

**Metabolic Costs and Honest Signalling of Need during
the Development of Endothermy in American White
Pelicans**

By

Christine Abraham

A thesis
presented to the University of Manitoba
in partial fulfillment
of the degree of Master of Science
in the
Department of Zoology

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**Metabolic Costs and Honest Signalling of Need During the Development of
Endothermy in American White Pelicans**

BY

Christine Abraham

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University
of Manitoba in partial fulfillment of the requirements of the degree**

of

MASTER OF SCIENCE

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Abstract

I examined the development of endothermy in American white pelican chicks (*Pelecanus erythrorhynchos*) during the first 16 days after hatching. My results suggest that, while pelican chicks reached a modest degree of incipient endothermy by day 7, thermoregulatory self-sufficiency was not well developed until day 16. The age of endothermy in pelicans was similar to those reported for other large pelecaniform species studied to date.

Honest signalling models predict that if offspring solicitation is a true reflection of need, then solicitation should be costly and costs should increase with need. I measured the metabolic costs of vocal heat solicitation calls given by pelican chicks in response to anticipated thermal need on days 1, 4, 7, 10 and 13. Call rates, metabolic rates ($\dot{V}O_2$) and body temperatures were measured during exposure to both warm (mid-thermoneutral) and cold (5°C below thermoneutral) ambient temperatures. At all ages, call rates were greater during cold trials than in warm trials. Absolute costs ($\dot{V}O_2$) and relative costs of calling were greatest during cold trials up to day 10, followed by a reversal at day 13. Absolute costs per call were greater in cold trials from days 1 to 7, followed by a reversal at days 10 and 13. Relative costs per call were greater in the cold trials from days 1 to 10, followed by a reversal at day 13.

I also measured the call rates, $\dot{V}O_2$ and body temperatures of pelican chicks (days 1, 4, 7, 10 and 13) exposed to warm (mid-thermoneutral) and cold

(5°C below thermoneutral) ambient temperatures, and those given the opportunity to vocally thermoregulate. Without the option to vocally thermoregulate, chicks in the cold group typically had the highest call rates, the lowest cloacal temperatures and the highest metabolic rates. At all ages, chicks in the warm group typically had the lowest call rates, the highest cloacal temperatures and the lowest metabolic rates. At all ages, chicks in the vocal thermoregulation group typically showed intermediate values with respect to all of these parameters. My results generally support the prediction that vocal heat solicitation is an honest signal of anticipated thermal need, and that signal costs increase with anticipated thermal need. Furthermore, my results suggest that pelican chicks are able to effectively communicate their needs to their parents and maintain their body temperature via a reliable, energetically efficient vocal-signalling system.

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General Introduction

Need for Heat in Nestling Pelicans

The development of thermoregulation has been described for several peleciform species (Howell and Bartholomew 1962; Bartholomew 1966; Dunn 1975, 1976; Kirkham and Montevecchi 1982). Cool ambient temperatures present a thermoregulatory challenge to essentially ectothermic altricial nestlings, especially during the period before endothermy is fully established. Hatchling pelicans are relatively immobile and naked, with an insulative downy covering not appearing until about 6 days post-hatching (Daniels 1997). Very young American white pelicans rely almost exclusively on a strategy of behavioural thermoregulation, using vocalizations to solicit the attending parent to provide additional heat in the form of brooding warmth (Evans 1992). This behaviour is most pronounced during the first week after hatching when thermoregulatory capabilities appear to be negligible (Evans 1984a). If young pelicans are left unattended for even short periods of time, they may become comatose and die if not rewarmed (Evans and Knopf 1993). When chilled for extended periods of time, young pelicans also experience reduced locomotor activity (Evans 1984a), which may inhibit acquisition and ingestion of food, while even a moderate drop in temperature may inhibit begging for food (Evans 1994).

Vocal Signalling of Need for Heat: Conflict and Resolution

The energy expenditure associated with signalling systems between avian parents and their offspring has generated much recent interest among physiologists and behavioural ecologists (Leech and Leonard 1996; McCarty 1996; Kilner and Johnstone 1997; Bachman and Chappell 1998; Chappell and Bachman 1998; Abraham and Evans 1999). Much of this interest stems from considerations of signal evolution, particularly when the receiver (parent) relies on a signal to reveal an otherwise cryptic condition (hunger, thermal need) of the sender (offspring). If offspring can benefit from false advertisement, then the relationship between offspring and parent may become evolutionarily unstable because responding to a dishonest signal reduces the fitness of the parent, resulting in a conflict of interest. Most theoretical analyses indicate that in such a signalling system, honesty is evolutionarily stable only if signal production has a fitness cost (such as energy expenditure or predation) that limits escalation of dishonest signalling (Zahavi 1975; Maynard Smith 1985; Grafen 1990; Godfray 1991, 1995; but see Maynard-Smith 1991). These costs are assumed to be an increase in either the risk of attracting predators (Haskell 1994) or energy expenditure (Godfray 1991, 1995).

