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# The ontogeny of thermal independence in nestling Gannets

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Gannets *Sula bassanus,* very large altricial birds, exhibit well developed thermolytic behaviour (panting, gular fluttering, posturing, etc.) by two days posthatch. In contrast, interactive mechanisms of heat conservation and thermogenesis developed gradually during the first three weeks posthatch, with a transitional phase from thermal dependence to independence during posthatch weeks 2 to 3. From hatching through 12 d slight increases in shivering capacity and down growth and an approximate 25% decrease in relative surface area were thermally ineffective. Shivering thermogenesis improved markedly from 13 to 24 d and was the primary determinant of the emergence of thermal independence. The ontogenetic contrast between early onset of heat tolerance and gradual development of heat conservation and thermogenic capacities suggests that heat stress is a greater threat to nestling survival than cold and that parental behaviour can cope more effectively with cold.

Adaptive protection against hyperthermia in newly hatched young is widespread, as indicated by the onset of thermolysis before thermogenesis and heat conservation in most open-nesting seabirds. Insulation associated with down growth complements thermogenic development for many large altricial nonpasserines and more precocious species but not for passerines. The former nest in the open and are exposed to the cooling effects of wind, whereas the latter tend to be buffered from the wind by nest-sites and nests. Comparatively, leg musculature functionally matures before flight muscles and is the primary source of thermogenesis for most large altricial nonpasserines, whereas pectoral muscles assume this role for smaller nonpasserines, passerines, and precocial species.

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## Introduction

Maintenance of young nestlings within thermally nonstressful temperature zones is a primary parental activity. As an extension of incubation (e.g. Beer 1966), most birds brood chicks until they can behavourally and physiologically cope with fluctuations in environmental temperature (e.g. Evans 1984). The duration of nestling ectothermy and parental brooding is closely associated with developmental precocity (Ricklefs 1983).

Temperature regulation during cold depends on thermogenesis and heat retention, whereas overheating is prevented by heat tolerance and dissipation (e.g. panting, posturing). Thermal independence in a cold environment develops from a complex of basic ontogenetic events: decreasing surface/volume relationships, skeletal muscle elaboration (i.e. enhancement of shivering capacity and resultant metabolic responsiveness), increasing insulation (that may include vasomotor influences on heat flow between core and skin), and nervous (and possibly hormonal) control mechanisms (Dawson and Hudson 1970, McNabb and McNabb 1977, Ricklefs 1983, Eppley 1984, Lustick 1984). Unlike mammals, almost all birds lack brown fat, and only very limited nonshivering thermogenesis is known to occur in the nestlings of a few species (Freeman 1971, Palokangas

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and Hissa 1971, Whittow 1971). Metabolic reactions of chicks exposed to cold can be linked directly to shivering and activity (see West 1965). For sedentary altricial chicks, activity thermogenesis can be ruled out.

Gannets *Sula bassanus,* large altricial seabirds (mean adult mass ca 3.25 kg, W. A. Montevecchi and R. E. Ricklefs unpubl.), increase in mass approximately 12-fold from about 80 g at hatching to about 1000 g by 3 weeks posthatch (Montevecchi and Porter 1980, Montevecchi et al. 1984). During this period, chicks are vulnerable to chilling and overheating and require varying degrees of thermal protection from parents. From 2 to 3 weeks posthatch, young attain endothermy, and parental brooding becomes progressively more sporadic; by 3 weeks chicks are too large to be effectively brooded (Kirkham and Montevecchi 1982, see also Nelson 1978, Evans 1984).

The present investigation examines the interactive roles of surface/volume relationships (body size), shivering thermogenesis (its metabolic consequences), and down insulation during thermal development. Observations on the onset of thermolytic behaviour are also included. The development of thermal mechanisms among large and small altricial and precocial birds is compared.

## Methods and materials

Research with live chicks was carried out in July 1978 on Baccalieu Island (48°07'N, 52°47'W), Newfoundland, in June and July 1979 on Great Bird Rock (47°07'N, 61°09'W), Magdalen Islands, Quebec, and in August 1980 on Funk Island (49°46'N, 53°11'W), Newfoundland. In September 1984, two birds approximately 46 d posthatch were captured on the mainland nesting area at Cape St. Mary's (46°50'N, 54°12'W, Montevecchi and Wells 1984), Newfoundland. In August 1983 and 1984, 11 chicks aged 2 to 24 d were collected at Funk Island, then frozen and later tested at Memorial University of Newfoundland. Ages were determined from hatching dates whenever possible or estimated from wing length and/or mass (Kirkham and Montevecchi 1982).

