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MINI REVIEW

BODY TEMPERATURE IN BIRDS

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Abstract—1. Mean levels of body temperatures (Tb) for all birds are (resting/active phase/high activity) 38.54 ± 0.96 ($N = 203$), 41.02 ± 1.29 ($N = 724$) and 43.85 ± 0.94°C ($N = 74$).

2. Tb is higher in birds than in mammals: 1.87°C higher during rest and 2.43°C higher during the active phase.

3. As in mammals, the range of Tb-oscillation (day/night) decreases with increasing body mass (bm). For birds between 10 and 100,000 g this range is 2.48–1.25°C.

4. Tb decreases slightly with increasing bm. During the resting phase the correlation is not pronounced.

5. During the resting phase there is no marked difference in Tb between different taxonomic groups. Flightless birds and birds with high bm show lower values during activity.

6. Slight nocturnal decrease in Tb ("hypothermia") is shown in many birds as an adaptation to low food supply and/or heavy cold load.

7. Daily torpor is a special physiological ability. Tb may fall during the night to a minimum range of 18–20°C with active rewarming. During "estivation" Tb may even fall to + 5–7°C without obvious ill effects.

8. Exogenous, artificial rewarming allows Tb to fall lower than normal torpor-levels.

9. Many other parameters are involved in the regulation of body temperature (circannual rhythms, hormones etc.).

INTRODUCTION

Much work has been done on the energetics of endotherms (birds and mammals). One major parameter of endothermy is a high and endogenously controlled body temperature (Tb) which is relatively easy to measure and, thus, has been often studied. Nevertheless there exists only one general analysis of Tb in birds and mammals: McNab's (1966a,b) review is based on about 86 species of birds.

In the last 25 years much additional data have been obtained to justify a new review of this problem to address the following issues:

—Mean levels and differences of Tb during diurnal cycle.
—The correlation of Tb with taxonomic group.
—Tb and body mass.
—Tb-difference between mammals and birds.
—Tb and other parameters.

MATERIALS AND METHODS

Most data were obtained from the literature but include our unpublished values for 61 bird species. Most measurements were done cloacally (73%), and 21.6% were obtained in the proventriculus. Other places include the axilla (1.5%), the skin (1.1%), the throat (1.1%) and the breast muscle (1%). Only 0.9% of Tb-data were obtained telemetrically by implanted temperature-transmitters.

In many cases we had some problems integrating published data in our review because of the lack of information in the papers on time (day/night) and/or circumstances (darkness, light, number and/or type of data collection) under which measurements were taken. All data included in this review were treated equally, independent of number and/or how values were obtained. A detailed differentiation of all figures would not allow us to present a general overview of the subject—the major aim of this paper.

The large number of published works does not make it practical to cite all birds (more than 720) and papers (≥ 300) in the text but all are listed in the references. A copy of the data and appropriate citations may be obtained by sending two formatted disks ($5\frac{1}{4}$ or $3\frac{1}{2}$ inches) to the authors.

RESULTS AND DISCUSSION

Mean levels and diurnal cycle of body temperature

Mean levels of body temperature for all birds are as follows (N = number of bird species):

resting phase	38.54 ± 0.96°C ($N = 203$), range 35.0–40.8
active phase	40.02 ± 1.29°C ($N = 724$), range 35.6–44.6
high activity	43.85 ± 0.94°C ($N = 74$), range 40.4–47.7.

This results in a mean day–night-difference in the diurnal cycle of 2.48°C. High activity (flying/running) may raise Tb up to a mean of 2.84°C above normal activity levels. The highest Tb ever recorded from a bird was 47.7°C in the white-crowned sparrow *Zonotrichia leucophrys* (Southwick, 1973) and 47.0°C in the blue-breasted quail *Excalfactoria chinensis* (Bernstein, 1973).

Based on data from Aschoff (1981) comparable values (resting/active phase) from mammals are as follows: 36.67/38.58°C ($N = 50$), resulting in a mean difference of 1.91°C.

Higher Tb-values in birds (+1.87°C for the resting phase and +2.43°C for the active phase) seem to be mainly caused by their higher level of energy metabolism (McNab 1966). The greater oscillation in diurnal rhythm is presumably caused by higher behavioural activity requirements (e.g. flying) in birds. In mammals and birds the range of oscillation decreases with increasing body mass. Based on the correlations of Fig. 1 the following values were calculated:

Body mass (g)	Range of oscillation (°C)
10	2.48
100	2.16
1000	1.86
10,000	1.55
100,000	1.25

The true (empirical, not calculated) values of a 100 kg ostrich are obviously below 1°C.

