

Convection and thermoregulation in two Antarctic seabirds*

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Summary. 1. Metabolism and heat transfer were measured at different wind speeds (V) and ambient temperatures (T_a) in Adelie penguins (*Pygoscelis adeliae*) and blue-eyed shags (*Phalacrocorax atriceps*). Five age classes of penguins (adults, fledglings, and 1-, 2-, and 3-kg downy chicks) and three age classes of shags (adults and 2- and 3-kg chicks) were studied.

2. In penguins, rates of oxygen consumption (\dot{V}_{O_2}) in the absence of forced convection increased with decreasing T_a in downy chicks. The \dot{V}_{O_2} of fledglings and adults increased marginally at -20°C . Lower critical temperatures (T_{lc}) were approximately $15\text{--}20^\circ\text{C}$ for 1-kg chicks, -5°C for 2-kg chicks, and -10°C for 3-kg chicks, fledglings, and adults. In shags, T_{lc} was approximately 0°C for all age classes, and \dot{V}_{O_2} increased substantially at -20°C .

3. Wind speeds of $3\text{--}6\text{ m}\cdot\text{s}^{-1}$ elicited significantly increased \dot{V}_{O_2} in all age classes of both species at -20°C . The largest increases were observed in adult and fledgling penguins (averaging 190% compared to \dot{V}_{O_2} in the absence of forced convection). At 0°C , \dot{V} had smaller but still significant effects in shags, but in penguins wind had little effect on \dot{V}_{O_2} at this T_a . The \dot{V}_{O_2} of all age classes of both species was independent of V at 20°C .

4. The response of thermal conductance (C) to changing V and T_a resembled that for \dot{V}_{O_2} . The C of fledglings and adults of both species increased rapidly with increasing V at low T_a but was independent of V at high T_a . In shags, minimal C did

not differ significantly among age classes, but in penguins C was highest in 1-kg chicks and lowest in adults.

5. In both penguins and shags, the responses of \dot{V}_{O_2} and C to changing V were similar in 3-kg downy chicks and adults, indicating that convection effects on down and feather plumages do not differ.

Key words: Convection – Energetics – Thermoregulation – Penguin – Shag

Introduction

The Adelie penguin (*Pygoscelis adeliae*) and the blue-eyed shag (*Phalacrocorax atriceps*) breed in large colonies on sub-Antarctic islands and on the coast of the Antarctic continent. Their reproductive seasons coincide with the austral spring and summer (mid-October through February), a period of relatively mild weather. Nevertheless, breeding Adelies, shags and their chicks often experience cold and windy weather, a combination which may produce high rates of convective heat loss. For adult birds, heat loss due to convection increases the drain on available energy supplies – a potentially important problem for Adelies, which undergo prolonged fasts during the early stages of the breeding cycle. For chicks, thermogenesis to replace body heat lost to convection reduces the energy available for growth, and in severe conditions wind chill may result in potentially lethal hypothermia. Thermal problems for chicks are compounded by nests that provide little shelter or insulative properties, and by the behavior of adults: in both Adelies and blue-eyed shags, hatchlings and young chicks are continuously brooded, but older chicks are left unattended and exposed for

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long periods while the parents forage (Ainley et al. 1983; Bernstein and Maxson 1982, 1985).

Convection has long been recognized as a major pathway for heat flow (Porter and Gates 1969; Monteith 1973; Bakken 1976), and the effects of convection on thermal balance have been examined in a number of birds (reviewed by Goldstein 1983). Unfortunately, there have been few studies of convective effects on young birds. A recent paper by Taylor (1986) reported that insulation of the downy plumage of penguin chicks may actually increase with increasing wind speed – a counterintuitive result opposite to previous observations. Taylor proposed that his results derived from the unique structural properties of downy plumages and suggested that penguin chicks experience reduced heat loss as wind speed increases. These predictions are based on measurements of heat transfer through pelt samples, and it is unclear if they can be extrapolated to intact, living chicks.

In this paper the effects of convection and ambient temperature on the heat transfer properties and metabolism of Adelie penguins and blue-eyed shags are examined. Adults and chicks of several ages were used in unrestrained conditions in order to approximate as closely as possible the behavioral and physiological responses of free-living birds. Data is discussed with respect to the influence of body size and the interaction of wind speed and temperature on metabolism. Using data from adults and similar-sized downy chicks, Taylor's hypothesis on the effects of plumage characteristics on convective heat exchange is tested. Finally, the effects of convection in shags and penguins are compared and discussed in relation to the probable importance of wind on temperature regulation and energy balance in the birds' natural habitat.

Materials and methods

Animals. Adelie penguins were obtained from a breeding colony on Torgersen Island, about 1 km west of the U.S. base at Palmer Station. Palmer is located on Anvers Island off the west coast of the Antarctic Peninsula (65°46' S, 64°05' W). Blue-eyed shags were obtained from a colony on Cormorant Island, about 4 km southeast of Palmer Station. Birds were captured by hand or with hand nets. Adults (penguins, $n=11$, mass 3.98 ± 0.31 kg; shags, $n=11$, mass 2.63 ± 0.24 kg) were held for 24–48 h and released after the completion of measurements. We studied penguin chicks of 4 age classes: '1-kg' downy chicks ($n=9$, mass 1.06 ± 0.09 kg, age 12–16 days), '2-kg' downy chicks ($n=9$, mass 2.09 ± 0.11 kg, age 22–26 days), '3-kg' downy chicks ($n=9$, mass 3.07 ± 0.14 kg, age 33–38 days), and fully-feathered fledglings ($n=11$, mass 3.10 ± 0.12 kg, age 40–45 days). Penguin chicks were held in the lab for 18–48 h and then returned to their capture locations.

