The Condor 101:832–841

THE DEVELOPMENT OF ENDOTHERMY IN AMERICAN WHITE PELICANS[1]

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Abstract. We examined the development of endothermy in White Pelican (*Pelecanus erythrorhynchos*) chicks during the first 16 days after hatching, which corresponds with the age at which parent pelicans begin to cease brooding behavior. At ambient temperatures between 20 and 25°C, pelican chicks progressively increased their thermoregulatory capabilities with age; average thermal competence increased with each age increment while average cooling rates declined with each age increment. Thermoneutral metabolic rates increased initially with age, reaching a maximum at day 10, then declined. Whole body conductance and minimum conductance generally declined with age. Our results suggest that, although pelican chicks reach a modest degree of incipient endothermy by day 7, thermoregulatory self-sufficiency is not well developed until day 16. The age at which endothermy becomes well developed in pelicans is similar to those reported for other large pelecaniform species.

Key words: *altricial, development of endothermy, nestling American White Pelicans,* Pelecanus erythrorhynchos, *thermal competence, thermoregulation.*

INTRODUCTION

Cool ambient temperatures present a thermoregulatory challenge to essentially ectothermic altricial nestlings, especially during the period before endothermy is established. Very young American White Pelicans, *Pelecanus erythrorhynchos,* rely almost exclusively on a strategy of behavioral thermoregulation, using vocalizations to solicit the attending parent to provide additional heat in the form of brooding warmth (Evans 1992). This behavior is especially pronounced during the first week after hatching, when thermoregulatory capabilities appear to be insufficient for maintaining a high body temperature during prolonged cold exposure at ambient temperatures between 10–20°C (Evans 1984a).

Approximately 16 days after chicks hatch, adult pelicans begin to terminate brooding behavior, enabling both parents to leave on extended foraging trips of up to 24 hr (Evans 1984b). Until about this age, young pelicans are almost constantly attended by at least one parent at the nest and presumably are not exposed to prolonged periods of cooling. Based on the ability of young pelicans to defend body temperature against low ambient temperatures, Evans (1984a) concluded that the development of endothermy is largely complete by about day 16. This suggests a strong correspondence between the establishment of competent endothermy and the termination of continuous parental brooding behavior in this species. Little is known regarding the physiological development of endothermy in young pelicans during the nestling period. Previous studies have shown that across large pelecaniform species, thermoregulation becomes well developed at similar ages, at approximately 20–25% of adult mass and by approximately 16–26% of the way through the nestling period (Bartholomew 1966, Dunn 1976, Kirkham and Montevecchi 1982). In contrast, nestlings of most small altricial species typically do not become fully endothermic until they have gained at least 70% of adult mass (Dunn 1975).

The main objective of this study was to document thermoregulatory development and responses to short-term exposure to temperature in young pelicans during the first 16 days posthatch. We examined the development of physiological endothermy and the mechanisms (metabolic rate, plumage development, and thermal conductance) by which pelican chicks improve their thermoregulatory abilities during short-term cold exposure. We also tested for the presence and magnitude of any incipient endothermic response to cold exposure in these chicks. Our objective included defining the limits of the thermoneutral zone (TNZ), which are unknown for this species, and describing adjustments in

[1] Received 21 December 1998. Accepted 25 June 1999.

the TNZ as chicks age. Our approach was to measure the metabolic rates of 1- to 16-day-old pelican chicks exposed to a range of ambient temperatures. We predicted that the stages of thermoregulatory development observed in pelicans would be similar to those described for most other altricial species (Thomas et al. 1993), but that the age of competent endothermy would fall within the range reported for other large pelecaniform species.

METHODS

STUDY ANIMALS

We collected a total of 12 pelican eggs, 1 per 2-egg clutch (to minimize effects on productivity), from a colony at East Shoal Lake, Manitoba, Canada, in June 1997. At the time of collection, eggs were externally pipped, or pipped approximately 24 hr prior to hatching. Eggs were hatched in a commercial poultry incubator set at 37.8 ± 0.5°C. On day 1 (where day 0 = day of hatch), we transferred chicks to a small brooder held at the same temperature. On day 4 we transferred chicks to larger brooding cages (46 × 41 × 61 cm) in a controlled-environment room with ambient temperature (T_a) controlled by heat lamps and monitored with a thermostat placed near the front of the cages. We set the heat lamps away from, but directed toward, the front of the brooding cages, resulting in a maximum temperature gradient of approximately 2°C inside each cage (from front to back). In order to avoid potential heat stress, we progressively lowered ambient brooding temperature (measured at the front of the cages) from 32°C at day 4, to 26°C at day 16. We placed a small fan inside the brooding room to provide air circulation. By day 4, chicks were sufficiently mobile to select an area of the cage that was thermally comfortable. We housed chicks in this fashion for the remainder of the study. It was not known during the rearing stages of this study whether the brooding temperatures utilized were indeed thermoneutral, but we monitored chicks closely to ensure there were no signs of heat or cold stress. We monitored cloacal temperature in the incubator and brooding cages for about 10 min prior to testing to determine body temperature during brooding. Brooding cloacal temperature (T_{cl}) remained relatively consistent across age, ranging from 37.9°C at day 1 to 39.0°C at day 16.

