

Thermoregulation, gas exchange, and ventilation in Adelie penguins (*Pygoscelis adeliae*)

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Summary. Adelie penguins (*Pygoscelis adeliae*) experience a wide range of ambient temperatures (T_a) in their natural habitat. We examined body temperature (T_b), oxygen consumption (\dot{V}_{O_2}), carbon dioxide production (\dot{V}_{CO_2}), evaporative water loss (\dot{m}_{H_2O}), and ventilation at T_a from -20 to 30 °C. Body temperature did not change significantly between -20 and 20 °C (mean $T_b = 39.3$ °C). T_b increased slightly to 40.1 °C at $T_a = 30$ °C. Both \dot{V}_{O_2} and \dot{V}_{CO_2} were constant and minimal at T_a between -10 and 20 °C, with only minor increases at -20 and 30 °C. The minimal \dot{V}_{O_2} of adult penguins (mean mass 4.007 kg) was 0.0112 ml/[g · min], equivalent to a metabolic heat production (MHP) of 14.9 Watt. The respiratory exchange ratio was approximately 0.7 at all T_a . Values of \dot{m}_{H_2O} were low at low T_a , but increased to 0.21 g/min at 30 °C, equivalent to 0.3% of body mass/h. Dry conductance increased 3.5 -fold between -20 and 30 °C. Evaporative heat loss (EHL) comprised about 5% of MHP at low T_a , rising to 47% of MHP at $T_a = 30$ °C. The means of ventilation parameters (tidal volume [V_T], respiration frequency [f], minute volume [\dot{V}_I], and oxygen extraction [E_{O_2}]) were fairly stable between -20 and 10 °C (V_T did not change significantly over the entire T_a range). However, there was considerable inter- and intra-individual variation in ventilation patterns. At $T_a = 20$ – 30 °C, f increased 7 -fold over the minimal value of 7.6 breaths/min, and \dot{V}_I showed a similar change. E_{O_2} fell from 28 – 35% at low T_a to 6% at $T_a = 30$ °C.

Abbreviations: C thermal conductance; EHL evaporative heat loss; E_{O_2} oxygen extraction; f respiratory frequency; MHP metabolic heat production; \dot{m}_{H_2O} evaporative water loss; LCT lower critical temperature; RE respiratory exchange ratio; T_a ambient temperature; T_b body temperature; \dot{V}_{O_2} rate of oxygen consumption; \dot{V}_{CO_2} rate of carbon dioxide production; \dot{V}_I inspiratory minute volume; V_T tidal volume

Introduction

Recent research has revealed considerable flexibility and variation in the responses of avian ventilatory systems to changing ambient temperature (Bucher 1981, 1985; Bech and Johansen 1980; Brent et al. 1984; Kaiser and Bucher 1985; Chappell and Bucher 1987). These responses presumably reflect the dual function of the respiratory system as a pathway for both gas exchange and, secondarily, for heat loss. At high ambient temperatures (T_a), many species greatly enhance evaporative heat loss by panting. At low T_a , increased thermogenesis is supported by elevated rates of oxygen consumption (\dot{V}_{O_2}) and carbon dioxide production (\dot{V}_{CO_2}). These increased gas exchange requirements may be accommodated by increasing lung ventilation (minute volume, \dot{V}_I), oxygen extraction (E_{O_2}), or both. Minute volume is itself a function of respiration frequency (f) and tidal volume (V_T). In some birds (e.g., pigeons, prairie falcons, parrots, and chukar partridges), E_{O_2} remains high but relatively constant at T_a below thermoneutrality, and increasing oxygen demand is accommodated by increases in \dot{V}_I (Bech et al. 1985; Bucher 1981, 1985; Kaiser and Bucher 1985; Chappell and Bucher 1987). Other species (e.g., mallard ducks and European coots) show a contrasting pattern: E_{O_2} increases with increasing \dot{V}_{O_2} at T_a below thermoneutrality (Bech et al. 1985; Brent et al. 1984). Because temperature effects on \dot{V}_I and E_{O_2} have been studied in a limited number of species, the physiological, phylogenetic, and/or ecological foundations and adaptive significance, if any, for these differences are unclear.

High E_{O_2} at low T_a is often interpreted as an adaptation for reducing the metabolic cost of thermoregulation by decreasing respiratory heat loss (Johansen and Bech 1983). However, in the studies

performed to date the estimated energy savings due to high E_{O_2} are minor – ca. 3–6% of total thermoregulatory costs (Bucher 1981; Chappell and Bucher 1987). Moreover, it is difficult to separate the influence on E_{O_2} of low T_a from that of high \dot{V}_{O_2} , since all of the species studied thus far show substantial thermogenic \dot{V}_{O_2} at low T_a .

