Weather, microclimate, and energy costs of thermoregulation for breeding Adélie Penguins

M.A. Chappell, K.R. Morgan*, and T.L. Bucher**

Biology Department, University of California, Riverside, CA 92521 USA

Summary. We measured meteorological conditions and estimated the energy costs of thermoregulation for young and adult Adélie Penguins (*Pygoscelis adeliae*) at a breeding colony near the Antarctic Peninsula. Air temperatures averaged $< 5°$ C and strong winds were frequent. Operative temperatures (T_e) for adults ranged from -8 to $28°$ C, averaging 5–6° C, for the period from courtship to fledging of chicks. The average energy cost of thermoregulation (C_{th}) for adult penguins was equivalent to 10–16% of basal metabolism. C_{th} comprised about 15% of the estimated daily energy budget (DEB) of incubating adults, but only about 1% of the DEB of adults feeding chicks. The T_e's for chicks older than 14 days ranged from 0 to 31° C, averaging 8.0 C. The C_{th} for downy chicks ranged from about 31% of minimal metabolic rate (MMR) in 1 kg chicks to about 10% of MMR in 3 kg chicks. Between initial thermal independence (age 12–14 days) and the cessation of parental feeding (age 35–40 days), chicks use about 10–11% of assimilated energy for thermoregulation. C_{th} is equivalent to about 17% of the MMR of fledglings during their 2–3 week fast. We observed no indication of thermal stress (i.e., conditions in which birds cannot maintain stable T_b) in adults and no indication of cold stress in any age class. However, on clear, calm days when air temperature exceeds 7–10° C for several hours, downy chicks are vulnerable to lethal hyperthermia.

Key words: Adélie Penguin – Energetics – Microclimate – Reproduction – Thermoregulation

Adélie penguins (*Pygoscelis adeliae*) breed on sub-Antarctic islands and the coast of Antarctica. Although breeding coincides with the relatively benign austral spring and summer, adults and chicks must cope with weather patterns ranging from subzero temperatures and high winds (Taylor 1962; Yeates 1971) to calm, sunny days which engender substantial heat loading (Murrish 1973; Muller-Schwarze 1984). Thermoregulatory challenges are exacerbated by extensive fasting, minimal parental attentiveness, and prolonged exposure of chicks to ambient conditions. Adults arrive at colonies in October and fast for 3–4 weeks while establishing territories, courting, and making nests. Females feed at sea after laying their eggs (usually two), but males continue fasting for another 10–16 days during the first incubation shift. Parents alternate nest attendance for the rest of the 32–35 day incubation period. Hatchlings are brooded continuously, but chicks older than 12–15 days encounter their parents only during brief, twice-daily feedings. Fledglings are abandoned at 5–6 weeks and must fast for 2–3 weeks while they complete the molt from natal down into juvenile plumage and learn to swim and capture prey (Ainley et al. 1983; Trivelpiece et al. 1987).

How important are weather and microclimate to Adélie Penguin breeding ecology? The thermal milieu in the colony could affect reproductive success through a variety of mechnisms, but two seem most plausible. Conditions exceeding the birds' capacity to thermoregulate would require adults to abandon nests or chicks, and could induce large-scale mortality of unprotected eggs or young. Less dramatic, but perhaps of greater long-term importance, are conditions requiring diversion of energy to thermoregulation (e.g., for metabolic heat production). High thermoregulatory expenditures reduce the duration of fasts that adults can undertake during courtship and incubation, slow the growth and maturation of chicks, and/or decrease the energy reserves and survival rate of young birds during molt and fledging.

Numerous authors have discussed the influence of weather on behavior, survival or reproduction in penguins (e.g., Taylor 1961; Stonehouse 1967, 1970; Le Resche and Boyd 1969; Drent and Stonehouse 1971;

Offprint requests to: M.A. Chappell

* *Present addresses:* Department of Zoology, University of Washington, Seattle, WA 98195, USA; ** Department of Biology, University of California, Los Angeles, CA 90024, USA

Yeates 1975; Pinshow et al. 1976; Le Maho et al. 1976; Taylor 1985; Culik 1989), but the energy cost of thermoregulation for Adélies has not been rigorously quantified. In this paper we present results from a study of an Adélie colony near the Antarctic Peninsula. We describe weather patterns and microclimate during courtship, incubation, chick rearing, and fledging and assess the importance of wind, sunlight, and air temperature to thermal balance. From these data and previously published information on the thermoregulatory physiology and heat transfer characteristics of Adélies (Chappell and Souza 1988; Chappell et al. 1989), we calculate the energy cost of thermoregulation and estimate its importance to the energy budgets of adults and chicks.

