

Metabolic response to wind of downy chicks of Arctic-breeding shorebirds (Scolopacidae)

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Summary

Wind is a significant factor in the thermoregulation of chicks of shorebirds on the Arctic tundra. We investigated the effect of wind at speeds typical of near-surface conditions ($0.1\text{--}3\text{ m s}^{-1}$) on metabolic heat production, evaporative cooling and thermal conductance of 1- to 3-week-old downy scolopacid chicks (least sandpiper *Calidris minutilla*; short-billed dowitcher *Limnodromus griseus*; whimbrel *Numenius phaeopus*). Body mass ranged from 9 to 109 g. To accurately measure the interacting effects of air temperature and wind speed, we used two or more air temperatures between 15° and 30°C that produced cold stress at all wind speeds, but allowed chicks to maintain normal body temperature (approximately 39°C). Thermal conductance increased by 30–50% as wind speed increased from 0.1 to 3 m s^{-1} . Conductance in

these chicks is somewhat lower than that of 1-day-old mallard ducklings of similar mass, but higher than values reported for downy capercaillie and Xantus' murrelet chicks, as well as for adult shorebirds. Evaporative water loss was substantial and increased with mass and air temperature. We developed a standard operative temperature scale for shorebird chicks. The ratio of evaporative cooling to heat production varied with wind speed and air temperature.

Key words: shorebird, thermoregulation, wind speed, conductance, insulation, standard operative temperature, metabolism, evaporative water loss, down, least sandpiper, *Calidris minutilla*, short-billed dowitcher, *Limnodromus griseus*, whimbrel, *Numenius phaeopus*.

Introduction

Many shorebird species (Scolopacidae and Charadriidae) migrate long distances to breed on the Arctic tundra (Piersma et al., 1996). On arrival, energy reserves of individuals are small, and consequently the energy needed to provide for eggs and chicks comes from the brief summer abundance of arthropod food items (Järvinen and Väisänen, 1978; Klaassen et al., 2001). Shorebird chicks leave the nest soon after hatching to follow their parents and forage for food (Nice, 1962). Success requires chicks to grow to maturity quickly while food is available, and to do this while exposed to the frequently cold and windy Arctic microclimate.

Because downy chicks are poorly insulated compared to adults (McNabb and McNabb, 1977; Taylor, 1986; Visser, 1998), foraging and thermoregulation costs are high, accounting for 25–30% of the total energy budget (Schekkerman and Visser, 2001). Moreover, foraging requires physiological maturity of muscle tissue for effective locomotion and thermoregulation, while rapid growth is typically associated with physiological immaturity (Ricklefs et al., 1994; Visser and Ricklefs, 1995; Starck and Ricklefs, 1998;

Krijgsveld et al., 2001). This conflict limits the peak metabolic rate of young chicks.

Thus, foraging chicks often cannot, or at least do not, maintain a stable body temperature (T_b). Chicks of some species can continue foraging until T_b falls as low as 30°C (Norton, 1973), but nevertheless parental brooding eventually becomes necessary. Because brooding prevents foraging by both the chicks and the brooding parent, adverse weather can depress growth (Beintema and Visser, 1989a; Schekkerman et al., 1998; Schekkerman and Visser, 2001). To understand the behavior, physiology and energetics of Arctic breeding one must therefore relate foraging time and thermoregulatory costs to thermal conditions. Given the scarcity of shelter on the tundra, wind is likely to be a significant factor in the cost of Arctic shorebird thermoregulation (Piersma and Morrison, 1994; Wiersma and Piersma, 1994). Although some authors have remarked that down seems rather sensitive to wind (Taylor, 1986; Visser, 1998), the effect of wind on downy chicks has received but limited attention (Bakken et al., 1999), and no data are available on shorebird chicks.

We measured oxygen consumption in relation to temperature and wind speed in downy scolopacid chicks of different ages varying in mass by an order of magnitude. Chicks were from species with small, medium and large adults: least sandpipers *Calidris minutilla* (approx. 20–30 g), short-billed dowitchers *Limnodromus griseus* (approx. 100–130 g) and whimbrels *Numenius phaeopus* (approx. 300–400 g). Heat loss from the legs and bill during cold stress is minimized by countercurrent heat exchange in a wide range of species (Ederstrom and Brumleve, 1964; Steen and Steen, 1965; Kilgore and Schmidt-Nielsen, 1975; Hagan and Heath, 1980; Midtgård, 1980). Consequently, the variation in relative leg and bill length of growing shorebird chicks of different species is probably unimportant. As their morphology is otherwise similar, we describe thermoregulatory responses by a single allometric model. We also use our data to define a standard operative temperature (T_{es}) scale that may be useful in field studies of shorebird chick behavior and energetics. Standard operative temperature is the temperature of a standard respirometer with essentially no wind, within which the same animal would have the same net heat production (Bakken, 1976, 1992).