Shag chicks of two age classes were studied: '2-kg' chicks ($n=5$, mass 1.96 ± 0.22 kg, age 30–35 days) and '3-kg' chicks

($n=5$, mass 2.79 ± 0.13 kg, age 40–45 days). The ages of shag chicks are approximate. Complete growth curves are not available for this population, and because of heavy sea ice we could not reach Cormorant Island to mark hatchlings. The 2-kg chicks showed little feather growth aside from newly-emerged sheathed primaries and secondaries. Considerably more feathering, including some of the wing coverts and retrices, was apparent in 3-kg chicks. However, most of the body surfaces of both age classes were covered with thick natal down. Shag chicks were returned to their nests within 24 h after capture.

Measurements. We determined gas exchange rates with open-circuit respirometry. For measurements in the absence of forced convection, we used lucite chambers of two volumes (12 and 92 L) to accommodate the size range of the birds. The chambers were placed within a larger environmental cabinet which controlled ambient temperature (T_a) ± 0.5 °C. Birds were unrestrained and stood on screen-wire platforms over a layer of mineral oil, which covered voided excreta. The T_a was measured with a copper-constantan thermocouple in the excurrent air line at its junction with the respirometer. Significant free convection occurs even in the absence of forced convection, and the chambers were perfused with a constant air flow. Therefore, a wind speed of $0.1 \text{ m} \cdot \text{s}^{-1}$ was assumed for these measurements (Robinson et al. 1976; Chappell and Holsclaw 1984).

For measurements in forced convection recirculating wind tunnels of two sizes were used, constructed of aluminum and lucite. Wind speed (V) was adjusted with variable-speed centrifugal fans powered from a voltage regulator (Fig. 1). The smaller tunnel had a test section 24 cm wide, 24 cm high, and 30 cm long; it was used for 1- and 2-kg chicks and could generate V up to $9 \text{ m} \cdot \text{s}^{-1}$. Internal volume was approximately 160 l. The larger tunnel's test section measured 31 cm wide, 32 cm high, and 45 cm long; it was used for 3-kg chicks, fledglings, and adults. Maximal V in the large tunnel was $5.5 \text{ m} \cdot \text{s}^{-1}$; internal volume was approximately 300 l. For both tunnels, variation of V across the test sections (measured with a hot-wire anemometer) was less than 10%, except in the extreme corners and within 2 cm of the walls.

'Ideal' wind tunnels have completely laminar flow, but this is difficult to achieve in practice. We estimated general patterns of turbulence from the streaming of fine threads suspended within test sections. Quantitative assessments were determined from short-term fluctuations of air velocity about a mean value, measured for several seconds with a hot-wire anemometer. Turbulence levels varied somewhat with V and with position in the cross-section, but were 4–8% of V within areas occupied by the birds.

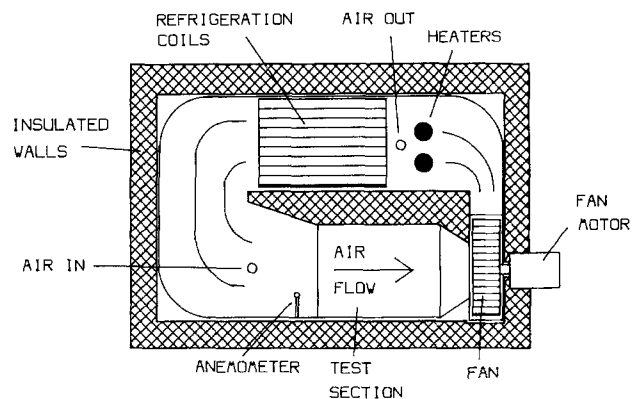


Fig. 1. Schematic diagram (top view) of recirculating wind tunnel respirometers

Wind speed was determined with hot-ball anemometers (Chappell and Bartholomew 1981) placed immediately upstream from the test section (Fig. 1). These anemometers measured V as the temperature difference between two polished aluminum spheres (diameter 1.3 cm), one of which was heated by a known power input. They were calibrated against a precision hot-wire anemometer. Measured V were corrected for velocity enhancement caused by reduced cross-sectional area within the test section due to the volume occupied by the birds. Since enhancement varies over a bird's body surface (being least at the beak and tail and greatest at the point of maximum girth for a bird facing upwind), we computed enhancement based on mean girth (integrated along the long axis) for a spheroid with dimensions similar to the bird in question. For the largest individuals used in either tunnel, the enhancement factor was 16% for penguins and 12% for shags.

Both tunnels were equipped with refrigeration coils and resistance heaters and could maintain $T_a \pm 0.5^\circ\text{C}$. The T_a was measured with copper-constantan thermocouples suspended immediately upstream from the test sections. Birds stood on plastic-coated screen-wire platforms within the test sections and were unrestrained.

To minimize handling time and stress, wind tunnel measurements were restricted to two wind speeds ($2.4\text{--}3\text{ m}\cdot\text{s}^{-1}$ and $5.5\text{--}7.9\text{ m}\cdot\text{s}^{-1}$) at each of three T_a (-20.0 , and 20°C). In the absence of forced convection, the same T_a was used, with additional measurements at -10 and 10°C for penguins and adults shags. After completing measurements at each combination of T_a and V , a thermocouple was inserted into the proventriculus to measure body temperature (T_b) within 45 s of opening the respirometer. All gas exchange measurements were made in the dark. Data from hypothermic individuals ($T_b < 35^\circ\text{C}$) were discarded.