Materials and methods

Study area

We worked on Torgersen Island, about 1 km from the U.S. Palmer Station base off the northwest coast of the Antarctic Peninsula (64°46'S, 64°05'W). Torgersen is a low, rocky island (diameter 0.5 km) which supported 7000–8000 breeding pairs of Adélies during our study. Nests were clustered into several subcolonies in level, open areas where ground was first exposed during the spring snowmelt. Within subcolonies, nests were densely packed, and pairs vigorously defended small territories about 1 m in diameter. The birds tolerated observers well and showed no reaction unless a person approached closer than 2–3 m.

Microclimate measurements

We recorded microclimate in one subcolony during the 1986–1987 and 1987–1988 breeding seasons. Equipment was placed in typical habitat within 1–2 m of several active nests. The local breeding pairs quickly habituated to the instruments and to our periodic visits.

Incident solar radiation (Q_r) was measured with a Li-Cor LI-200s pyranometer, mounted atop a 2 m sensor mast and equipped with an integrating dome which greatly reduced directional sensitivity. The dome-equipped sensor was calibrated to an accuracy of $\pm 5\%$ against an unmodified LI-200s.

Wind speed (V) was measured with 1.3 cm diameter hot-ball anemometers (HBA's; Buttemer 1981; Chappell and Bartholomew 1981). HBA's were calibrated in a wind tunnel against an accurate hot-wire anemometer. Accuracy varied with V because of recorder resolution limits. At $V<3$ m/s accuracy was $\pm 7\%$; at V of 3–9 m/s accuracy was $\pm 12\%$; at higher V accuracy was ± 15–20%. Wind speeds >20 m/s were recorded only as exceeding that value. Two HBA's were deployed from the sensor mast, one 14–16 cm above ground level (the height of a small chick or prone adult) and the other 35 cm above ground level (the height of a standing adult or large chick).

Temperatures were recorded to a resolution of $\pm 0.2°$ C with copper-constantan thermocouples calibrated to an accuracy of $\pm 0.5°$ C against a common reference thermistor. We measured air temperatures (T_a) with 0.2 mm diameter thermocouples adjacent to the HBA's. Operative temperatures (T_e; Bakken 1976) were obtained from hollow taxidermic mounts of penguin pelts, equipped with internal thermocouples (Chappell et al. 1984). T_e is the equilibrium temperature a metabolically inert penguin would attain in a given combination of T_a, V, Q_r. The difference between body temperature (T_b) and T_e is an index of the gradient for heat flux between animal and environment. Actual heat flux is determined by the T_b–T_e gradient and by thermal resistance, which in turn is a function of the convective regime and the animal's

physiological characteristics (Bakken 1976; Robinson et al. 1976). We used three mounts of adults in different orientations and postures (prone or erect), and two mounts of chicks (1 kg and 3 kg). Simultaneous measurements from different mounts revealed effects of any color asymmetry (fledglings and adults are black dorsally and white ventrally; downy chicks are a uniform gray-brown) on absorbed solar radiation and T_e. Response times to complete 90% of a change to a new equilibrium T_e (τ_{90}) were 8–12 min at high V (>4 m/s) and 14–22 min at low V (0–2 m/s). We covered chick mounts with a light wire cage to prevent damage by skuas (*Catharacta maccormacki* and *C. lonnbergi*). The cage had no measurable affect on T_a, V, Q_r, or T_e.

Sensors were connected to a battery-powered microcomputer and 12-bit analog-to-digital converter (Remote Measurement Systems ADC-1). Data were recorded every 30 or 60 min throughout the day, stored in memory, and archived onto floppy disks every 1–3 days. Records were continuous for most of the study, but we lost data occasionally because of equipment malfunction or weather or sea ice conditions that prevented us from servicing the instruments. T_e and V data from periods of rain or snowfall were discarded, as sensors for these parameters were inaccurate when wet.

