

THERMAL ENERGETICS OF CHICKS OF ARCTIC-BREEDING SHOREBIRDS

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(Received 19 June 1979)

Abstract—1. The heat-transfer characteristics of young and adults of several arctic-breeding shorebirds were examined. Heated, skin-covered metal casts were used for measurements difficult to perform on live birds.

2. Heat transfer coefficients are high in small chicks, but decrease rapidly with age. Both heat transfer coefficients and body resistances to heat flow (i.e. insulation) are linearly related to the square root of wind speed.

3. Energy budget analysis indicates that chicks cannot maintain body temperature in typical environmental conditions in the breeding area until at least half grown. During this interval they require periodic brooding by the parent birds.

4. Efficiency of the brooding-activity cycle is enhanced by the thermolability of chicks.

INTRODUCTION

Several species of small shorebirds (sandpipers, plovers, phalaropes) breed in arctic tundra areas of northern Alaska (Pitelka *et al.*, 1974). Their chicks face severe thermoregulatory problems, because of low ambient temperatures, small size, and poor insulation. Further, the chicks are nidifugous, leaving the nest almost immediately upon hatching and wandering over the tundra. As a result, they are exposed to stressful wind and radiation conditions which would be ameliorated by the microclimate of a nest. Norton (1973) reported metabolic rates and body temperatures of sandpiper chicks as part of a study of breeding ecology and energetics. Of particular interest was his finding that the body temperatures of chicks vary widely, over a range of 30–40°C, without severely affecting locomotor abilities or other aspects of behavior.

The work described here expands upon Norton's data, utilizing techniques which describe thermal energy balance in terms of animal surface properties and the radiative and convective characteristics of the environment (Campbell, 1977; Monteith, 1973; Robinson *et al.*, 1976). Two main questions are examined: (1) How do the rapid size increases of growing chicks affect their thermal balance in the context of the different wind speed and insolation regimes they are subjected to, and (2) what are the advantages or disadvantages of the highly labile body temperature of chicks?

MATERIALS AND METHODS

Chicks and adults of four species of shorebirds were collected in the vicinity of Barrow, Alaska, during the months of July and August 1978 (Table 1). Shorebird chicks are thermolabile, making them difficult to work with in wind tunnels and other situations where steady-state measurements are desired. Therefore, much of the heat exchange data was gathered from skin-covered, internally heated Wood's metal casts. Rates of heat exchange from casts should closely resemble those in live birds, since size,

shape, and plumage characteristics are similar. The casts were constructed as described in Heller (1972) and Bakken (1976).

The metabolic requirements of the birds were calculated in terms of equivalent environmental temperatures (T_e), which are the sum of air temperature (T_a) and a temperature increment due to radiation and convection (Morhardt & Gates, 1974; Mahoney & King, 1977):

$$T_e = T_a + R_{ni} \cdot r_e / \rho c_p \quad (1)$$

The r_e term is an external resistance to heat flow:

$$r_e = (r_r \cdot r_a) / (r_r + r_a)$$

where $r_r = \rho c_p / 4\epsilon\sigma T_a^3$ and $r_a = k(d/u)^{0.5}$. At wind speeds of 1 m s^{-1} or less, a free convection resistance was added in parallel to the forced convection resistance r_a , as described in Robinson *et al.* (1976). At wind speeds greater than 1 m s^{-1} , free convection becomes negligible compared to forced convection (*ibid.*). The parameters in these equations are as follows: u = wind velocity (m s^{-1}), d is animal diameter (m), k is a constant (310 for laminar flow and about 30–50% less in naturally turbulent conditions—Nobel, 1974), ϵ is surface emissivity (≈ 1 for most integuments), σ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$), and the product of ρ (air density) and c_p (specific heat of air) is a constant ($1200 \text{ J m}^{-3} \text{ K}^{-1}$ at 20°C). The tables in Tracy *et al.* (1978) were used to obtain ρc_p values at other T_a 's. Climatological and microclimate information for the Barrow area was obtained from Kelley & Weaver (1969), Coyne & Kelley (1975), Myers & Pitelka (1979), and U.S. Weather Service data.