Materials and methods

Animals

We conducted this study at the Churchill Northern Studies Centre, Churchill, Manitoba, Canada, during the summer of 1997. We collected eggs from different clutches of least sandpiper *Calidris minutilla* Vieillot, short-billed dowitcher *Limnodromus griseus* Gmelin and whimbrel, *Numenius phaeopus* L., and transported them to the laboratory, where they were incubated at 37°C and 80% relative humidity. After hatching, chicks were kept in boxes with an elevated wire mesh floor over sawdust. A light bulb in one corner of each box allowed chicks to thermoregulate behaviorally until they were fully homeothermic at room temperature. The lights were then removed. Food (turkey starter, canned tuna, boiled eggs and fresh insects) and water were provided *ad libitum* (for details, see Krijgsveld et al., 2001). Eggs were collected under permit from the Canadian Wildlife Service, and laboratory procedures were approved by the Institutional Animal Care and Use Committee of the University of Missouri – St Louis.

Experiments were begun when body mass was equal to or greater than 9 g (approx. 7 days post-hatching) for least sandpipers ($N=4$), 20 g (5 days) for dowitchers ($N=8$), and 63 g (7 days) for whimbrels ($N=4$). Studies were continued until contour feathers began to appear, at which time body mass was less than 18 g (14 days) for least sandpipers, 56 g (19 days) for dowitchers and 109 g (11 days) for whimbrels.

Body temperature

We measured T_b at 1 min intervals to within $\pm 0.1^\circ\text{C}$ with a 36AWG (0.13 mm conductors, 0.14 mm \times 0.69 mm overall) Teflon[®]-insulated duplex thermocouple (type TT, Omega

Engineering, Stamford, CT, USA). We looped one full turn of the wire through the thread holes of a clothing button, cemented it in place with the sensing junction extending 1–2.5 cm beyond the button, and rounded the sensing junction with a drop of epoxy cement. We matched button diameter and probe length to the size of the chick. At the time of the experiment, we lubricated the sensing junction with petroleum jelly, and inserted it into the cloaca. We then secured the assembly by folding several nearby feathers over the button and gluing them to the button with cyanoacrylate adhesive. At the end of the experiment, the glue was dissolved with acetone to release the feathers so that the thermocouple could be removed. Because some down was lost each time, we limited body temperature measurements to approximately 40% of our runs to avoid increasing normal rates of heat loss. We monitored T_b during the first experiments in each size class to avoid conditions leading to hypothermia. We also monitored T_b on a random sample of chicks thereafter.

Experimental conditions

Our experimental conditions excluded solar radiation and simulated the cold, windy conditions experienced by chicks during storms, heavy overcast days, or the brief Arctic night. Our small-volume wind tunnel metabolism chamber was limited to winds of speeds less than 3.5 m s^{-1} (Bakken et al., 1989). However, this range of wind speed is sufficient to determine the quantitative trend of wind effects. Further, wind speed varies logarithmically with height (Campbell et al., 1980), such that wind measured at 10 cm height over tundra is only 20–35% of that measured 3 m above the surface (G.S.B., unpublished data from four tundra sites near the Churchill Northern Studies Centre). Thus, our data can be used directly with standard wind speeds up to $8\text{--}15\text{ m s}^{-1}$ ($30\text{--}50\text{ km h}^{-1}$). Finally, internal temperature gradients and peak metabolic rates vary with body temperature, which complicates accurate measurements of thermal conductance on cooling animals (Eppley, 1994; O'Conner, 1999). Consequently, we used experimental air temperatures chosen such that chicks were normothermic but below their lower critical temperature at all wind speeds.

Gas exchange

We measured oxygen consumption and evaporative water loss at four wind speeds (u ; 0.1, 0.8, 1.8 and 3.0 m s^{-1}) and at least two air temperatures (T_a) between 15° and 30°C , the exact value of T_a depending on the age and mass of the chick. Procedures generally follow those detailed in earlier studies (Bakken et al., 1991, 1996), with some changes in instrumentation. We measured oxygen consumption using an open-circuit system supplied with dry, CO_2 -free, outdoor air at 1.1 l min^{-1} , measured using a precision rotameter (Brooks Full View, Emerson Electric, Hatfield, PA, USA) calibrated on-site against a bubble meter (Levy, 1964). We measured the oxygen content of a dry, CO_2 -free subsample (200 ml min^{-1}) of chamber air with an electrochemical oxygen analyzer (FC-1,