Physiological data

We measured T_b in the field by catching penguins with a hand net and quickly inserting a thermocouple 20–40 cm into the proventriculus. T_b ($\pm 0.1°$ C) was read with Bailey BAT-12 thermometers. Energy metabolism and thermal resistance were calculated from rates of oxygen consumption ($\dot{V}_{O_2}$) at T_a from -20 to 30° C and V from 0.1 to 8 m/s. $\dot{V}_{O_2}$ was measured using open-circuit respirometry (details of protocols and results are in Chappell and Souza 1988 and Chappell et al. 1989).

Calculations and analysis

Dates of first ovoposition and first hatching differed by only 1–2 days during 1986–1987 and 1987–1988, so we combined data from both seasons for analyses.

We calculated the metabolic heat production (MHP) required to maintain normal T_b for adults, 1 kg chicks (the smallest chicks thermally independent of their parents), 2 kg chicks, 3 kg chicks, and fully-feathered fledglings. The T_b's used in these calculations were derived from both laboratory and field measurements. MHP for V and T_e recorded in the field was computed by interpolating (occasionally extrapolating for $V>8$ m/s) from $\dot{V}_{O_2}$ measured in the laboratory over a range of V and T_a. We used adult T_e to calculate fledgling MHP, since fledglings are similar to adults in size and coloration. T_e's obtained from the two chick mounts were similar, so we used the mean value for all chick sizes when calculating MHP. For 1 kg chicks we used V measured by the lower HBA; for other ages we used the mean V from both upper and lower HBA's. We defined the energy cost of thermoregulation (C_{th}) as the difference between MHP and minimal resting metabolic rate at thermoneutral T_a (MMR; = BMR in adults and fledglings).

Data were analyzed using t-tests, ANOVA, and multiple regression. Skewed data were log- or square-root transformed as necessary to yield normal distributions. Data for V and Q_r were highly skewed, so these parameters were analyzed with the nonparametric Kruskal-Wallis method. Results differing at probability levels of 0.05 or less are considered significant. Values are given as mean $\pm$ SD.

Results

We monitored microclimate from 17 November 1986 to 31 January 1987 and from 6 November 1987 to 20 Feb-

Table 1. Chronology of Adélie Penguins breeding at Torgersen Island during the 1986–1987 and 1987–1988 reproductive seasons. Dates encompass 90–95% of each event; earliest observations in parentheses

Event	Dates
courtship, nest construction	mid-October to 25 November
egg laying	12 November to 1 December (8 November)
hatching	14 December to 1 January (10 December)
1 kg chicks (age 11–16 days)	25 December to 16 January (22 December)
2 kg chicks (age 20–25 days)	4 January to 22 January
3 kg chicks (age 29–35 days)	15 January to 3 February
fledglings (age 40–50 days)	31 January to 20 February (28 January)

Fig. 1. Frequency distributions of air temperature (T_a), wind speed (V), and incident solar radiation (Q_r) during the 1986–1987 and 1987–1988 breeding seasons. Distributions include all measurements from both years

ruary 1988 (N = 183 days). Sampling was evenly distributed with respect to season and time of day. Cumulatively, we lost about 18 days of data to malfunctions or other problems (longest single interval 4.5 days).

In both years egg laying was spread over 17–20 days (Table 1). Consequently there was considerable overlap between incubation and chick rearing and among various sizes of chicks. Subsequent discussion of phases of the breeding cycle refer to the following periods: courtship and incubation, 6 November to 20 December; chick rearing, 15 December to 3 February; fledging, 31 January to 20 February.

General weather patterns

During courtship and nest construction, snow covered all breeding sites but the central portions of some subcolonies. Except for a few peripheral nests, subcolonies were snow-free by the early stages of incubation (mid to late November). Snowfalls occurred during courtship and incubation and once each year enough snow fell to cover some incubating birds completely. Heavy mist and rain occurred sporadically during chick rearing but seldom lasted longer than a few hours. A few brief snowfalls occurred during fledging, but the new snow melted quickly.