During heat stress tests, chicks 1 to 14 d posthatch (n = 8) were removed from nests and tested nearby on foil blankets in direct sunlight for 20 to 60 min, during which substrate ($T_s$), ambient ($T_a$, ca 25 cm above ground) and core body ($T_b$) temperatures were recorded with Yellow Springs Instrument banjo and flexible thermal probes (ser. 400), the latter were inserted into either cloaca or proventriculus (depending on ease of insertion). Latency to first vocalization and number of calls were recorded. During testing $T_a$ and $T_s$ averaged (± SD) 25.1 ± 6.7°C and 32.9 ± 2.4°C, respectively.

For cooling tests, chicks 1 to 21 d posthatch (n = 23) were removed from nests, carried in a bag for $\leq$ 8 min to the basement of a nearby lighthouse, tested for 1 h or until $T_b$ dropped to 20°C in $T_a$ range of 10° to 15°C. A total of 57 tests were conducted with 14 chicks used from two to eight times each at different ages. Vocal behaviour and $T_b$ were measured as indicated above.

Metabolism tests of 30 to 60 min were run on 18 chicks (1 to 21 d old) and two adults at lighthouses on Great Bird Rock and Baccalieu Island. Metabolism was measured in air-tight plastic buckets, containing soda lime to absorb $CO_2$ and Drierite$^R$ to absorb moisture, attached to manometers and Yellow Springs Instrument thermometers. Different aged chicks were tested at a range of $T_a$ from 15° to 38°C in different sized buckets. The change in pressure between chamber and outside air was converted to rates of $O_2$ consumption ($\dot{V}O_2$) using appropriate equations (Ricklefs et al. 1985). Eighteen animals were retested (up to seven times) at different ages up to 3 weeks posthatch. After testing, young were returned to nests, where they were readily accepted by their parents.

$T_b$ of each carcass was raised to 40°C by steam heating in plastic bags. Down was fluffed with a hot air blower before testing. A carcass was then placed in a styrofoam cooler on an elevated platform of heavy gauge wire above a 15 cm layer of snow or ice, ca 12 cm above which a temperature probe was suspended. Another probe was inserted into cloaca or proventriculus, and the cooler was covered. Initial $T_a$ in the cooler ranged from 0° to 8°C, and during tests $T_a$ ranged from 0° to 10°C for 1 to 18 d old chicks and from 0° to 14°C for 19 to 47 d old birds (differences due to greater heat losses from larger chicks). $T_a$ and $T_b$ were recorded at 0, 5 and 10 min and at 10 min intervals until $T_b$ decreased to 17°C (at which point a live chick would be torpid) or for 1 h whichever came first. This procedure was followed for all carcasses in two conditions: (1) two replicate trials were run on INTACT birds (n = 39), and (2) down was plucked as cleanly as possible (NAKED, n = 17). Down was weighed whenever it was removed or added. Two live ca 46 d old chicks were tested, killed then immediately retested to examine metabolic and shivering effects on body cooling. Carcasses were then plucked, frozen and retested after a few days.

To assess developmental change, chicks were grouped into five age classes: 1–6, 7–12, 13–18, 19–24 and 46 d. Owing in part to (1) rapid initial cooling of ectothermic chicks during transport from nests and (2) termination of cooling procedures when $T_b$s of young chicks reached 20°C, linear regressions provided the best fits of $T_b$–$T_a$/time cooling curves. Multiple linear regressions (SPSS$^x$) of the percentage of variance attributable to age, condition and time were run on INTACT vs NAKED data. Linear regressions of $T_b$–$T_a$ vs time for different pairs of conditions were also analyzed. Regressions of INTACT tests were compared with regressions of means of INTACT ones when the initial $T_b$s of each INTACT test were identical. When initial $T_b$s were unequal, the INTACT test with initial $T_b$ nearest to the initial $T_b$ of the NAKED test was used. Significant differences between regression slopes were determined with standard errors