We fed chicks to satiation, 5 times per day, on a diet of moist commercial fish-based mink food. We provided water ad libitum from an eye dropper at least 10 times per day. We fed and watered all chicks approximately 45 min prior to each test. We tested chicks every third day for 16 days, after which they were euthanized with an injection of Phenobarbitol, according to the guidelines of the Canadian Council on Animal Care. We tested a total of six age classes: days 1, 4, 7, 10, 13, and 16, respectively.

RESPIROMETRY SET-UP

We performed metabolic tests on chicks placed in plastic respirometry chambers of varying sizes, depending on age class (2.2 L at day 1 to 11.3 L at day 16). We painted the insides of the chambers flat black to minimize radiative heat transfer. The removable lids had several openings to accommodate thermocouples, microphones, and incurrent and excurrent air ports positioned at opposite ends of each lid. A small fan inside the chamber assisted in air circulation. A coil of copper tubing (6.5 mm outside diameter) installed in each chamber surrounded the chick during testing. A barrier of plastic mesh separated the copper coil from the chick to minimize conductive heat transfer between the bird and the metal tubing. We controlled chamber ambient temperature by circulating water from a temperature-regulated water bath through the coil (Evans 1990).

We monitored cloacal temperature during testing with a 30-gauge thermocouple inserted 1–2 cm into the cloacal opening depending on age, and these values were assumed to represent core body temperature. We monitored chamber ambient temperature with the same type of thermocouple taped to the plastic mesh separating the chick from the surrounding ring of copper coil.

We monitored vocalizations continuously using a sound operated relay and an Esterline Angus event recorder. A second microphone placed in the lid of each chamber allowed us to continuously monitor and record any motor activity (shuffling, turning around) or vocalizations during testing. In addition, we installed clear Plexiglas chamber lids to further monitor movement, with a black cloth covering the lids during testing.

We obtained metabolic measurements using a single channel, open-flow respirometry system (after Fig. 4c, Stack and Rossi 1988). Flow rates

ranged from 435 to 2,200 ml min^{-1} (depending on age class of chick), which were adequate to maintain the fractional oxygen content of the excurrent gas above 19% in all cases (Stack and Rossi 1988). We monitored flow rates < 800 ml min^{-1} with an AMETEK R-1 flowmeter calibrated according to the bubble flow method (Levy 1964). We monitored flow rates > 800 ml min^{-1} with a Gilmont flowmeter calibrated against a Brooks Vol-U-Meter (model 1057). Chamber excurrent air was scrubbed of H_2O and CO_2 (using Drierite, soda lime, and Drierite again), then was drawn through the oxygen sensor and flow meter. We monitored the fractional oxygen content of chamber excurrent air with an AMETEK S-3A oxygen analyzer equipped with an N-22M sensor. We recorded fractional O_2 content, ambient temperature, and cloacal temperature every 5 sec using a Sable System (Sable Systems, Salt Lake City, Utah) data acquisition and analysis program (DATACAN V). This program simultaneously recorded all temperatures to 0.1°C.

We calibrated the oxygen analyzer to room air (taken as 20.94%) before and after each trial. At the end of the study, the system latency and washout characteristics for each chamber were measured using a pulse of respired, oxygen-depleted air drawn through the chamber containing a dummy pelican chick of appropriate mass.

TESTING PROTOCOL

We measured metabolic rates during exposure to relatively constant (within about 0.25°C of the target test temperature) ambient temperatures ranging from 16 to 39°C, depending on chick age. For each age class, we chose a range of ambient temperatures that would likely include at least some temperatures which fell outside of the thermoneutral zone. During testing, we placed individual chicks in the metabolic chamber pre-set to a specified test temperature. We terminated tests after 30 min or when cloacal temperature fell by more than 3°C below brooding cloacal temperature. This ensured that chicks had sufficient time to rest and return to brooding T_{cl} before further testing. We tested individual chicks 4 times at each age at randomly chosen temperatures within the pre-defined temperature range. We weighed chicks to the nearest gram immediately before and after each test, and recorded the mean. We averaged the body masses of all chicks tested at each age to obtain a mean daily body mass. Between tests, we returned chicks to their cages to rest, rewarm, and feed.