R_{ni} can be calculated from absorbed radiation (R_{abs}) and T_a :

$$R_{ni} = R_{abs} - \epsilon\sigma T_a^4$$

R_{abs} was obtained from Porter & Gates (1969), where it is expressed as a function of T_a , sky conditions, and short-wave absorptivity. Absorptivity was assumed to be about 0.7–0.75, which is average for similarly-colored animals (Porter & Gates, 1969; Morhardt & Gates, 1974; DeJong, 1977).

The energy balance of the bird can be expressed as:

$$M - \lambda E = \rho c_p (T_b - T_e) / (r_b + r_e) \quad (2)$$

where M is metabolic rate, λE is evaporative heat loss, and r_b is whole-body resistance. The r_b term can be derived

Table 1. Specimen parameters. D = diameter, A = surface area, A_1 = leg area, T = feather thickness (average of measurements from back and abdomen)

Specimen, wt (g)	D (m)	A (cm ²)	A_1 (cm ²)	A_1/A	T (mm)
CHICKS					
<i>Calidris</i>					
<i>pusilla</i> 1 5	0.023	24	2.6	0.108	4.0
<i>C. pusilla</i> No. 2 5.1	0.024	24	2.6	0.108	4.2
<i>C. bairdii</i> No. 1 6.5	0.028	28	2.9	0.103	3.8
<i>C. bairdii</i> No. 2 6.5	0.030	28	2.8	0.100	4.2
<i>C. pusilla</i> No. 3 11.5	0.032	41	3.5	0.085	4.6
<i>C. bairdii</i> No. 3 18	0.041	56	4.6	0.082	6.1
<i>C. melanotos</i> No. 1 18	0.039	56	4.8	0.083	6.2
<i>C. melanotos</i> No. 2 21	0.040	62	4.7	0.086	6.8
<i>Charadrius</i>					
<i>semipalmatus</i> No. 1 20	0.037	60	5.0	0.076	6.2
ADULTS					
<i>Phalaropus</i>					
<i>fulicarius</i> No. 1 60	0.051	125	5.0	0.040	8.8
<i>P. fulicarius</i> No. 2 60	0.052	125	6.2	0.049	8.6
<i>C. melanotos</i> No. 3 50	0.050	110	5.6	0.051	8.6

from known rates of heat loss in a metabolism chamber or wind tunnel:

$$r_b = \rho c_p (T_b - T_c) / (M - \lambda E) - r_c \quad (3)$$

The final term, λE , was calculated as a percent of M from equation 56 in Calder & King (1974):

$$\lambda E = 5 + 1.48e^{0.087T_c} \quad (4)$$

The derivation of the above equations is explained in detail in Robinson *et al.* (1976) and Mahoney & King (1977).

The casts did not include the legs, so the magnitude of heat loss from legs was estimated separately. Leg areas were calculated from lengths and circumferences of the various sections (tarsus, toes, etc.). Leg surface temperatures were obtained from several live chicks in natural habitats. Thin (40-gauge) thermocouples were attached to the bird's legs with contact adhesive. Temperatures were recorded after the chicks had calmed and were no longer crouched in alarm postures. Wind speed on the legs was estimated to be about 0.3 m s^{-1} on an average day when wind speed at the height of a chick's body (5–7 cm) is about 1 m s^{-1} . Heat loss from the legs was calculated from equation 2, assuming $r_b = 0$ because leg surface temperatures instead of core temperatures were used.

The surface areas of chicks were difficult to measure directly, due to the delicate natal down. Therefore, areas were calculated from body mass using the allometric relationship $A = 8.11 M^{0.667}$, where A is in cm² and M is in g (Walsberg & King, 1978). This equation gives good results for birds of diverse body configurations over a body mass range of four orders of magnitude. Cast diameter (d) was measured from side to side across the thorax with calipers.

A wind tunnel was used to measure thermal conductance

($\text{W m}^{-2} \text{C}^{-1}$) and the body resistance r_b at various wind speeds. The casts were suspended in the center of the tunnel where airflow was approximately laminar (determined from observing smoke trails). Power to the cast heater was then adjusted until cast temperature (T_c) stabilized within the physiological range (35–45°C). Conductance and r_b could then be calculated from heater wattage, wind speed, surface area, T_c , and T_a .

