

AN ANALYSIS OF THE BODY TEMPERATURES OF BIRDS

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Recently there has been much work done on the energetics of homoiotherms. One parameter of energetics, body temperature, is relatively easy to measure and, thus, has been often studied. An analysis of the body temperatures of mammals was proposed by McNab (1966), but none has been made of bird temperatures. The purpose of this report is to analyze the factors responsible for the level of body temperatures of birds.

Two conclusions on bird temperatures can be drawn from the available data (table 1): (1) they are almost always above those of mammals, and (2) they are low in ratites and penguins, high in passerines, and intermediate in other birds. These differences have no obvious explanation.

Usually the difference in body temperature between mammals and birds is ignored. If an explanation is offered, it generally consists of the correlation that flying birds have higher body temperatures than mammals or flightless birds. Why this should be, however, is not clear, since the low body temperatures of temperate-zone bats indicate that a high resting body temperature is not a rigid requirement for flight. Rodbard (1950) suggested that small birds have higher body temperatures than small mammals because feathers are better insulators than hair; this suggestion will be examined later.

The correlation of body temperature with taxonomic group is either ignored or the suggestion is made that it represents the evolutionary attainment of good thermoregulation (Sutherland, 1899; Wetmore, 1921). This explanation disregards the correlation of body temperature with weight. Large birds tend to have low body temperatures and small birds, high body temperatures (Rodbard, 1950); this correlation, in itself, requires an explanation, since there is apparently no dependence of body temperature on weight in mammals (Morrison and Ryser, 1952), in spite of a proposal to that effect by Rodbard (1950).

ANALYSIS

What factors determine the level of body temperature in homoiotherms? The level of body temperature in some 30 species of mammals can be predicted ($r = 0.92$) by the equation

$$T_b = 4.7(M/C) + 32.2 \quad (1),$$

where M is the basal rate of metabolism and C is the rate of heat loss (or conductance), when both parameters are expressed relative (in per cent) to the values expected for a mammal of a given weight (McNab, 1966). Thus, body temperature in mammals does not appear to be a character that can show an adaptation to the environment independent of the behavior of M and C .

A question immediately arises as to whether body temperature in birds is determined as it is in mammals. Unfortunately, only birds in the limited weight range of 10 to 100 g. have been extensively studied with respect to their energetics. Therefore, one cannot use empirically determined values for M and C , but must rely on estimating them from a general relation to weight that ignores variations due to factors other than weight. One would expect, then, that the ability to predict T_b in birds would be less successful than it is in mammals.

In this paper the energetics of birds will be compared with that of mammals. The relationship between the basal rate of metabolism and weight is given for mammals by

$$M_m \text{ (kcal./day)} = 70W^{0.75} \quad (2),$$

where W is body weight in kilograms (Kleiber, 1961). Rewritten, this relationship becomes

$$M_m/W \text{ (cal./g.-hr.)} = 16.4W^{-0.25} \quad (3),$$

where W is in grams. Conductance is given by

$$C_m \text{ (cal./g.-hr.-}^\circ\text{C.)} = 4.8W^{-0.50} \quad (4),$$

(Morrison and Ryser, 1951).

King and Farner (1961) give two functions that relate the basal rate of metabolism to weight in birds. One of these is similar to that of mammals. But increasing evidence on small birds (*e.g.*, King, 1964; Lasiewski *et al.*, 1964) suggests that this equation is not appropriate. Their second equation, which is used in this paper, appears to be most appropriate for the entire weight range:

$$M_b \text{ (kcal./day)} = 80.1W^{0.66} \quad (5),$$

or

$$M_b/W \text{ (cal./g.-hr.)} = 35.0W^{-0.34} \quad (6).$$

Thus, large birds and large mammals of the same weight have approximately the same rates of heat production, but small birds have greater rates of heat production than small mammals of the same weight.