DATA ANALYSIS

Traditional methods of calculating rates of oxygen consumption ($\dot{V}O_2$) using an open system assume that steady-state conditions prevail. This assumption was not met in this study, as we were interested in relatively short-term changes in $\dot{V}O_2$ (maximum of 30 min). Under these conditions, short-term (approaching "instantaneous") measures are more appropriate (Bartholomew et al. 1981). When actual oxygen uptake changes, for example due to decreasing T_{cl}, O_2 levels in the excurrent air stream change exponentially, only gradually approaching a new equilibrium. We calculated the equilibrium value that would have eventually been reached if no further changes in oxygen consumption were to occur, according to the equations developed by Bartholomew et al. (1981), which are incorporated into the DATACAN V software analysis package.

We calculated mass-specific oxygen consumption ($\dot{V}O_2$), corrected to STP, using equation 4a of Withers (1977) and expressed as ml g^{-1} hr^{-1}. Validation of the accuracy of these calculations for this system was obtained by calculating $\dot{V}O_2$ over successive 5-sec periods during washout. The computed value for each chamber size was close to the actual $\dot{V}O_2$ value of zero (all means $\pm$ SD $\leq$ 0.013 $\pm$ 0.281 ml g^{-1} hr^{-1}) during washout measurement (no live animal in the chamber).

We took mean $\dot{V}O_2$ as the mean of all averages of consecutive series of 5-sec recordings of $\dot{V}O_2$ during periods of inactivity in each trial. We are confident that we were able to isolate periods of inactivity during tests for analysis. Vocalizations were monitored and recorded continuously and periods of physical activity were easily identified (live microphone and visual observations) and manually recorded. We excluded any periods of vocal behavior and physical activity from the analysis. We compared $\dot{V}O_2$ measurements across the range of ambient temperatures tested to detect any metabolic response to ambient cooling. Any differences in $\dot{V}O_2$ helped delineate the thermoneutral zone (TNZ) for each age, as well as how the relationship between metabolic heat production and ambient temperature changes as chicks age. It is important to note, however, that we did not apply the three-

phase Scholander model in the traditional sense (Hill and Wyse 1989), in that the assumption of a stable body temperature in the TNZ was not always met. We therefore caution that our interpretations of the TNZ should be considered in a more unconventional sense, given that the above assumption was occasionally violated.

We performed statistical analyses using Statistix (Analytical Software, version 4.1) and Microsoft Excel (version 5.0). We modified the two-phase regression model of Nickerson et al. (1989) as a three-phase model for evaluating the relationship between metabolic rate and ambient temperature, and used the two-phase regression model for assessing the relationship between whole body conductance and ambient temperature. We used Excel's "solver" function to calculate all critical inflection points for the above models using regression functions which minimized the sum of squares of the error terms. We could not compute ANOVAs due to disproportionate missing values at some age classes. Those missing values were due to the fact that, as chicks aged (particularly after day 13), they became increasingly intolerant of being confined in the metabolic chamber, and any questionable trials were not included in the analysis. Therefore, we used paired *t*-tests (one-tailed) to make comparisons across age groups. We used a significance level of $\alpha < 0.01$ for all *t*-tests (Bonferroni correction), and Pearson's correlations were used to describe trends within age classes. Values presented are means ± SE.

RESULTS

PATTERNS OF GROWTH

Chick mass increased significantly with each age increment (all $t \geq 20.9$, df ≥ 17, $P < 0.001$), by about 11 fold between days 1 to 16. The largest absolute and relative increase in body mass occurred between days 10 to 13 (increase of 430.8 g and 75.6%, respectively). Masses observed in this study were similar to but significantly lower than those reported by Evans (1997) for wild pelican chicks at days 4, 7, and 10 (one-sample *t*-tests, all $t \geq 7.66$, df ≥ 45, $P < 0.001$). Parents feed small young up to 4 times daily, with feeding frequencies declining by the second week after hatching (Evans and Knopf 1993). Therefore, masses obtained in the field (Evans 1997) may have varied slightly from the real average daily body mass, depending on how many feedings the wild chicks had received prior to weighing. Masses obtained in the present study indicate that the lab-reared chicks were growing and developing at a similar rate to wild pelicans (8.2-fold increase in lab-reared vs. 8.4-fold increase in wild pelicans, over the first 13–14 days post-hatching).