Cooling rates of chicks were estimated by placing casts in the natural environment or in simulated natural conditions in the laboratory. Casts were heated to 38°C and then supplied with power equal to metabolic heat production (measured by Norton, 1973). The time necessary for T_c to fall to 30°C was recorded, along with T_a , wind speed, and estimated radiation load. The end points of 30 and 38°C were derived from Norton's data: 30°C is the T_b below which chicks experience motor dysfunction and emit distress notes, and 38°C is the average T_b of freshly-brooded chicks in the field.

Approximate heating rates for brooded chicks were obtained in an analogous manner. Casts were cooled to 30°C and supplied with power equivalent to normal metabolic heat production. To simulate the brooding parent, a rubber hot-water bottle filled with 40°C water was placed over the cast, and the time needed for T_c to rise from 30°C to 38°C was recorded.

The accuracy of equation 2 for estimating necessary metabolic rate was tested as follows: Casts were placed in the field and heated to constant T_c (35–45°C) with the internal heater. The microclimate (T_a , R_{obs} , wind speed) was determined and this data used to predict necessary heat production. Actual power requirements for maintaining cast homeothermy could then be compared to the predicted requirement; the magnitude of the error is an index of predictive accuracy.

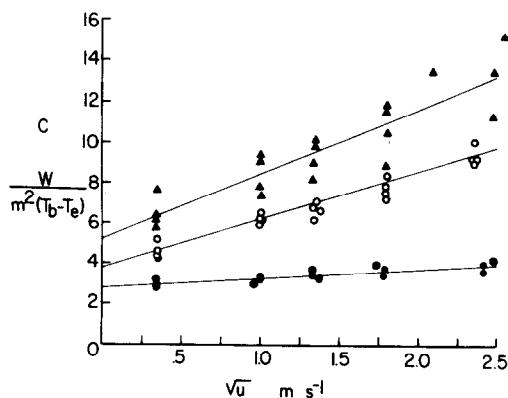


Fig. 1. Changes in heat transfer coefficients (C) with size and wind speed (u). Triangles represent data points from four chicks weighing 5–6.5 g; open circles are points from four 18–21 g chicks, and dark circles are points from two 60 g adult birds. Each point is an average of 3–5 measurements; variances in most cases were so small as to be concealed behind the symbols. Regression equations are given in Table 2.

RESULTS

Heat loss coefficients (thermal conductance) of adults and young, as derived from wind-tunnel measurements of casts, are shown in Fig. 1. The data points from the 11 casts were combined into three groups: newly hatched chicks (5–6.5 g), half-grown chicks (18–21 g), and adult birds (50–60 g). Conductance values for the single cast of an 11.5 g chick (not plotted) fall between those of the smaller and larger chicks. For all groups, thermal conductance can be expressed as a linear function of the square root of wind speed (u ; Table 2), as was assumed for calculations of the external thermal resistance r_e . Linear relationships between conductance and $u^{0.5}$ were also noted by Gessaman (1972) for the much larger Snowy Owl and by Robinson *et al.* (1976) with the White-crowned Sparrow.

Increased conductance at higher wind speeds is due to a combination of two factors: decreased external thermal resistance resulting from augmented forced convection, and lowered thermal resistance (r_b) within the feather coat itself. The r_b change is illustrated in

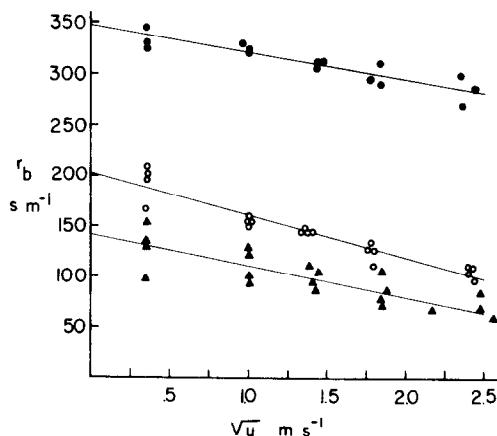


Fig. 2. Changes in body resistance to heat flow (r_b) with size and wind speed (u). Symbols as in Fig. 1; regression equations in Table 3.