The vocal signalling behaviour of nestling birds provides a good system for investigating signal evolution. Although parents and young may disagree over the amount and allocation of resources (food, brooding warmth) the parents deliver

(Parker 1985; Stamps et al. 1985; Smith and Montgomerie 1991; Godfray 1995), several studies indicate that offspring solicitation is an honest signal of needs or condition (Redondo and Castro 1992; Leonard and Horn 1996; Price et al. 1996; Kilner and Johnstone 1997; Iacovides and Evans 1998) and that parents use offspring solicitation to make appropriate decisions about resource allocation.

Most empirical experiments to date have focused on the context and costs associated with offspring solicitation for food. Pelicans are among the few avian species whose young have two functionally and structurally distinct vocal signals. One is a begging call for food and appears soon after hatching, and the other is a 'squawk' call for incubation/brooding warmth that first occurs at the pipped-egg stage (Evans 1992). Pelican chicks employ an effective strategy of behavioural thermoregulation by vocally soliciting brooding warmth from a parent to maintain a warm (high) body temperature (Evans 1992) and to fine-tune the parental brooding response. These studies suggest that young pelicans make use of vocal heat solicitation calls to transfer honest information regarding thermal needs and condition to an attending parent (Evans 1990, 1994).

Given these findings, several investigators have looked for evidence that the energy costs associated with vocal signals produced by avian nestlings might be sufficient to select for honesty. Recent studies of passerine nestlings (Leech and Leonard 1996; McCarty 1996; Bachman and Chappell 1998) suggest that vocal signals produced by nestlings have a low energetic cost when expressed as

a fraction of the daily energy budget. This may be due in part to the small fraction of time that young spend vocalizing, as well as to adequate food availability and low sibling competition. However, in nestling house wrens (Bachman and Chappell 1998) and nestling tree swallows (Leech and Leonard 1996), rates of energy expenditure during begging are elevated substantially above resting levels.

The need to quantify metabolic costs associated with signalling has recently emerged as a significant gap in our knowledge of communication systems (Gittleman and Thompson 1988; Mock and Forbes 1992; Godfray 1991, 1995). Parent-offspring conflict (POC) theory predicts that natural selection acting on genes expressed in the young will favor offspring solicitation of more resources than the parent is selected to provide (Hamilton 1964; Trivers 1974). Models of POC have shown that an evolutionarily stable equilibrium can exist at which an offspring solicits resources in a way that reduces its fitness and a parent provides extra resources to prevent further costly solicitation (Parker and Macnair 1979; Stamps et al. 1978; Feldman and Eshel 1982; Parker 1985; Hussell 1988; Eshel and Feldman 1991). Godfray (1991) presented a resolution model relevant to POC, but from a somewhat different perspective. He suggested an alternative explanation for costly solicitation by showing that the level of offspring solicitation can be a true reflection of the offspring's needs so long as solicitation is costly and that the benefits of resources received increase with the need of the offspring. Godfray assumed that offspring need is not static and that offspring will increase their level of costly solicitation if their physical

need increases. The requirement that signalling incurs a cost is a direct consequence of the potential for POC. Godfray (1991) suggested that the following strategy pair can be evolutionarily stable: (1) the young signal at a rate that is strictly determined by their condition, and that some characteristic of the signal increases as condition worsens or needs increase; (2) the parent allocates resources to young using the level of display as an accurate indicator of offspring needs or condition. For the signalling system to remain evolutionarily stable, the model also requires that any increments in offspring benefit be balanced by a corresponding increase in cost (Godfray 1991, 1995). It follows that signalling costs should also increase with need, for example, as illustrated graphically by Johnstone (1997, figure 7.2b).

The first Chapter of this thesis documents the development of physiological thermoregulation and varying responses to ambient temperature in young pelicans during the first 16 days post-hatch. My objective included defining the age-specific limits of the thermoneutral zone (TNZ) which were previously unknown for this species, and describing adjustments in the TNZ as chicks age. These measurements were essential for the studies reported in Chapters 2 and 3 when it was necessary to know at what ambient temperatures pelican chicks do and do not experience thermal need. In the second study (Chapter 2), I tested for the presence and magnitude of the metabolic costs associated with vocal heat solicitation calls given by young pelicans in response to anticipated thermal need (at ambient

temperatures within and below the TNZ during the period before endothermy is fully functional). In the third study (Chapter 3), I assessed the overall metabolic costs and benefits associated with vocal thermoregulation and the maintenance of a high body temperature in young, cold-challenged pelicans during the period before endothermy is fully functional. In the second and third Chapters, I also discuss the relevance of the costs and benefits associated with vocal thermoregulation to Godfray's (1991) evolutionary model of honest signalling.