Inspection of the data assembled by Lasiewski *et al.* (1964) on the relationship of conductance to body weight in birds suggests that C_b is about 70 per cent that of mammals of the same weight. Feathers may be better insulators than hair because of greater overlap, thus isolating air pockets more effectively from the atmosphere. Yet there is only a limited weight range, from 20 to 200 g., over which the difference between the insulating properties of feathers and hair is shown. The rate of heat loss is influenced by at least two factors: (1) the quality of the fur or feather coat and (2) the ratio of surface to volume. The insulative increment due to feathers decreases in importance with an increase in weight as a result of the decrease in the surface-to-volume ratio. Consequently, large birds have conductances similar to large mammals. On the other hand, in very small species the effectiveness of the feather coat is reduced to that of hair, because of its reduced thickness.

Therefore, the body temperatures of birds, if determined as they are in mammals, should be given by

$$\begin{aligned} T_b &= 4.7 (M_b/M_m) (C_m/C_b) + 32.2 \\ &= 4.7 \left(\frac{35.0W^{-0.34}}{16.4W^{-0.25}} \right) \left(\frac{1.0}{0.7} \right) + 32.2 \\ &= 14.3W^{-0.09} + 32.2 \end{aligned} \quad (7).$$

DISCUSSION

Data on body temperatures and weights are summarized in table 1 and figure 1. Equation (7) is illustrated graphically in figure 1. Clearly, this equation fits the data reasonably well for weights greater than 30 g., both in terms of the differential dT_b/dW and the position of the curve on the y-axis (T_b). This fit is remarkable when

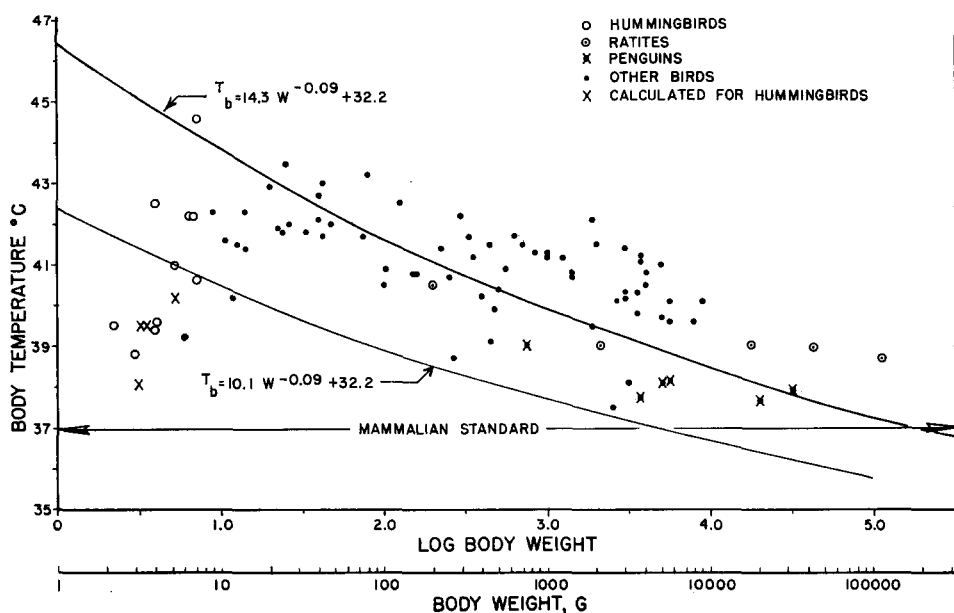


Figure 1. The relationship of body temperature to weight in birds. The equations are derived in the text.

it is remembered that the equation was derived from relative rates of heat production and loss, rather than from body temperatures. Still, there is a marked variation about the curve at weights greater than 30 g. and a deviation from the curve in small species. An explanation for these phenomena will be sought.

The two factors that determine body temperature, M and C, are capable of modification to suit the requirements of the environment (McNab, 1965). A marked modification of M or C would alter T_b . Thus, the data of Enger (1957) indicated that the Turkey Vulture (*Carthartes aura*) has a basal rate of metabolism that is 70

TABLE 1
BODY WEIGHTS AND TEMPERATURES IN SELECTED SPECIES*

Species	Body temperature (°C.)	Weight (g.)	References
Sphenisciformes			
<i>Aptenodytes patagonica</i>	37.7	20,000	K-F*
<i>Aptenodytes forsteri</i>	37.9	32,000	Prévost and Sapin-Jaloustre, 1964
<i>Pygoscelis papua</i>	38.1	5,000	K-F
<i>Pygoscelis adeliae</i>	38.2	5,500	K-F; Prévost and Sapin-Jaloustre, 1964
<i>Megadyptes antipodes</i>	37.8	3,700	K-F
<i>Eudyptula minor</i>	39.0	765	White (see Wetmore, 1921)

* This table is essentially a revision of Table 9 of King and Farner, 1961 (K-F).