To address these problems, additional comparative data are needed, particularly from birds with thermoneutral zones which extend to very low T_a . In these species, \dot{V}_{O_2} is ‘decoupled’ from T_a , allowing study of temperature effects on ventilation without the confounding influence of changing requirements for oxygen uptake. Accordingly, we investigated thermoregulatory physiology, ventilation, and gas exchange in the Adelie penguin (*Pygoscelis adeliae*). This species routinely experiences subzero air and seawater temperatures in its natural habitat, and is well insulated. Consequently it shows little elevation of \dot{V}_{O_2} at T_a as low as -20°C . During the nesting season, Adelies may also experience considerable heat stress. On warm, sunny days, both chicks and adults may pant for hours at a time (Murrish 1973, 1982).

Materials and methods

Animals. We made preliminary measurements in July 1986 on adult birds from a colony maintained at Sea World, in San Diego, California. These penguins ($N=8$) were obtained from wild populations, but had been held in captivity for 10 to 15 years. They were kept in a large group aviary maintained at -5 to 5°C , and were fed a diet of fish and squid supplemented with vitamins. We also obtained data from wild penguins collected during December 1986 and January 1987 in the breeding colony on Torgersen Island, near Palmer Station off the west coast of the Antarctic Peninsula ($64^\circ46'S$, $64^\circ05'W$). These birds ($N=6$) were captured in hand nets, held in the laboratory for 2 to 3 days, and released after measurements were completed. Most of the wild penguins were obtained from small ‘resting’ groups; none were captured while attending nests. Ventilation data from wild birds was much more uniform than those from captives, and \dot{V}_{O_2} of wild birds was substantially lower than the \dot{V}_{O_2} of captives (see Results). Accordingly, we restricted most of our analyses to wild penguins. Unless otherwise specified, all reported measurements refer to wild penguins.

Measurements. Rates of gas exchange were measured in a plexiglas respirometry chamber (internal volume 92 l) placed in a larger environmental chamber which controlled ambient temperature (T_a) $\pm 0.5^\circ\text{C}$. The Sea World birds were run at T_a of -20 , -10 , 0 , 10 , 20 , and 25°C ; at Palmer Station we used T_a of -20 , -10 , 0 , 10 , 20 , and 30°C . The T_a was measured with copper-constantan thermocouples in the excurrent air line at its junction with the respirometry chamber. Penguins were unrestrained in the chamber, and had adequate room to stretch, groom, or lay prone. They stood on a screen-wire platform over a layer of mineral oil which covered voided excreta. After completing measurements of each T_a , we measured body temperature (T_b) with a thermocouple inserted into the proventricu-

lus within 45 s of removing the bird from the chamber. Penguins were fasted at least 12 h (usually >20 h) before experiments. All measurements were made during local daylight (0700–1900 Palmer time).

Oxygen consumption (\dot{V}_{O_2}), carbon dioxide production (\dot{V}_{CO_2}), and evaporative water loss (\dot{m}_{H_2O}) were measured using open-circuit respirometry. Flow rates of dry air (12 l/min at low T_a to 25 l/min at high T_a) were regulated $\pm 1\%$ with Tylan mass flow controllers. A fraction (50–100 ml/min) of the excurrent air was diverted through a Viasala humidity sensor, dried and passed through an Anarad AR-50 CO_2 sensor, scrubbed of CO_2 with Ascarite and redried, and passed through an Applied Electrochemistry S-3A O_2 sensor. Before and after measurements, all sensors were referenced against dry air diverted from upstream of the respirometry chamber. The humidity probe resolved 0.1% R.H. and was calibrated over salt solutions to within 1% of actual R.H. The CO_2 sensor was calibrated weekly with a precision reference gas to an accuracy of 0.005% CO_2 . Both CO_2 and O_2 analyzers resolved concentrations of 0.001%. During experiments, O_2 concentration was always $>20.3\%$ and CO_2 concentration never exceeded 0.6%. Chamber humidity was kept below 50%, except at $T_a < 10^\circ\text{C}$. Ventilation and gas exchange data were taken only after birds had been held at one T_a for at least 1 h and \dot{V}_{O_2} was low and stable. Gas exchange data were recorded by a microcomputer equipped with an analog-to-digital converter. The sample interval was 5 s, which allowed 53 min of uninterrupted measurements between pauses for data storage. \dot{V}_{O_2} was calculated as:

$$\dot{V}_{O_2} = \dot{V} \cdot (F_{iO_2} - F_{eO_2}) / [M \cdot (1 - F_{eO_2})] \quad (1)$$

where \dot{V} is flow rate (STPD), F_{iO_2} is the fractional concentration of O_2 in incurrent air, F_{eO_2} is fractional O_2 concentration in excurrent air, and M is body mass. \dot{V}_{CO_2} was calculated as:

$$\dot{V}_{CO_2} = \dot{V} \cdot (F_{eCO_2} - F_{iCO_2}) / M \quad (2)$$

where F_{eCO_2} is the fractional concentration of CO_2 in excurrent air and F_{iCO_2} is the fractional concentration of CO_2 in incurrent air. Rates of evaporative water loss (\dot{m}_{H_2O}) at $T_a > 0^\circ\text{C}$ were computed by substituting water vapor concentrations for CO_2 concentrations in Equ. (2). Data on vapor pressures and vapor densities were obtained from Tracy et al. (1980). No condensation within the flow system was observed at $T_a > 0^\circ\text{C}$. Plexiglas adsorbs small quantities of water vapor, which can decrease the accuracy of water loss measurements in conditions of low humidity, flow rate, and \dot{m}_{H_2O} . Potential errors from this source were minimized by the relatively high humidities and flow rates we used, and by the 1–2 h equilibration period between measurements. At $T_a \leq 0^\circ\text{C}$ frost formed in the excurrent air line, preventing direct measurement of \dot{m}_{H_2O} . Accordingly we used Equ. (56) in Calder and King (1974) to compute water loss from \dot{V}_{O_2} at these T_a . This approximation, which predicts \dot{m}_{H_2O} from T_a and metabolic rate, may not be completely accurate for Adelie penguins. However, any errors are probably unimportant for calculations of heat balance because, at $T_a < 0^\circ\text{C}$, evaporative heat loss is typically $<6\%$ of metabolic heat production. We computed thermal conductance by converting \dot{V}_{O_2} and \dot{m}_{H_2O} into their heat flux equivalents, using values of 21 J/[ml O_2] (typical for fat metabolism) and 2404 J/[g H_2O] to yield metabolic heat production (MHP) and evaporative heat loss (EHL), respectively. Dry thermal conductance (C , W/[g $^\circ\text{C}$]) was calculated as:

$$(MHP - EHL) / (T_b - T_a) \quad (3)$$

The respirometer functioned as a whole-body plethysmograph, allowing simultaneous measurements of gas exchange and ventilation (Bucher 1981; Chappell and Bucher 1987). Pressure

changes caused by the warming and humidification of tidal air were measured with a pressure transducer connected to a microcomputer. Sampling intervals for ventilation data were 0.1 s for low-frequency breathing (yielding 64 s of continuous measurements) and 0.05 s for high-frequency breathing (yielding 32 s of continuous measurements). The system was calibrated by serial injections of known volumes of air into the chamber after each set of measurements at a particular T_a . Inspiratory tidal volume was computed by comparing ventilation deflections with calibration deflections according to Malan (1973). For these calculations we assumed that lung temperature = T_b . Chamber pressure was 8–15 Torr over ambient and the total pressure experienced by the penguins was approximately 765–770 Torr.

The \dot{V}_{O_2} and \dot{V}_{CO_2} are corrected to STP; V_T and $\dot{V}_I (=f \times V_T)$ are calculated at BTPS and indicate actual volumes in the respiratory tract. The E_{O_2} was computed from \dot{V}_I (adjusted to STP) and \dot{V}_{O_2} as $E_{O_2} = [\dot{V}_{O_2} / (0.2095 \cdot \dot{V}_I)] \times 100$, after accounting for ambient humidity and CO_2 concentration.

Statistics. We made 4–10 measurements of ventilation and gas exchange at each T_a for all penguins, but only used samples for which \dot{V}_{O_2} was within 10% of its lowest 10-min average for a particular T_a . All data that met this criterion were used for comparisons which did not directly involve T_a (e.g., the effects of f on E_{O_2} or the relationship between \dot{V}_{O_2} and ventilation parameters). For comparisons between different T_a , single values were computed for each individual in order to avoid biasing results in favor of birds with many data points. The lowest 10-minute moving average from the 53 min measurement period was used for gas exchange; for ventilation parameters, the single value was the average of all data points for that T_a . ANOVAs or t -tests were used to compare means; regressions were fitted by the method of least squares. The E_{O_2} data (expressed as %) were arcsine transformed for t -tests or ANOVAs (this transformation converts percentage or proportion data, in which variance is necessarily a function of the mean, into a form appropriate for standard statistical tests; Sokal and Rohlf 1981). Results differing at the 0.05 probability level are considered significantly different; data are given as mean \pm 95% confidence intervals.

Results

Penguins adapted well to the experimental apparatus. Most birds sat quietly during experiments, except for occasional episodes of preening. Activity levels increased at high T_a (20–30 °C), but never to a degree which prevented us from obtaining useful measurements. The mean mass of the six penguins was 4007 ± 363 g (range 3513–4955 g).

Body temperature

Body temperatures of wild-caught penguins were very stable at all T_a below 30 °C (Fig. 1a). Mean T_b at these T_a was 39.3 ± 0.2 °C ($N=30$, range 38.3–40.2 °C). The T_b at 30 °C was slightly higher: 40.1 ± 0.58 °C ($N=6$, range 39.2–41.1 °C). However, the difference is only marginally significant ($P=0.042$, $F=2.65$, $N=36$). Similar results were obtained from captive penguins at Sea World.