Sable Systems, Henderson, NV, USA) and the water vapor density of a separate subsample (200 ml min^{-1}) using a dewpoint hygrometer (880, EG&G, Waltham, MA, USA). We corrected all values to standard temperature and pressure (STP) using an electronic readout barometric pressure transducer (Model 2014-27/31.5, YSI Instruments, Yellow Springs, OH, USA). We calibrated fan-shaft revs min^{-1} , measured with a dedicated phototachometer, against wind speed, measured with a Prandtl-design Pitot tube and electronic hook gauge (Dwyer Instruments, Michigan City, IN, USA). We measured various temperatures with copper-constantan thermocouples (type TT, Omega Engineering, Stamford, CT, USA). A digital data logger (CR-21X, Campbell Scientific, Logan, UT, USA) recorded T_a , T_b and rotameter temperature, analyzer outputs and fan revs min^{-1} . Control outputs were used to automatically step through a predetermined randomized sequence of wind speeds and switch a solenoid valve at 1 min intervals to alternate sample and reference gas flow to the FC-1 for continuous baseline correction. The FC-1 equilibrated within 40 s of switching, including washout time for the analyzer gas scrubbers. We used Z-transform methods to compute 'instantaneous' oxygen consumption and evaporative water loss for each 2 min sample interval (Bartholomew et al., 1981; Bakken, 1991a).

After weighing the chick, we installed the cloacal thermocouple and placed it in the chamber, before allowing 30 min for it to recover from handling. We then conducted measurements for 30 min at each wind speed. At the end of the run, we removed the thermocouple, reweighed the chick, and returned it to its box no more than 3.5 h after it was first removed. Because we needed to maintain normal growth patterns while making maximum use of a limited number of chicks, we made no attempt to ensure that chicks were post-absorptive. Consequently, the respiratory exchange ratio may have varied during the run. The order of wind speeds was randomized during each series to minimize any resulting bias in our estimates of the effect of wind on heat loss. Total chick metabolism included basal, thermoregulatory and active metabolism, the heat increment of feeding (SDA) and growth. We assumed full thermoregulatory substitution of all forms of metabolic heat production, which may or may not be correct (Hart, 1952; Paladino and King, 1984; Klaassen et al., 1989; Webster and Weathers, 1990; Zerba and Walsberg, 1992; Zerba et al., 1999).

Data analysis

Data were converted to heat production M (W) and evaporative cooling E (W), assuming $20.08 \text{ J ml}^{-1} \text{ O}_2$ consumed and $2427 \text{ J g}^{-1} \text{ H}_2\text{O}$ evaporated. We discarded all data from chicks that became hypothermic during the experiment ($T_b < 37^\circ\text{C}$). Also, data points identified as outliers (studentized residuals > 3) in a preliminary multiple-regression model were further scrutinized, and the entire run was discarded if there was evidence of hyperactivity or abnormal experimental conditions during the measurements.

To allow comparison of thermoregulatory responses across

the full range of age and body mass, we computed overall thermal conductance, K_o :

$$K_o = (M - E) / (T_b - T_a), \quad (1a)$$

and, for comparison with older studies, wet thermal conductance, K_{ow} :

$$K_{ow} = M / (T_b - T_a), \quad (1b)$$

where both K_{ow} and K_o are $\text{W } ^\circ\text{C}^{-1}$.

We used SYSTAT 7.0 (SPSS, Chicago, IL, USA) for all statistical analyses. Because of the considerable inter- and intraspecific variation in mass, we conducted allometric analyses using \log_{10} -transformed data when appropriate to ensure homogeneity of variances. Homogeneity of variance was then verified by examining residual plots. To allow statistical analysis, we assumed that rapid growth justified treating each measurement as independent. This assumption is not strictly correct, and consequently our results apply only to the specific animals studied. In any event, the greatest source of uncertainty in applying our data to wild chicks is systematic rather than statistical, namely the effects of captive rearing. For example, captive shorebird chicks may have lower total energy requirements and higher average growth rates than wild ones (Beintema and Visser, 1989b; Schekkerman and Visser, 2001).

Results

Body temperature

The variation in T_b values in an individual chick during a run generally exceeded the variation among birds. Therefore, we treated the mean T_b value at each wind speed as an independent measurement. For each run, this yielded four temperature measurements spaced at 30 min intervals. Nearly all such T_b measurements fell within the $38\text{--}40^\circ\text{C}$ range. The main exceptions were for a few of the smallest sandpipers and dowitchers near the end of measurements at the highest wind speed, 3 m s^{-1} . Generally, if T_b fell below 37°C it would continue to decrease. We excluded these cases as incipiently hypothermic. For the remaining data, average T_b values were $39.24 \pm 0.45^\circ\text{C}$ (mean \pm S.D., $N=15$) for whimbrels, $38.73 \pm 0.56^\circ\text{C}$ ($N=38$) for dowitchers, and $38.56 \pm 0.80^\circ\text{C}$ ($N=9$) for least sandpipers. These values are consistent with other data on chicks of the same species (J.B.W., unpublished data), and were assumed in calculations for experiments when T_b was not measured.