Daily means of T_a, Q_r, and V changed relatively little over the breeding season, but there was substantial within-day variation. Individual records of T_a (N = 5172) ranged from −8.0 to 14.8° C, with an overall mean of 4.0 ± 2.9° C. More than 90% of the records were between −1 and 8° C (Fig. 1). Mean T_a changed slightly but significantly (P ≪ 0.001; ANOVA) from 2.7 ± 2.9° C (N = 2151) during courtship and incubation to 5.0 ± 2.6° C (N = 2969) during chick rearing to 3.8 ± 2.0° C (N = 765) during fledging.

The distribution of Q_r was strongly skewed (Fig. 1), with 44% of 5277 readings < 100 w/m² and 90% of the readings < 700 w/m². Mean Q_r over the breeding season was 244 w/m² and maximum Q_r was 1350 w/m² (when reflected radiant loads off snow augmented direct insolation). Mean Q_r was significantly higher during courtship
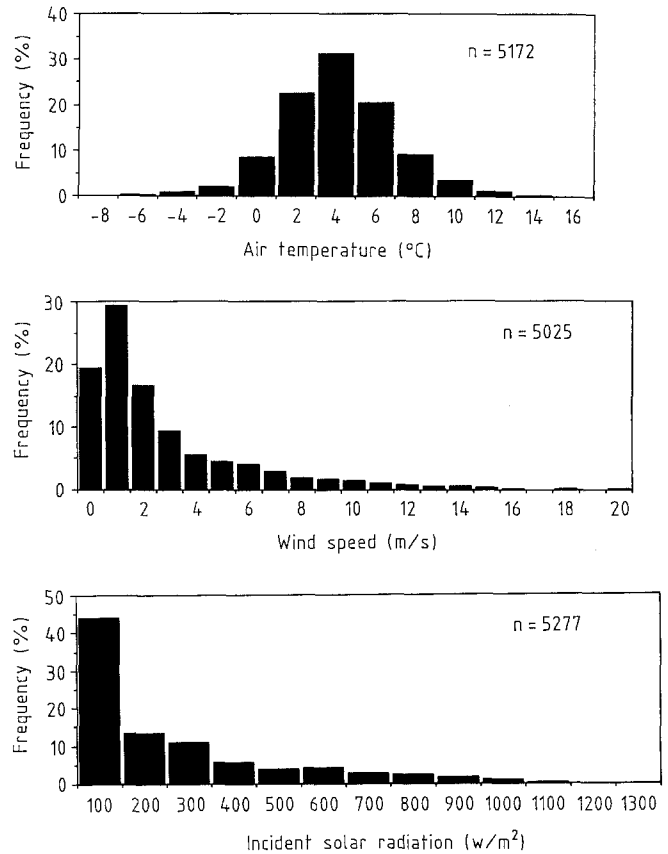
and incubation (311 w/m², N = 2195) than during chick rearing (191 w/m², N = 3056) or fledging (133 w/m², N = 775; P < 0.001, Kruskal-Wallis test).

The distribution of V was skewed towards low V (Fig. 1). Nevertheless, V was greater than 1 m/s in more than 80% of 5025 records and averaged 2.6 m/s, with occasional measurements approaching or exceeding 20 m/s. Mean V was highest during courtship and incubation (3.5 m/s; N = 2160), decreasing to 2.0 m/s (N = 3065) during chick rearing and 2.3 m/s during fledging (N = 538; P < 0.001, Kruskal-Wallis test).

Operative temperatures

Daily means of T_e changed only slightly over the breeding season but there was substantial within-day variation of T_e (Fig. 2). Adult T_e often fluctuated by 12–16° C in a single day, with a maximum daily change of 25° C. Maximum diel variation of chick T_e was 28° C.