Young American white pelicans that vocalize in response to chilling provide a simple, readily controllable system for studying the metabolic costs associated with vocal heat solicitation in relation to thermal need and the maintenance of an elevated body temperature. Young pelicans do not make use of posturing or other visual or behavioural displays to transfer information, so presumably the parent must rely solely on the young chick's ability to vocally communicate thermal needs and condition. In addition, because young pelicans do not attain physiological endothermy until about 16 days post-hatch, any metabolic responses detected, especially in younger chicks, are unlikely to be confounded by endothermic thermoregulatory processes. In addition, predation occurs rarely in this species and is unrelated to chick vocalizations (Evans and Knopf 1993), hence, the chief costs of signalling are likely energetic.

Chapter 1: The Development of Endothermy in American White Pelicans

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 behavioural thermoregulation, using vocalizations to solicit the attending parent to provide additional heat in the form of brooding warmth (Evans 1992). This behaviour 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 and 20°C (Evans 1984a).

Approximately 16 days after chicks hatch, adult pelicans begin to terminate brooding behaviour, 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 to 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 behaviour 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% 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 altered ambient temperatures in young pelicans during the first 16 days post-hatch. I examined the development of physiological endothermy, including ontogenic changes in metabolic rate, plumage development and thermal conductance, of pelican chicks. I also tested for the presence and magnitude of any incipient endothermic response to short-term cold exposure in these chicks. My objectives included defining the limits of the thermoneutral zone (TNZ) which are unknown for this species, and describing adjustments in the TNZ as chicks age. My approach was to measure the metabolic rates of 1- to 16-day-old pelican chicks exposed to a range of ambient temperatures. I 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

I collected a total of 12 pelican eggs, one per two-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 $37.8 \pm 0.5^\circ\text{C}$. On day 1 (where day 0 = day of hatch), I transferred chicks to a small brooder held at the same temperature. On day 4 I transferred chicks to larger brooding cages (46 x 41 x 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. I 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, I progressively lowered ambient brooding temperature (measured at the front of the cages) from 32°C at day 4, to 26°C at

day 16. I 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. I 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 I monitored chicks closely to ensure there were no signs of heat or cold stress. I 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 ages, ranging from 37.9°C at day 1 to 39.0°C at day 16.

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

Respirometry Set-up

I 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). I 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. I controlled chamber ambient temperature by circulating water from a temperature-regulated water bath through the coil (Evans 1990).

I monitored cloacal temperature during testing with a 30-gauge thermocouple inserted 1-2 cm into the cloacal opening (depth depending on age), and assumed these measurements represented core body temperature. I 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.

I 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 me to continuously monitor and record any motor activity (shuffling, turning around) or vocalizations during testing. In addition, I installed clear Plexiglas chamber lids to visually monitor movement, with a black cloth covering the lids during testing.

I obtained metabolic measurements using a single channel, open-flow respirometry system (after Fig. 4c, Stack and Rossi 1988). Flow rates ranged from 435 to 2200 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). I monitored flow rates < 800 ml·min⁻¹ with an AMETEK R-1 flowmeter calibrated according to the bubble flow method (Levy 1964). I 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 H₂O and CO₂ (using Drierite, soda lime, and Drierite again), then was drawn through the oxygen sensor and flow meter. I monitored the fractional oxygen content of chamber excurrent air with an AMETEK S-3A oxygen analyzer equipped with an N-22M sensor. I recorded fractional O₂ content, ambient temperature and cloacal temperature every 5 sec using a Sable System (Sable Systems, Salt Lake City, Utah, U.S.A.) data acquisition and analysis program (DATACAN V). This program simultaneously recorded all temperatures to 0.1°C.

I calibrated the oxygen analyzer with room air (O₂ content 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

I measured metabolic rates during exposure to relatively constant (within about 0.3°C of the target test temperature) ambient temperatures ranging from 16 to 39°C, depending on chick age. For each age class, I chose a range of ambient temperature that would likely include at least some temperatures which fell outside of the TNZ. During testing, I placed individual chicks in the metabolic chamber pre-set to a specified test temperature. I 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. I tested individual chicks 4 times at each age at randomly chosen temperatures within the pre-defined temperature range. I weighed chicks to the nearest gram immediately before and after each test, and recorded the mean. I averaged the masses of all chicks tested at each age to obtain a mean daily mass. Between tests, I 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-flow system assume that steady-state conditions prevail. This assumption was not met in this study, as I was 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. I 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.