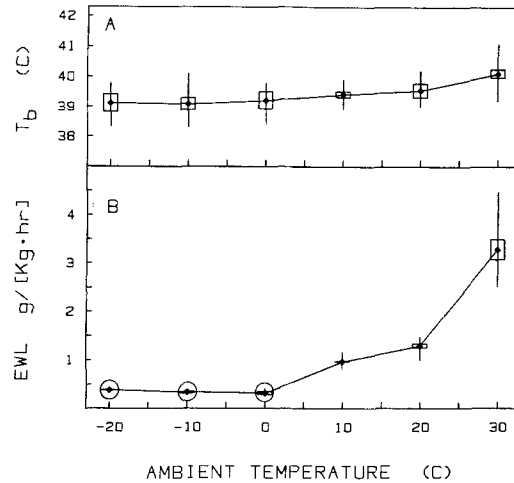


Fig. 1. **A** Body temperature (T_b) in Adelle penguins vs ambient temperature. Vertical lines indicate range; boxes indicate 95% confidence intervals; $N=6$ for all temperatures. **B** Evaporative water loss (EWL) vs ambient temperature. Data for T_a 's of -20 to 0 °C are estimated from a generalized regression for birds (see text)

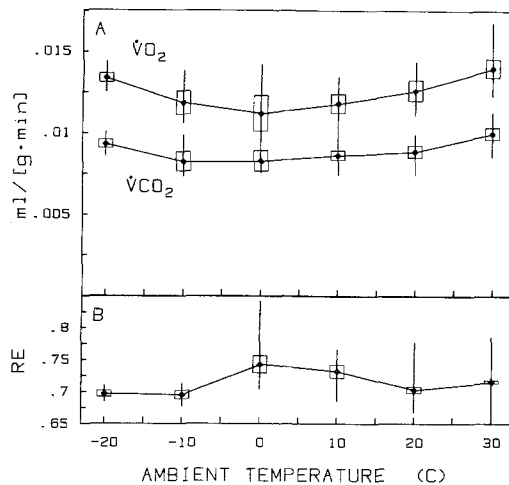


Fig. 2. **A** Oxygen consumption (upper line) and carbon dioxide production (lower line) vs ambient temperature. Symbols as in Fig. 1. **B** Respiratory exchange ratios (RE) vs ambient temperature

Gas exchange

Rates of evaporative water loss (Fig. 1 B) were low (0.025 – 0.063 g H_2O /min) at T_a of 10 °C and below, but increased rapidly at higher T_a . At 30 °C, \dot{m}_{H_2O} was 0.21 ± 0.04 g H_2O /min. That rate is equivalent to a loss of 0.3% of body mass per hour.

The \dot{V}_{O_2} and \dot{V}_{CO_2} of wild penguins (Fig. 2A) varied only slightly between T_a 's of -20 and 30 °C. The minimal \dot{V}_{O_2} (0.0112 ± 0.0013 ml/[g·min], $N=6$) occurred at 0 °C, but there was no significant difference in \dot{V}_{O_2} between T_a 's of -10 to 20 °C ($P=0.37$; $F=1.12$, $N=24$). \dot{V}_{O_2} was

slightly but significantly elevated above the minimal value at $-20\text{ }^{\circ}\text{C}$ ($0.01333 \pm 0.0007\text{ ml}/[\text{g} \cdot \text{min}]$; $P=0.016$; $F=3.76$, $N=30$) and at $30\text{ }^{\circ}\text{C}$ ($0.01397 \pm 0.0014\text{ ml}/[\text{g} \cdot \text{min}]$; $P=0.003$; $F=5.32$, $N=30$). Because these increases are so small, it is difficult to define the limits of the thermal neutral zone with any precision. However, for most purposes Adelie penguins can be considered to be effectively thermoneutral at all T_a between -10 and $20\text{ }^{\circ}\text{C}$. The increase in \dot{V}_{O_2} at $-20\text{ }^{\circ}\text{C}$ (compared to the minimal \dot{V}_{O_2} at $0\text{ }^{\circ}\text{C}$), though statistically significant, was only 17%.

\dot{V}_{CO_2} closely paralleled \dot{V}_{O_2} (Fig. 2A). Respiratory exchange ratios (RE, Fig. 2B) averaged 0.70 to 0.74 at all T_a , indicating that fat was the primary metabolic substrate. Even though they were fasted prior to experiments, we cannot be sure the birds were completely postabsorptive because adult penguins often retain food in the stomach for long periods. However, values of RE did not differ between individuals fasted 12–20 h and those fasted for 36–48 h, indicating that the birds were not digesting during measurements.