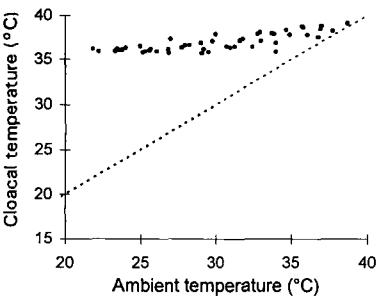

FIGURE 1. Mean cloacal temperature of day 4 pelican chicks during trials for each ambient temperature tested. The dashed line indicates $T_{cl} = T_a$.

DEVELOPMENT OF ENDOTHERMY

Effects of age and ambient temperature on cloacal temperature. Chicks of all ages were capable, to at least some degree, of defending body temperature at some test ambient temperatures below ambient brooding temperature. At all ages tested, mean cloacal temperature during each trial was significantly greater than mean ambient temperature (all $t \geq 6.86$, df ≥ 20, $P < 0.001$). At no age did cloacal temperature conform to ambient temperature, as is typical of ectotherms, although this was in part due to relatively short exposure times, especially during the first week (Fig. 1). The proportion of chicks that maintained cloacal temperature within 3°C of brooding cloacal temperature for the entire 30-min test period at all test temperatures was highly correlated with age ($r = 0.91$, $P < 0.01$), ranging from 45.7% at day 1 to 84.6% at day 16.

The ability of young pelicans to defend body temperature against ambient temperature was quantified and defined as thermal competence (TC). Typically, chicks of a given age are judged to be effective homeotherms if they are able to maintain a body temperature of at least 75% of the adult body temperature (Dunn 1975, Ricklefs 1987). The index of homeothermy of Ricklefs (1987) was modified and defined as:

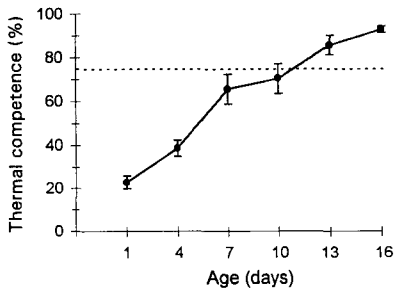

FIGURE 2. Mean ± SE thermal competence of pelican chicks at T_as between 20 and 25°C (n = 7–12 at each age). The dotted line represents 75% thermal competence.

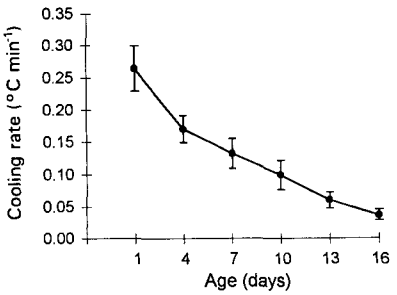

FIGURE 3. Mean ± SE cooling rates of pelican chicks during metabolic trials at T_as between 20 and 25°C (n = 7–12 at each age).

$$TC = [(T_{cl(final)} - T_1)/(T_{cl(initial)} - T_a)](D_t/30 \text{ min}) \times 100$$

where the value of TC represents percent thermal competence, $T_{cl(final)}$ represents the cloacal temperature at the end of the trial, $T_{cl(initial)}$ represents the cloacal temperature at the start of the trial (rather than adult body temperature, which is unknown), T_a represents the mean ambient temperature for the duration of each trial, D_t represents individual trial duration (min), and 30 min was the maximum duration of any trial. This time correction reflected the fact that some trials were terminated prematurely (before 30 min) if cloacal temperature fell by more than 3°C below brooding cloacal temperature, otherwise the computed TC values for these early terminations would have overestimated thermal competence.

Chicks showed an increasing ability to defend body temperature against decreasing ambient temperature with age. TC was significantly correlated with ambient temperature (all $r \geq 0.4$, $P \leq 0.01$) at all ages, with the exception of day 1 ($r = 0.29$, $P = 0.06$). Average TC was calculated for ambient test temperatures only between 20 and 25°C. Average TC increased with each age increment (Fig. 2), although this was significant only between days 4 and 7 ($t_6 = 3.83$, $P = 0.002$). At days 7 and 10, average TC was not significantly different than 75% (all $t \leq 1.40$, df ≥ 15, $P \geq 0.09$), whereas at days 13 and 16, average TC was significantly greater than 75% (all $t \geq 2.35$, df ≥ 10, $P \leq 0.02$).

Average cooling rates of chicks during tests also were calculated for ambient test temperatures between 20 and 25°C. Average cooling rates declined, although not significantly, with each age increment, (all $t \leq 3.03$, df ≥ 2, $P \leq 0.02$; Fig. 3). The largest decline in average cooling rates occurred between days 1 and 4.