Fig. 2. As with thermal conductance, r_b is approximately a linear function of $u^{0.5}$ (Table 3). Again, a similar relationship was reported by Robinson *et al.* (1976). The change in r_b is probably due to wind-induced disruption and penetration of the feather layer, resulting in increased intraplumage air movement. Theoretically r_b should be constant up to a critical windspeed (Davis & Birkebak, 1974), but no non-zero critical windspeed is discernible from my data. Slopes of the regression equations of r_b on $u^{0.5}$ are comparable to those of Robinson *et al.* (1976) and Monteith (1973).

The decrease in r_b with increasing wind speed has a greater net influence on total heat balance in chicks than in adult birds. Although the slopes of the r_b vs $u^{0.5}$ regressions for chicks and adults are essentially alike, the absolute r_b 's of chicks are much smaller than those of adults. Consequently, a change in wind speed from 0.1 $m s^{-1}$ to 5 $m s^{-1}$ decreases the r_b of an adult by only 15–20%, but a similar windspeed change reduces a chick's r_b by half (Fig. 2). The differential effects of wind on adult and chick r_b 's may be attributable to plumage differences; intuitively, the delicate natal down would seem to be more vulnerable to disruption by wind than the stronger, less flexible adult plumage. In unstirred air (u approximately

Table 2. Regression equations for heat transfer coefficient (C) on wind speed (u)

Weight (g)	Regression equation	r	N
5–6.5	$C = 5.1 + 3.27(u^{0.5})$	0.909	20
18–21	$C = 3.8 + 2.28(u^{0.5})$	0.972	20
50–60	$C = 2.3 + 3.92(u^{0.5})$	0.928	15

Table 3. Regression equations for body resistance to heat flow (r_b) on wind speed (u)

Weight (g)	Regression equation	r	N
5–6.5	$r_b = 139 - 26.7(u^{0.5})$	0.80	20
18–21	$r_b = 202 - 41.7(u^{0.5})$	0.94	20
50–60	$r_b = 347 - 25.2(u^{0.5})$	0.89	15

0.1 m s^{-1}) there seems to be no large difference in insulatory properties between adult feathers and down; the r_b values of both scale to coat thickness (t) according to the equation $r_b = 40.6t - 39$ ($r = 0.93$; $N = 17$, including unpublished data for Snow Buntings).

Leg skin temperatures were obtained from five chicks at ambient temperatures of 3.8°C , but data was limited because the chicks were easily frightened and quickly became hypothermic (data was rejected if T_b was below 30°C after a reading was made). Leg skin temperatures ranged from 7 to 13°C and averaged about 4.5°C above ambient temperature and 24°C below body temperature ($N = 7$). At typical T_a 's, heat loss from the legs amounts to 10–20% of total heat loss.

Ontogenic changes in the thermoregulatory capabilities of shorebird chicks in comparison with the thermal characteristics of the environment are diagrammed in Fig. 3. Except in unusual weather conditions (low wind speed, high T_a , and direct sunlight), chicks cannot attain energy balance and maintain constant T_b until they weigh 20–30 g.

Field tests of the predictive accuracy of equation 2 were limited by the rarity of sufficiently stable microclimate conditions during the time available for experiments. Data points from runs in which wind speed changed more than 25%, or air temperature shifted more than 2°C , were discarded. A total of 14 complete runs with the nine casts of chicks were obtained. Despite the paucity of data, the results indicate that equation 2 has good predictive value. The average error was about 9% (range 3.5–21%) in a variety of microclimates varying from the summer tundra surface in sunlight to snow surfaces exposed to the clear night sky in winter. There was no tendency to