I calculated mass-specific oxygen consumption ($\dot{V}O_2$), corrected to STP, using equation 4a of Withers (1977) and expressed as $ml \cdot g^{-1} \cdot hr^{-1}$. Validation of the accuracy of these calculations for this system was obtained by calculating $\dot{V}O_2$ over successive 5 s 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 $\leq 0.013 \pm 0.281 ml \cdot g^{-1} \cdot hr^{-1}$) during washout measurement (no live animal in the chamber).

I took mean $\dot{V}O_2$ as the mean of all averages of consecutive series of 5 s recordings of $\dot{V}O_2$ during periods of inactivity in each trial. I am confident that I was 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. I excluded any periods of vocal behaviour and physical activity from the analysis. I 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 I 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. I therefore caution that my interpretations of the TNZ should be considered in an unconventional sense, given that the above assumption was occasionally violated.

I performed statistical analyses using Statistix (Analytical Software, version 4.1) and Microsoft Excel (version 5.0). I 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. I 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. I 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, I used paired *t*-tests (one-tailed) to make comparisons across age groups. I used a significance

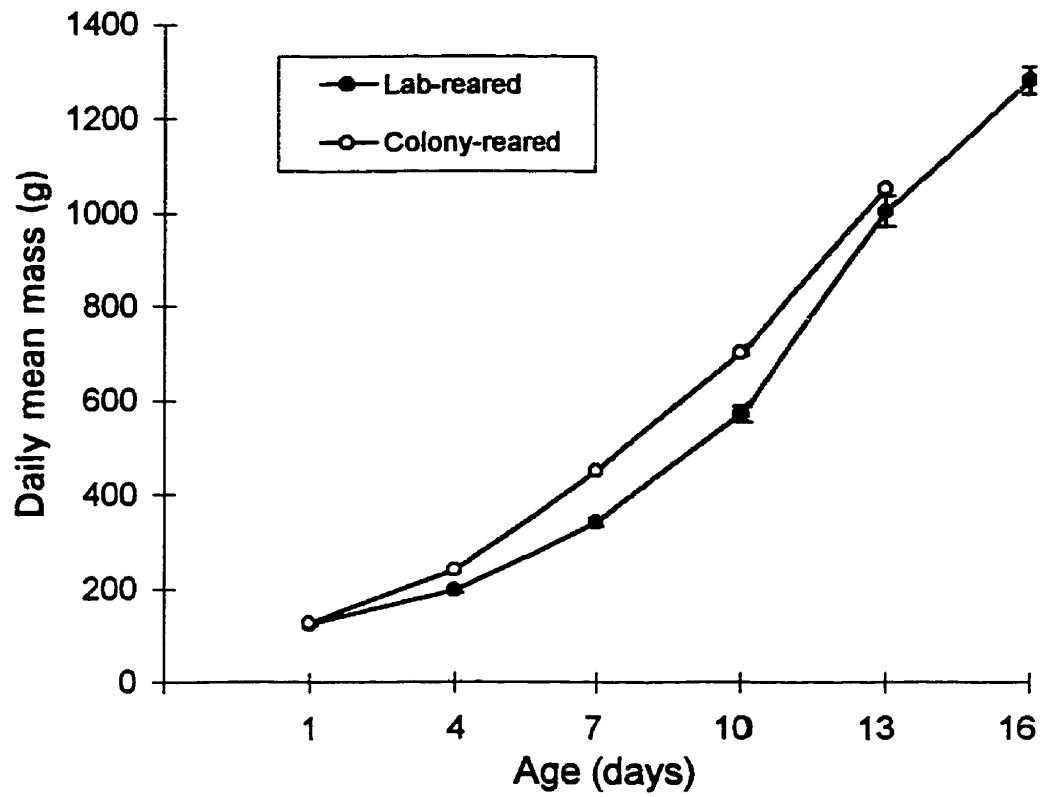
level of $\alpha < 0.01$ for all t -tests (Bonferroni correction), and Pearson's correlations were used to describe trends within age classes. Values presented are means \pm SE.

Results

Patterns of Growth

Chick mass increased significantly with each age increment (all $t \geq 20.9$, $df \geq 17$, $P < 0.001$), and by about 11-fold between days 1 and 16 (Fig. 1-1). The largest absolute and relative increase in mass (relative to mass at previous age) occurred between days 10 and 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 $t \geq 7.66$, $df \geq 45$, $P < 0.001$; Fig. 1-1). 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 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

Figure 1-1. Daily mass (mean \pm SE) of lab-reared pelican chicks at each age tested ($n = 12$ at each age) and masses of wild pelican chicks reported by Evans (1997).



at a similar rate to wild pelicans (8.2-fold increase in lab vs. 8.4-fold increase in wild pelicans over the first 13-14 days post-hatching).