Adult T_e (average of three mounts in different orientations) ranged from −8.0 to 22.9° C with an overall mean of 5.8 ± 3.9° C (N = 5173; Figs. 2, 3). The highest T_e recorded from a single adult mount was 27.6° C. Mean adult T_e was slightly lower during courtship and incubation (5.0 ± 4.4° C, N = 2195) than during chick rearing (6.7 ± 3.6° C, N = 2945; P < 0.001, *t*-test).
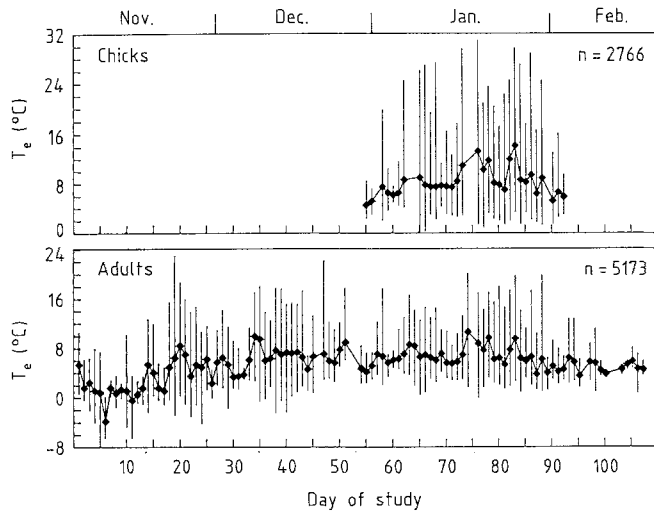
Fig. 2. Operative temperatures (T_e, °C) for Adélie Penguin adults and chicks during the 1986–1987 and 1987–1988 breeding seasons. Adult T_e is the mean of temperatures from three taxidermic mounts in different orientations; chick T_e is the mean of temperatures from two mounts. Diamonds indicate 24-h means and vertical lines indicate ranges
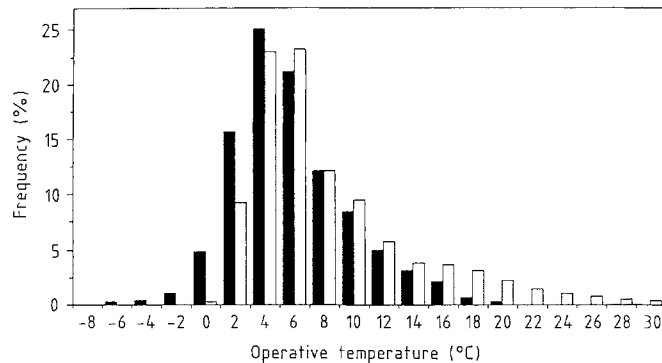

Fig. 3. Frequency distributions of adult and chick T_e during the 1986–1987 and 1987–1988 breeding seasons. ■ Adults N = 5173; □ Chicks N = 2766

Mounts with their dark backs towards the sun attained T_e's 2–7° C higher than the T_e's of otherwise identical mounts with the white ventral plumage facing the sun (the T_e difference between orientations varied with solar azimuth and V).

Chick T_e averaged 8.3±5.6° C (range 0–30.8° C, N = 2766), somewhat higher than simultaneously measured adult T_e ($P < 0.001$, t-test). Orientation to the solar beam had little effect on chick T_e. Temperature excess (T_{ex}; = T_e-T_a) also averaged significantly higher for chicks than for adults (3.3±4.9° C versus 1.8±2.8° C, N = 2766 and 5172, respectively; $P < 0.001$, t-test). Maximum T_{ex} was 21.8° C for adults and 26.1° C for chicks.

We used multiple regression to examine the influence of T_a, Q_r, and V on T_e, according to the following logic: $T_e = T_a$ in all blackbody convective environments; at constant V and T_a, T_e changes in proportion to Q_r. At moderate V and constant T_a and Q_r, T_e is inversely related to $V^{0.5}$ (Monteith 1973; Robinson et al. 1976; Mit-
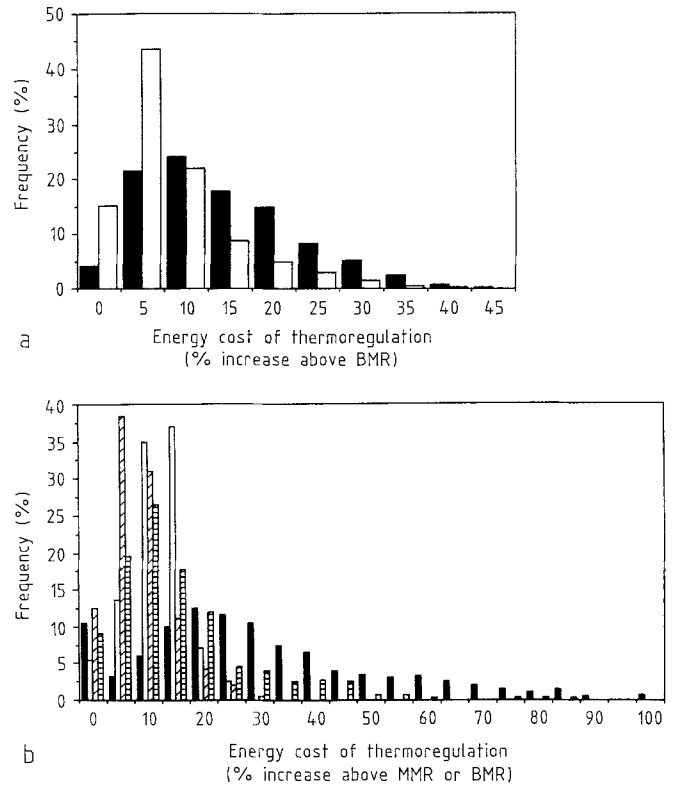