Heat is stored or released when chick T_b changes, and this needs to be included in the overall energy budget (Eppley, 1994). We estimated the maximum rate of heat storage or release as $c_p m (\Delta T_b / \Delta t)$, where m is body mass (g), c_p is tissue heat capacity (3.48 J g^{-1}) and t is time (s). However, for the T_b variation observed in our normothermic chicks, heat storage was negligible relative to the average energy expended during a 30 min interval.

Evaporative water loss

Evaporative water loss from shorebird chicks varied with

Table 1. Allometric models describing overall thermal conductance K_o and wet thermal conductance K_{ow} for adult nonpasserine birds and shorebird chicks

	Model			Statistics	
	C_0	$\log_{10}(m)$	u	Adj. r^2	F
Dependent variable $\log_{10}(K_o)$, $K_o=(M-E)/(T_b-T_a)$					
Adult nonpasserines ^a	-2.427	0.52			
Shorebird chicks	-2.122	0.466	0.0594	0.88	$F_{2,116}=429$
Dependent variable $\log_{10}(K_{ow})$, $K_{ow}=M/(T_b-T_a)$					
Adult nonpasserines ^b	-2.326	0.46			
Adult summer nonpasserine ^c	-2.505	0.57			
Adult winter nonpasserine ^d	-2.655	0.59			
Adult nonpasserine active phase	-2.278	0.52			
Adult shorebirds ^f	-2.467	0.56		0.97	$F_{1,6}=281$
Shorebird chicks	-1.869	0.399	0.0433	0.86	$F_{2,116}=361$

^aCalder and King (1974), equation 14b.

^bCalder and King (1974), equation 14.

^cKendeigh et al. (1977), equation 5.8.

^dKendeigh et al. (1977), equation 5.

^eAschoff (1981), active-phase nonpasserines.

^fOur regression fitted to data from Kersten and Piersma (1987), table 3, for *Arenaria interpres*, *Pluvialis squatarola* and *Haematopus ostralegus* adults (118–540 g), plus data for *Charadrius dubius* (36 g) and *Scolopax rusticola* (mass 430 g) from Kendeigh et al. (1977), Appendix 5.1.

mass and T_a . The best-fit (adj. $r^2=0.76$, $F_{2,117}=188$) model for evaporative cooling E (W) was:

$$\log_{10}E = -1.53 + 0.395\log_{10}m + 0.00926T_a\log_{10}m. \quad (2)$$

The interaction term between T_a and m was highly significant ($t=5.02$, $P<0.00001$) and resulted in a 10% decrease in the standard error of the estimate. This indicates that the effect of air temperature on evaporation varied with chick size, possibly because convective heat and mass transport vary with body size (Gates, 1980). Evaporative water loss in these shorebird chicks appears relatively high compared to other birds (Fig. 1). The published regression lines included for comparison are for thermally neutral temperatures, and consequently our data and regression in Fig. 1 have been adjusted to $T_a=25^\circ\text{C}$ using Equation 2. Note that we measured evaporative water loss primarily to estimate the effect of wind on dry thermal conductance, and did not attempt to standardize chamber vapor pressure. Consequently, our evaporative water loss data should be used with caution.

Thermal conductance

Wind speed u affects both boundary layer convection processes, which are proportional to $u^{0.5}$, and dynamic processes (wind displacement of and penetration among insulating fibers), which are proportional to u^2 (Bakken, 1991b). The net result is that overall thermal conductance is related to u raised to an intermediate exponent, the value reflecting the weighting of convective and dynamic processes by the structure of the insulation. Therefore, we first fitted a preliminary model of the form $a+bu^c+dm^f$ to our data, where a , b , c , d and f are fitted coefficients. The best-fit wind speed

exponents were $c=1.04$ – 1.09 . The exact value of c was not critical, and consequently $u^{1.0}$ was used in the final allometric models (Table 1).

We also plotted conductance as a function of body mass (Fig. 2A,B), using LOWESS (locally weighted scatterplot smoother) regressions (Cleveland, 1985) to data at each of the four wind speeds. The LOWESS lines suggest that the

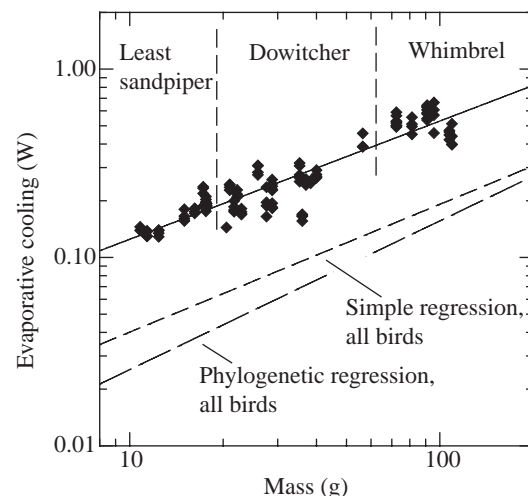


Fig. 1. Logarithmic plots of daily total evaporative water loss (g day^{-1}) as a function of body mass. As evaporative water loss from birds is sensitive to ambient temperature, Equation 2 was used to adjust both plotted data and the regression line to a nearly thermally neutral 25°C for comparison with simple and phylogenetic allometric regression models for birds in thermally neutral conditions (equations 2 and 7 in Williams, 1996).