Development of Endothermy

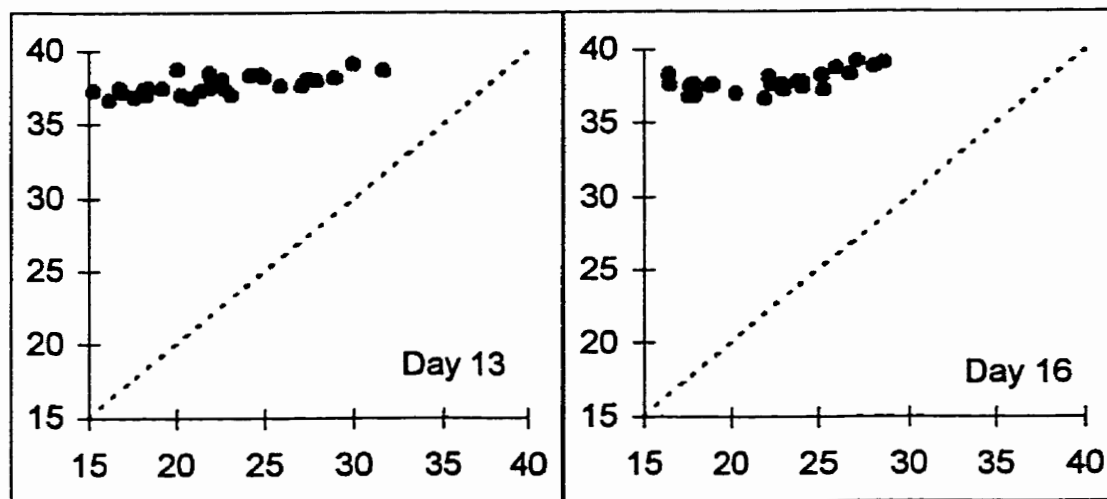
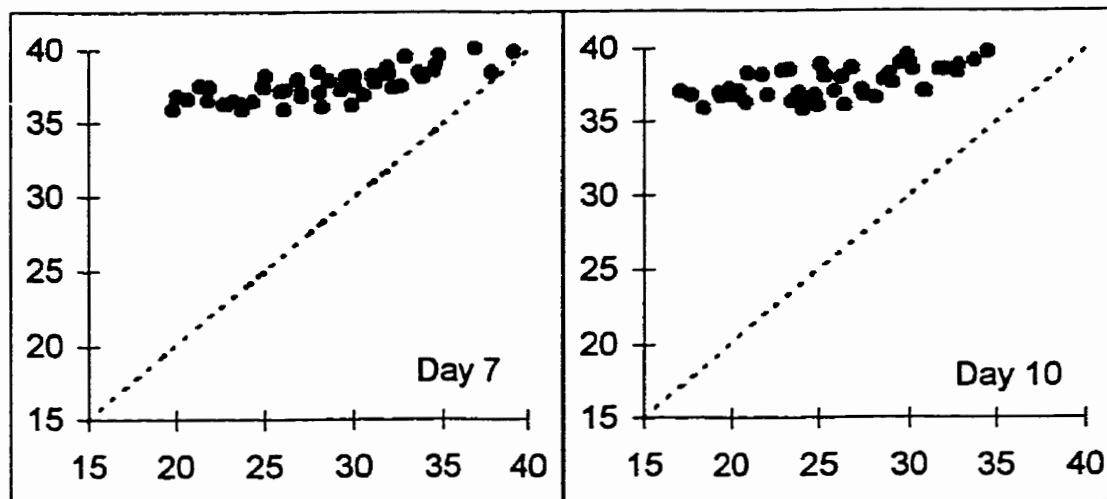
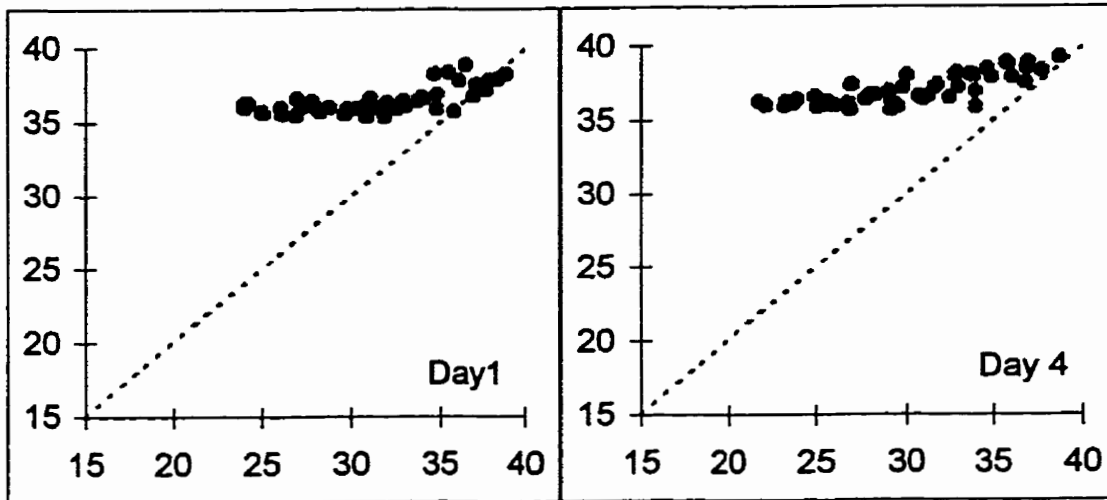
Effects of Age and Ambient Temperature on Cloacal Temperature