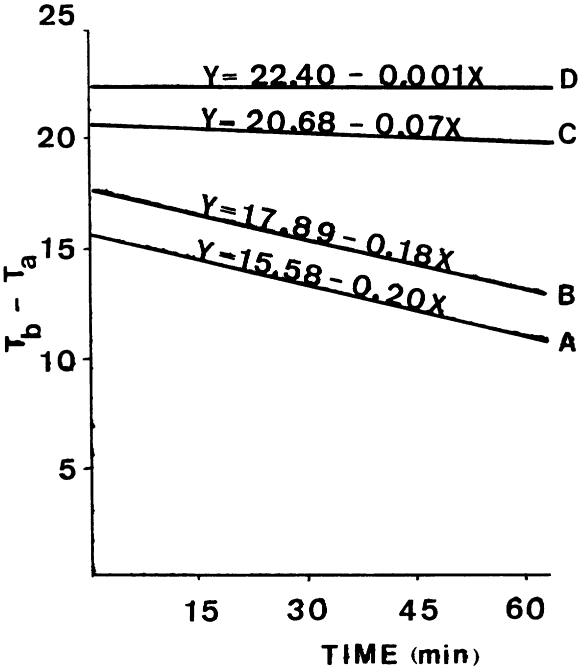

Fig. 1. Linear regressions of $T_b$–$T_a$ of different-aged Gannet nestlings removed from nests and exposed to $T_a$ of 10–15°C.

(S.E.): when 2 × SE of slopes did not overlap, regressions were considered to differ significantly. Following tests for homogeneity of variance, vocalization data and coefficients of homeothermy (Ricklefs 1987) were tested with 1-way analyses of variance; call latency data were tested with Kruskal-Wallis nonparametric 1-way analyses of variance.

## Results

### Ontogeny of temperature regulation

Gradual thermal development, i.e. a decreasing gradient between $T_b$–$T_a$ and time, is evident during the first 3 weeks posthatch. Regressions for the two youngest age groups each differed significantly from each of the two older groups, which also differed from each other (Fig. 1). Thermal conductance rates, reflected by regression slopes, declined markedly from 1 to 24 d (see top of Tab. 3). Coefficients of homeothermy increased consistently and significantly with age ($H_{1\text{–}6d}$ = 0.58 ± 0.08; $H_{7\text{–}12d}$ = 0.74 ± 0.08; $H_{13\text{–}18d}$ = 0.89 ±0.09; $H_{19\text{–}24d}$ = 0.92 ± 0.05; $F_{3,52}$ = 50.52, $P < 0.001$) Intercepts increased with age due to (1) greater heat loss of young nestlings between time parents left the nest and testing and (2) increasing $T_b$ with age (see also LIVE intercepts in Tab. 3).

Except for two trials with 1 d old chicks, all nestlings peeped during cooling. Chicks < 1 week took significantly longer to begin calling, called at lower $T_b$s and called less than older chicks (Tab. 1).

### Body size/surface relationships of growing nestlings

From hatching until attainment of effective endothermy at 3 weeks, surface/volume ratios were estimated to decrease by > 50% (Tab. 2). To asses size effects on thermal conductance, comparisons were made among NAKED age groups. No significant differences were obtained between mean cooling rates of 7–12, 13–18 and 19–24 d groups. The cooling rate of INTACT 1–6 d group, which included chicks that were virtually naked, was significantly greater than that of the 13–18 d and of the 19–24 d INTACT groups. Cooling rates of INTACT and NAKED 46 d old nestlings were virtually identical.

### Insulative down growth

Gannets were essentially naked at hatching but down growth was rapid. By 2 weeks chicks were covered dorsally, though ventral down was sparser, and by 3 weeks down filled in completely (Fig. 2). Amount of down approximately doubled every three to four days up to 3 weeks posthatch (Fig. 3), increasing from 0.2 to 0.7% of total body mass, which increased about 10-fold during this time.