Flow rates of dry air through the respirometers and wind tunnels were regulated to within $\pm 1\%$ with Tylan mass flow controllers calibrated against a Singer dry volume meter. Flow rates (STPD) varied from $41\text{ l}\cdot\text{min}^{-1}$ for small chicks in the respirometer to $231\text{ l}\cdot\text{min}^{-1}$ for large individuals in the wind tunnels. A fraction ($50\text{--}100\text{ ml}\cdot\text{min}^{-1}$) of the excurrent air was diverted, dried and passed through an Anarad AR-50 CO_2 sensor, then scrubbed of CO_2 with Ascarite, redried, and passed through an Applied Electrochemistry S-3A O_2 sensor. Both analyzers resolved concentrations of $\pm 0.001\%$. During measurements, O_2 concentration was always $> 20.3\%$, and CO_2 concentration never exceeded 0.6% . Data were taken only after birds had been held at a particular combination of T_a and V for at least 1 h and oxygen consumption (\dot{V}_{O_2}) was minimal and stable. \dot{V}_{O_2} was calculated as:

$$\dot{V}_{\text{O}_2} = F \cdot (F_i\text{O}_2 - F_e\text{O}_2) / [M \cdot (1 - F_e\text{O}_2)] \quad (1)$$

where F is flow rate (STPD), $F_i\text{O}_2$ is the fractional concentration of O_2 in incurrent air, $F_e\text{O}_2$ is fractional O_2 concentration in excurrent air, and M is body mass. Carbon dioxide production (\dot{V}_{CO_2}) was calculated as:

$$\dot{V}_{\text{CO}_2} = F \cdot (F_e\text{CO}_2 - F_i\text{CO}_2) / M \quad (2)$$

where $F_e\text{CO}_2$ is the fractional concentration of CO_2 in excurrent air and $F_i\text{CO}_2$ is the fractional concentration of CO_2 in incurrent air.

At T_a of 0°C and below, equation 56 in Calder and King (1974) was used to compute evaporative heat loss (EHL) from \dot{V}_{O_2} and T_a . At higher T_a , evaporative water loss (mH_2O) data obtained in the absence of forced convection was used to compute EHL (using a conversion factor of $2404\text{ J}\cdot\text{g}\text{ H}_2\text{O}^{-1}$). The Calder-King approximation, which estimates EHL as a fraction of metabolic heat production (MHP), is unlikely to be completely accurate for these species. However, potential errors

are probably unimportant for calculations of heat balance, because at low T_a EHL is typically $< 6\%$ of MHP. \dot{V}_{O_2} was converted into its heat equivalent using a value of $21\text{ J}\cdot\text{ml}\text{ O}_2^{-1}$ (typical for fat and protein catabolism) to yield MHP. Net heat production (HP_n) equals MHP-EHL. Dry thermal conductance (C , $\text{watts}\cdot[\text{kg}\cdot^\circ\text{C}]^{-1}$) was calculated as:

$$C = \text{HP}_n / (T_b - T_a) \quad (3)$$

Data analysis and statistics. Data were analyzed with one- and two-way ANOVA, least-squares regression, and ANCOVA using the General Linear Models procedure of the Statistical Analysis System (SAS). The \dot{V}_{O_2} and conductance data are presented in mass-specific units in order to facilitate comparison with other studies. Interpretive errors occasionally arise from use of ratios (Packard and Boardman 1988). Accordingly, we analyzed both absolute and mass-specific data. In most cases, identical qualitative results were obtained from both data sets; the interpretations and significance values we report are from data not converted to mass-specific units. Where necessary, data were \ln -transformed to yield equal variances. Results differing at the 0.05 probability level are considered significantly different; unless otherwise stated, data are given as mean $\pm 95\%$ confidence intervals.

Results

Behavior

Both species adapted well to laboratory protocols. Most individuals were calm and quiet; several were asleep when chambers were opened for T_b measurements. Since measurements were made in the dark, we could not determine posture during experiments. However, when lights were turned on at the conclusion of measurements, shags and adult and fledgling penguins were generally prone. In the wind tunnel adults faced upwind or downwind with approximately equal frequency. Penguin chicks assumed a variety of postures (upright, prone, or intermediate); the orientation of chicks of both species with respect to wind direction appeared random. Head, foot, and wing position varied from extended to completely tucked within the plumage.

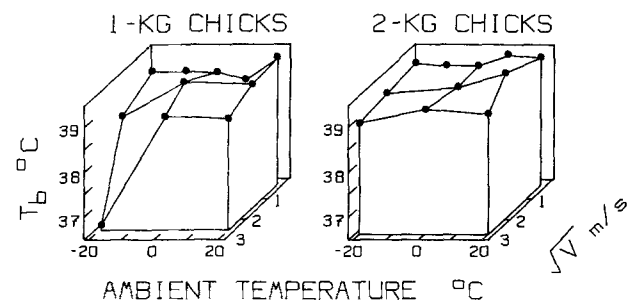


Fig. 2. Body temperatures (T_b) of 1- and 2-kg Adelie penguin chicks at various combinations of ambient temperature and wind speed. Dots are means of data from at least 4 (usually 5) individuals

Body temperature

Shags and penguins of all ages tested had remarkably stable T_b 's. At all combinations of T_a and V , the mean T_b for penguins ranged from 38.6 to 39.6 °C, with one exception. At high V at -20 °C, 1-kg chicks became slightly hypothermic (Fig. 2). At this T_a , mean T_b fell from 38.8 ± 0.14 °C in the absence of forced convection to 36.6 ± 1.52 °C at $V = 6.7$ m·s⁻¹ ($n = 4$ at each V ; $P = 0.03$).

There was no difference between the T_b means of 2- and 3-kg shag chicks (both 39.3 °C), but the T_b of adults (40.6 ± 0.2 °C) was significantly higher than that of chicks ($P < 0.001$, t -test). The only significant effect of wind on T_b in shags occurred in 2-kg chicks. Their T_b at -20 °C fell from 39.9 ± 0.6 °C ($n = 5$) in the absence of forced convection to 37.5 ± 2.4 °C at $V = 7.9$ m·s⁻¹ ($n = 4$; $P = 0.03$).

Hypothermia ($T_b < 35$ °C) occurred in two 1-kg penguin chicks and one 2-kg shag chick subjected to high V at -20 °C. These individuals recovered rapidly when returned to room temperature, and the shag and one penguin were able to tolerate identical regimes when retested a few hours later.

Oxygen consumption and carbon dioxide production

Respiratory exchange ratios (RE; $\dot{V}_{CO_2}/\dot{V}_{O_2}$) of penguins did not differ significantly with age, T_a , or V . Mean RE was 0.71 ± 0.005 . The RE's of shags differed slightly but significantly with age, ranging from 0.69 ± 0.003 in adults to 0.73 ± 0.01 in 2-kg chicks. Mean RE was 0.71 ± 0.005 . These values are consistent with use of lipid as the primary substrate for energy metabolism.