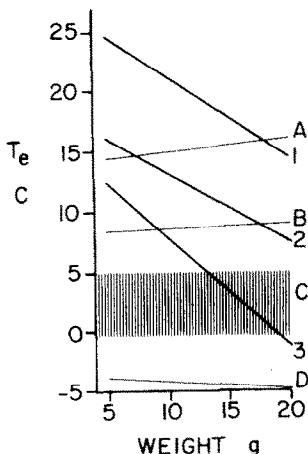


Fig. 3. Minimum tolerable effective environmental temperatures (T_e , heavy lines) for chicks of various sizes, as compared to ambient conditions (thin lines and shaded area). Line 1: $T_b = 38^\circ\text{C}$, wind speed (u) 1.0 m s^{-1} . Line 2: $T_b = 30^\circ\text{C}$, $u = 1.0 \text{ m s}^{-1}$. Line 3: $T_b = 30^\circ\text{C}$, $u = 0.1 \text{ m s}^{-1}$ (unusually low). Line A: $T_a = 10^\circ\text{C}$, $u = 0.1 \text{ m s}^{-1}$, direct sunlight (optimum conditions). Line B: $T_a = 5^\circ\text{C}$, $u = 1.0 \text{ m s}^{-1}$, direct sunlight. Area C: $T_a = 0.5^\circ\text{C}$, $u = 1.0 \text{ m s}^{-1}$, overcast (typical conditions, prevailing for most of a normal breeding season). Line D: $T_a = 0^\circ\text{C}$, $u = 1.0 \text{ m s}^{-1}$, shaded from sun but exposed to clear sky.

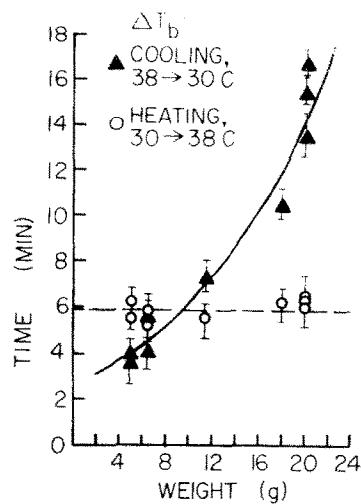


Fig. 4. Cast-derived heating and cooling times of chicks. Cooling conditions: maximum metabolic rate, $T_a = 0^\circ\text{C}$, $u = 1 \text{ m s}^{-1}$. Heating conditions: maximum metabolic rate, $T_a = 40\text{--}41^\circ\text{C}$ (hot-water bottle fitted around cast).

over or underestimate cast energy requirements (eight over and six underestimates), and no apparent difference in predictive accuracy among the different chick size groups.

The cooling times in simulated tundra microclimates and heating times in simulated brooding conditions are shown in Fig. 4. These are corrected for the difference in volumetric specific heat between animal tissue and Wood's alloy, and for the slightly larger conductances expected in living birds due to the heat loss from legs. Cooling times increase rapidly with increasing body size and are predicted accurately from mass (M) by the exponential curve: cooling time = $2.69 e^{0.0835M}$ ($r = 0.98$, $N = 35$). Measurements of cooling rates of casts in the field were very similar to those obtained in the laboratory, but were limited in number because of the same difficulties described for other field tests. Independent estimates of cooling rates, calculated from thermal conductances, are also similar to the laboratory measurements. Rather surprisingly, the heating rates do not change significantly as body size increases; in all cases the heating time was about 6 min (see Discussion).

DISCUSSION

Applicability of cast-derived measurements

Heat transfer coefficients obtained from metal casts should accurately simulate radiative and convective transfer across the skin and feathers. However, cast-derived measurements do not include the latent heat loss found in live birds, and casts cannot reproduce the possible insulative effects of peripheral vasoconstriction. Corrections for these factors must be made before the cast data can be used in calculations of energetics.

At the relatively low ambient temperatures encountered by shorebird chicks, evaporative water loss is probably quite small compared to other pathways of heat loss; equation 2 predicts that total latent heat loss will be only 5–7% of metabolic heat production at typical arctic summer T_a 's. Accounting for vaso-

constriction (tissue thermal resistance as opposed to coat thermal resistance) is more difficult, but small size may prevent vasoconstriction from having large effects on heat transfer from the main body surfaces. The thermal resistance of even nonvascularized fatty tissue is much smaller than that of fur or feathers (Porter & Gates, 1969). In neonate shorebirds, the distance from body core areas to the skin surface is usually less than 1 cm, which is about the same as coat thickness. Therefore, the importance of vasoconstriction as a heat retention mechanism, and its effect on r_b , is probably minor compared to that of the plumage.

