FALCON TEMPERATURE REGULATION

James A. Mosher[1] and Clayton M. White

Department of Zoology, Brigham Young University, Provo, Utah 84601 USA

Abstract.—We measured tarsal and body temperatures of four species of large falcons in relation to rising ambient temperature and found that the tarsus has an apparent thermoregulatory function. Statistical efforts to separate the birds into ecological or plumage types yielded mixed results. An index of tarsal surface area per unit body weight was correlated with the temperature regimens of the birds, with species from the hottest climates having the greatest tarsal index values. *Received 28 July 1975, accepted 25 March 1977.*

In 1957, Bartholomew and Cade asserted, "Despite the number of falcons which have been trained and kept in captivity, remarkably few quantitative data are available on even the most obvious aspects of their physiology" (1957, Wilson Bull. 69: 149). They examined the role of the tarsometatarsus in temperature regulation and presented evidence for a countercurrent vascular mechanism in the American Kestrel (*Falco sparverius*). Their conclusions led us to investigate the same mechanism in larger falcons.

The genus *Falco* is virtually worldwide in distribution and occupies a wide range of thermal habitats. The existence of closely related forms adapted to varied environments presents an opportunity to examine adaptations of the tarsometatarsus to different thermal environments. Four species of the genus *Falco* were selected for study; *F. peregrinus* (Peregrine Falcon), *F. mexicanus* (Prairie Falcon), *F. jugger* (Lugger Falcon), and *F. biarmicus* (Lanner Falcon). They are of comparable size and are subject to distinctly different climates in their normal distribution. *Falco peregrinus tundrius* is a migratory population, breeding in subarctic regions of North America and wintering in South America. It is exposed to a moderate range of temperatures from about 25°C to −5°C. *Falco p. pealei* is a maritime, subarctic to north temperate year-round resident and is exposed to a narrower range of cold temperature from about 12°C to −5°C. *Falco mexicanus* breeds and winters over a wide range of thermal environments from arid northern Mexico to temperate Canada—a temperature range of about 42°C to −30°C. *Falco jugger* is restricted to the temperate environment of the northern India region and *Falco biarmicus* is found in arid Africa and the Middle East. Besides differences in habitat, *Falco peregrinus* differs from the other three species in plumage quality. Peregrines have a "hard, brittle" plumage, whereas the others have "soft, flexible" plumage.

Our objective was to determine whether or not differences exist in the tarsal thermoregulatory mechanism related to the observed ecological and plumage differences.