Body temperature and body mass

Figure 1 gives mean levels of Tb in relation to body mass. Tb shows a clear relationship with body mass.

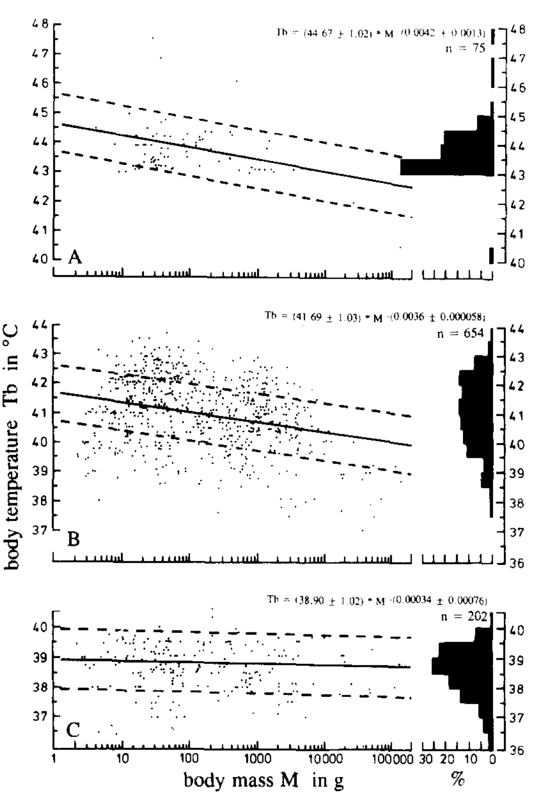

Fig. 1. Body temperature versus body mass in birds during high active phase (A; flight, running), activity time (B) and resting phase (C); see text. The corresponding regression equations are given in the figure (solid lines = regression curves; broken lines = range of SD). The right part of the figure gives relative portions (%) of the different body temperatures (see appendix).

In birds, body temperatures are lower in larger species. The correlation is more distinct in the active phase, and most pronounced during high activity. The corresponding correlation-exponents of mass are 3.4×10^{-4}, 36×10^{-4} and 42×10^{-4}.

The following calculated data in Table 1 are based upon the equations in Fig. 1 and show the relationship very clearly.

In mammals there seems to be no pronounced dependence of body temperature on weight. Therefore the correlation in birds requires an explanation: the mass-dependence during rest is negligible (0.12°C over the whole mass-range). Tb increases with increasing activity. From this it may be assumed that an increase in activity has a more distinct effect in birds than in mammals. Energy expenditure for flying in birds is much more mass-dependent than other forms of movement. Smaller birds need much more energy for flying than walking or running mammals of similar size, and this results in higher mass dependent Tb-increase. Flightless birds and/or those with a high body mass should have a low body temperature, and this was observed (see below). Here we wish to add a note of caution. All measurements of Tb may not be physiologically similar. For example, a Tb measured at a depth of 1 cm into the cloaca of a 10 g bird does not necessarily equate to a measurement made 10 cm deep in a 100 kg bird.

The large bird may have a higher deep core temperature than the one normally obtained. When this situation is taken into account the relationship between Tb and body mass may be less pronounced.

Body temperature and taxonomic group

Table 2 shows body temperature from birds in different orders. In some cases it is not possible to separate taxonomic and mass effects. For example all species of Struthioniformes and Casuariformes have high body masses and low Tb. Additionally it is difficult, if not impossible, to determine if these differences in Tb are statistically significant because of the great differences in number of species per order. If only biological relevant differences are taken into account, that means Tb-values which are not within a range of mean value ± SD/2 (resting: 38.0–39.0; activity 39.3–41.6°C), only in very few orders we can find statistically significant differences (see Table 2). In the resting phase we find no obvious differences. In the active phase Passeriformes have slightly increased Tb, whereas the ratites (Casuariformes, Struthioniformes, Apterygiformes), the petrels (Procellariformes) and the penguins (Sphenisciformes) show lower values. Petrels were measured during breeding, where they often show hypothermia (see

Table 1. Mass dependence of mean body temperature calculated from data in Fig. 1

Body mass (g)	Tb resting	Tb active	Tb highly active
10	38.87	41.30	44.24
100	38.84	41.00	43.81
1000	38.81	40.67	43.39
10,000	38.78	40.33	42.97
100,000	38.75	40.00	42.56
Range	0.12	1.35	1.68

Table 2. Body temperatures in different orders of birds. The first row shows resting levels, the second row active phase levels and the third row high activity levels. Significant difference to mean values of all birds: *(for explanation see text and Fig. 1)