correlations between both $\log_{10}K_o$ and $\log_{10}K_{ow}$ and $\log_{10}m$ are nonlinear, and that wind has a relatively greater effect on the smallest chicks, a result expected from convective transport theory. LOWESS does not assume a particular model, and thus

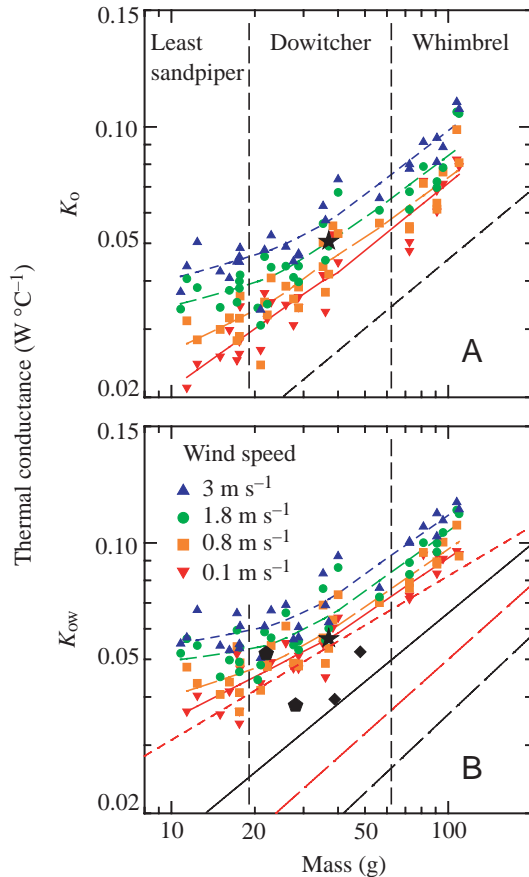


Fig. 2. Logarithmic plots of thermal conductance *versus* body mass for downy shorebird chicks showing that conductance increases markedly with wind, especially for smaller chicks. To show trends, LOWESS (locally weighted scatterplot smoother) regressions have been fitted to data taken at wind speeds of 0.1 m s^{-1} (solid red line), 0.8 m s^{-1} (broken orange line) 1.8 m s^{-1} (broken green line) and 3.0 m s^{-1} (dotted blue line). (A) Dry conductance $K_o = (M - E)/(T_b - T_a)$. The dashed black line is a regression to data on adult nonpasserines (Calder and King, 1974). For comparison, the conductance of 1-day-old mallard ducklings exposed to 0.1 m s^{-1} wind is indicated with a black asterisk (Bakken et al., 1999). (B) Wet conductance $K_{ow} = M/(T_b - T_a)$. The results for our 7- to 10-day-old chicks at 0.1 m s^{-1} are consistent with data on newly hatched (<24 h-old) shorebirds in still air (dotted red line; $K_{ow} = 0.0125m^{0.371}$) (Visser and Ricklefs, 1993). The conductances of notably cold-resistant downy chicks are shown for comparison, including 1-day-old mallards (asterisk; Bakken et al., 1999), 2-day and 6-day-old Xantus' murrelets (pentagon; Eppley, 1984), and 3-day and 6-day-old capercaillie (diamonds; Pis, 2002). Also shown are some regression models for adult conductance: broken red lines, our regression to data from adult shorebirds (36–540 g; Kersten and Piersma, 1987; Kendeigh et al., 1977); solid black lines, active phase adult nonpasserines (Aschoff, 1981); broken black lines, winter adult nonpasserines (Kendeigh et al., 1977). Model parameters are given in Table 1.

cannot provide statistical information on goodness-of-fit that might test the reality of, or hypotheses about, the curvature. (Indeed, the goodness of fit is set *a priori* by the LOWESS tension parameter.) We tested polynomial regressions on body mass, as well as regressions where each species was assigned a dummy variable equal to 1 if the data applied to that species and 0 otherwise (Draper and Smith, 1981). These models explained significantly more variance than the linear model, indicating the relation is indeed nonlinear. However, we cannot discriminate between phylogenetic and mass-related physical effects such as convection because mass and taxon are confounded.