In penguins, the effect of T_a on \dot{V}_{O_2} in the absence of forced convection differed among age classes. No significant effects were observed in fledglings (although \dot{V}_{O_2} at -20 °C was slightly elevated), and in adults the only significant change was a minor elevation of \dot{V}_{O_2} ($p = 0.016$) at -20 °C. \dot{V}_{O_2} increased significantly with decreasing T_a in all three age classes of downy chicks ($P < 0.02$; ANOVA). The change was greatest for 1-kg chicks (\dot{V}_{O_2} was 82% higher at -20 °C than at 20 °C). Minimal resting mass-specific \dot{V}_{O_2} (which occurred at 10 °C for adults and 20 °C for other age classes) decreased with increasing age. Lower critical temperature (T_{lc}) was approximately 15–20 °C in 1-kg chicks. T_{lc} was difficult to define in larger chicks and adults, partly due to small sample size and partly because these age classes are well insulated (Fig. 3; also Chappell and Souza 1988). Approximate values of T_{lc} were -5 °C for 2-kg chicks and -10 °C for larger birds.

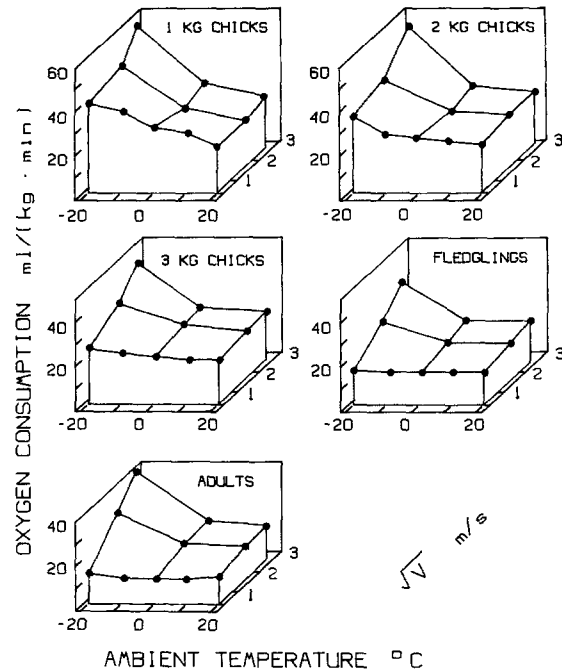


Fig. 3. Oxygen consumption of five age classes of Adelle penguins at various combinations of ambient temperature and wind speed. Dots are means of data from 4 to 6 individuals

In shags, temperature effects on \dot{V}_{O_2} in the absence of forced convection were similar among age classes. Significant elevation of \dot{V}_{O_2} at $T_a < 0$ °C was observed in all three age classes ($P < 0.01$; ANOVA). The increase in \dot{V}_{O_2} at -20 °C compared to \dot{V}_{O_2} at 20 °C was 59% in 2-kg chicks, 36% in 3-kg chicks, and 33% in adults. T_{lc} was approximately 0 °C for all ages. Minimal resting \dot{V}_{O_2} (which occurred at 20 °C for all ages) was 20.0 ± 4.0 ml·kg⁻¹·min⁻¹ in adults, 16.5 ± 1.3 ml·kg⁻¹·min⁻¹ in 3-kg chicks, and 19.3 ± 3.3 ml·kg⁻¹·min⁻¹ in 2-kg chicks. These values did not differ significantly and are similar to values reported by Ricklefs and Matthew (1983). Minimal \dot{V}_{O_2} in adult shags was twice the allometrically predicted value for non-passerines (8.55 ml·kg⁻¹·min⁻¹, Lasiewski and Dawson 1967; 7.95 and 10.2 ml·kg⁻¹·min⁻¹ for the inactive and active phases of the diel cycle, Aschoff and Pohl 1970). It was also larger than predicted by an allometric equation for pelecaniform birds (10.6 ml·kg⁻¹·min⁻¹, derived from Bucher 1986).

The combined effects of T_a and V on \dot{V}_{O_2} are shown for penguins in Fig. 3, and for shags in Fig. 4. Because there was considerably greater variance of \dot{V}_{O_2} at high versus low V , we \ln -transformed raw \dot{V}_{O_2} data prior to analysis. Similarly, we used the square-root of wind speed ($V^{1/2}$), since this transformation increased the linearity of regressions (Robinson et al. 1976; Goldstein 1983).

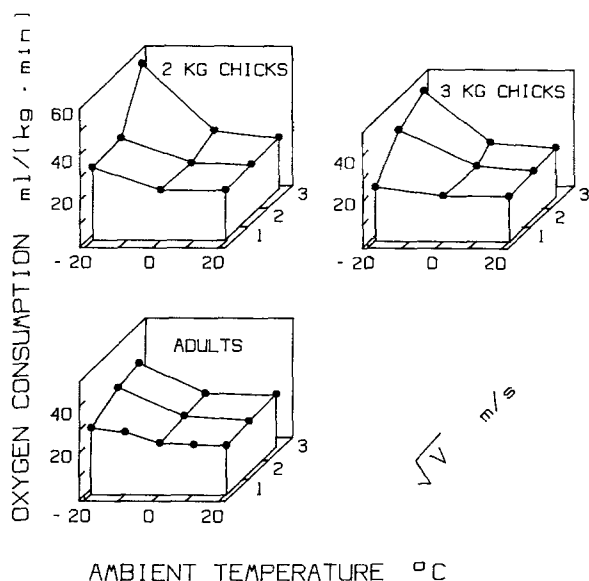


Fig. 4. Oxygen consumption of three age classes of blue-eyed shags at various combinations of ambient temperature and wind speed. Dots are means of data from 4 to 6 individuals