Order	N	Mean ± SD (range)	Significance
All birds	202	38.54 ± 0.96	
	724	41.02 ± 1.29	
	74	43.85 ± 0.93	
Passeriformes	59	38.9 ± 0.87 (36.0–40.8)	
	298	41.6 ± 1.13 (39.0–44.1)	*
	45	43.9 ± 0.78 (43.1–47.7)	
Piciformes	1	39.0	
	20	41.8 ± 0.95 (39.0–43.0)	*
	2	43.7 (43.3–44.2)	
Trochiliformes	19	38.1 ± 1.26 (35.3–39.5)	
	64	40.3 ± 1.48 (35.6–44.6)	
	—	—	
Caprimulgiformes	7	37.9 ± 1.51 (35.0–39.5)	
	9	39.7 ± 1.70 (37.0–42.4)	
	2	43.9 (43.5–44.3)	
Strigiformes	8	38.7 ± 0.56 (38.0–39.8)	
	20	40.2 ± 0.66 (38.6–41.2)	
	1	44.2	
Columbiformes	6	38.6 ± 0.66 (37.7–39.9)	
	20	40.9 ± 1.35 (38.6–43.3)	
	5	44.6 ± 0.91 (43.6–46.2)	
Charadriiformes	16	38.5 ± 0.99 (35.2–39.5)	
	64	40.9 ± 0.86 (38.3–42.4)	
	2	43.6 (43.3–43.9)	
Gruiformes	1	37.5	
	11	40.4 ± 0.77 (39.1–41.4)	
	—	—	
Galliformes	4	38.9 ± 1.16 (37.5–40.5)	
	39	41.4 ± 0.92 (38.2–42.5)	
	3	44.8 ± 1.59 (43.3–47.0)	
Falconiformes	5	39.0 ± 0.86 (38.0–40.3)	
	24	40.0 ± 0.96 (39.4–42.8)	
	1	43.3	
Anseriformes	5	39.0 ± 0.42 (38.3–39.5)	
	45	41.3 ± 0.77 (39.8–43.0)	
	4	43.2 ± 0.04 (43.1–43.2)	
Ciconiiformes	4	39.3 ± 0.38 (38.7–39.6)	
	15	40.5 ± 0.82 (39.5–42.3)	
	1	44.3	
Pelecaniformes	5	37.9 ± 0.73 (37.1–38.9)	
	17	40.6 ± 0.81 (39.0–42.7)	
	2	43.7 (43.2–44.2)	
Procellariformes	22	38.3 ± 0.68 (37.0–39.6)	
	24	39.4 ± 0.84 (37.5–41.0)	*
	—	—	
Casuariformes	6	38.6 ± 0.58 (37.7–39.2)	
	6	38.8 ± 0.43 (37.9–39.2)	*
Sphenisciformes	10	37.8 ± 0.76 (36.0–39.0)	*
	10	38.2 ± 0.68 (37.0–39.0)	*
	—	—	
Coliiformes	4	38.2 ± 0.93 (36.6–39.0)	
	5	39.5 ± 1.21 (38.0–41.5)	
	1	43.2	
Struthioniformes	3	38.3 ± 0.31 (38.0–38.7)	
	3	39.3 ± 0.58 (38.7–40.1)	*
	—	—	
Apterygiformes	3	38.2 ± 0.65 (37.4–39.0)	
	3	38.3 ± 0.51 (38.1–39.0)	*
	—	—	
Tinamiformes	1	39.2	
	1	40.5	
	—	—	
Gaviiformes	2	39.2 ± 0.25 (39.0–39.5)	
	2	39.3 ± 0.35 (39.0–39.0)	
	—	—	
Podicipediformes	2	38.9 ± 0.40 (38.5–39.3)	
	4	39.5 ± 0.65 (38.5–40.2)	
	—	—	
Psittaciformes	2	37.9 ± 0.20 (37.7–38.1)	
	6	41.3 ± 0.20 (41.0–41.5)	
	1	43.5	
Apodiformes	3	38.6 ± 0	
	4	40.0 ± 1.43 (38.6–41.8)	
	—	—	
Coraciiformes	1	39.2	
	3	40.0 ± 0.24 (40.0–40.5)	
	—	—	
Cuculiformes	—	—	
	8	41.3 ± 0.81 (39.9–42.3)	
	1	43.5	

Table 3 and below) and all other species are large and flightless ("mammal-like"). By this, all taxonomic effects can easily be explained by mass-specific and/or behavioural parameters. The lack of distinct differences in the resting phase (the best phase for comparisons) shows, that there are no marked differences between the taxonomic groups.