Gas exchange of captive penguins at Sea World differed from that of wild-caught Adelies. At all T_a below $20\text{ }^{\circ}\text{C}$, the \dot{V}_{O_2} and \dot{V}_{CO_2} of captive birds were significantly higher than those of wild-caught individuals ($P < 0.003$ in all cases). The difference increased with decreasing T_a , and at $-20\text{ }^{\circ}\text{C}$ the \dot{V}_{O_2} of Sea World birds was 85% larger than for wild penguins (0.0240 vs $0.01333\text{ ml}/[\text{g} \cdot \text{min}]$). Moreover, in captive penguins the lower limit of the thermal neutral zone was approximately $0\text{ }^{\circ}\text{C}$, instead of $-10\text{ }^{\circ}\text{C}$ for wild-caught birds.

Thermal conductance

Dry thermal conductance (C) increased with increasing T_a (Fig. 3A). Minimal conductance ($0.0712 \pm 0.0040\text{ W}/[\text{kg} \cdot ^{\circ}\text{C}]$, $N=6$) occurred at $-20\text{ }^{\circ}\text{C}$. Although there was no significant difference in C between -20 and $-10\text{ }^{\circ}\text{C}$ ($P=0.12$, $N=12$, t -test), differences were significant between all other T_a . At $30\text{ }^{\circ}\text{C}$, C was $0.2457 \pm 0.0147\text{ W}/[\text{kg} \cdot ^{\circ}\text{C}]$, or 3.45 times larger than at $-20\text{ }^{\circ}\text{C}$. The proportion of total heat loss due to evaporation (EHL) was less than 10% at $T_a \leq 0\text{ }^{\circ}\text{C}$, but reached 16.4% at $10\text{ }^{\circ}\text{C}$, 20.5% at $20\text{ }^{\circ}\text{C}$, and 46.9% at $30\text{ }^{\circ}\text{C}$ (Fig. 3B).

Ventilation

Ventilation parameters (f , V_T , \dot{V}_I , and E_{O_2}) of wild-caught Adelies are summarized in Table 1 and plotted as a function of T_a in Fig. 4.

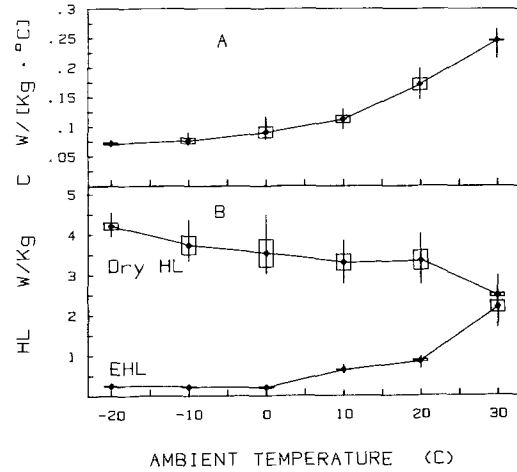


Fig. 3. A Dry thermal conductance (C) vs ambient temperature. Symbols as in Fig. 1. B Heat loss (HL) from evaporation (EHL) and by dry conductance ($dry\ HL$) at different ambient temperatures. Data at T_a of $0\text{ }^{\circ}\text{C}$ and below (circled) were obtained from metabolic rate using equ. 56 in Calder and King (1974); see text for details

Table 1. Ventilation parameters of Adelie penguins at different ambient temperatures (T_a)

T_a	V_T	f	\dot{V}_I	E_{O_2}
-20	123.4 (33.2)	8.4 (1.9)	1004 (244)	27.8 (7.4)
-10	124.0 (53.2)	7.8 (1.9)	910 (277)	27.7 (5.9)
0	101.4 (30.4)	7.8 (1.9)	751 (169)	32.1 (7.7)
10	96.3 (16.4)	7.8 (1.7)	742 (139)	35.0 (4.8)
20	109.9 (55.4)	18.1 (9.4)	1657 (635)	21.2 (7.9)
30	105.2 (38.5)	54.1 (13.7)	5111 (1107)	6.4 (1.5)

Symbols: V_T , tidal volume (ml); f respiration frequency (breaths/min); \dot{V}_I minute volume (ml); E_{O_2} oxygen extraction (%). Data are shown as means and 95% confidence intervals (in parentheses)

Respiration frequency (Fig. 4A) did not change significantly between T_a 's of -20 to $10\text{ }^{\circ}\text{C}$ ($P=0.97$; $F=0.087$, $N=24$); mean f over this T_a range was 7.96 ± 0.86 breaths/min. Breathing under these thermal conditions was characterized by rapid inhalations and exhalations separated by 6–10 s apneas. In some birds, apneas of up to 35 s were observed, usually followed by 2–5 breaths in rapid succession. Although we have no direct data on arousal states, we suspect these long apneas occurred in sleeping individuals. Respiration frequency increased and apneas disappeared at higher T_a . Some individuals showed little or no increase