Effects of age and ambient temperature on metabolic rate. The upper and lower critical temperatures of the thermoneutral zone (TNZ) were calculated by modifying Nickerson's et al. (1989) two-phase regression model for determination of critical points as a three-phase regression model describing the relationship of $\dot{V}O_2$ to ambient temperature.

A three-phase regression was calculated for all age classes of chicks (Fig. 4). Third-order polynomial curves applied to these data conformed closely to the calculated regression lines (Fig. 4). The lower critical temperatures (LCT) and upper critical temperatures (UCT) generally declined with age (Table 1), with the exception of slight increases in both at day 10. The width of the TNZ declined from days 1 to 7, then increased from days 7 to 16 (Table 1). Both the

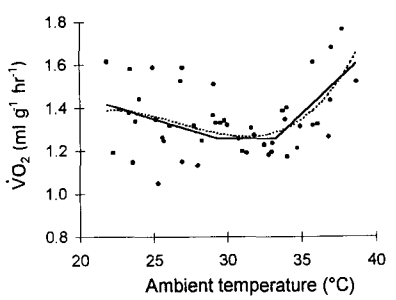

FIGURE 4. The relationship of mass-specific metabolic rates to ambient temperature of day 4 pelican chicks. The solid line represents the calculated regression lines (lines of best fit) of metabolism in relation to ambient temperature. The dashed line represents a third-order polynomial curve fitted to the data.

TABLE 1. The calculated lower (LCT) and upper critical temperatures (UCT) and width of the thermoneutral zone (TNZ derived from the calculated inflection points illustrated in Fig. 4), and inflection temperatures calculated for whole body conductance (as illustrated in Fig. 6). Also present are test temperatures at or below which shivering was observed, and test temperatures at or above which gular fluttering was observed.

Age (days)	LCT (°C)	UCT (°C)	Width of TNZ (°C)	WBC inflection (°C)	Shivering (°C)	Gular fluttering (°C)
1	34	38	4	36	—	—
4	29	33	4	36	28	36
7	28	30	2	36	24	34
10	28	32	4	29	23	33
13	23	28	5	27	19	31
16	24	28	4	27	—	—

LCT and UCT showed a significant negative correlation with chick age (LCT: $r = -0.94$, $P < 0.01$; UCT: $r = -0.89$, $P < 0.02$), whereas the width of the TNZ was not significantly correlated with age ($r = 0.40$, $P = 0.43$).

Thermoneutral metabolic rate (MR_{TN}) was calculated as the average mass-specific MR measured between the upper and lower critical temperatures. Incremental increases in MR_{TN} were significant only from days 1 to 4 ($t_6 = 3.82$, $P < 0.01$) and from days 7 to 10 ($t_5 = 8.34$, $P < 0.001$; Fig. 5a). There was a significant incremental decrease in MR_{TN} from days 10 to 13 ($t_4 = 4.1$, $P < 0.01$). The largest absolute increase in MR_{TN} occurred from days 7 to 10 (increase of 0.41 ml g^{-1} hr^{-1}), with chicks at day 10 having the highest MR_{TN} of all ages tested. MR_{TN} showed an absolute decrease of 0.48 ml g^{-1} hr^{-1} from days 10 to 13. There was a slight, although insignificant, increase in MR_{TN} between days 13 and 16 ($t_2 = 1.0$, $P = 0.41$).

Total (whole-animal) metabolic rate (MR_{total}, expressed in ml hr^{-1}) was calculated for all thermoneutral measures. MR_{total} increased significantly from days 1 to 16 ($t_2 = 7.1$, $P < 0.01$; Fig. 5b). Incremental increases in MR_{total} were significant only from days 1 to 4 ($t_6 = 10.6$, $P < 0.001$), days 7 to 10 ($t_5 = 9.7$, $P < 0.001$), and days 13 to 16 ($t_2 = 60.7$, $P = 0.01$).

Effects of age and ambient temperature on whole-body conductance. Whole body conductance (C) was defined as (McNab 1980): $C = \dot{V}O_2/(T_{cl} - T_a)$, where $\dot{V}O_2$ = average metabolic rate (ml g^{-1} hr^{-1}), T_{cl} = average body temperature, and T_a = average ambient temperature during each test. A two-phase regression model (Nickerson et al. 1989) was used to test for the existence of an inflection point in the relationship between conductance and ambient temperature (Thomas et al. 1993). Minimum conductance (C_{min}) was calculated as the average conductance below the critical inflection T_a.