(Continued on next page)

TABLE 1 (Continued)

Species	Body temperature (°C.)	Weight (g.)	References
Struthioniformes			
<i>Struthio camelus</i>	38.7	113,000	Bligh and Hartley, 1965
Casuariiformes			
<i>Casuarus</i> sp.	39.0	17,600	Sutherland, 1899; Benedict and Fox, 1927
<i>Dromiceius novae-hollandiae</i>	39.0	43,000	Sutherland, 1899
Apterygiformes			
<i>Apteryx australis</i>	39.0	2,200	K-F
Tinamiformes			
<i>Nothura maculosa</i>	40.5	ca 200	Sutherland, 1899
Podicipediformes			
<i>Podiceps caspicus</i>	40.2	380	K-F
Procellariiformes			
<i>Diomedea exulans</i>	39.6	8,200	K-F
<i>Diomedea nigripes</i>	38.1	3,100	Howell and Bartholomew, 1961
<i>Diomedea immutabilis</i>	37.5	2,500	Howell and Bartholomew, 1961
<i>Daption capensis</i>	39.1	450	Prévost, 1964
<i>Pachyptila turtur</i>	39.9	470	K-F
<i>Puffinus tenuirostris</i>	40.9	550	K-F
<i>Pagodroma nivea</i>	38.7	270	Prévost, 1964
Pelecaniformes			
<i>Pelecanus occidentalis</i>	40.3	3,500	K-F
<i>Morus bassanus</i>	41.4	2,950	K-F
<i>Phalacrocorax auritus</i>	40.1	2,720	K-F
<i>Phalacrocorax carbo</i>	39.8	3,630	K-F
Ciconiiformes			
<i>Ardea herodias</i>	39.5	1,850	Benedict and Fox, 1927
<i>Jabiru mycteria</i>	40.1	5,470	Benedict and Fox, 1927
<i>Leptoptilos javanicus</i>	39.6	5,710	Benedict and Fox, 1927
<i>Phoenicopterus antiquorum</i>	40.2	3,040	Benedict and Fox, 1927
Anseriformes			
<i>Cygnus buccinator</i>	40.1	8,880	Benedict and Fox, 1927
<i>Branta canadensis</i>	41.1	3,800	K-F
Domestic Goose	41.0	5,000	K-F
<i>Anas platyrhynchos</i>	41.2	1,220	K-F
<i>Anas cyanoptera</i>	41.7	340	K-F
<i>Anas carolinensis</i>	41.2	360	K-F
<i>Anas acuta</i>	41.3	980	K-F
<i>Mareca penelope</i>	41.5	710	K-F
<i>Aythya affinis</i>	41.3	850	K-F
Domestic duck	42.1	1,870	K-F
Falconiformes			
<i>Geranoaëtus melanoleucus</i>	40.3	2,860	Benedict and Fox, 1927
<i>Gypaëtus barbatus</i>	39.7	5,070	Benedict and Fox, 1927
<i>Falco sparverius</i>	40.5	100	K-F
Galliformes			
<i>Lagopus lagopus</i>	41.7	620	K-F
<i>Lophoryx californicus</i>	40.6	150	K-F
<i>Lophoryx gambelii</i>	40.6	150	K-F
Domestic turkey	41.2	3,700	K-F
Domestic chicken	41.5	2,000	K-F

TABLE 1 (Continued)