To assess some of the insulative properties of down, cooling rates of dead INTACT and NAKED chicks were compared. Nestlings 1–6 d have very sparse down

Tab. 1. Vocal behaviour of Gannet chicks during cooling.

| | Age (d) | Call latency (s) | $T_b$ at 1st call | Maximum calls (5 min)$^{-1}$ | $T_b$ at maximum calling |
|---|---|---|---|---|---|
| 1–6 | $\overline{X}$±SD | 459.5±93.6$^a$ | 26.6±1.0$^b$ | 55.7±8.7$^c$ | 23.4±0.7$^d$ |
| | Median | 262.5 | 25.5 | 51.5 | 23.0 |
| 7–12 | $\overline{X}$±SD | 1.4−1.4$^a$ | 30.8±0.8$^b$ | 109.9±8.6$^c$ | 25.4±0.4$^d$ |
| | Median | 0 | 31.0 | 103.5 | 25.0 |
| 13–18 | $\overline{X}$±SD | 11.5±11.5$^a$ | 35.1±0.5$^b$ | 149.7±9.0$^c$ | 31.6±0.9$^d$ |
| | Median | 0 | 35.8 | 150.0 | 32.2 |
| 19–24 | $\overline{X}$±SD | 150±150$^a$ | 37.6±0.4$^b$ | 108.0±50.3$^c$ | 36.4±1.2$^d$ |
| | Median | 0 | 38.0 | 104.0 | 37.1 |

a. $H_3$ = 22.32, $P < 0.001$. b. $F_{3,52}$ = 16.56, $P < 0.001$. c. $F_{3,52}$ = 15.96, $P < 0.001$. d. $F_{3,52}$ = 34.10, $P < 0.001$.

Tab. 2. Estimates of changing surface/volume relationships of Gannet nestlings during the growth period when thermal independence is achieved.

| Age (d) | Surface area ($cm^2$) | Volume[a] ($cm^3$) | Surface area / volume |
|---|---|---|---|
| 1–6 | 108 | 106 | 1.02 |
| 7–12 | 192 | 250 | 0.77 |
| 13–18 | 363 | 650 | 0.56 |
| 19–24 | 528 | 1140 | 0.46 |

a. Calculations assume that specific gravity of chicks = 1, i.e. 1 g = 1 $cm^3$ of tissue. Based on hypothetical spherically shaped chicks with mean masses of 3, 9, 15 and 21 d old nestlings.

and were excluded from this analysis. Variance attributable to age (size) was significant ($F_{1,6} = 7.71$, $P < 0.05$), but that due to down was not ($F_{1,6} = 3.86$, $P > 0.05$). There were no significant differences between INTACT and NAKED conditions in any age group (Tab. 3). Analysis of variance of INTACT chicks and same-aged young that were covered with a full coat of down removed from a 24-d chick revealed significant effects of age ($F_{1,4} = 19.62$, $P < 0.025$) and condition ($F_{1,4} = 16.35$, $P < 0.025$). Comparison of regression equations of these conditions for each age group yielded significant effects within 7–12 and 13–18 d groups.

### Shivering thermogenesis and metabolism

Muscle tremors developed gradually during the first 3 weeks posthatch (Tab. 4). During cold exposure, chicks < 1 week exhibited no overt signs of shivering, whereas gross leg tremors were evident in most chicks during week 2. Vigorous shivering was first seen at about 2 weeks, and by 3 weeks all chicks shivered vigorously when exposed to cold. This development was associated with a sharp decrease in cooling rates (see Fig. 1). Significant shivering (metabolic) effects are indicated by cooling rates of LIVE and INTACT chicks 46 d posthatch (Tab. 3). Chicks ≤ 3 weeks old were tested in the field and returned to nests, so there were no matched comparisons of cooling rates of live and dead nestlings of these ages. Relative changes between same age groups of LIVE and INTACT chicks 1 to 24 d, though not strictly comparable, are real indications of thermogenic effects. Cooling rates of 1–6 and 7–12 d groups about doubled from LIVE to INTACT conditions, the 13–18 d group almost tripled and the 19–24 d group increased about 30-fold (Tab. 3).