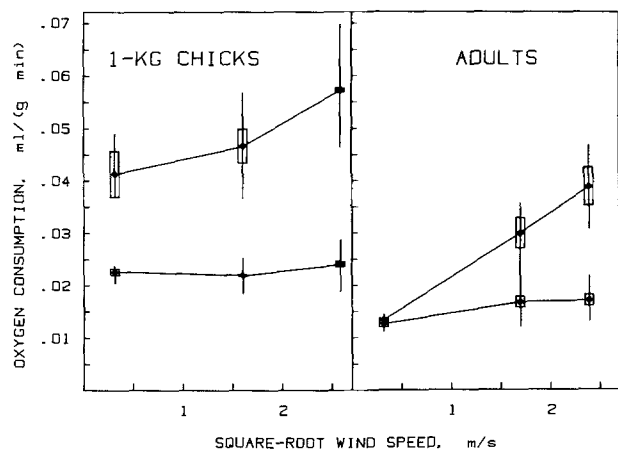


Fig. 5. The effect of wind speed on oxygen consumption in 1-kg Adelle penguin chicks and adults. Upper lines are for data taken at -20°C ; lower lines are for data taken at 20°C . Vertical lines are ranges and boxes enclose 95% confidence intervals

Results from ANCOVA revealed significant interaction effects between T_a and $V^{1/2}$ for all age classes of penguins ($P < 0.03$). Especially in older age classes, wind had little effect on \dot{V}_{O_2} at a T_a of 0 or 20°C , but large effects at -20°C . Surprisingly, the effects of wind were greatest in the oldest and largest age classes (Fig. 5). At -20°C , the relative increase in \dot{V}_{O_2} between $V = 0.1 \text{ m}\cdot\text{s}^{-1}$ and $V = 5.5\text{--}6.7 \text{ m}\cdot\text{s}^{-1}$ was 39% for 1-kg chicks (41.2 ± 5.3 to $57.1 \pm 9.7 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$), but 191% for adults (13.3 ± 0.6 to $38.7 \pm 6.2 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$).

In shags, there were significant interaction effects for 2-kg chicks ($p = 0.03$) and 3-kg chicks ($P < 0.01$), but not for adults ($P = 0.13$). As with pen-

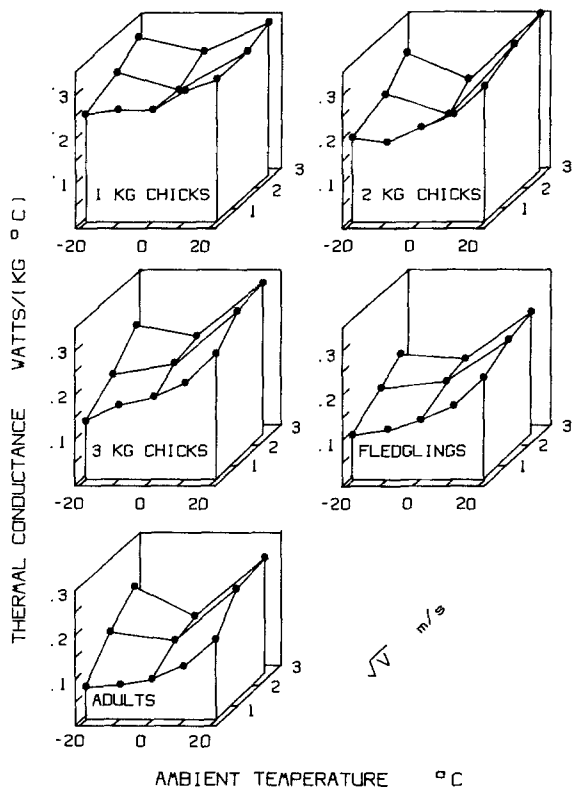


Fig. 6. Thermal conductance of five age classes of Adelle penguins at various combinations of ambient temperature and wind speed. Dots are means of data from 4 to 6 individuals

guins, the effects of wind on \dot{V}_{O_2} were generally larger at -20°C than at higher T_a .

Thermal conductance

In the absence of forced convection, C for most age classes of both species was minimal at -20°C and increased with increasing T_a (Figs. 6, 7). In 2-kg chicks, C for both species was constant and minimal between -20 and 0°C . In penguins, overall conductance decreased rapidly with increasing body mass and age. At -20°C , C for 1-kg chicks was three times larger than for adults (0.232 ± 0.03 versus $0.0737 \pm 0.004 \text{ watts}\cdot\text{kg}^{-1}\cdot^{\circ}\text{C}^{-1}$, respectively). In contrast, the minimum conductance of shags did not change significantly among age classes. Minimal C of adult shags ($0.155 \text{ watts}\cdot\text{kg}^{-1}\cdot^{\circ}\text{C}^{-1}$) was substantially greater than predicted for a 3.63 kg bird in the active phase of the diel cycle ($0.117 \text{ watts}\cdot\text{kg}^{-1}\cdot^{\circ}\text{C}^{-1}$; Aschoff 1981).

We used ANCOVA to examine the combined effects of T_a and $V^{1/2}$ on C , after \ln -transforming C to equalize variances at high and low V . Significant interactions between temperature and wind were observed in all age classes of both species ($P < 0.023$), except adult shags ($P = 0.45$). Generally, C increased with increasing $V^{1/2}$ at particular T_a , but slopes varied at different T_a .