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 $t \geq 6.86$, $df \geq 20$, $P < 0.001$; Fig. 1-2). 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. 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 1-2. Mean cloacal temperatures (T_{cl}) of 1- to 16-day-old pelican chicks during trials for each ambient temperature (T_a) tested. In each case, the dashed lines indicate $T_{cl} = T_a$ ($n = 12$ at each age).

Cloacal temperature (°C)



Ambient temperature (°C)

$$(1) \text{ TC} = [(T_{\text{cl}(\text{final})} - T_{\text{a}})/(T_{\text{cl}(\text{initial})} - T_{\text{a}})] (D_{\text{t}}/30\text{min}) \times 100$$

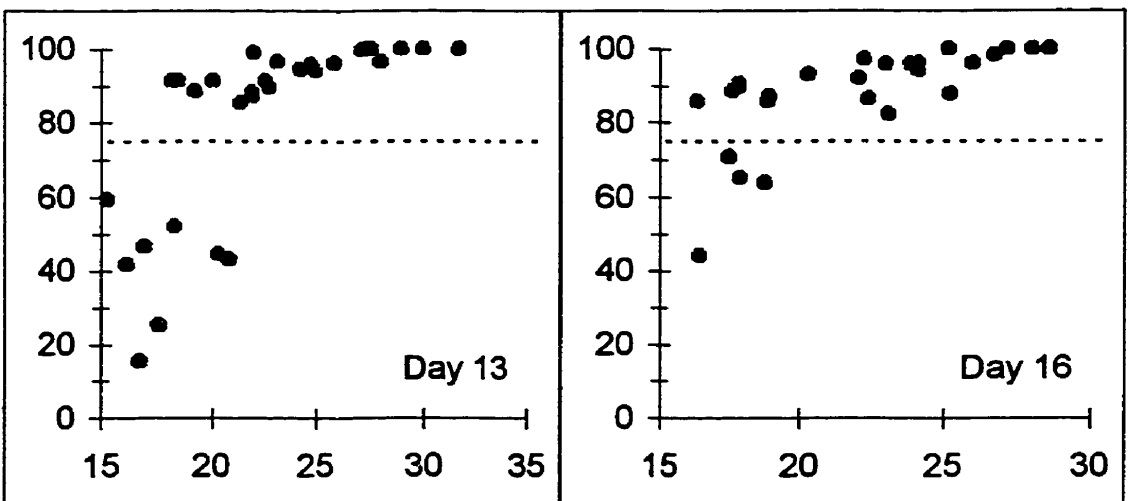
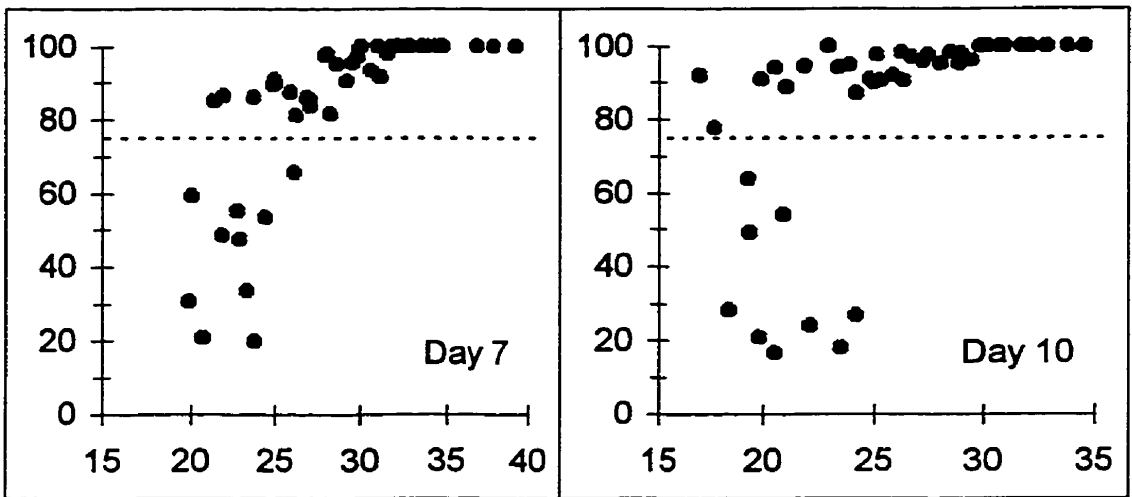
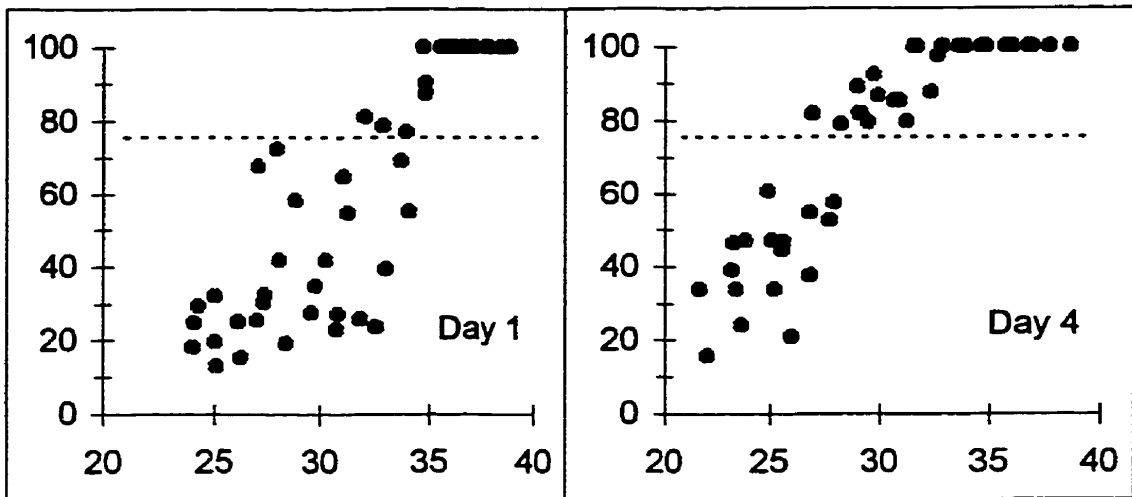
where the value of TC represents percent thermal competence, $T_{\text{cl}(\text{final})}$ represents the cloacal temperature at the end of the trial, $T_{\text{cl}(\text{initial})}$ represents the cloacal temperature at the start of the trial (rather than adult body temperature, which is unknown), T_{a} 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 (Fig. 1-3). 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. 1-4), 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 $t \leq 1.40$, $df \geq 15$, $P \geq 0.09$), whereas at days 13 and 16, average TC was significantly greater than 75% (all $t \geq 2.35$, $df \geq 10$, $P \leq 0.02$).