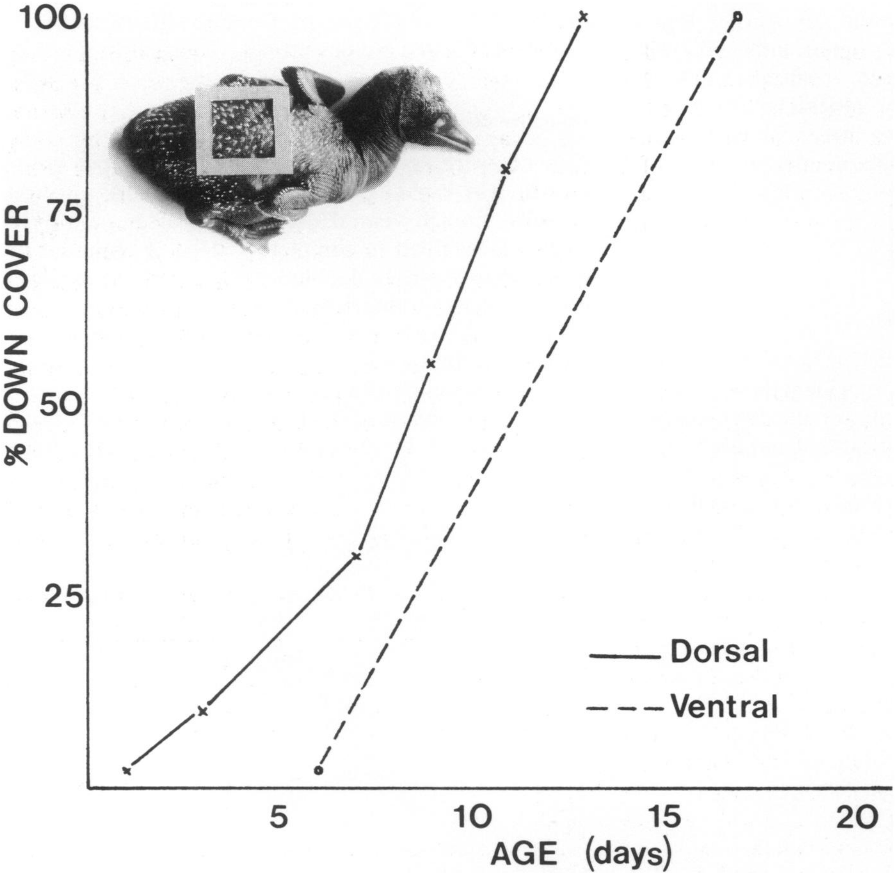

Fig. 2. Percentage of down cover as a function of nestling age. Inset shows 2.5 $cm^2$ area used to estimate percentage of down on dorsal and ventral surfaces of young chicks. Chick in the Fig. is 3 d posthatch.

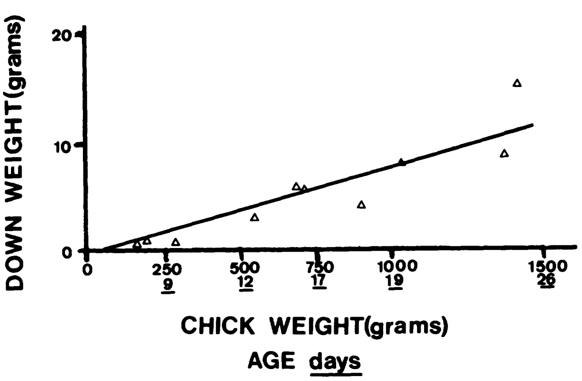

Fig. 3. Mass of down as a function of body mass (age) of Gannet chicks. For comparison, the down mass of a 45 d chick weighing 2790 g was 47 g, that of a 47 d chick weighing 3075 g was 60.5 g.

During metabolic tests run at < 22°C ($\bar{T}_a$ did not differ among age groups), older chicks exhibited significantly lower $\dot{V}O_2$ than younger ones (Tab. 5). These age effects were also significant in tests run at ≥ 22°C and in all tests combined (Tab. 5); $\bar{T}_a$ was significantly lower for older chicks in the latter two data sets (Tab. 5).

### Heat tolerance

When exposed to high $T_a$, nestlings < 7 d showed a more rapid rise in $T_b$ ($Y = 33.33 + 0.41X$) than 7–12 d ($Y = 30.83 + 0.30X$) and 13–18 d chicks ($Y = 35.10 + 0.17X$). Chicks ≥ 2 d posthatch always showed panting or gular fluttering during heat stress tests, whereas a 1 d old chick did not. All chicks peeped during these tests, and cloacal elevation and wing drooping were common.