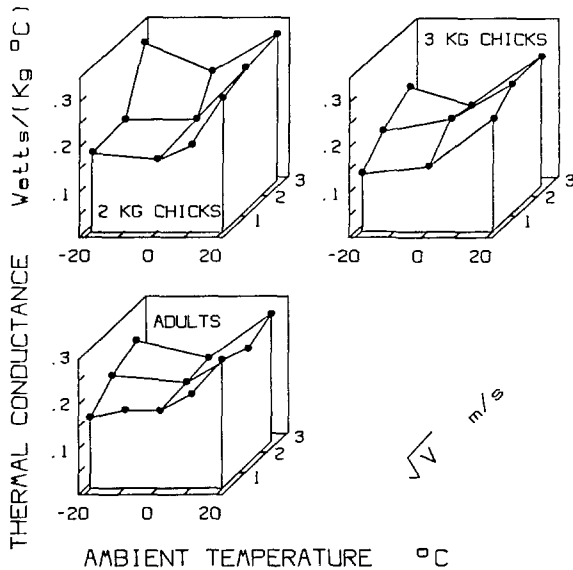


Fig. 7. Thermal conductance of three age classes of blue-eyed shags at various combinations of ambient temperature and wind speed. Dots are means of data from 4 to 6 individuals

Differences between plumage types

We examined the possibility that convective heat transfer may vary according to plumage type (Taylor 1985, 1986) by comparing regressions predicting $\ln \dot{V}_{O_2}$ and $\ln C$ as functions of $V^{1/2}$ at a T_a of -20°C (all age classes of both species are strongly affected by V at this T_a). For penguins we compared 3-kg chicks and fledglings. These groups have similar masses (3.07 and 3.19 kg, respectively) and differ in age by only 7–14 days. For shags we compared 3-kg chicks and adults; again, both groups had similar masses (2.79 and 2.63 kg, respectively).

For both shags and penguins, slopes of regressions predicting $\ln \dot{V}_{O_2}$ as a function of $V^{1/2}$ in downy versus feathered plumages were not significantly different ($P > 0.2$; ANCOVA). Intercepts were similar in shags, but differed significantly in penguins. Quantitatively identical findings (similar slopes and intercepts for shags, similar slopes but different intercepts for penguins) were obtained for thermal conductance. These findings indicate that convection has approximately equivalent effects on downy and feathered plumages of both species, but that \dot{V}_{O_2} and C in penguins are significantly lower in feathered fledglings than in downy chicks of similar mass.

Discussion

Analytical techniques

Convective heat exchange is often analyzed by converting heat flow into heat transfer resistances or

dimensionless Nusselt and Reynolds numbers (Monteith 1973; Mitchell 1976; Robinson et al. 1976; Stahel et al. 1987). These approaches facilitate comparisons of species of different size and shape. Our protocols produced good measurements of metabolism and heat transfer, and the data can be used for rigorous estimates of metabolism in natural weather conditions. However, two factors precluded the effective use of resistance calculations or Nusselt-Reynolds numbers. First, resistance calculations require good measurements of body surface area. We were unable to obtain consistent and accurate estimates of surface area due to the wide variety of postures used. Second, comparisons based on Nusselt-Reynolds numbers assume a consistent airflow over an object, but because our birds often lay prone, air velocity varied considerably and unpredictably over the body surface. For example, V over prone birds was maximal on the dorsal surface, close to zero on the ventral surface, and intermediate on lateral surfaces. Because of these complications, we restricted our analyses of heat flow to whole-body conductances.

Comparisons between downy and feathered plumages

The natal down of penguin and shag chicks is strikingly different from the adult plumage. Taylor (1986) reported that thermal flux through pelt samples from downy penguin chicks (*Pygoscelis papua* and *P. antarctica*) was highly dependent on orientation to wind. Down had greater insulative value than adult feathers, and in some orientations the thermal resistance of down increased with increasing wind speed (opposite to results obtained from all other species thus far studied). On the basis of these measurements, Taylor hypothesized that *Pygoscelis* chicks would not suffer increased heat loss at high V .

Our data appear to invalidate this hypothesis. All three age classes of downy Adelie chicks we tested, as well as the 2- and 3-kg downy shag chicks, showed substantial increase in metabolic rate at wind speeds within the range of V used by Taylor. Moreover, Taylor measured higher insulative values for down from large chicks than for the feathers of fledglings in gentoo penguins (*P. papua*), but in Adelies we found that standard metabolic rate (SMR), C , and T_{lc} are all considerably lower in fledglings than in 3-kg downy chicks. Several factors may contribute to the apparent discrepancies between our results with intact birds and Taylor's data on pelt samples. First, thermal resistance of pelt samples increased with increasing

V only when wind flow was parallel to the pelt; in other orientations, resistance decreased with increasing V . As Taylor points out, part of the plumage of a live bird will be parallel to wind flow, part will be normal to wind flow, and a variety of intermediate orientations will occur around the curved body surface. Second, turbulence levels around a live bird will differ from those adjacent to a flat plumage sample (Stahel et al. 1987). Third, Taylor's pelt samples were taken from the relatively thick ventral plumage. Intact birds have many regions covered with much thinner insulation than that on the ventral body surface. These areas (e.g. the head, flippers, legs, and feet) may act as windows for heat flow, especially in high winds.

Comparisons with other species

Qualitatively, the effects of convection on Adelie penguins and blue-eyed shags are similar to those reported for all other birds thus far studied: at T_a below T_{lc} , increasing wind speed elicits increased heat loss and metabolic heat production. Goldstein (1983) reviewed the existing literature and developed equations describing the combined effects of T_a and V on metabolism in birds. His equation 2 predicts the slope (b , watts·[m·s]^{1/2}) of the regression of metabolism on V at temperatures below T_{lc} :

$$b = 0.0092M^{0.66} \cdot \Delta T^{0.32} \quad (4)$$

where M is mass in g and ΔT is $T_{lc} - T_a$. For a given combination of V and T_a , metabolic rate (MR, in watts) is calculated as:

$$MR = SMR + b \cdot V^{1/2} \quad (5)$$

where SMR is standard metabolic rate (in watts) at that T_a in the absence of forced convection. For the 8 species Goldstein examined (including passerines, galliforms, strigiforms, and falconiforms, mass range from 13.5 g to 3.85 kg), equations 4 and 5 explained almost 97% of the variance in MR.