Standard operative temperature scale

Standard operative temperature T_{es} is the temperature defined by an enclosure with free-convection conditions ($u=0$) in which the animal with the same body temperature T_b would have the same net heat loss as it does in its actual environment (Bakken, 1976, 1992). We defined a standard operative temperature (T_{es}) scale appropriate for use in the absence of thermally significant visible radiation. For this case, operative temperature T_e equals air temperature T_a , and:

$$T_{es} = T_b - (K_o/K_{os})(T_b - T_a). \quad (3a)$$

The overall thermal conductance in the reference enclosure is K_{os} , and the overall thermal conductance in the actual environment is K_o . Using the regression equations in Table 1 to define K_o and K_{os} gives T_{es} scales based on dry conductance:

$$T_{es} = T_b - 10^{0.059u}(T_b - T_a), \quad (3b)$$

and wet conductance

$$T_{esw} = T_b - 10^{0.043u}(T_b - T_a). \quad (3c)$$

However, these equations may slightly underestimate the effect of wind on the T_{es} experienced by the smallest chicks, because of the known greater importance of convective heat transfer for smaller animals noted earlier.

Discussion

Standard operative temperature

In the absence of solar radiation, the main factor causing T_{es} to differ from T_a is wind speed. Early studies of the effect of wind speed on thermoregulation almost always presented their data as regressions using $u^{1/2}$ as the independent variable. This practice was based on engineering relationships developed for smooth metal surfaces (Porter and Gates, 1969). This $u^{1/2}$ response was imposed on the relationship between wind and thermal conductance, and carried over to T_{es} scales based on these published data. This includes the general passerine scale proposed by Bakken (1990):

$$T_{es} = T_b - (1 + 0.26u^{1/2})(T_b - T_a). \quad (4)$$

This dependence is incorrect for porous insulation, as noted earlier (Campbell et al., 1980; Bakken, 1991b; Bakken et al., 1999). Correlations based on $u^{1/2}$ overestimate the effect of

small increases in wind speed, but the practical significance is not obvious. Given the observation that the thermal conductance of contour feathers varies as approximately $u^{0.7}$, and fur or down as $u^{1.0}$, (present study; Bakken, 1991b; Bakken et al., 1999), the overall effect of imposing a $u^{1/2}$ on the T_{es} scale should be evaluated for both down and contour feathers.

A suitable published T_{es} scale for adult birds with contour feathers is not available, so we reanalyzed data on dark-eyed juncos from Bakken et al. (1991). The best-fit relation had conductance vary as $u^{0.7}$. The corresponding T_{es} scale is:

$$T_{es} = T_b - [(0.015 + 0.00023T_a + 0.0026u^{0.7}) / (0.015 + 0.00023T_{es})](T_b - T_a). \quad (5)$$

For downy chicks that respond to $u^{1.0}$, we used Equations 3a and 3b, plus a T_{es} scale developed for 1-day-old mallard ducklings (equations 4 and 5 in Bakken et al., 1999). The junco and mallard T_{es} scales involve recursive relations, and were solved numerically (Bakken et al., 1991).

Because these T_{es} scales have different mathematical forms, they are best compared graphically (Fig. 3). Comparisons assume the average conditions of the present study, $T_a=20^\circ\text{C}$ and $u=0-3\text{ m s}^{-1}$. The importance of wind is evident, as even at room temperature, a wind speed of 3 m s^{-1} decreases T_{es} by $7-8^\circ\text{C}$ and increases heat loss by 40–50%. The overall effect of wind, and thus the effect of differences in wind response among temperature scales, is greater at lower T_a values. While the relative effect of wind on T_{es} is similar among the downy chicks and adult passerines, the effect on required heat production also depends on the baseline conductance at low wind speed:

$$M - E = K_{os}(T_b - T_{es}). \quad (6)$$

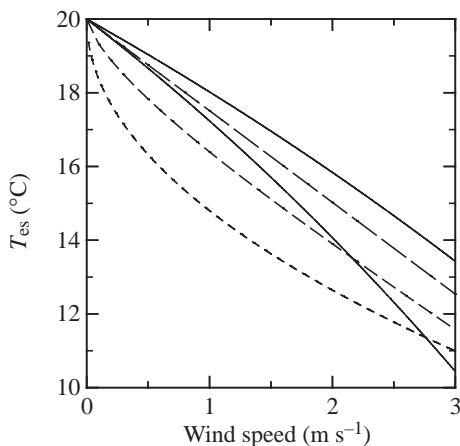


Fig. 3. Comparison of the effect of wind speed on operative temperature T_{es} given by different T_{es} scales. Solid lines, 25 g shorebirds (upper line, Equation 3b; lower line, Equation 3c). Long broken lines, dark-eyed junco modeled using the best-fit wind speed dependence of $u^{0.7}$ (junco data taken from Bakken et al., 1999). Short broken lines, mallard ducklings using the best fit wind-speed dependence of $u^{1.0}$ (Bakken et al., 1999). Dotted line, Equation 4, based on published data using $u^{0.5}$ (Bakken, 1990). See text for discussion.

Thus, the substantially higher conductance of chicks (Fig. 2) means they experience a greater absolute change in energetic cost for a given change in T_{es} .