Average cooling rates of chicks during tests also were calculated for ambient test temperatures between 20 and 25°C. Average cooling rates declined,

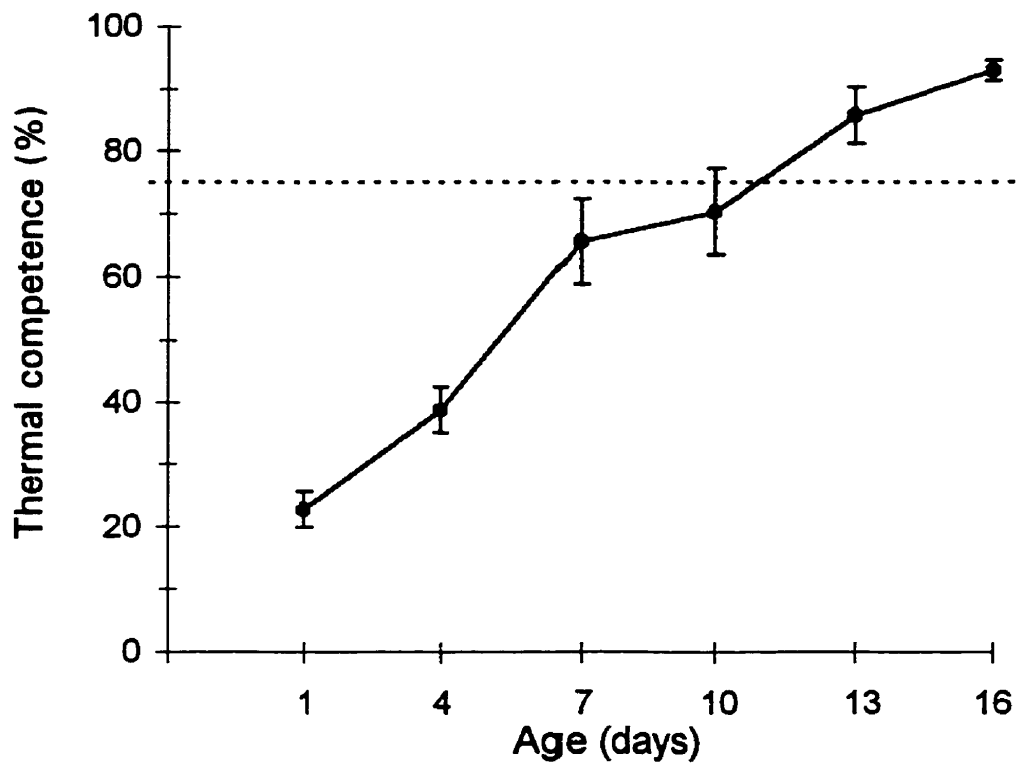
Figure 1-3. Thermal competence of 1- to 16-day-old pelican chicks in relation to ambient temperature ($n = 12$ at each age). Note the different scales on the x-axes.