METHODS

The birds used in this study were all captive falcons varying in degree of tameness. The two Prairie Falcons were falconers' trained birds that were not being flown at the time of the study. They were all housed in free flight enclosures in Provo, Utah (about 40°N, 112°W), exposed to ambient temperature conditions and photoperiod. The birds were maintained on a diet of cockerels and quail (*Coturnix coturnix*). The data were collected between 14 November and 5 March.
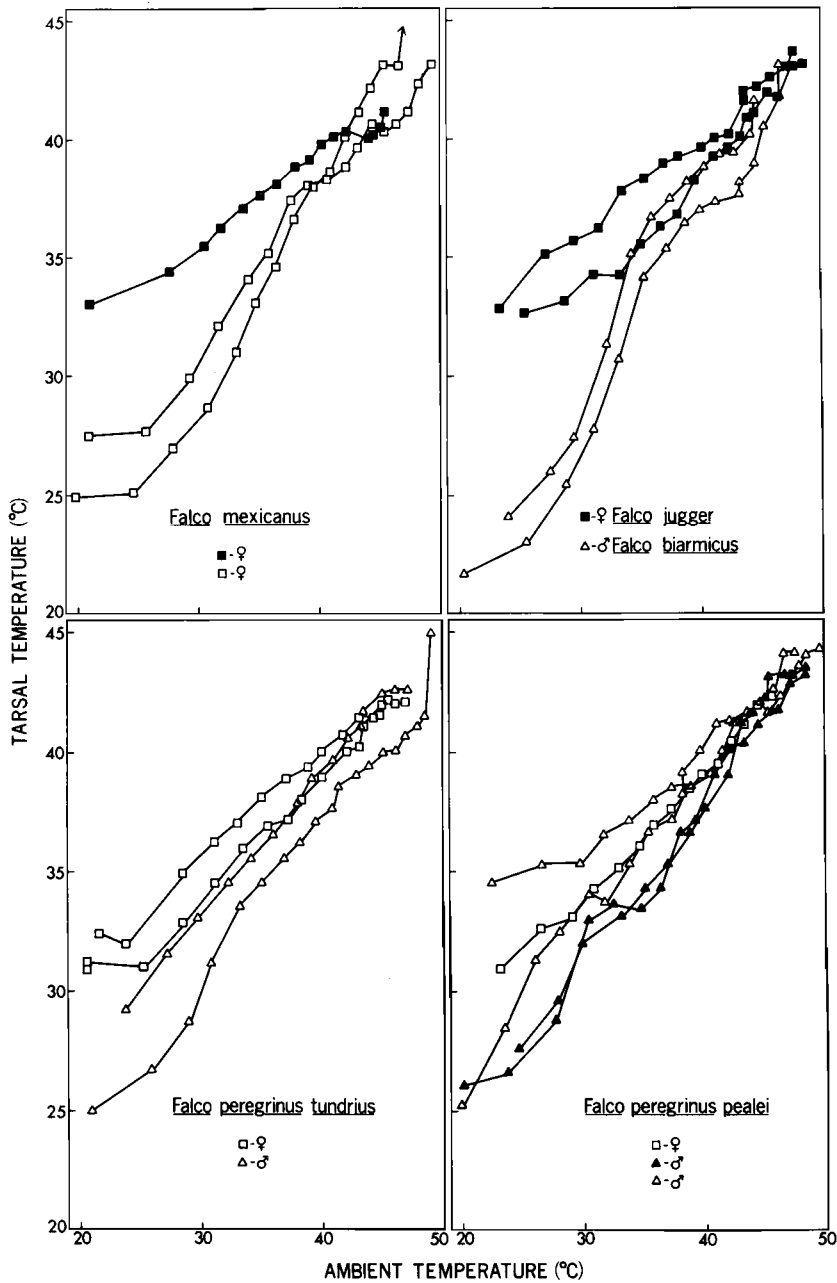

Fig. 1.   Response of tarsal temperatures of large falcons to increasing ambient temperature.

Cloacal, tarsal, and ambient temperatures were read to the nearest 0.1°C on a YSI multichannel telethermometer. One flexible YSI thermistor probe was taped (masking tape overlaid with furnace tape) to the midsection of the bare tarsus, and one was placed, following sterilization with ethanol and lubrication with petroleum jelly, approximately 2 cm through the cloaca into the colon. The third temperature probe was placed within 30 cm of the bird at perch level. The birds were tethered in the middle of a 30-cm perch and were free to move its length.

The birds were placed in a temperature-controlled room (2.24 m wide × 2.57 m long × 2.44 m high) on
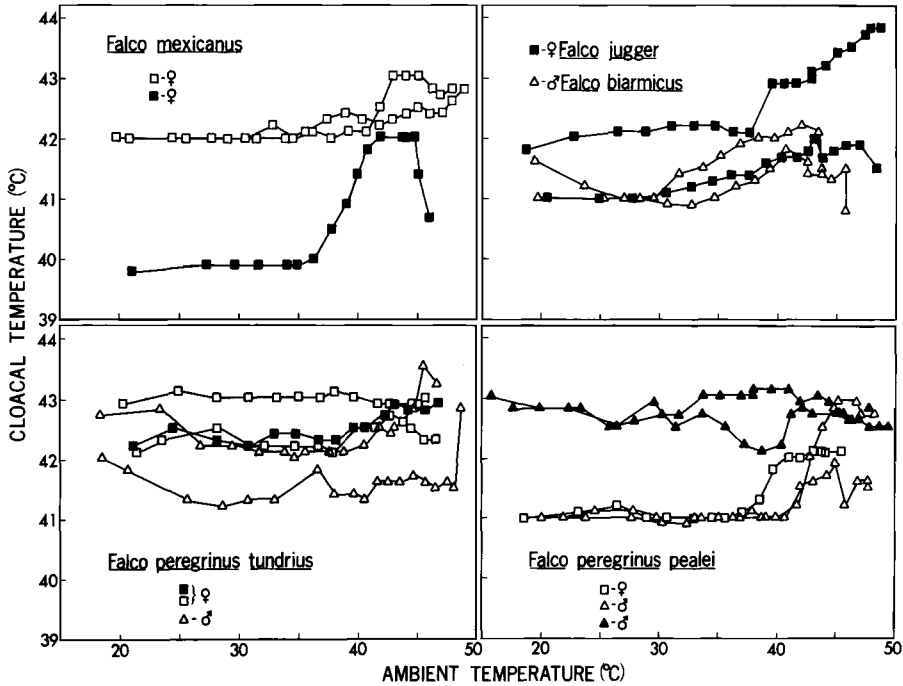
Fig. 2. Response of cloacal temperatures of large falcons to increasing ambient temperature.