The only clear conclusion about the effect of different wind speed exponents is that the correlation using $u^{1/2}$ is too sensitive to wind speeds from 0.5 to 1.5 m s^{-1} , and that the discrepancy is most significant for downy chicks. Otherwise, the shorebird chick scales based on wet and dry thermal conductance bracket the mallard scale and overlap the junco scale. These differences are within experimental error.

Evaporative water loss

During the experiments, humidity was generally higher than has been recommended for making standardized evaporative water loss measurements (Lasiewski et al., 1966). The high chamber humidities were unexpected, as we were examining the response of animals below their lower critical temperature, where evaporative water loss is generally low. The dewpoint increased significantly ($P<0.001$) with the size of the bird. Consequently, the E of small birds may be exaggerated compared to the larger ones, and this may account for the shallower slope of the shorebird chick regression compared to the adult correlation (Fig. 1). High chamber humidity should have decreased evaporation, but nevertheless our measured values of evaporative water loss from shorebird chicks, adjusted to $T_a=25^\circ\text{C}$ using Equation 2 (Fig. 1), are substantially higher than comparable values for adult birds under thermally neutral conditions (Williams, 1996).

Calder and King (1974) suggested that, to a first approximation, the ratio E/M should be mass-independent. Briefly, they argued that metabolism is proportional to respiratory minute volume, as is respiratory water loss. Further, metabolism is proportional to mass, as is surface area, and cutaneous water loss is proportional to surface area. Indeed, their review of published data demonstrated that, at a given temperature, E/M had a consistent relationship to ambient temperature, across a wide range of body mass. It is particularly interesting that while E and M are positively correlated with each other and with mass at one temperature, they are negatively correlated across temperatures, such that $E/M=0.05+0.0148\exp(0.087T_a)$. Bartholomew (1972) suggested that the remarkable ability of birds to decrease E when M , and thus minute volume, was increasing was because colder inspired air chilled the respiratory tract, and thus water condensed on the respiratory passages when exhaled. Respiratory passages were increasingly chilled as ambient air temperature decreased, and consequently the temperature of exhaled air decreased, and therefore its water content. This mechanism is not affected by wind, and E should thus remain constant or even increase when convective cooling increases M . Consequently, one expects E/M should track T_a as in Calder and King's equation, and perhaps even increase when wind increased M at a given T_a .

In shorebird chicks, we found that M and E are correlated with each other ($r=0.66$, $P<0.00001$), and with body mass. However, we were unable to fit Calder and King's exponential

to our data. Using a linear model, we found E/M increased with T_a ($P < 0.00001$) as expected, but contrary to expectation, E/M decreased rather than increased with wind speed u ($P < 0.00001$):

$$E/M = -0.016 + 0.0136T_a - 0.0282u \quad (7)$$

(adjusted $r^2 = 0.65$, $F_{2,117} = 111$). Evaporation thus appeared to respond to aggregate cold stress rather than air temperature. When we used T_{es} to incorporate convective cooling in the temperature variable, the Gauss–Newton least-squares routine in SYSTAT easily fitted Calder and King’s exponential:

$$E/M = 0.064 + 0.055 \exp(0.062T_{es}) \quad (8)$$

(adjusted $r^2 = 0.641$, $N = 120$). These data, Equation 8 and Calder and King’s correlation have been plotted in Fig. 4. This relationship to T_{es} is consistent with earlier work, which found that T_{es} was a better predictor of E/M than T_a when radiation was present (Bakken, 1980), but begs a physical explanation.

We suggest that reduced skin temperature and relatively high cutaneous evaporative water loss may account for the wind effect. Because down is relatively poor thermal insulation, a significant part of the overall resistance to heat loss is provided by tissue. Thus, a wind-induced increase in heat loss reduces skin temperature with no change in air temperature. Reduced skin temperature may reduce E via two mechanisms unrelated to M , and thus decrease E/M : (1) a low skin temperature causes vasoconstriction and reduces water movement to the skin by increasing the diffusion distance for liquid water; (2) the vapor pressure of the water that does reach the stratum corneum decreases with air temperature.

This wind effect on E/M was not seen in a study of adult juncos (Bakken et al., 1991), possibly because they are better insulated so that skin temperature is less affected by wind

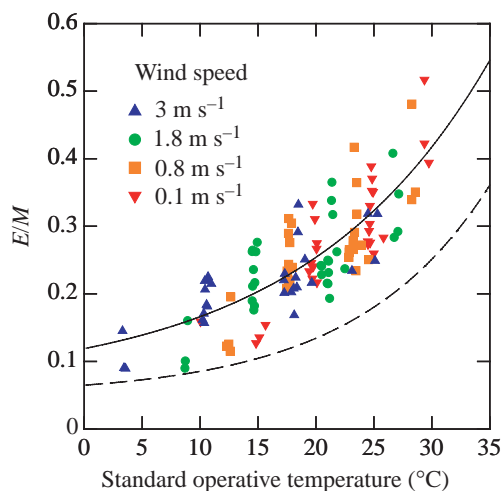


Fig. 4. The ratio of evaporative cooling E to metabolic heat production M for shorebird chicks varies with standard operative temperature T_{es} , and is independent of body mass. The solid curve is an exponential function fitted to these data (see text), and the broken line is the correlation found by Calder and King (1974).