Based on the applied two-phase regression model, chicks of all ages, with the possible exception of day 16, showed an obvious inflection point where the slope of conductance changed significantly (Fig. 6). In all cases, C_{min} was sig-

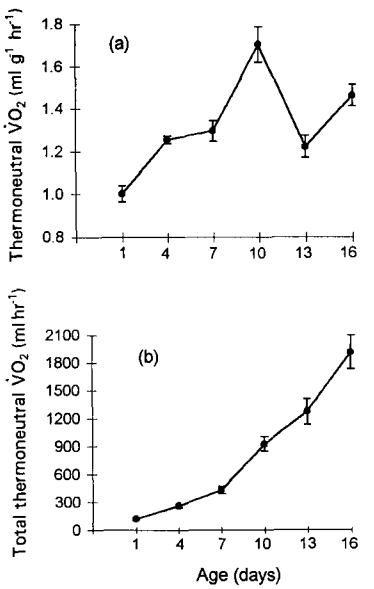

FIGURE 5. Mean ± SE (a) mass-specific and (b) mass-independent thermoneutral metabolic rates of pelican chicks (n = 3–12 at each age).

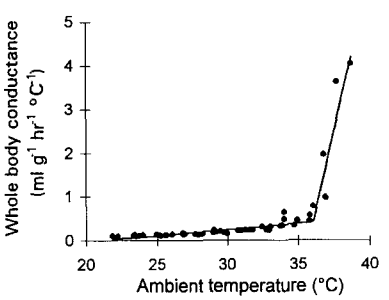

FIGURE 6. Whole body conductance of day 4 pelican chicks. The solid lines represent the calculated regression lines of conductance in relation to ambient temperature.

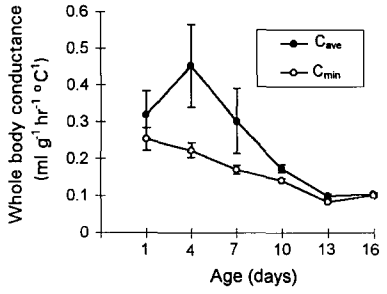

FIGURE 7. Average and minimum conductances (mean ± SE) of pelican chicks (n = 12 at each age).

nificantly greater than zero (one-sample t-tests, all $t \geq 8.13$, df ≥ 22, $P < 0.001$), and was significantly correlated with T_a (all $r \geq 0.77$, $P < 0.001$). T_a values at calculated inflection points were negatively correlated with age ($r = -0.91$, $P = 0.01$).

Average conductance (C_{ave}) declined significantly from days 1 to 16 ($t_{20} = 3.0$, $P < 0.01$; Fig. 7). The largest absolute incremental decrease in C_{ave} occurred from days 4 to 7 (decrease of 0.15 ml g^{-1} hr^{-1} $°C^{-1}$), although this was not significant ($t_{43} = 0.9$, $P = 0.34$). C_{ave} showed an absolute increase of 0.13 ml g^{-1} hr^{-1} $°C^{-1}$ from days 1 to 4; this also was not significant ($t_{30} = 0.4$, $P = 0.67$). Average C_{min} declined significantly from days 1 to 16 ($t_{19} = 2.7$, $P = 0.01$; Fig. 7). The only significant incremental decrease in C_{min} occurred from days 10 to 13 ($t_{20} = 9.77$, $P < 0.001$).

DISCUSSION

THERMOREGULATORY ABILITIES OF PELICAN CHICKS

Chicks showed a significant and increasing ability to defend body temperature against ambient temperature with age. Thermal competence (TC) increased with each age increment, with the largest increase occurring between days 4 and 7 (Fig. 2). According to one commonly applied definition (Dunn 1975), young altricial birds are considered effective homeotherms if they can maintain their body temperature at 75% of the adult body temperature for the duration of a trial. Our measure of average TC differs from Dunn's (1975) index of homeothermy in that our age-specific mean values of TC incorporate ambient temperatures between 20 and 25°C, whereas Dunn used data between 15 and 25°C. Pelican chicks were close to a 75% level of average TC on day 7 (Fig. 2). Average cooling rates also declined with each age increment, with the largest decrease occurring between days 1 and 4 (Fig. 3).

Our results imply that pelican chicks have developed a significant ability to defend body temperature against reduced ambient temperature by day 7. This conclusion is consistent with the fact that by day 7, pelican chicks have developed a strong observable shivering response to periods of cold stress (Evans 1994). Shivering is the major, if not sole, means of increasing heat production in the inactive bird (see review in Calder and King 1974). The heat increment of feeding in growing chicks may not compensate for any of the thermoregulatory costs incurred by cold exposure, because the act of feeding apparently stimulates peripheral blood circulation and thus facilitates heat loss (see review in Weathers 1996). Shivering intensity is closely correlated with the development of endothermy, with the degree of cold stress, and with the rate of oxygen consumption below thermoneutrality (Calder and King 1974, Visser and Ricklefs 1993). The first appearance of natal down feathers occurs in wild pelicans on about day 6, with plumage length increasing from 0.1 to 1.9 mm from days 6 to 8, and increasing to about 11 mm by day 14 (Daniels 1997). However, the length of plumage at day 7 probably does not increase insulation enough to contribute significantly to an improved thermoregulatory ability of pelican chicks at that age.