a perch about 15 cm above the floor at an initial ambient temperature of 20°C ± 2°C. After ½ to 1 h (when tarsal and cloacal temperatures stabilized) the temperature control was reset to 50°C. The temperature increase from 20°C to 50°C required about 1 h and was linear. Relative humidity was not controlled but did not exceed 40%.

RESULTS

The results of our tests are displayed in Figs. 1 and 2. The relationship between tarsal temperature (T_t) and ambient temperature (T_a) was essentially linear over the

TABLE 1. Results of regression analyses of tarsal temperatures on ambient temperature for several large falcons

| Species | Sex | Regression | | |
		Slope	Intercept	r^2
Falco peregrinus pealei	♂	0.70	9.88	0.98
F. p. pealei	♀	0.53	17.96	0.97
F. p. pealei	♂	0.52	18.71	0.94
F. p. pealei	♀	0.73	6.53	0.98
F. p. tundrius	♂	0.62	13.02	0.90
F. p. tundrius	♀	0.44	21.82	0.94
F. jugger	♀	0.49	19.42	0.89
F. biarmicus	♂	0.87	2.39	0.92
F. mexicanus	♀	0.55	7.91	0.95
F. mexicanus	♀	0.45	20.87	0.91
Ecological type 1[a]		0.57	15.90	0.84
Ecological type 2		0.63	13.19	0.78
Ecological type 3		0.58	14.94	0.85
Ecological type 4		0.51	18.31	0.83
Plumage type 1[b]		0.54	16.89	0.83
Plumage type 2		0.61	13.97	0.81

[a] Ecological type 1 = *F. p. pealei*, 2 = *F. jugger* and *F. biarmicus*, 3 = *F. mexicanus*, and 4 = *F. p. tundrius*.
[b] Plumage type 1 = *F. peregrinus*; 2 = *F. jugger, F. biarmicus* and *F. mexicanus*.

TABLE 2. Tarsal index values for several large falcons

Species	Sex	Body weight[a] (g)	Tarsal surface[b] area (mm²)	Index[c] (cm²·g⁻¹)
Falco peregrinus pealei	♀	1,152	832	0.723
F. p. pealei	♂	730	634	0.868
F. p. anatum	♀	991	813	0.820
F. p. anatum	♂	639	556	0.871
F. p. tundrius	♀	993	809	0.814
F. p. tundrius	♂	612	559	0.913
F. jugger	♀	745	552	0.741
F. mexicanus	♀	759	817	1.076
F. mexicanus	♂	479	605	1.262
F. biarmicus	♂	489	657	1.345

[a] Body weights were taken from specimens in the Brigham Young University collection and from Brown and Amadon (1968, Eagles, hawks and falcons of the world, New York, McGraw-Hill Co.), and represent an average.

[b] Tarsal surface area was computed as the surface area of a cylinder using the averages of longest and shortest tarsal diameters from both tarsi and the average of the ventral and dorsal lengths from both tarsi. Measurements were taken from study skins in the Brigham Young University Collection.

[c] The tarsal index is tarsal surface area divided by body weight.

range of our tests, and the results of the analyses are presented in Table 1. The response of cloacal temperatures (T_c) to increasing T_a was variable and depended largely on the initial T_c.