Controlled hypothermia

In some birds, food scarcity and/or cold load can lead to a marked decrease in Tb during the resting phase which is well below normal Tb (e.g. "hypothermia"). These birds have the ability to actively and spontaneously increase their Tb (therefore referred to as "controlled" hypothermia). In this review only those cases where Tb was clearly well below +35°C were used because a decrease of only 1–3°C below normal resting levels is presumably characteristic of all birds (and mammals). Torpor (see below), on the other hand, is a totally different physiological (lethargic) state not to be confused with controlled hypothermia. When in controlled hypothermia birds can respond instantly to external factors, such is not the case when birds are in deep torpor. Therefore, Tb values below +25°C were omitted here as this range of temperatures probably reflects birds that were in a state of torpor. Table 3 lists birds in which controlled hypothermia has been recorded. This table contains birds from six orders, nine families and 38–40 species. It is possible that controlled hypothermia occurs in all species of birds if hunger and/or cold load is exceptionally severe. This question needs to be investigated more thoroughly in the future.

Table 3. Deep body temperature (°C) during resting phase (controlled hypothermia) caused by hunger and/or cold load in birds. Listed are only Tb-values ⩾30 ⩽35°C (with few exceptions)

Species	Minimal recorded Tb	Ref.*
Ancanthis flammea (redpoll)	32.0	1
Carduelis chloris (greenfinch)	33.0	1
Cathartes aura (black vulture)	34.0	2
Columbia livia (rock pigeon)	35–37	17, 18
Crotophaga ani (smooth-billed ani)	32.6	4
Lichenostomus virescens (singing honeyeater)	32.0	5
Lichmera indistincta (brown honeyeater)	32.0	5
Loxia curvirostra (red crossbill)	34.0	3
Neopelma sulphureiventer (sulphur-bellied manakin)	30.5	6, 12
Nyctea scandiaca (snowy owl)	32.6	7
Parus atricapillus (black-capped tit)	33.8	8
Parus carolensis (Carolina tit)	30.0	9
Parus cincta (Siberian tit)	32.1	10
Parus major (great tit)	29–31	11, 16
Passer montanus (tree-sparrow)	28–31	1
Pipra mentalis (red-capped manakin)	29.0	6, 12
Scardafella inca (inca dove)	28.5†	11
Turdus merula (common blackbird)	37.0	13
Nectariniidae (sunbirds)	down to 35.5	14
Coliidae (mousebirds)	down to 35.0	15

*References: 1. Steen (1958), 2. Heath (1962), 3. unpubl. own data, 4. Warren (1960), 5. Collins and Briffa (1984), 6. Bucher and Worthington (1982), 7. Gessaman and Folk (1969), 8. Grossman and West (1977), 9. Mayer *et al.* (1982), 10. Haftorn (1972), 11. MacMillen and Trost (1967), 12. Bartholomew *et al.* (1983), 13. Biebach (1977), 14. Prinzinger *et al.* (1989a), 15. Prinzinger (1988), 16. Reinertsen (1985), 17. Ostheim (1990), 18. Graf *et al.* (1989).

†Threshold for spontaneous arousal (values with exogenous rewarming down to +22°C).

Torpor

Torpor is treated here as defined by Swan (1974). Body temperature and metabolism can drop to extremely low levels. Entrance, maintenance and arousal from this lethargic state is an active and regulated process. However, arousal can take up to 20 min. Tb can approximate ambient temperatures clearly below +25°C (in contrast to controlled hypothermia). Metabolism may be reduced to less than 1/50 of basal levels without ill effects. Some (possibly all) birds have the ability to regulate Tb down to a range between +25 and +30°C. There are many references in the literature of birds being "in torpor" with Tb in this range (some authors even use the term "torpor" when the bird has a Tb clearly above +35°C; this is not correct). It should be proven in every case if this is not only controlled hypothermia (see above). In most birds minimal critical Tb during daily torpor should principally be able to drop to between +18–20°C. This same range is reported for mammals during torpor.

Tb lower than those reported above, in most cases, do not represent deep core Tb as measured via the cloaca. Lower Tb may also occur in birds that will suffer ill effects after rewarming. Exceptions do occur, however, as in the case of the long-fasting poorwill (*Phalaenoptilus nuttallii*) and in the European nightjar (*Caprimulgus europaeus*). These species are reported to maintain Tb of between +5–7°C during torpor and also to undergo spontaneous arousal (e.g. Peiponen, 1970; Ligon, 1970). It is often stated that sunbirds can maintain Tb as low as +25°C, but this value was obtained from only one bird, an eastern double-collared sunbird (*Nectarinia mediocris*) that was in poor physical condition and died shortly after the experiment (Cheke, 1971). Table 4 contains only groups of birds that undergo torpor as defined above. Geiser (1988) presents an overview of the occurrence of torpor in mammals.