## Discussion

### Thermal development in nestling Gannets

The thermal independence of Gannet nestlings develops gradually during the first 3 weeks posthatch, with a marked transition period during week 3. Between weeks 1 and 2, a 25% decrease in relative surface area and slight increases in down and shivering capacity were thermally ineffective. Marked improvement in thermal competence by 13–18 d nestlings was associated with a significant increase in shivering (metabolic) thermogenesis. Thermally independent 19–24 d nestlings showed further significant increases in shivering thermogenesis, which was the major determinant of effective endothermy in still air (see also Hissa et al. 1983).

Leg shivering thermogenesis is functional in Northern Gannets by ca 12 d posthatch. Leg muscles comprise a significantly larger proportion (~50%) of relative adult size in the neonatal period than pectoral muscles (~12%); they also grow faster and contain less water (Ricklefs et al. 1985), indications of greater functional maturity (Ricklefs 1979a). Metabolic potential is greatly enhanced during early development, as reflected in a doubling of the energy density of nestlings during the first 3 weeks (Montevecchi et al. 1984). For nestlings from different developmental modes, BMR decreases with age (mass) (e.g. Chappell et al. 1984, Epply 1984, O'Connor 1984), as $T_b$ increases (Evans 1984, Barrett 1985).

Tab. 3. Summary of regression analyses of the cooling rates (°C $min^{-1}$) of Gannet chicks tested in various conditions (see text).

| Condition | Age (d) | Cooling rate (b) | SE | (a) |
|---|---|---|---|---|
| LIVE | 1–6 | –0.20 | 0.02 | 15.58 |
| (n = 61) | 7–12 | –0.18 | 0.01 | 17.89 |
| | 13–18 | –0.07 | 0.01 | 20.68 |
| | 19–24 | –0.001 | 0.01 | 22.40 |
| | 46 | –0.002 | 0.01 | 39.60 |
| INTACT | 1–6 | –0.36 | 0.01 | 31.20 |
| (n = 39) | 7–12 | –0.32 | 0.03 | 32.64 |
| | 13–18 | –0.18 | 0.02 | 29.33 |
| | 19–24 | –0.16 | 0.04 | 28.27 |
| | 46 | –0.09 | 0.01 | 38.15 |
| NAKED | 7–12 | –0.33 | 0.04 | 32.62 |
| (n = 17) | 13–18 | –0.28 | 0.03 | 31.93 |
| | 19–24 | –0.22 | 0.03 | 32.07 |
| | 46 | –0.09 | 0.01 | 39.20 |

Nestlings gain thermodynamic advantages as they grow. Heat loss is proportional to relative surface area, and heat production is a function of metabolic tissue. Neonatal chicks coped with prolonged cold by going into a torpid state. After one week chicks were much less likely to undergo torpidity during cold exposure; they also called almost immediately, at much higher rates and much more than newly hatched young when exposed to cold. Presumably, solicitation of parental warming is more critical for chicks with some positive termal capability (Ricklefs 1974, 1983). Body size effects found in the present studywere not of crucial importance for the transition to thermal independence.

Body size effects on thermal relationships can be seen across taxa. Large altricial nonpasserine nestlings (> 1500 g adult mass) attain thermal independence at about 20–25% adult mass, whereas intermediate sized (100–1500 g) altricials and small passerines (< 100 g)

Tab. 4. Leg shivering of different-aged Gannet chicks exposed to 10°–15°C $T_a$.

| Age (d) | Visible shivering | | |
|---|---|---|---|
| | Vigorous | Slight[a] | None |
| 1–6 | 0 | 2 | 24 |
| 7–12 | 1 | 10 | 8 |
| 13–18 | 5 | 6 | 0 |
| 19–24 | 8 | 0 | 0 |

a. Slight shivering = low frequency gross tremors.