Although attainment of an average thermal competence near 75% by day 7 indicates that endothermy is developing at this time, further development is almost certainly needed prior to pelican chicks achieving thermoregulatory self-sufficiency, as this level would probably be insufficient to prevent a significant and detrimental decline in body temperature if chicks were left exposed in the nest for prolonged periods of time. Indeed, Evans (1984a) demonstrated that 7-day-old pelican chicks showed only a slight ability to thermoregulate during 2 hr cold exposure to 10°C and 20°C in the lab, with cloacal temperature falling almost linearly with ambient temperature.

Day 16 pelican chicks have previously been shown to maintain body temperature at or above 35°C during 2 hr exposures to ambient temperatures as low as 10°C (Evans 1984a). Mean minimum ambient temperature in southern Manito-

ba during June, when most chicks reach 2–3 weeks of age, averages 10.7°C (Annual Meteorological Summary, 1977–1997). It is not surprising that the improvement in average TC and the decline in average cooling rates by day 16 correlates closely with the chick age when parents begin to terminate brooding. Additionally, grouping of chicks is known to reduce metabolic effects of low ambient temperature in this species, and is consistent with the observation (Evans 1984b) that at about day 16, pelican chicks begin to form overnight and diurnal creches (consisting of from 2 to 4 individuals from different broods at this age) in the absence of parental brooding under natural rearing conditions.

DEVELOPMENTAL CHANGES IN METABOLIC RESPONSE TO TEMPERATURE

For all ages tested, the three-phase regression model revealed a thermoneutral zone (TNZ), in which metabolic rate was relatively constant, bounded by increases in metabolic rate as ambient temperature moved away from the upper and lower critical temperatures (Fig. 4, Table 1). The fact that a TNZ was present at all ages, suggests that altricial pelican chicks as young as day 1 have some degree of an incipient endothermic capacity which represents a significant development beyond the earlier ectothermic stage typical of altricial avian embryos (Whittow and Tazawa 1991). Although the assumption that body temperature remains stable in the TNZ was not always met, there is some support that the calculated inflection points do indeed represent a zone of thermoneutrality. Young pelicans began to show visible signs of shivering in response to cool ambient temperatures on day 4. In addition, young pelicans begin to flutter their gular pouch in response to heat stress on day 1 (Evans 1984a). Shivering was only observed at ambient temperatures below the calculated lower critical temperatures (Table 1), and gular fluttering was only observed at ambient temperatures above the calculated upper critical temperatures (Table 1). In addition, cloacal temperatures within the calculated TNZ during testing were close to cloacal temperatures in the brooding cages, which were held at ambient temperatures within the limits of the TNZ. These results suggest that, within the limits of the calculated TNZ, chicks were not experiencing any thermal stress, whereas outside of the TNZ, increases in metabolic rates may be due in part to shivering and gular fluttering as an attempt to regulate body temperature.

Thermoneutral metabolic rates increased from days 1 to 10, declined from days 10 to 13, and finally increased from days 13 to 16 (Fig. 5a). This trend of an initial increase in metabolism followed by a decrease near the age of functional endothermy has been observed in some other altricial species (Double-crested Cormorants *Phalacrocorax auritus,* Dunn 1976; Red-winged Blackbirds *Agelaius phoeniceus,* Olson 1992; Cockatiels *Nymphicus hollandicus,* Pearson 1998). The decline in metabolic rate near the age of endothermy may be due in part to the fact that the largest increase in body mass observed in this study occurred from days 10 to 13, with a concomitant large decline in surface area-to-volume ratio (Thomas et al. 1993). According to Weathers (1996), increases in growth rates may be facilitated by a decrease in heat production. In addition, the largest absolute increases in flank plumage length (Daniels 1997) occur in young pelicans from days 10 to 12 (4.0 to 6.8 mm) and days 12 to 14 (6.8 to 10.5 mm). The resulting insulative effects by day 13 would be expected to promote a lower metabolic rate, with less energy spent maintaining body temperature. The increase in metabolic rates from days 13 to 16 (Fig. 5a), although not significant, is not typically observed in other altricial species. As chicks aged and became more mobile (particularly after day 13), they became increasingly intolerant of being confined in the metabolic chamber (pers. observ.). Therefore, an increase in mobility and a corresponding undetected increase in activity in the metabolic chamber could account for the increase in metabolic rate at day 16.

