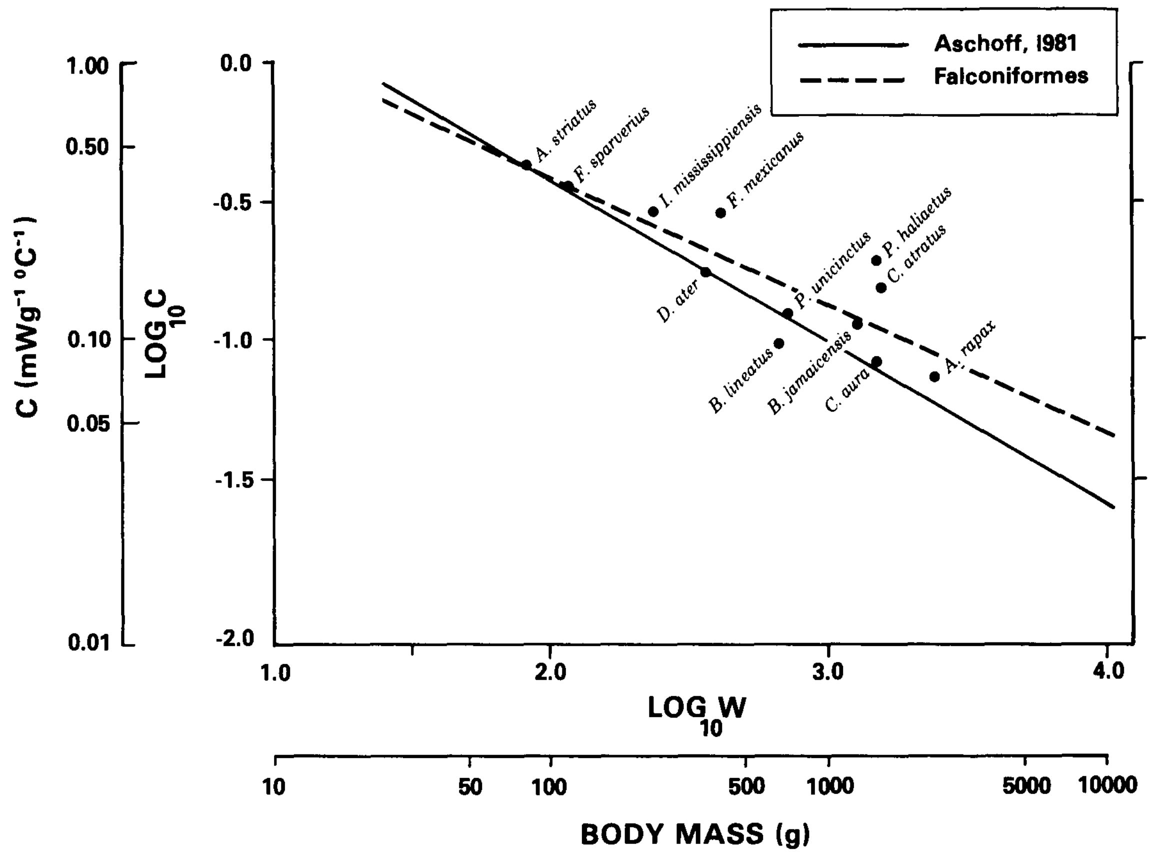

FIGURE 4. The relationship of thermal conductance to body mass in falconiforms. Mean curves for non-passerine birds during their resting phase (Aschoff 1981) and falconiforms (this study) are indicated. Sources as in Figure 2.

or a thermistor probe (Yellow Springs Instruments). For the purpose of this study, I defined "resting metabolic rate" as the mean of the metabolic heat production measured within the thermoneutral zone while an animal was quiet at night (Aschoff and Pohl 1970a, b). I did not feed these birds from 12 to 72 hours before the experiments, depending on their mass. Measurements were confined therefore to animals in the post-absorptive condition. I made all these experimental measurements between dusk and dawn and made multiple measurements of each individual over the range of temperatures tested. I ended an experiment when a bird was calm and its oxygen consumption was judged to be in a steady state. I weighed the birds to the nearest 0.5 g immediately after each experiment.

BODY TEMPERATURE

I measured body temperatures (T_b) either in the cloaca with a thermistor probe or in the proventriculus with a radio telemeter (Minimitter Company, Sun River, Oregon) that was calibrated in a temperature-controlled water bath and was then force-fed to birds before the experiment. I measured T_b with the thermistor probe immediately after each experiment and periodically throughout the experiment with the radio telemeter.

THERMAL CONDUCTANCE

I estimated mean minimal thermal conductance (C) by calculating thermal conductance values for each value of metabolic rate below the estimated lower critical temperature, according to the formula

$$C = \frac{\dot{H}_m}{(T_b - T_a)},$$

where C is the thermal conductance (mW $[g°C]^{-1}$), $\dot{H}_m$ is the rate of metabolic heat production (mW g^{-1}), T_b is the body temperature (°C), and T_a is the environmental temperature (°C; McNab 1980). I drew a graph on which the mean thermal conductance line intersected the mean body temperature line at a metabolic rate equal to zero and with a slope equal to C (Fig. 1). I then determined the lower limit of thermoneutrality from the intersection of the line representing the mean resting metabolic rate and the line representing minimal thermal conductance. Since I did not measure evaporative water loss, these estimates are of "wet" conductance.

CLIMATE

I classified falconiforms by specific habitat according to information from Brown and Amadon (1968) and Bock and Lepthien (1976).