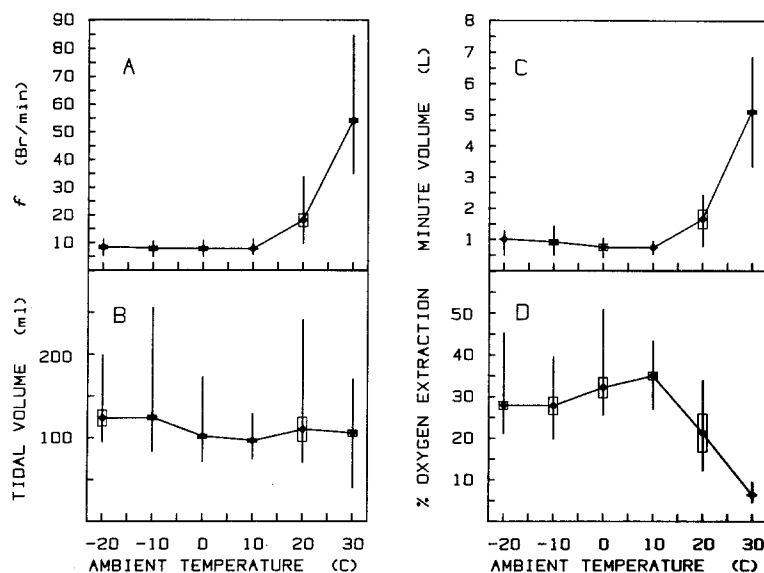


Fig. 4A–D. Ventilation parameters vs ambient temperature. Symbols as in Fig. 1. A Respiration frequency (f). B Tidal volume. C Minute volume. D Oxygen extraction

in f at 20 °C. All birds panted at 30 °C and the mean f at this T_a was 54.1 ± 13.7 breaths/min, an increase of about 7-fold over minimal levels. The highest f observed was 87 breaths/min.

Mean V_T (110 ± 15.6 ml; Fig. 4B) did not change significantly over the entire range of T_a , even during high-frequency panting ($P=0.89$; $F=0.328$, $N=36$). However, there was considerable variation both within and especially between individuals. For example, at -10 °C V_T varied more than 3-fold (83 to 255 ml). At 20 and 30 °C the range was even greater. Minimal V_T (96.2 ± 16.4 ml) occurred at 10 °C.

Minute volume (Fig. 4C) declined slightly between -20 °C (1004 ± 244 ml/min) and 10 °C (742 ± 139 ml/min), but the decline was not significant ($P=0.27$; $F=1.42$, $N=24$). At higher T_a , \dot{V}_I increased rapidly and significantly as birds began to pant, reaching 5111 ± 1107 ml/min at 30 °C. As with f and V_T , there was considerable variation in \dot{V}_I , especially at high T_a .

The ventilation parameters of Adelies from the Sea World colony were much more irregular than those of wild-caught penguins. In most of the Sea World birds, V_T and f showed considerable variation (apparently random) over time intervals as short as a few seconds. In contrast, ventilation in wild penguins was usually quite stable for periods of several minutes at a time (variation within individuals did occur, but over much longer periods than in captive birds).

Oxygen extraction

Rates of oxygen extraction are shown in Fig. 4D. The highest mean E_{O_2} occurred at 10 °C

($35.0 \pm 4.8\%$), and the maximum observed E_{O_2} was 65.5% (also at 10 °C). At lower T_a , E_{O_2} declined, reaching $27.8 \pm 7.4\%$ at -20 °C, but the difference was not significant ($P=0.32$; $F=1.24$, $N=24$). E_{O_2} declined sharply and significantly at 20 and 30 °C as birds began to pant; the minimal value (at 30 °C) was $6.4 \pm 1.5\%$. Substantial inter- and intra-individual variation was apparent, especially at 10 and 20 °C. Nevertheless, all birds showed a qualitatively similar overall relationship of E_{O_2} with T_a .

Considerable variation between individuals is evident in Fig. 5, which shows the relationship between f and E_{O_2} . In general, when birds were not panting E_{O_2} was high but showed no relationship to f . The E_{O_2} dropped suddenly at the onset of panting (i.e., at f exceeding about 15 breaths/min). Similar trends were apparent within individuals. However, points for different birds are clustered around different 'preferred' combinations of f and E_{O_2} , particularly during panting.

Discussion

Differences between wild and captive birds

At low T_a , the \dot{V}_{O_2} of wild-caught penguins was considerably less than that of long-term captives. The difference reflects lower thermal conductance in wild birds, which may result from unequal thermal acclimation regimes or from seasonal differences in physiology (Palmer birds were in the midst of the summer breeding season, while Sea World birds were measured during local 'winter'). We have no adequate explanation for the highly irregular f and V_T of captive penguins; a remote possi-