Fig. 4a, b. Frequency distributions of energy costs of thermoregulation for adults a ■ Incubation N = 2441; □ Chick rearing N = 3013 and chicks b ■ 1-kg Chicks N = 1146; □ 2-kg Chicks N = 1323; ▨ 3-kg Chicks N = 1428; ▤ Fledglings N = 914

chell 1976; Goldstein 1983; Stahel et al. 1987). The magnitude of convective heat flux depends on the gradient between surface and air temperature (Monteith 1973), so the absolute change in T_e resulting from a change of V is proportional to Q_r. Accordingly, the convection term was expressed as a multiple of Q_r and $V^{0.5}$:

$$\text{Adult } T_e = 0.85(T_a) + 0.013(Q_r) - 0.0032(Q_r \cdot V^{0.5}) + 0.56$$
$$P < 0.001, \text{ N} = 4867, r^2 = 0.83 \tag{1}$$

$$\text{Chick } T_e = 0.69(T_a) + 0.028(Q_r) - 0.0056(Q_r \cdot V^{0.5}) + 1.47$$
$$P < 0.001, \text{ N} = 2307, r^2 = 0.74 \tag{2}$$

The coefficient for T_a is less than 1 because T_e can be less than T_a if Q_r is low and birds are exposed to a clear sky. We attribute most residual variance to unequal sensor $\tau_{90\%}$. Sensors for Q_r and T_a responded almost instantaneously, but $\tau_{90\%}$ for HBA's and taxidermic mounts was tens or hundreds of seconds (depending on V). Rapid changes in T_a, Q_r, or V therefore produced readings not matched to equilibrium T_e.

Body temperatures

Adults and chicks maintained T_b within narrow limits. Adult T_b (38.7±0.4° C; range 37.4–39.6; N = 42) did not differ significantly between sunny and overcast days. The T_b's of unbrooded chicks (mass 1 kg or larger) did

Table 2. Energy cost of thermoregulation in Adélie Penguins. Abbreviations: MHP, metabolic heat production in watts, calculated from microclimate measurements and data on oxygen consumption in different combinations of air temperature and wind speed; MMR, minimal metabolic rate (= BMR in adults and fledglings); C_{th}, energy cost of thermoregulation, max C_{th}, maximum value of C_{th} (minimum $C_{th} = 0$ for all age classes). Values are mean ± S.D.

age class	MHP (watts)	MMR[a] (watts)	C_{th} (watts)	C_{th} (% MMR)	max C_{th} (% MMR)	N
incubating adults	17.2 ± 1.3	14.7	2.5 ± 1.3	16.8 ± 8.5	46	1973
adults rearing chicks	16.5 ± 1.1	14.7	1.8 ± 1.1	11.9 ± 7.6	36	2944
1 kg chicks	9.2 ± 1.4	7.1	2.1 ± 1.4	30.8 ± 20.1	104	1054
2 kg chicks	16.8 ± 0.7	14.7	2.1 ± 0.7	14.2 ± 5.1	30	1242
3 kg chicks	23.8 ± 1.2	21.5	2.3 ± 1.2	10.8 ± 5.5	33	1302
fledglings	20.8 ± 2.1	17.8	3.0 ± 2.1	16.8 ± 11.7	87	688

[a] from Chappell and Souza (1988) and Chappell et al. (1989)

not differ significantly with mass on either overcast or sunny days. On sunny days with little wind, more than 80% of the chicks in the colony panted heavily (no panting was observed on overcast days). However, mean chick T_b was only slightly higher on sunny days (39.5 ± 0.55, range 38.4–41.6, N = 122) than on overcast days (39.0 ± 0.55, range 37.5–39.7, $P < 0.01$, N = 27).