Species	Body temperature (°C.)	Weight (g.)	References
Gruiformes			
<i>Grus canadensis</i>	40.8	3,890	Benedict and Fox, 1927
<i>Tetrapteryx</i> (= <i>Anthropoides</i>) <i>paradisea</i>	40.5	4,030	Benedict and Fox, 1927
Charadriiformes			
<i>Charadrius vociferus</i>	41.7	76	K-F
<i>Limosa fedoa</i>	40.7	250	K-F
<i>Catoptrophorus semipalmatus</i>	41.4	222	K-F
<i>Limnodromus griseus</i>	40.9	103	K-F
<i>Ereunetes mauri</i>	41.8	24	K-F
<i>Lobipes lobatus</i>	41.8	33	K-F
<i>Catharacta skua</i>	41.2	1,000	K-F
<i>Larus glaucus</i>	40.7	1,400	K-F
<i>Rissa tridactyla</i>	41.5	460	K-F
<i>Cepphus grylle</i>	40.4	500	K-F
Columbiformes			
Domestic Pigeon	42.2	300	K-F
<i>Zenaidura macroura</i>	42.5	123	K-F
Strigiformes			
<i>Bubo virginianus</i>	40.8	1,450	K-F
Apodiformes			
<i>Eupetomena macroura</i>	40.6	7.0	Morrison, 1962
<i>Melanotrochilus fuscus</i>	42.2	6.8	Morrison, 1962
<i>Colibri serrirostris</i>	42.5	3.9	Morrison, 1962
<i>Lophornis magnificus</i>	39.5	2.2	Morrison, 1962
<i>Chlorestes notatus</i>	38.8	3.0	Morrison, 1962
<i>Hylocharis cyanus</i>	38.8	3.0	Morrison, 1962
<i>Thalurania furcata</i>	39.6	4.1	Morrison, 1962
<i>Polytmus guainumbi</i>	41.0	5.3	Morrison, 1962
<i>Amazilia leucogaster</i>	39.4	4.0	Morrison, 1962
<i>Aphantochroa cirrocholoris</i>	44.6	6.9	Morrison, 1962
<i>Clytolaema rubricauda</i>	42.2	6.8	Morrison, 1962
Piciformes			
<i>Dendrocopos pubescens</i>	41.9	23	K-F
Passeriformes			
<i>Empidonax flaviventris</i>	42.3	14	K-F
<i>Eremophila alpestris</i>	43.0	43	K-F
<i>Riparia riparia</i>	41.4	14	K-F
<i>Parus carolinensis</i>	42.3	9	K-F
<i>Parus cinctus</i>	41.5	12.5	K-F
<i>Telmatodytes palustris</i>	41.6	10.5	K-F
<i>Mimus polyglottos</i>	42.7	40	K-F
<i>Turdus migratorius</i>	43.2	77	K-F
<i>Passer domesticus</i>	43.5	25	K-F
<i>Estrilda troglodytes</i>	39.2	6.2	Cade <i>et al.</i> , 1965
<i>Taeniopterygia castanotis</i>	40.2	11.7	Calder, 1964
<i>Richmondia cardinalis</i>	42.1	40	K-F
<i>Pipilo fuscus</i>	41.7	43	K-F
<i>Pipilo aberti</i>	42.0	47	K-F
<i>Junco hyemalis</i>	42.9	19	K-F
<i>Zonotrichia leucophrys</i>	42.0	26	King, 1964

per cent of that expected for its weight (1200 g.) and a conductance of 90 per cent, when equations (6) and (4), respectively, are used for comparison. The body temperature calculated from these data is about 36.4°C. Although Enger (1957) reports a body temperature of 41°C., Heath (1962) gives values between 34 and 39°C. on the basis of more complete data. The low M in the Turkey Vulture may be an adaptation to its undependable food supply, permitting it to tolerate prolonged periods of food scarcity, but having the effect of lowering the T_b .