Do Adelie penguins and blue-eyed shags fit Goldstein's general model for convection effects? The question is particularly pertinent to Adelies. All of the species Goldstein studied are capable of flight; accordingly, the structural characteristics of their plumages are relatively conventional. In contrast, penguins are extensively adapted for aquatic locomotion and have a unique plumage morphology. Their feathers are relatively short, grow from tracts covering almost the entire skin surface, and form a dense, essentially waterproof plumage. Several investigators have suggested that penguin plumages might confer unusual resistance

Table 1. Comparison of measured metabolic rates (MR_m ; watts) for Adelie penguins and blue-eyed shags at different wind speeds (V) at an ambient temperature of -20°C versus predicted values (MR_p) based on Goldstein (1983)

Age class (mass)	n	T_{lc}	SMR	V	MR_m	MR_p	m/p
Penguins:							
1-kg chicks	4	20	11.9	2.6	15.7	16.3	0.96
(1.06 kg)	4			6.7	20.9	19.3	1.08
2-kg chicks	5	-5	24.7	3.1	24.6	30.6	0.80
(2.09 kg)	5			8.1	36.4	34.2	1.06
3-kg chicks	5	-10	28.2	3.0	36.6	34.8	1.05
(3.07 kg)	5			6.0	46.6	37.6	1.24
Fledglings	5	-10	19.0	2.7	32.9	25.5	1.29
(3.19 kg)	5			5.4	41.5	28.2	1.47
Adults	5	-10	19.0	2.9	39.0	26.7	1.46
(3.98 kg)	5			5.7	50.6	29.9	1.69
Shags:							
2-kg chicks	4	0	20.2	2.4	23.0	25.7	0.89
(1.96 kg)	5			7.9	35.6	30.1	1.17
3-kg chicks	4	0	23.0	2.3	32.8	29.9	1.10
(2.79 kg)	4			5.8	40.8	33.9	1.20
Adults	6	0	21.6	2.3	34.5	28.2	1.22
(2.63 kg)	6			5.7	38.5	32.0	1.20

Other abbreviations: T_{lc} , lower critical temperature ($^\circ\text{C}$), SMR, standard metabolic rate in the absence of forced convection (watts); m/p; ratio of measured to predicted metabolic rate

to convective heat transfer (Drent and Stonehouse 1967; Stonehouse 1967; Le Maho et al. 1976; Taylor 1986).

We used our data on mass, SMR, and T_{lc} in equations 4 and 5 to predict the metabolic rates of penguins and shags at different V . We used data from -20°C only in order to insure that T_a was below T_{lc} for all age classes. Results from these comparisons (Table 1) should be regarded with caution, since Goldstein's data came from birds that stood or were perched above the substrate, while our birds sat directly upon it or lay prone. Nevertheless, it seems clear that downy penguin chicks and shags conform fairly well to the model. For 3 sizes of downy penguin chicks, measured MR averaged within 3% of predicted MR ($P=0.2$ that measured=predicted, $n=56$, t -test). Slight (10–20%) but significant differences were observed for 3-kg shag chicks and adult shags, but for both groups the difference was significant for only one of the two wind speeds tested.

In fledgling and adult penguins, measured MR was much higher (by an average of 48%) than predicted values ($P<0.001$, $n=40$, t -test). The difference between the measured/predicted ratio for downy versus feathered age classes of penguins was also significant ($P<0.001$, $n=48$, t -test). The high values for fledgling and adult penguins are

especially impressive considering that these individuals usually lay prone, thereby shielding a large fraction of their ventral surface from the air flow.

It seems unlikely that the cause of these large heat losses is related to plumage structure. If this were the case, convection should strongly affect MR and conductance at 0 °C (and possibly 20 °C), rather than at -20 °C only. The unfeathered feet are a possible source of heat loss at low T_a . However, in cold conditions penguins keep their feet sheltered under the body feathers. The most likely avenues for high heat loss at subzero T_a are the poorly insulated flippers. Penguin flippers have evolved for efficient aquatic propulsion. They are covered with small, scale-like feathers that confer good hydrodynamic properties but provide little resistance to heat flow. Penguins have excellent vasomotor control and countercurrent heat exchangers in the vasculature supplying the flippers (Hammel et al. 1976; Simon et al. 1976). These mechanisms enable swimming penguins to reduce flipper temperature (T_f) essentially to that of the surrounding water, minimizing heat loss even at the lowest possible water temperatures (0 to -1 °C). However, since they are poorly insulated and (unlike the feet) cannot be hidden under the body feathers, the flippers are vulnerable to frostbite injury. At subzero T_a , penguins must perfuse their flippers with enough warm blood to keep T_f above the freezing point of tissue. Hence, minimal T_f is 'fixed' at approximately 0 °C and high rates of heat loss through the flippers will occur when subzero T_a combines with high wind speed.

This hypothesis explains the paradoxical observation that feathered penguins are more affected by convection at low T_a than are small downy chicks: even though their overall thermal conductivity is much greater than that of fledglings or adults, chicks are less vulnerable to frostbite injury because their flippers are covered with insulative down. It may also explain why Stahel et al. (1987) reported convection effects in adult little penguins (*Eudyptula minor*) which are approximately the same as predicted by Goldstein's equations: Stahel and his colleagues did not use $T_a < 6$ °C, so their birds were never threatened by frostbite.

Comparisons between blue-eyed shags and Adelie penguins

It is instructive to compare thermoregulation and convection in shags and Adelies. These species have roughly similar masses, live in similar habitats, and nest at the same time of year (often in the same rookeries). Both forage by diving after

active aquatic prey. Shag chicks are highly altricial while penguin chicks are metabolically precocial (Bucher 1987), but by the age at which they are routinely left unattended by their parents, the young of both species have robust thermoregulatory capabilities. However, shag morphology and plumage structure are conventional for flying birds, while the flightless penguins are specialized for aquatic locomotion.