Thermoregulatory costs

For Adélies breeding on Torgersen, the energy cost of thermoregulation was generally moderate but changed markedly with age (Fig. 4; Table 2). It was lowest in adults rearing young and in 3 kg chicks (mean C_{th} 12% and 11%, maximum 46% and 36% of MMR, respectively), and highest in 1 kg chicks (mean C_{th} 31%, maximum 104% of MMR). Mean C_{th} differed significantly among the three age classes of chicks (N = 3897; $P < 0.001$, ANOVA) and among incubating and chick rearing adults (N = 5145; $P < 0.001$, t-test). Since it is a function of T_e and V, C_{th} showed considerable diel variation. In 1 and 2 kg chicks and fledglings, C_{th} often varied from 0 to > 50% of MMR within a few hours. Diel fluctuations in C_{th} were proportionally smaller in adults and 3 kg chicks; in these age classes C_{th} seldom exceeded 25–30% of MMR.

Discussion

Adélie Penguin colonies are colder than most avian breeding habitats. The uninsulated nest sites offer little protection from frequent winds, chicks are left unattended at a relatively early age, and adults and fledglings undergo substantial fasts. Accordingly, it is reasonable to assume that microclimate conditions could have an important influence on breeding biology. We addressed three related questions: (1) Is thermal stress (environmental conditions that exceed the birds' physiological or behavioral ability to maintain a normothermic T_b) a significant factor in reproductive success? (2) How large are energy costs of thermoregulation, and what fraction of the birds' overall energy budgets do they

comprise? (3) Which climatic factors have the greatest impact on thermal balance and C_{th}?

Thermal stress

We saw few indications that Adélies at Torgersen experienced appreciable cold stress. Laboratory measurements of thermogenic capacity demonstrate that penguins of all the age classes we studied can withstand combinations of low T_a and high V much more severe than any we measured (or are likely to occur) in the Torgersen colony. Even 1 kg chicks (the smallest birds not continuously attended by parents) maintain T_b of 36–38° C for several hours in winds of 6–8 m/s at a T_a of −20° C (Chappell et al. 1989; see also Taylor 1985, 1986).

Adélies of all ages are vulnerable to heat stress and hyperthermia at temperatures above 25–30° C (unpublished data; Murrish 1973, 1983), but during our study heat stress was never severe for adults or fledglings. We never observed them vigorously panting and measured no T_b above 40° C. At the highest T_e we recorded (22–28° C), adults pant at moderate rates, slightly elevate T_b, and increase evaporative water loss (EWL) to about 0.54% of body mass/hr (Chappell and Souza 1988). They tolerate these conditions for many hours and are limited only by eventual depletion of body water stores or possibly by hypocapnia from increased ventilation (Murrish 1982).

Heat stress is a greater problem for chicks. In the laboratory, exposure to T_a above 20–25° C elicits sustained and vigorous panting, elevated T_b, and high EWL. Many 1 and 2 kg chicks develop uncontrollable, rapidly lethal hyperthermia when exposed to $T_a > 25$–27° C for more than 30–60 min (unpublished data). Heat stress at similar temperatures (T_e) may be somewhat lower in the natural habitat, where chicks can take advantage of behavioral options and rates of convective heat loss not available during the laboratory studies. Although sunny days were frequent at Torgersen, high T_e were uncommon: we recorded only five incidents when chick T_e exceeded 25° C for more than 30 min (durations 1.0, 2.0, 2.5, 3.0, and 5.5 hr). During these episodes all chicks panted vigorously and many lay

prone with feet and wings extended. While we observed no mortality directly attributable to heat stress, extrapolation from laboratory studies and eq. (2) suggests that mortality would be substantial if T_a exceeded 7–10° C for prolonged periods on sunny days with $V < 1$ m/s.