Tab. 5. Metabolic rates ($cm^3\ O_2[g \cdot h]^{-1}$) of different-aged Gannet chicks at different $T_a$s (°C).

| Age (d) | $\bar{X} \pm SD$ | | | | | |
|---|---|---|---|---|---|---|
| | $T_a$ | $\dot{V}O_2$ | $T_a$ | $\dot{V}O_2$ | $T_a$ | $\dot{V}O_2$ |
| | < 22°C | | > 22°C | | All tests | |
| 1–6 | $18.9-2.3^a$ | $0.32\pm0.11^b$ | $30.2\pm3.3^c$ | $0.43\pm0.12^d$ | $28.7\pm5.0^e$ | $0.42\pm0.12^f$ |
| 7–12 | $18.1\pm2.7^a$ | $0.46\pm0.18^b$ | $26.0\pm2.2^c$ | $0.40\pm0.18^d$ | $23.4\pm4.4^e$ | $0.40\pm0.18^f$ |
| 13–18 | $17.3\pm0.5^a$ | $0.26\pm0.11^b$ | $23.3\pm0.5^c$ | $0.23\pm0.13^d$ | $19.0\pm2.8^e$ | $0.25\pm0.11^f$ |
| 19–24 | $18.7\pm2.1^a$ | $0.29\pm0.10^b$ | $24.1\pm2.1^c$ | $0.30\pm0.07^d$ | $20.2\pm3.2^e$ | $0.29\pm0.09^f$ |

a. $F_{3,35} = 1.06$, NS. b. $F_{3,35} = 4.87$, $P > 0.01$. c. $F_{3,76} = 17.91$, $P < 0.01$. d. $F_{3,76} = 3.66$, $P < 0.05$. e. $F_{3,119} = 29.5$, $P < 0.01$. f. $F_{3,119} = 7.58$, $P < 0.01$.

are not usually endothermic until they reach 40–45% and ≥ 50% adult mass, respectively (Hudson et al. 1974, Dunn 1975, 1976, Marsh 1979, 1980, Kirkham and Montevecchi 1982, Ricklefs et al. 1985). Reduced relative surface area obviously affords large altricial species thermal advantages. Barn *Hirundo rustica* and Cliff Swallow *Petrochelidon pyrrhonata* nestlings are unusual in attaining full endothermy after exceeding adult mass (Dunn 1975). Their nests are well protected from environmental fluctuation (see also Morton and Carey 1971).

Our experiments failed to demonstrate any marked effects of down during the transition to thermal independence. Measurement of cooling rates of dead birds cannot account for heat conservation due to plumage adjustments made by live birds, which can reduce thermal conductance substantially (Herreid and Kessel 1967, Dawson and Hudson 1970, Lustick 1984). Moreover, in our experiments freezing of carcasses reduced down loft (i.e. effectiveness), though we attempted to minimize this effect by fluffing down with hot air before testing. Using dead birds thus underestimates heat retention attributable to plumage insulation. Freezing may have also disrupted the cellular integrity of body tissues. Most critically, tests run in still air exclude the important function of down in reducing wind effects on evaporative cooling (Robinson et al. 1976, Kersten and Piersma 1987). Assessment of physiological development in studies of thermal ontogeny standardly excludes wind effects and hence is not generalizable to natural conditions (Ricklefs 1987). Owing to this circumstance, our developmental study was precluded from detecting the most important thermal effects of down (see below).

Decreases in skin permeability (e.g. McNabb and McNabb 1977) and accumulation of subcutaneous fat could also serve insulative functions. The former factor requires investigation, whereas the latter seems improbable, because Gannet nestlings accumulate lipid *after* endothermy is achieved (Montevecchi et al. 1984). Delayed thermal independence in birds is associated with rapid structural growth rather than fat storage.

In sharp contrast to the ontogeny of cold adaptation, Gannets (the only sulid with a temperature breeding range) exhibit a wide variety of robust thermolytic behaviour to cope with heat stress within a day or two of hatching. The developmental precedence of thermolysis and heat tolerance before thermogenesis and heat conservation is presumably an outcome of a stronger selection by heat stress than cold (Lustick et al. 1978, Dawson and Bennett 1981, Grant 1982). This developmental sequence is a widespread adaptation as parental birds are much less well equipped to cool overheated nestlings than they are to warm cold ones (Ricklefs and Hainsworth 1968).

### Comparative overview

A fundamental difference in thermal ontogeny occurs between large altricial nonpasserines that conserve heat by down insulation and small altricial passerines that do not. Most passerine nestlings do not develop extensive down, and for many shivering thermogenesis precedes plumage insulation (e.g. Odum 1942). In contrast, large altricial nonpasserine young (e.g. gannets, pelicans, cormorants, herons) develop extensive down early in the nestling period, and processes of heat conservation and production show close temporal association (Evans 1984, Bartholomew and Goldstein 1984). Breitenbach and Baskett (1967) suggested that some thermoregulatory processes of altricial nonpasserine Mourning Doves *Zenaidura macroura* are attained only after insulative feather growth is complete.