When individual birds are grouped by ecological type, correlation coefficients decline and no significant differences in the slopes of the T_t vs. T_a regressions can be detected. However, when grouped by plumage type the slopes of this relationship differ significantly ($\propto$ = 0.025). The T_t of Peregrines appears to increase more slowly as T_a increases when compared with the Lugger, Lanner and Prairie falcon group.

Table 2 summarizes the data on tarsal surface area and tarsal index (tarsal surface area per gram of body weight).

DISCUSSION

The animals we studied are subject to quite different thermal environments, which vary seasonally as well as geographically. Being endothermic, they must have adaptive mechanisms for maintaining a stable internal body temperature. Bartholomew and Cade (ibid.) established that the bare tarsus is an effective heat exchanger in the Falconiformes. Based on this earlier work we hypothesized that there might be differences in this tarsal mechanism related to differences in environmental conditions. These differences could be in the extent of the bare tarsus, the control of circulation to the tarsus, or a combination of both. They might be adapted to extreme hot or cold environments or to a broad range of temperature.

Theoretically, if the bare tarsus was always maintained at the ambient temperature the bird would neither gain nor lose heat via that avenue. Several evolutionary adaptations are possible. If subject to extreme cold, it would be adaptive to be able to reduce tarsal temperature as low as physiologically possible (near freezing, Paynter 1974, Publ. Nuttall Ornithol. Club No. 15) and/or reduce the surface area of the bare tarsus by shortening or by increasing insulation. With the strong selective pressures on the tarsus related to prey capture, modifying tarsal dimensions seems improbable. In environments in which T_a exceeds body temperature (T_b), the tarsus cannot function in heat dissipation but rather heat gain from the environment is inevitable. A reduction in bare tarsal dimension and reduction of peripheral circulation could minimize this heat gain. If reduced circulation takes place, the T_t would passively follow T_a but transfer of heat from the tarsus to body core would be inhibited.

At the upper temperature extremes it would be advantageous to be able to permit body temperature to rise in order to reduce the gradient between T_b and T_a. Respiratory water loss associated with panting is probably the most important avenue of heat loss at high ambient temperatures (Bartholomew and Cade, ibid.). We have only a few observations of the onset of panting for the birds we tested. However, these observations suggest a problem with humidity and respiratory water loss. Some preliminary test runs were made with the birds placed inside a plywood box ($42 \times 42 \times 58$ cm) so that we could simultaneously measure oxygen consumption. The flow rate was about 2.5 l/min. We discontinued this procedure when it became apparent that above 30°C humidity was very high (the observation window showed condensation) and the birds were experiencing heat stress. During these preliminary tests the birds began to pant between 25°C and 35°C, whereas in the following tests with very low humidity panting did not begin until ambient temperature reached about 40°C to 45°C. Bartholomew and Cade (ibid.) also observed the onset of panting at these higher temperatures with low himidity. These observations further demonstrate the importance of respiratory water loss in heat dissipation. Under conditions of high humidity, respiratory water loss is inhibited and at ambient temperatures above body temperature there is no other avenue for heat loss.

As can be seen in Fig. 2, T_c increased markedly as T_a approached T_c with only two exceptions and in both these cases (*F. p. pealei* and *F. p. tundrius*) initial T_c was very high. The declines observed at even high T_a were probably due to increased respiratory rates (panting) with the consequent heat loss via evaporation. Continued high T_a would inevitably lead to dehydration and a fatal T_b increase.

Cloacal temperature responses to increasing T_a were highly variable; however, both *F. lugger* and *F. biarmicus* appear to respond sooner and more gradually than either *F. peregrinus* or *F. mexicanus*.

We conclude that the tarsal thermoregulatory mechanism first described for raptors by Bartholomew and Cade (ibid.) is probably universal among Falconiformes, and varies only slightly if at all in adaptive efficiency. Although our analyses showed some statistical differences, the biological meaning remains in doubt. Extent of bare tarsus shows good correlation with thermal habitat, but may be confounded by prey capturing adaptations. The effect of humidity as it relates to respiratory water loss needs further attention.