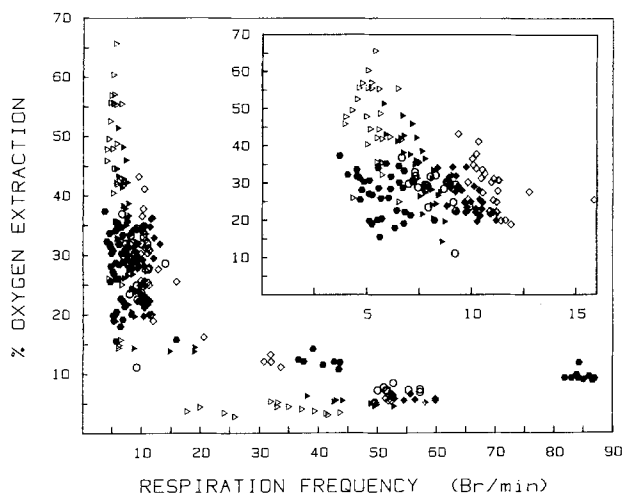


Fig. 5. Oxygen extraction vs respiration frequency (inset shows enlargement of data for f of 0–16 breaths/min). Symbols indicate data from different individuals

bility is that the irregularity was related to the long period of captivity and/or old age (> 14 years) of these individuals.

Thermoregulation

Adelie penguins have impressively wide thermoneutral zones. Although it is difficult to discern the lower critical temperature (LCT) from our data, the \dot{V}_{O_2} of wild Adelies did not increase significantly above minimal levels until T_a was reduced below -10°C . This LCT is one of the lowest yet reported for birds and is roughly equivalent to the LCT of the much larger emperor penguin (Pinshow et al. 1976; LeMaho et al. 1976). Nevertheless, the Adelie's tolerance of low T_a is not exceptional for a bird of its mass: feathered chicks of the similar-sized, congeneric chinstrap penguin (*P. antarctica*) also have LCT's of approximately -10°C (Taylor 1985), and the predicted LCT for a 4.007 kg nonpasserine is -6.6°C (Calder and King 1974). Somewhat surprisingly, the thermal conductance of Adelies is approximately 25% higher than predicted from regressions for nonpasserines (Calder and King 1974), and is substantially greater than that of several other birds from cold climates (e.g., snowy owls, Gessaman 1972; Peruvian penguins, Drent and Stonehouse 1971; Pinshow et al. 1976). The higher than expected heat transfer coefficient of Adelies is balanced by a relatively high resting metabolism. Rates of metabolic heat production (calculated from \dot{V}_{O_2}) within the thermal neutral zone are 14.9 W, or about 23% higher than predicted for a 4.007 kg nonpasserine in the active phase of the diel cycle (12.1 W,

Aschoff and Pohl 1970). By comparison, Kooyman et al. (1976) estimated the minimal metabolic rate of Adelies to be about 11 W at T_a of $13\text{--}15^\circ\text{C}$, and Hammel et al. (1976) and Simon et al. (1976) reported minimal metabolic rates of 17–23 W.

Adelies are surprisingly tolerant of high T_a . During our experiments they withstood temperatures of 30°C for several hours with no apparent discomfort and only minor elevation of T_b and \dot{V}_{O_2} , despite intense panting. Heat loss under these conditions was facilitated by a large increase in dry conductance (about 3.5-fold greater than the minimal conductance), and by substantial evaporative water loss. At 30°C , almost half the metabolic heat production was dissipated by evaporation. The increase in dry conductance was probably due to peripheral vasodilation in the flippers, feet, and facial area (Hammel et al. 1976; Simon et al. 1976).

Rates of evaporative water loss were relatively low, even at high T_a . At 30°C , Adelies lost only 0.3% of body mass/h by evaporation. Adelies can tolerate somewhat higher T_a than we used in this study. Murrish (1973, 1982) reported that they withstood T_a 's of $33\text{--}37^\circ\text{C}$ (however, the birds often incurred severe respiratory alkalosis under these conditions). Assuming that dry conductance cannot be increased above the maximal level we observed, we estimate that Adelies need to evaporate about 0.5% of body mass/h to maintain thermal balance at $T_a = 35^\circ\text{C}$. These low rates of EWL are consistent with observations of Adelies panting continuously for many hours while incubating eggs or shading chicks on sunny days. If Adelies can tolerate a depletion of the body water pool equivalent to 10% of initial body mass, they can pant for 20 h at $T_a = 35^\circ\text{C}$ (assuming they are not limited by respiratory alkalosis), and for 33 h at $T_a = 30^\circ\text{C}$. Long-duration panting is important for the reproductive ecology of Adelies. Relatively high heat loads are engendered by calm, sunny days (unpublished data), and individual incubation bouts can last for several days before a bird is relieved by its mate (Ainley et al. 1983).

Ventilation at low T_a

The ventilation parameters of Adelies were remarkably constant over a wide range of T_a . No significant change occurred in f , V_T , \dot{V}_I , or E_{O_2} between T_a 's of -20 to 10°C . This stability is probably due to the wide thermoneutral zone of Adelies, which results in unchanging gas exchange requirements between -10 and 20°C and a very small increase in \dot{V}_{O_2} (17%) at -20°C . In several

other birds (e.g., pigeons, Bech et al. 1985; prairie falcons, Kaiser and Bucher 1985; parrots, Bucher 1981, 1985; chukar partridges, Chappell and Bucher 1987), f , \dot{V}_T , and \dot{V}_I increased with decreasing T_a . However, these changes occurred at T_a considerably below thermoneutrality. The increased ventilation presumably functioned to support increased \dot{V}_{O_2} and \dot{V}_{CO_2} .