The width of the TNZ was smallest at day 7 and largest at day 13 (Table 1). Over this same period, the TNZ was shifted to the left. Consequently, developing pelican chicks can withstand progressively broader and cooler ambient temperature ranges due to behavioral modifications, such as postural changes which decrease surface area-to-volume ratio, rather than to increasing metabolic rate.

DEVELOPMENTAL CHANGES IN CONDUCTANCE

Chicks of all ages showed two significantly different phases of conductance (C; Fig. 6), with C

decreasing rapidly at first, then at a markedly slower rate as ambient temperature declined. The critical inflection temperature calculated from the 2-phase regression of C has been used to indicate the lower critical temperature (LCT) in at least some other avian species (Thomas et al. 1993). In this study, the critical inflection temperature was consistently higher than the LCT, but it was significantly correlated with age.

A potential explanation as to why this method did not accurately confirm the LCT is that birds tend to deviate from the typical mammalian model where conductance reaches its minimum value at an ambient temperature very close to the LCT (Calder and King 1974). In contrast, as found in the present study, birds typically continue to decrease conductance at ambient temperatures below the TNZ. Conductance may reach its minimum value substantially below the LCT, perhaps in part due to continued ptiloerection, vasomotor, or postural changes as T_a declines below the LCT (Calder and King 1974). Even essentially naked young pelican chicks may be able to decrease conductance via postural changes until the appearance of natal down plumage at about day 6, after which C could be further altered by a combination of postural changes, peripheral vasoconstriction, and ptiloerection.

THE DEVELOPMENT OF ENDOTHERMY

With the exception of the Red-tailed Tropic bird (*Phaethon rubricauda*), which is essentially endothermic upon hatching (Howell and Bartholomew 1962), the age at which thermoregulation becomes well developed is relatively consistent across other large pelecaniform species studied. Masked Boobies *Sula dactylatra* (Bartholomew 1966), Double-crested Cormorants, *Phalacrocorax auritus* (Dunn 1976), Northern Gannets *Morus bassanus* (Kirkham and Montevecchi 1982), and White Pelicans (Evans 1984a, present study) all achieve endothermy at roughly 18–25% of adult body mass, all between 16–26% through the nestling period, all between 12 and 18 days after hatching, and all close to the age at which parents begin to terminate brooding. In contrast, nestlings of most small altricial species typically do not become endothermic until they have gained at least 70% of adult body mass (Dunn 1975). The development of endothermy, which relies primarily on shivering thermogenic capacity and on the relative size of skeletal muscle, appears to occur in a series of stages involving complex interactions between many physiological variables. The stages of thermoregulatory development observed in pelicans are similar to those reported for other altricial species (Thomas et al. 1993).

In the relative conformer stage, which includes only day 1, chicks are small, naked, have low average thermal competence, high rates of body cooling, and low metabolic rates. At this age, pelican chicks are continuously attended by at least one parent at the nest, and are typically not exposed to prolonged periods of ambient cooling.

The transitional stage, which appears to include days 4 to 13, is characterized by a large increase in body mass, the appearance and growth of downy plumage, the appearance and improvement of shivering ability, a reduced rate of body cooling, higher average thermal competence (near or above 75%), a leftward shift in the TNZ, and a higher mass-specific metabolic rate.

The regulator stage, which includes only day 16 (of ages tested), is characterized by a large body mass, improved physical mobility, complete covering of downy plumage, a low rate of cooling, high thermal competence (above 90%), low LCT and UCT, and a high metabolic rate. At this age, both parents may have already begun to terminate brooding behavior in order to forage, thus leaving chicks unattended for prolonged periods of time.

Our results indicate a gradual sequence of the development of endothermy, resulting in day 16 chicks being capable of effectively coping with prolonged periods of cooling due to parental absence. Because pelican chicks attain thermoregulatory self-sufficiency relatively early in development (compared to passerines), parent pelicans presumably benefit by being freed at an earlier stage to leave on long foraging flights. The gradual development of a complex mechanism to maintain body temperature when faced with an ambient thermal challenge is likely energetically efficient. Younger, more ectothermic pelicans are presumably able to save the metabolic costs associated with thermoregulation, thereby having the greatest portion of energy resources allocated to growth of body tissue (Weathers 1996).

ACKNOWLEDGMENTS

Funding was provided by the Duff Roblin and H. E. Welch Postgraduate Fellowships to C. L. A. and by an operating grant from the Natural Sciences and Engineering Research Council, Ottawa, to R. M. E. We thank R. A. MacArthur, K. L. Campbell, and D. M. Gillis for their technical assistance and helpful advice.

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