Wind exposure is likely the primary ecological factor responsible for the importance of down during the thermal ontogeny of nonpasserines. Thermoregulatory costs associated with wind elevate metabolic rates (Kersten and Piersma 1987, see also Birt-Friesen et al. 1989). Altricial nonpasserines are usually raised in open nests exposed to wind and wet, whereas passerines are protected from wind by nest-sites and nests. Although the present experiment did not assess wind effects on cooling, it is clear in comparative perspective that such effects have probably been pervasive in producing developmental differences among avian groups. For precocial and to a lesser extent for semi-precocial chicks (reared in either exposed or sheltered conditions), insulation *and* shivering capacity are well developed at hatching.

To assess adaptive patterning of thermogenic mechanisms, we reviewed studies on relative sizes, growth and structural development of major skeletal muscle masses. Neonatal leg muscles were relatively larger than pectoral muscles (Ricklefs 1975, 1979b, Aulie 1976, Dawson et al. 1976, Austin and Ricklefs 1977, O'Connor 1977, Aulie and Grav 1979, Marsh and Wickler 1982, Tatner 1984, Ricklefs et al. 1985), revealing a potential role for legs during early thermogenesis. Generally, neonatal and adult leg muscle proportions are smaller in large altricial nonpasserines (2–4% total body mass) than in passerines (5–13%). For the latter, leg proportions may be 15–100% larger at maturity than at hatching. The proportion of leg in adult Gannets (4.1%) is double that of hatchlings (2.0%, Ricklefs et al. 1985). Presumably owing to early ambulatory patterns, most precocial young are well endowed with leg muscle, e.g. Japanese Quail *Coturnix coturnix,* 18.1% of total body mass (Ricklefs 1979b). Yet simple generalizations about neonatal body proportions cannot be made, e.g. legs of precocial Willow Ptarmigan *Lagopus lagopus* hatchlings comprise only 3.5% of total body mass (Aulie 1976), and semi-precocial Common Terns *Sterna hirundo,* like most precocials, also have well developed leg muscles at hatching (15.8% total body mass, Ricklefs 1979b). Relative proportions of neonatal pectoral muscles varied from 0.5 to 2.9% of total body with no apparent relationship to developmental mode. Mass of pectoral muscles usually exceeded that of leg muscles in adults. Pectoral muscle increased much more markedly from hatching to maturity (range = 2.4 to > 400) than leg muscle, an outgrowth of attaining flight late in nestling development. Leg muscle contains less water than pectoral muscle, indicating earlier functional capacity of the former among young of many species with different developmental modes (Ricklefs 1968, 1979b, Austin and Ricklefs 1977, O'Connor 1977, Ricklefs 1979b, Ricklefs et al. 1985, Ricklefs and Webb 1985).

The potential early thermogenic roles of leg muscles are not realized on a wide taxonomic scale. Only large altricial nonpasserines and some semi-precocial larids are known to use neonatal leg shivering (Keskpaik and Davydov 1966, Hudson et al. 1974, Dawson and Bennett 1981, Evans 1984, present study). Smaller nonpaserines (e.g. doves) and many precocial and passerine nestlings hatch with relatively much larger legs than large alticial nonpasserines but rely primarily on pectoral shivering for heat production (Morton and Carey 1971, Aulie 1976, Hohtola 1982, Montevecchi unpublished data). Many passerines show a rapid transition to endothermy late in the nestling period (Morton and Carey 1971, Marsh and Wickler 1982), and early thermogenic involvements of leg muscle are less important for them than subsequent development of pectoral musculature. Well developed leg musculature early in the nestling period of passerines and small nonpaserines may undoubtedly facilitate other important functions including behavioural interactions involved in the procurement of food from parents and in preventing young from falling out of nests. Simultaneous recording of EMG potentials from leg and pectoral muscles (Stevens et al. 1986) throughout thermoregulatory development, particularly in large altricial nonpasserines and gulls that use both types of shivering, could help to clarify the thermogenic roles of major skeletal muscle masses.

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