A third factor missing from the heated-cast conductance measurements is heat loss from the birds' legs. For all sizes of chicks the calculated heat loss from the legs is 10–20% of total heat loss in typical environmental conditions. The low leg surface temperatures result in substantial heat conservation; if chicks maintained leg temperatures of 20°C above ambient (instead of 4–6°C), leg heat loss would be 40–60% of total heat flux. These loss rates are maximum values which assume the legs are completely extended. Normally, some parts of the legs are withdrawn under the feathers, and resting chicks often squat, completely covering the legs.

A partial check on the accuracy of the cast-derived heat transfer coefficients for unstirred air can be made by calculating conductances from the metabolic data of Norton (1973). The two approaches produce very compatible results: the metabolically derived values are about 15% higher than the heated-cast values. The difference is roughly equal to the estimated correction factors for evaporative and leg-surface heat loss. The close agreement suggests that, at least at low wind speeds, the casts accurately mimic the heat-exchange characteristics of living birds.

Energy balance of chicks in the natural habitat

Young chicks of arctic-breeding sandpipers tolerate an unusually wide range of T_b , apparently without large effects on behavior or locomotory ability (Norton 1973, personal observations). The ability to function at a T_b of 30°C has the obvious thermoregulatory advantage of reducing the thermal gradient between body and environment. Nevertheless, it is clear from this study and Norton's metabolic work that newly hatched chicks cannot independently maintain steady-state heat balance during typical summer weather conditions, despite the thermal advantages of the unusually low minimum T_b (Fig. 3). Except in rare circumstances (combinations of low wind speed, high T_a , and direct sunlight), environmental T_e 's are usually between 0 and 5°C, some 15–20°C below the minimum possible T_e for homeothermy of a 6 g chick. The maximum heat production of a chick this size would have to be more than doubled to attain thermal balance at $T_e = 5^\circ\text{C}$. There is a rapid increase in cold tolerance as chicks age (Fig. 3), due primarily to greater surface-area specific metabolism (increasing by 60% as a chick grows from 6 to 20 g), augmented by increasing r_b (Fig. 2) and decreasing convective losses (due to larger body diameter). However, chicks do not attain the ability to maintain constant T_b until they are at least half grown (20–30 g). Until this time,

they will require occasional parental brooding to supplement their own metabolic heat production.

The maximum metabolism values for chicks, used in Fig. 3, are not compensated for Q_{10} effects, although these are certainly possible over the 10°C range of tolerated T_b 's. Norton (1973) does not provide any direct empirical information on this problem. Body temperatures of chicks were not monitored continuously during his metabolism determinations, but they were measured at the completion of experimental runs. At this time-chick T_b 's varied from a high of 41°C to considerably less than 30°C, so the maximum metabolism figures are "averages" from chicks at many T_b 's. However, an examination of the individual data points (Norton 1973, chapter 4, Fig. 5) reveals surprisingly little variation in maximum metabolic rate, as long as T_b remained above 30°C. There was some indication that chicks with T_b less than 30°C (the approximate temperature for the onset of distress calls and locomotory dysfunction) were not able to produce as much heat as chicks with higher T_b .

Metabolic heat production should be increased somewhat during exercise; this could lower the minimum T_e limits of active chicks. However, in many small mammals and birds, exercise heat can substitute for thermoregulatory heat only partially or not at all (Bartholomew, 1977). If, as seems likely, the same is true for young shorebirds, exercise will have little effect on lower T_e limits. This problem deserves further investigation, but field observations (see below) indicate that chicks do not accrue substantial thermoregulatory benefits from exercise heat.

Advantages of chick thermolability

The low T_b 's tolerated by sandpiper chicks were interpreted as an energy-saving adaptation by Norton (1973). He reasoned (quite correctly) that it would be energetically cheaper for chicks to operate at low rather than high T_b in the face of cold ambient conditions. This interpretation is somewhat questionable, however, in view of the fact that even at $T_b = 30^\circ\text{C}$, small chicks (<20 g) cannot maintain steady-state energy balance during typical weather conditions. An alternative explanation is that chick thermolability increases foraging ability. The dependance of chicks on parental brooding imposes a cycle on foraging behavior: Chicks will feed actively until T_b falls below the critical minimum of 30°C, at which point brooding is solicited with distress notes. After warming by the parent birds, the chicks initiate another bout of foraging (Norton 1973, personal observations). Maximizing the foraging time–brooding time ratio, and the lengths of each bout of activity, is obviously important for the energetic efficiencies of both parents and chicks. The ability of chicks to function within a wide range of T_b 's helps maximize foraging time; a chick with a large T_b tolerance will obviously take longer to cool to minimum tolerable T_b than will a similar chick with smaller tolerance. This situation is closely analogous to the use of hyperthermia and hypothermia to extend activity periods in chipmunks from hot, arid habitats (Chappell *et al.*, 1978).