In European coots and mallard ducks, both \dot{V}_I and E_{O_2} increased with decreasing T_a below the lower critical temperature (Brent et al. 1984; Bech et al. 1985). Elevated E_{O_2} at low T_a reduces air convection requirements and hence the rate of respiratory heat loss, and is often interpreted as a thermoregulatory adaptation (Bucher 1981; Johansen and Bech 1983). However, in those species for which respiratory heat loss has been quantified, the potential reduction in heat loss accruing from high E_{O_2} is minor. In small parrots (Bucher 1981), European coots (Brent et al. 1984), and chukar partridges (Chappell and Bucher 1987), elevated E_{O_2} could reduce total heat loss by only 3–6%. For Adelies, assuming that the exhaled air temperature is 0 °C at $T_a = -20$ °C (Murrish 1973), respiratory heat loss (including evaporative heat loss) amounts to 3.8% of metabolic heat production. Hence, a 1.5-fold increase in E_{O_2} (from 30–35% to 52%) would reduce heat loss by only 1.9% at this T_a .

The minimal f for Adelies was about 7.8 breaths/min in this study; Murrish (1982) reported a resting f for Adelies of 8 breaths/min. These values are approximately as expected for an unrestrained bird with mass of 4.007 kg (6.6 breaths/min, Bucher 1985), but are considerably less than predicted by a regression obtained from restrained birds (11.2 breaths/min, Lasiewski 1972).

Panting

Evaporative heat loss by panting is surprisingly effective in Adelies, considering their high-latitude distribution and tolerance of low T_a . Large increases in \dot{V}_I occurred at $T_a \geq 20$ °C, and were accompanied by elevated \dot{m}_{H_2O} . At the mean \dot{V}_I (5.11 l/min) and \dot{m}_{H_2O} (0.21 g/min) we measured at $T_a = 30$ °C, the temperature of exhaled air at 100% saturation would be 35 °C (Tracy et al. 1980). The difference between this temperature and the mean T_b of 40.1 °C is probably due to cooling within the nasal cavities (Murrish 1973).

The 5 to 7-fold increase in \dot{V}_I at high T_a is of similar magnitude to changes in \dot{V}_I observed

in other species. However, the manner in which Adelies accomplish the increase is unusual: the change is due entirely to a relatively moderate increase in f , with no change in \dot{V}_T . In most birds, \dot{V}_T declines sharply when panting commences, and f increases to a much greater degree (15 to 25-fold) than observed in Adelies (Bucher 1981, 1985; Kaiser and Bucher 1985; Chappell and Bucher 1987). We saw no evidence of the 'compound panting' reported by Ramirez and Bernstein (1976) and Bernstein and Samaniego (1981) for pigeons and by Chappell and Bucher (1987) for chukar partridges. In these species, high-frequency panting involves very low \dot{V}_T , such that effective ventilation is limited to the trachea. This prevents overventilation of the gas exchange surfaces and a resultant hypocapnia. Periodic deep 'flush-out' breaths (Bernstein and Samaniego 1981), which comprise a small portion of total \dot{V}_I , ventilate the parabronchi and allow for gas exchange.

Panting rates during our study were considerably greater than previously reported for Adelies. At 30 °C, the mean f for our birds (54 breaths/min) was approximately twice the rate observed by Murrish (1982) at the same T_a (his penguins did not attain an f of 50 breaths/min until T_a exceeded 35 °C). Moreover, Murrish described increases in arterial blood pH when f exceeded 25 breaths/min, and his birds developed substantial respiratory alkalosis at the f we observed. We did not measure blood pH, but two observations suggest that respiratory alkalosis was not severe during our measurements. First, our penguins withstood f of 50–60 breaths/min for periods exceeding 2 h (occasionally considerably longer) without obvious distress. Many birds tolerate considerable alkalosis during heat stress (Calder and Schmidt-Nielsen 1968), so this observation is not strong evidence. However, we saw no evidence of decreasing f over time, as might be expected from negative feedback if blood pH became too alkaline. Murrish was convinced that \dot{V}_T increased at high f (although he did not measure it directly), whereas \dot{V}_T remained constant in our experiments. If Murrish was correct, the \dot{V}_I of his birds would have been higher than we measured at similar f , thereby increasing the likelihood of alkalosis.

The reason for the difference in panting rates (and possibly \dot{V}_T) between the two studies is unclear, but might be due to the irritative effect of the catheters and thermistor probes used by Murrish. Ventilation parameters (including f and \dot{V}_T) in many birds are known to be sensitive to even minor disturbances (Bucher 1981; Chappell and Bucher 1987).

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