RESULTS

METABOLIC RATES

An analysis of covariance indicated a significant difference ($P < 0.01$) between the slope of the falconiform line and that shown by Aschoff and Pohl (1970a; Fig. 2). The relationship between body mass and resting metabolic rate for falconiforms from this study may be expressed as

$$\dot{H}_m = 34.62W^{-0.36}$$

($r = 0.91$, $S_b = 0.248$, $S_{y \cdot x} = 0.09$, $n = 22$), where $\dot{H}_m$ is the metabolic heat production (mW g^{-1}) and W is mass (g).

BODY TEMPERATURE

Body temperatures of the birds tested fell within a range of 37.1°C to 41.3°C ($\bar{x} = 39.5$°C, SE = 0.292, $n = 16$) and were independent of body size and climate (Table 1, Fig. 3).

THERMAL CONDUCTANCE

An analysis of covariance indicated a significant difference ($P < 0.05$) between the slope of the falconiform line and that shown by Aschoff (1981; Fig. 4). The relationship between body mass and minimal thermal conductance for falconiforms from this study may be expressed as

$$C = 2.96W^{-0.45}$$

($r = 0.83$, $S_b = 0.230$, $S_{y \cdot x} = 0.147$), where C is the minimal thermal conductance (mW $[g°C]^{-1}$) and W is mass (g).

DISCUSSION

METABOLIC RATE

I have generated a predictive equation that describes the relationship between mass and resting metabolic rate and is a better predictor for falconiforms than the non-passerine equation of Aschoff and Pohl (1970a). Aschoff and Pohl's (1970a) relationship for non-passerine birds during their normal sleep period may be expressed as

$$\dot{H}_m = 22.42W^{-0.27},$$

where $\dot{H}_m$ is the resting metabolic heat production (mW g^{-1}) and W is mass (g). The relationship of metabolic rate to mass of falconiforms does not conform well to this equation, perhaps because of the narrow phylogenetic base from which Aschoff and Pohl derived their equation (four orders, seven species, no falconiforms). Zar (1969) derived an expression for the metabolism vs. body weight relationship for falconiforms but based his equation on only five data points and, by his own admission, this equation is not very reliable.

BODY TEMPERATURE

My data indicate that variations in body temperature do not correlate with climate in falconiforms from hot habitats. This conclusion supports those of Scholander et al. (1950a, b) and Dawson and Schmidt-Nielsen (1964) for other birds.

CLIMATE AND RESTING RATE OF METABOLISM

The resting metabolic rates of falconiforms from hot habitats are lower than expected from rates based on mass alone. The results of a two-tailed Mann-Whitney *U*-test indicate a significant difference ($P < 0.05$) between the average metabolic rate of the five falconiforms that occur almost exclusively in hot environments (the Yellow-throated Caracara, Tawny Eagle, Harris' Hawk, Gray Eagle Buzzard [*Buteo frutescens*], and the Black Vulture [*Coragyps atratus*; $\bar{x} = 88.9$% of expected, SE = 7.33, $n = 5$]) and that of the remaining species ($\bar{x} = 110.0$% of expected, SE = 5.13, $n = 17$). Because I could not obtain specimens from arctic species, I was unable to test whether the metabolic rates of falconiforms from cold habitats are higher than those rates predicted from mass alone. My results for falconiforms from hot habitats are therefore in agreement with the conclusions of Kendeigh and Blem (1974), Dawson and Bennett (1973), and Weathers (1979) that the resting metabolic rates of birds from warm climates tend to be lower than those rates expected from mass alone, an adaptation that presumably helps prevent excessive heat stress in these birds.

THERMAL CONDUCTANCE

Although I expected falconiforms from hot habitats to have high minimal thermal conductances, the only exclusively tropical falconiform in this study, the Yellow-throated Caracara, had a thermal conductance of only 82.8% of the value expected. The Harris' Hawk and the Tawny Eagle, both from predominantly hot habitats, have minimal thermal conductances of 72.2% and 81.3% of the expected values, respectively. My results contradict the conclusions of Scholander et al. (1950a, b), who reported high minimal thermal conductances in the tropical birds that they studied. The somewhat low resting metabolic rates of these three species may provide adequate adaptation to climate. The Osprey (Florida population), a falconiform from a hot habitat, has a high minimal thermal conductance of 171.9% of the value expected. The Osprey also has a high resting metabolic rate and this, combined with its living in a hot habitat, may require a high minimal thermal conductance to avoid heat stress. Whether the northern populations of the Osprey have the same resting metabolic rates and minimal thermal conductances as the southern birds that I measured is not known.

A factor complicating my analysis of climatic adaptations in energetic variables of falconiforms is that, while many of the species that I analyzed may be found in hot habitats, they are found in temperate habitats as well. Additionally, some of the temperate species that I used in this study migrate to the tropics for part of the year, where they are exposed to the climatic stresses of a hot environment. Additional data on resting metabolic rate and minimal thermal conductance of falconiforms from either exclusively hot habitats or exclusively cold habitats are necessary before a more definitive statement on the relation of energetic variables and climate can be made.

In conclusion, I have demonstrated that a better estimate of resting metabolic rate and minimal thermal conductance based on mass for falconiforms can be obtained by using the allometric equations that I have derived in this study rather than the general expressions for non-passerines. I have also shown that, at least for species from predominantly hot habitats, the energetic variables of falconiforms exhibit the climatic correlations found in other birds by Weathers (1979) and others.

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