Some members of the family Caprimulgidae show marked modifications in both M and C. The most extensive data are from the Common Nighthawk (*Chordeiles minor*; Lasiewski and Dawson, 1964). Using these data, where the weight is about 70 g., M is 65 per cent, C is 92 per cent, and the calculated body temperature is 37.1°C. Actual body temperatures vary between 35 and 40°C. In the Poorwill (*Phalaenoptilus nuttalli*), which weighs about 40 g., M is 38 per cent and C is 62 per cent (Bartholomew *et al.*, 1962), leading to a calculated T_b of 36.6°C. Unfortunately, there is little mention of the body temperature of nonhibernating, but quiescent, Poorwills; the few data suggest that it is between 35 and 38°C. (Marshall, 1955; Bartholomew *et al.*, 1957; Howell and Bartholomew, 1959). Finally, the data of Scholander *et al.* (1950) on two 43-g. Pauraques (*Nyctidromus albicollis*) suggest that their M is 76 per cent and their conductance is 72 per cent; the calculated T_b is 39.8°C. No normal body temperatures were given, but a low value of 37°C. indicates that the T_b is typically higher.

Conductances and basal rates of metabolism account reasonably well for the body temperatures found within these caprimulgids. These parameters, in turn, are probably associated with the radiative heat gain from the sun resulting from roosting and nesting in exposed places. When exposed to the sun, caprimulgids prevent their body temperature from approaching a lethal level by gular fluttering (Bartholomew *et al.*, 1962; Lasiewski and Dawson, 1964). As a result of a low M caprimulgids can lose more heat by evaporation than is produced by the metabolism of a quiet individual, and thus dissipate some of the heat gained from the environment. In fact, the lowest rate of metabolism, and the greatest capacity for the evaporative dissipation of heat in this group, has been found in the desert-dwelling Poorwill, the species that may well have the greatest environmental heat load.

Yet the capacity for thermoregulation cannot be eliminated in a homoiotherm that lives in an environment marked by wide temperature fluctuations. Good thermoregulation in mammals demands a high M/C ratio (McNab, 1966). Therefore, to have good thermoregulation and a low M requires, in compensation, a low C. If the Poorwill had, coupled with its low M, a conductance equal to that of the Nighthawk, the body temperature of the Poorwill would be approximately 35°C. This is the lowest body temperature compatible with good thermoregulation under moderate cold stress (2-hour exposure at 10°C.; McNab, 1966), and is inadequate for lower temperatures or longer exposures. The Poorwill, in fact, has a marked capacity for thermoregulation (Bartholomew *et al.*, 1962), presumably due to its low conductance. This situation is identical to the case found in desert *Peromyscus* (McNab and Morrison, 1963; McNab, 1966), where a low rate of heat production is compensated by a low rate of heat loss.

From this analysis one can argue that caprimulgids not exposed to intensive solar radiation (forest-dwelling Chuck-will's-widow and Whip-poor-will) would have higher rates of metabolism and higher body temperatures. Furthermore, it can be concluded that much of the scatter of body temperatures about the values expected from equation

TABLE 2
PREDICTED BODY TEMPERATURES IN HUMMINGBIRDS^a

Species	Weight (W) (g.)	Basal rate of Metabolism (M)		Conductance (C)		M/C %/%	T _b °C ^d
		(cc. O ₂ /g.-hr.)	% expected ^b	(cc. O ₂ /g.-hr.°C)	% expected ^c		
<i>Calypte costae</i>	3.10	3.30	61	0.55	96	64	38.0
<i>Archilochus alexandri</i>	3.45	3.65	78	0.50	96	81	39.5
<i>Selasphorus rufus</i>	3.60	3.35	71	0.46	87	82	39.5
<i>Calypte anna</i>	5.35	3.85	93	0.44	102	91	40.1

^a Data taken from Lasiewski (1963, 1964) and Lasiewski *et al.* (1964).

^b Calculated from $M(\text{cc. O}_2/\text{g.-hr.}) = 7.3W^{-0.34}$.

^c Calculated from $C(\text{cc. O}_2/\text{g.-hr.}^\circ\text{C.}) = 1.0W^{-0.50}$.

^d Predicted from $T_b(^\circ\text{C.}) = (10.1)(M/C)W^{-0.09} + 32.2$.

(7) at weights greater than 30 g. is due to the deviation of the basal rates of metabolism from those expected from equation (6).