One seeming disadvantage of a wide T_b tolerance is that longer brooding periods are necessary to bring T_b back up to high levels. This tradeoff is ameliorated

by the shift in thermal gradients as T_b changes: The increase in heating time required for low minimum T_b 's is proportionately less than the increase in cooling time they provide. A chick at low T_b loses heat to the environment slowly (due to the reduced thermal gradient), but gains heat rapidly when brooded. Conversely, a warmer chick cools rapidly, but heats slowly. If a chick could increase its T_b tolerance $2 \times$ (minimum T_b of 20°C), the cooling time in typical climatic conditions would increase by about $2.4 \times$, but heating time would only increase about $1.5 \times$. This is an increase of $1.6 \times$ in the cooling time-heating time ratio. Expansion of the already wide T_b tolerance is probably limited by biochemical factors, especially the difficulty of maintaining efficient enzyme function over such a wide temperature range.

The ontogenic changes in the activity time-brooding time ratio can be seen in Fig. 4. Warming time from $T_b = 30^\circ\text{C}$ to 38°C remains constant at about 6 min as chicks grow from 6 to 20 g, due to the compensating effects of decreasing surface-volume ratio and increasing surface-area specific metabolism. Cooling time, however, increases dramatically and exponentially as chicks age; as a result a much greater proportion of total time can be spent active. When a chick reaches a weight of 25–30 g, cooling times become essentially infinite; the ability to maintain T_b without brooding has been attained.

Unfortunately, there is little good field data on chick activity times, due to the difficulty of observing chicks without influencing their behavior. Norton (1973) reported 1- and 2-day old chicks (6 g) foraging continuously for up to 30 min at T_a 's of $0-5^\circ\text{C}$; however, the wind speed and radiation conditions were not recorded so T_c cannot be calculated. Thirty min is much longer than estimated activity times for $T_c = 0-5^\circ\text{C}$, but if the sun is shining and wind speed is low, near-ground air temperature can be around 10°C and T_c as high as $15-20^\circ\text{C}$. This T_c is compatible with a 30 min cooling time. Observations of complete brooding-activity cycles at T_c 's ranging from 3 to 7°C yielded cooling times of the same magnitude as predicted experimentally ($N = 9$; weight range 6.5–18 g). Initial T_b was not measured, but was assumed to be about 38°C (Norton's average for chicks brooded >5 min); T_b at the onset of distress calls averaged 31°C (range $29-33^\circ\text{C}$). In no case was activity time more than 15% greater than predicted, even though all chicks were exercising vigorously; in six of nine observations activity time was less than the predicted maximum (average 85% of predicted). These findings argue against the hypothesis that exercise heat adds significantly to thermoregulatory heat, and indicate that the experimental cooling times are at least approximately correct.

Tundra-breeding shorebirds can take advantage of the huge burst of insect productivity that occurs during the arctic summer (Pitelka *et al.*, 1974), but in order to do so their chicks must be able to survive and grow in the face of severe cold stress. Small chicks are poorly insulated and have inadequate heat-production capacities for independent maintenance of thermal balance; the parents compensate for this deficiency by periodically brooding the chicks until they are half grown. The highly labile body temperature of chicks appears to be a key adaptation which

greatly enhances the efficiency of the brooding activity cycle.

Acknowledgements—This paper is a result of work done as a postdoctoral fellow at the Naval Arctic Research Laboratory under ONR contract N00014-77-0167. J. P. Myers, D. W. Norton, L. M. Philo, and E. H. Follmann provided much helpful advice, and G. A. Bartholomew critically read the manuscript.

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