Energy cost of thermoregulation

Although overt cold stress is not a serious problem for Adélies breeding on Torgersen, the cold and windy environment might be expected to engender high C_{th}. However, C_{th} was surprisingly low (Table 2). Even during courtship and incubation, the coldest and windiest part of the breeding season, mean C_{th} for adults was only 17% of BMR (with a maximum of 46% of BMR). Since incubating adults are inactive, C_{th} is the major component of the daily energy budget (DEB) in addition to BMR (Culik 1989). Hence, C_{th} comprises 14–15% of DEB during incubation and will reduce maximum fast duration by a similar percentage. This is similar to the energy cost of incubation in large subantarctic seabirds (e.g., Wandering, Gray-headed, and Black-browed Albatross; *Diomedia exulans*, *D. chrisostoma*, and *D. melanophrys*; Prince et al. 1981; Adams et al. 1986). Adult Adélies rearing chicks spend only 1–2 h/day ashore (Trivelpiece et al. 1987) and have high activity costs from foraging (Davis et al. 1983; Nagy et al. 1984). Therefore, C_{th} in the colony is probably a negligible fraction (ca. 1% or less) of adult DEB. We caution that C_{th} for adults may be considerably higher in colder, more southerly Adélie colonies (Taylor 1962), since MHP requirements in strong convection increase rapidly as T_e falls below 0° C (Chappell et al. 1989).

C_{th} for 1 kg chicks averaged 31% of MMR and 16% of cases exceeded 50% of MMR. C_{th} for large chicks and fledglings was more modest (10–17% of MMR). Between thermal independence at 12–14 days and the cessation of parental feeding at 35–40 days, C_{th} averaged about 17% of MMR for a total of approximately 7.7 megajoules (mj) per chick. During this time a chick consumes 20 kg of food (primarily krill, *Euphausia* sp.; Trivelpiece et al. 1987) containing 95–100 mj. Assuming an assimilation efficiency of 75–80% (Adams 1984; R. Herwig, personal communication), C_{th} comprises 10–11% of assimilated energy. By comparison, the 0.6–0.8 kg dry mass gain during this period comprises 23–30% of assimilated energy (Myrcha and Kaminski 1982).

The most important effects of C_{th} on breeding success probably occur during the fledging fast. The "window" of fasting time available, during which fledglings must finish molting into juvenile plumage and learn to swim and forage, is determined by DEB and by stored energy. C_{th} directly affects DEB and indirectly limits energy reserves through its effects on DEB during earlier growth stages. If we assume that DEB is 1.5–2.5 times MMR in a moderately active fledgling, C_{th} (average 17% of MMR) decreases maximum fast duration by 5–10%, which could make the difference between survival and starvation for a fledgling with subnormal fat stores. If fledglings experienced subzero T_a's combined with high

V's, C_{th} would increase several-fold (Chappell et al. 1989).

Relative importance of Q_r and V on energetics

Conceivably, Adélies could reduce C_{th} by seeking sunlit areas and/or avoiding windy areas. To examine this possibility we used equations 1 and 2 to calculate T_e and C_{th} if sunlight or forced convection were absent. For both adults and chicks, sunlight explains considerably more of the variance in T_e than is explained by V (partial r^2 for $Q_r = 0.55$ for adults and 0.49 for chicks; partial r^2 for the convection term $= 0.21$ for adults and 0.12 for chicks). If Q_r were lacking, T_e would be considerably lower for all age classes, but the effect on energetics would be surprisingly small: C_{th} would rise by only 2–4% of MMR in fledglings, adults, and large chicks, and by about 5% of MMR in 1 kg chicks. In contrast, the energetic consequences of wind are considerable because V influences resistance to heat flow as well as T_e (see also Culik 1989). If Q_r and T_a were unchanged and the environment lacked forced convection, C_{th} would be zero for fledglings, adults, and 3 kg chicks, and the C_{th} of 1 and 2 kg chicks would fall to 6–9% of MMR. We conclude that penguins could realize substantial energy savings by selecting sites sheltered from wind. However, sheltered areas (e.g., in boulder piles or adjacent to exposed rock faces) are scarce on Torgersen Island. Penguins tend to avoid those that do exist, perhaps because they are difficult for the birds to traverse and because they accumulate drifting snow and retain snow cover much longer than more open, exposed areas.

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