The marked reduction of T_b in the smallest birds also requires an explanation. We can consider conductance. If C_b = C_m, equation (7) becomes

$$T_b = 10.1W^{-0.09} + 32.2 \quad (8),$$

which is also plotted in figure 1. If the body temperatures of birds followed this curve, they would be some 2 to 4°C. lower than expected from equation (7). Contrary to the suggestion of Rodbard (1950), the difference in T_b between birds and mammals at weights less than 20 g. cannot be explained in terms of insulation. For example, Calder (1964), working on the energetics of the Zebra Finch (*Taeniopygia castanotis*), found that its basal rate of metabolism was that expected for a mammal of its weight (11.7 g.), but its conductance was that expected for a mammal of its weight. The body temperature calculated from equation (8) is 40.3°C., and the measured T_b is about 40.2°C., which is still well above the typical mammalian temperature of 37°C. Below 20 g., then, the body temperatures of birds depart from those predicted by equation (7) and approach those predicted by equation (8), because of a reduction in the insulating capacity of the plumage.

A family of birds worthy of comment, especially because of their small weight, is the Trochilidae. One can conclude from the data of Lasiewski (1963, 1964) and Lasiewski *et al.* (1964) that hummingbirds have low rates of metabolism (compared with those predicted by equation (6), which is appropriate for most birds), high conductances (approximately equal to those of mammals of the same weight), and low body temperatures. The body temperatures in four species calculated from these data vary from 38.0 to 40.1°C., and show a positive correlation with weight (figure 1, table 2). The actual body temperatures show great variability, but are usually between 35 and 41°C. Morrison (1962) has shown in a group of Brazilian hummingbirds that small species have lower body temperatures than large species.

The reduction of M, and therefore of body temperature, near the lower size limit is also found in small passerines, such as the Black-rumped Waxbill (*Estrilda troglodytes*; Lasiewski *et al.*, 1964; Cade *et al.*, 1965). This small finch (6.2 g.) has a conductance somewhat greater than expected for its weight and a basal rate of metabolism of 88 per cent; the calculated T_b is 39.6°C. The actual T_b is about 1°C. below that of the larger Zebra Finch (Cade *et al.*, 1965), or about 39.2°C. Among small finches, therefore, there is also a positive correlation between T_b and weight.

The low T_b in the smallest birds is therefore a result of two factors: relatively

high conductances and low rates of metabolism. The low rates of metabolism may be viewed as a means of reducing the energy expenditure required of a small (3 to 6 g.) bird, which, following equation (8), would otherwise maintain a T_b of 41.4 to 40.8°C.

CONCLUSIONS AND SUMMARY

Several conclusions can be made from this analysis. (1) The body temperature of birds, like that of mammals, appears to depend upon the rate of metabolism and the rate of heat loss, and is not an independent character in itself. Low body temperatures indicate low rates of metabolism or high conductances, or both, which in turn may reflect ecologic requirements. (2) Birds have higher body temperatures than mammals of the same weight because they have higher rates of metabolism and usually have lower rates of heat loss than mammals. (3) Small birds have higher body temperatures than large birds because they have higher rates of heat production, relative to their weight, than do large birds, even when compared with a mammalian standard. Mammals seem to have a balance between heat production and loss so that body temperature is independent of weight. Birds, however, have a greater power increase in weight-specific heat production than mammals, and it is this difference (0.09) that is responsible for the weight correlation of body temperature in birds. (4) The apparent correlation between the level of body temperature and the taxonomic group is really a correlation of weight and taxonomic group. (It should be noted that within both the ratites and penguins, small species have higher body temperatures than large species.) (5) Much of the departure of the body temperatures from those predicted by weight at weights greater than 30 g. is due to modifications of the rate of metabolism. (6) The insulation of birds that weigh less than 20 g. is equal to that of mammals of the same weight, resulting in lower body temperatures than expected in birds from weight alone. (7) The very small weight of hummingbirds and certain finches poses a problem of energy conservation, which is met by a reduction in the basal rate of metabolism, further reducing body temperatures near the lower weight limit. (8) The ability to predict the body temperature of birds from energetics suggests that the modification proposed by King and Farner (1961) of the Brody-Procter equation, relating the basal rate of metabolism to weight, is a good estimate of the "true" relationship.

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