Blue-eyed shags are members of an order most strongly represented in tropical and temperate regions, and adults are poorly insulated relative to their mass, an apparent disadvantage for thermoregulation in the cold Antarctic climate. Blue-eyed shags compensate for high rates of heat loss with high basal metabolic rates, yielding a T_{lc} of about 0 °C, approximately as predicted for a similar-sized non-passerine (Calder and King 1974). However, high MHP is an energetically expensive method of coping with cold environments. Adelie penguins have thermal conductances and basal metabolic rates only slightly greater than predicted; their T_{lc} is about -10 °C. Both species easily tolerate T_a at least as low as -20 °C. However, the metabolic costs of thermoregulation in the absence of forced convection are much higher in shags than in penguins, in both absolute and mass-specific units (shags: 9.8 watts·kg⁻¹ or 25.8 watts; penguins: 4.6 watts·kg⁻¹ or 18.3 watts; both for -20 °C).

Despite the large differences in heat-transfer properties of adults, the thermal characteristics of downy penguin and shag chicks are similar (Table 2). Although small penguin chicks (ca. 1 kg)

Table 2. Comparison of rates of oxygen consumption (ml·kg⁻¹·min⁻¹) for blue-eyed shags (BES) and adelie penguin (AP) chicks of similar mass

		2-kg chicks				
		$V=0.1 \text{ m}\cdot\text{s}^{-1}$			$V=5.5\text{--}7.9 \text{ m}\cdot\text{s}^{-1}$	
T_a	AP	BES	Significance	AP	BES	Significance
-20	34.1	30.7	ns	51.9	53.8	ns
0	24.3	19.6	0.028	26.9	28.2	ns
20	21.1	19.3	ns	24.4	20.2	0.045
		3-kg chicks				
		$V=0.1 \text{ m}\cdot\text{s}^{-1}$			$V=5.5\text{--}7.9 \text{ m}\cdot\text{s}^{-1}$	
T_a	AP	BES	Significance	AP	BES	Significance
-20	25.0	23.5	ns	44.6	41.8	ns
0	21.4	17.3	0.039	26.8	22.2	0.033
20	19.8	16.5	0.004	23.2	17.6	0.001

$n=4$ for all groups. Other abbreviations: T_a , ambient temperature (°C); V , wind speed (m·s⁻¹); ns, not significant

are more capable thermoregulators than young shags of similar mass (unpublished data), 2-kg chicks of both species can tolerate prolonged exposure to high winds and low T_a . Even though they are younger, 2- and 3-kg penguin chicks have somewhat higher metabolic rates than shag chicks of similar mass. However, differences are minor at most T_a . Responses to convection are also similar in penguin and shag chicks.

Convection has strikingly different effects on adult shags and penguins. Even though adult shags have high thermal conductances, their metabolic response to wind is moderate: at -20°C , a $6\text{ m}\cdot\text{s}^{-1}$ wind increases MHP by about 44% over MHP in the absence of forced convection. The change in MHP at similar T_a and V is more than four times larger (191%) in adult Adelies. As a result, the metabolic costs of thermoregulation are substantially lower in shags than Adelies when low T_a combines with higher V , a reversal of the ranking in the absence of forced convection.

Ecological considerations

How important is wind-induced heat loss for the thermoregulation and energy budgets of breeding Adelies and blue-eyed shags? From our data it is obvious that in cold, windy conditions the energy cost of heat production is substantial. However, such conditions do not occur throughout the breeding season, at least in colonies near Palmer

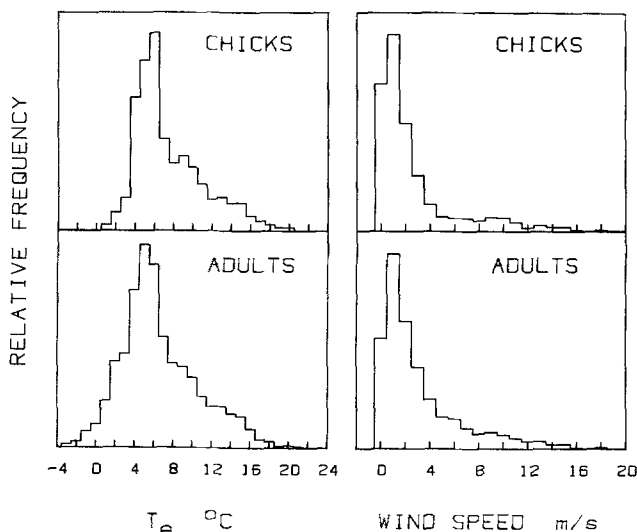


Fig. 8. Frequency histograms for environmental temperature (T_e) and wind speed in an Adelie penguin colony near Palmer Station. Data were obtained during the 1986–1987 breeding season. Upper plots include data for periods when 1-kg and larger chicks were present (December 26–January 31); lower plots include data for the entire season (November 15–January 31)

Station. Figure 8 shows frequency distributions of wind speeds and environmental temperatures (T_e) for adult and chick Adelies in the Torgersen Island colony during the 1986–1987 breeding season. The T_e incorporates sunlight and wind (but not convective effects on thermal conductance), and was measured from taxidermic mounts of penguins (see Bakken 1976 or Chappell and Bartholomew 1981 for details). Although wind speeds above $2\text{ m}\cdot\text{s}^{-1}$ were common, adults rarely experienced T_e lower than -2°C and chicks never experienced T_e lower than 1°C . At these temperatures, wind effects on heat loss and MR are minor for all age classes (Fig. 3). T_e data for shags are unavailable, but because shags are similar to penguins in size, coloration, nest sites, and breeding chronology, the conclusions drawn from Fig. 8 should also apply to shags.

In conclusion, the heat-transfer properties of Adelie penguins and blue-eyed shags seem to be adequate to protect the birds against serious energy drains from convective heat loss during the majority of environmental conditions encountered during the breeding season. Even in rarely-occurring combinations of high wind and subzero temperatures, the smallest chicks that are likely to be left unattended by their parents can probably maintain normal T_b as long as they have adequate energy reserves for thermogenesis. Convection may be a more important factor for Adelies during the cold, windy Antarctic winter. When temperatures drop more than a few degrees below 0°C , any wind speed greater than $1\text{--}2\text{ m}\cdot\text{s}^{-1}$ will require the birds to substantially increase rates of metabolic heat production.

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