(thermal conductance of shorebird chicks is 30–60% greater than that of juncos of similar mass).

Down versus contour feathers as insulation

Wind has a substantial effect on thermal conductance. For a 25 g bird (the approximate geometric mean for our study), increasing wind speed from 0.1 to 3 m s⁻¹ increased K_o by 50% and K_{ow} by 30%. Data from heated taxidermic mounts (Bakken, 1991b) indicated that the thermal conductance of contour feather insulation increases with wind speed as $u^{0.7} - u^{0.8}$. Fur is more affected by dynamic processes and responds as $u^{1.0}$, with some very soft furs on strongly curved surfaces responding as $u^{1.5}$. The best exponent for downy shorebird chicks was 1.04–1.09, which indicates a fur-like response to wind matching the fur-like appearance of down.

Because the chicks of Arctic-breeding shorebirds are often exposed to cold, one might expect their down to provide unusually effective insulation. In Fig. 2, we compare our data with other chicks and regressions to data on adult birds with contour feathers. The downy insulation of shorebird chicks was slightly better than that of day-old mallard ducklings (*Anas platyrhynchos*), but inferior to the extremely dense down of notably cold-hardy capercaillie (*Tetrao urogallus*; Pis, 2002) and Xantus’ murrelet (*Synthliboramphus hypoleucus*; Eppley, 1984) chicks. The down of the latter two approaches the insulating value of summer adult plumages (Fig. 2B). Comparison with various regressions for adults indicates that shorebird chicks are rather poorly insulated compared to adults. The regression coefficients for published adult regression models as well as a regression that we constructed from published data for adult shorebirds (Kendeigh et al., 1977; Kersten and Piersma, 1987) are listed in Table 1.

Energetic considerations are probably paramount in determining the use of down rather than contour feathers in chicks. The mass of contour feathers needed to give the same amount of insulation is approximately 3 times the mass of down (McNabb and McNabb, 1977), and the cost of synthesizing feathers appears to be considerably greater than for other proteins (Lindstrom et al., 1993). Apparently, the selective tradeoff between the thermal benefits of improved insulation and the cost of synthesizing contour feathers and keeping them properly preened favors the use of down by chicks.

Shorebird versus duckling insulation

Some data are available to compare the overall thermal conductance K_o of downy shorebirds to that of ducklings breeding in the same area. In another study at Churchill, we measured three long-tailed (oldsquaw) 4-day-old ducklings (*Clangula hyemalis*) averaging about 35 g, using the same equipment and protocol. These long-tailed ducklings had an average $K_o = 0.040 \text{ W } ^\circ\text{C}^{-1}$, increasing by 13% to $0.045 \text{ W } ^\circ\text{C}^{-1}$ at $u = 1 \text{ m s}^{-1}$. The conductance of shorebird chicks with the same body mass as the ducklings, 35 g, is similar, $K_o = 0.039 \text{ W } ^\circ\text{C}^{-1}$, increasing by 14% to $0.045 \text{ W } ^\circ\text{C}^{-1}$ at $u = 1 \text{ m s}^{-1}$ (Table 1).

Mallards (*Anas platyrhynchos*) typically breed at lower latitudes and have higher thermal conductance than Arctic-breeding shorebirds (Fig. 2). However, 1- to 2-day-old mallard ducklings are physiologically more mature, having greater thermogenic capacity than 1- to 2-week-old shorebirds of similar size (Visser and Ricklefs, 1995). Consequently, they are able to tolerate T_a values at least as low as 10°C for over an hour (Koskimies and Lahti, 1964; Bakken et al., 1999).

In conclusion, the insulation of Arctic-breeding shorebird chicks thus appears somewhat, but not greatly, better than that of many other downy chicks. However, shorebird chicks are considerably less well insulated than capercaillie or Xantus' murrelet chicks of similar mass. Wind can increase heat loss and metabolic rate by 30–50% under windy conditions (30–50 km h⁻¹). Thus, the success of Arctic breeding shorebirds depends on efficient parental care, the ability to use stored heat to enable foraging with falling body temperature, and perhaps behavioral adjustments such as foraging in such sheltered areas as may be available.

List of symbols

c_p	tissue heat capacity
E	evaporative cooling
K_o	thermal conductance in actual environment
K_{os}	thermal conductance in convection-free enclosure
K_{ow}	wet thermal conductance
m	body mass
M	heat production
t	time
T_a	air temperature
T_b	body temperature
T_e	operative temperature
T_{es}	standard operative temperature
u	wind speed

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