Table 4. Birds that show torpor as defined in text. o = Obligatory (regular) torpor during an endogenous diurnal rhythm independent of food supply. f = Faculative torpor in an energetic emergency state (h = hunger, food scarcity, c = cold load, low ambient temperature etc.)

Species/taxonomic group	Type of torpor	Ref.*
Caprimulgidae (nightjars)		
Caprimulgus europaeus (European nightjar)	f (h, c)	1
Eurostopodus guttatus (spotted nightjar)	f (h, c)	2
Chordeiles minor (common nighthawk)	f (h, c)	3
Chordeiles acutipennis (lesser nighthawk)	f (h, c)	4
Phalaenoptilus nuttallii (common poorwill)	o, f (?)†	5–7
Apodidae (swifts)		
Apus apus (common swift)	f (h, c)‡	8
Aeronautes saxatilis (white-throated swift)	f (h, c)‡	6
Trochilidae (hummingbirds)		
observed in all species	o	9
Coliidae (mousebirds)		
observed in all species tested (4 of 6)	f (h, c)	10, 11
Hirundinidae (swallows)		
Delichon urbica (house martin)	f (h, c‡	12–14
Hirundo rustica (barn swallow)	f (h, c)‡	13, 14
Riparia riparia (sand martin)	f (h, c)	13, 14
Tachycineta thalassina (violet-green swallow)	f (h, c)	15
Cheramocea leucosternum (white-backed swallow)	f (h, c)	16
Procellariidae (petrels)		
how many species? (all?)	f (h, c)‡	17

*References (examples): 1. Peiponen (1965, 1966, 1970), 2. Dawson and Fischer (1969), 3. Lasiewski and Dawson (1964), 4. Marshall (1955), 5. Jaeger (1948, 1949), 6. Bartholomew et al. (1957), 7. Howell and Bartholomew (1959), 8. Koskimies (1948, 1950), 9. summaries e.g. in Krüger et al. (1982) and Reinertsen (1985), 10. Bartholomew and Trost (1970), 11. Prinzinger et al. (1981a,b), Prinzinger (1988), 12. Prinzinger and Siedle 1986, 1988, 1989), 13. Keskpaik (1976, 1981a,b), 14. Keskpaik and Lyuleyeva (1968), 15. Lasiewski and Thompson (1966), 16. Serventy (1970), 17. Boersma (1986).

†Daily torpor and "estivation" for up to 85 days (and more?)

‡Observed as a survival strategy in young during hunger/bad weather conditions.

Other effects on Tb

There are reports of circannual variations in Tb. The gray jay (*Perisoreus canadensis*) shows a greater range of oscillation in Tb during periods of reduced gonadal activity (2.4°C, winter) than during summer (1.7°C) (Veghte, 1964). In the Japanese quail (*Coturnix coturnix japonica*) Tb at rest is lower during the reproductive season (mean values: 42.7/41.5°C in winter/summer). Sexually inactive (castrated) males have greater oscillations in Tb than active ones (Feuerbacher, 1981): the same effect has been observed in the starling (*Sturnus vulgaris*) (Rutledge, 1974). All increase in body mass during annual cycle leads to a decrease in Tb in migratory birds, e.g. in the robin (*Erithacus rubecula*) and the whitethroat (*Sylvia communis*) (Merkel, 1958).

Differences in Tb between males and females have been reported in many birds, with females exhibiting slightly higher (0.3–0.5°C) values (e.g. Simpson and Galbraith, 1905; Gilbreath and Ru-Chiung Ko, 1970; Becker and Harrison, 1975; Hänssler and Prinzinger, 1979; etc.).

Many hormones are involved in the regulation of Tb. After pinealectomy, for example, the circadian rhythm of Tb is abolished and the amplitude of the oscillation in Tb is reduced in the house sparrow (*Passer domesticus*) (Binkley et al., 1971). This topic, however, requires a separate review.

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APPENDIX

Recently found additional data from 70 birds (Oniki, 1974) result in the activity time of the slightly different correlation $\mathrm{Tb} = (41.56 \pm 1.03) \times M^{(-0.00294 \pm 0.0005)}$; $M = 724$. In all tables these data are included.