Thermal competence (%)



Ambient temperature (°C)

Figure 1-4. Average (\pm SE) thermal competence of 1- to 16-day-old pelican chicks at T_{as} between 20 and 25°C ($n = 12$ at each age). The dotted line represents 75% thermal competence.



although not significantly, with each age increment, (all $t \leq 3.03$, $df \geq 2$, $P \geq 0.02$; Fig. 1-5). 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. 1-6). Third-order polynomial curves applied to these data conformed closely to the calculated regression lines (Fig. 1-6). The lower critical temperatures (LCT) and upper critical temperatures (UCT) generally declined with age (Table 1-1), 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 1-1). Both the 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. 1-7a). There was a

Figure 1-5. Mean \pm SE cooling rates of 1- to 16-day-old pelican chicks during metabolic trials at $T_{a,s}$ between 20 and 25°C ($n = 12$ at each age).

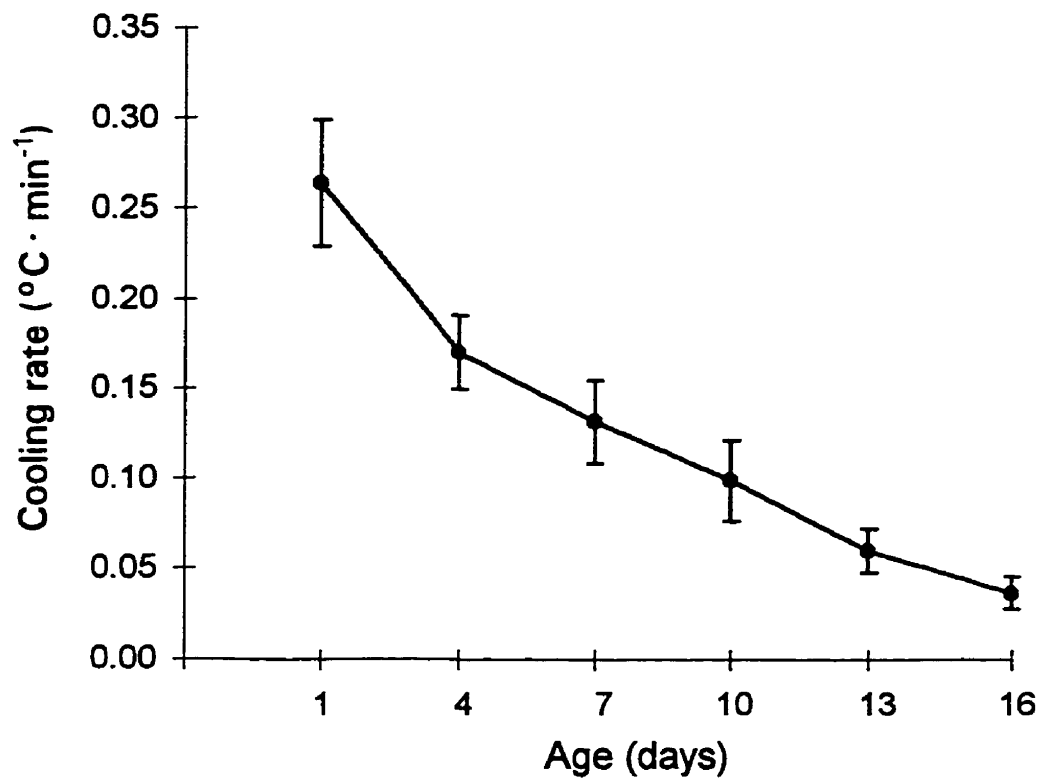
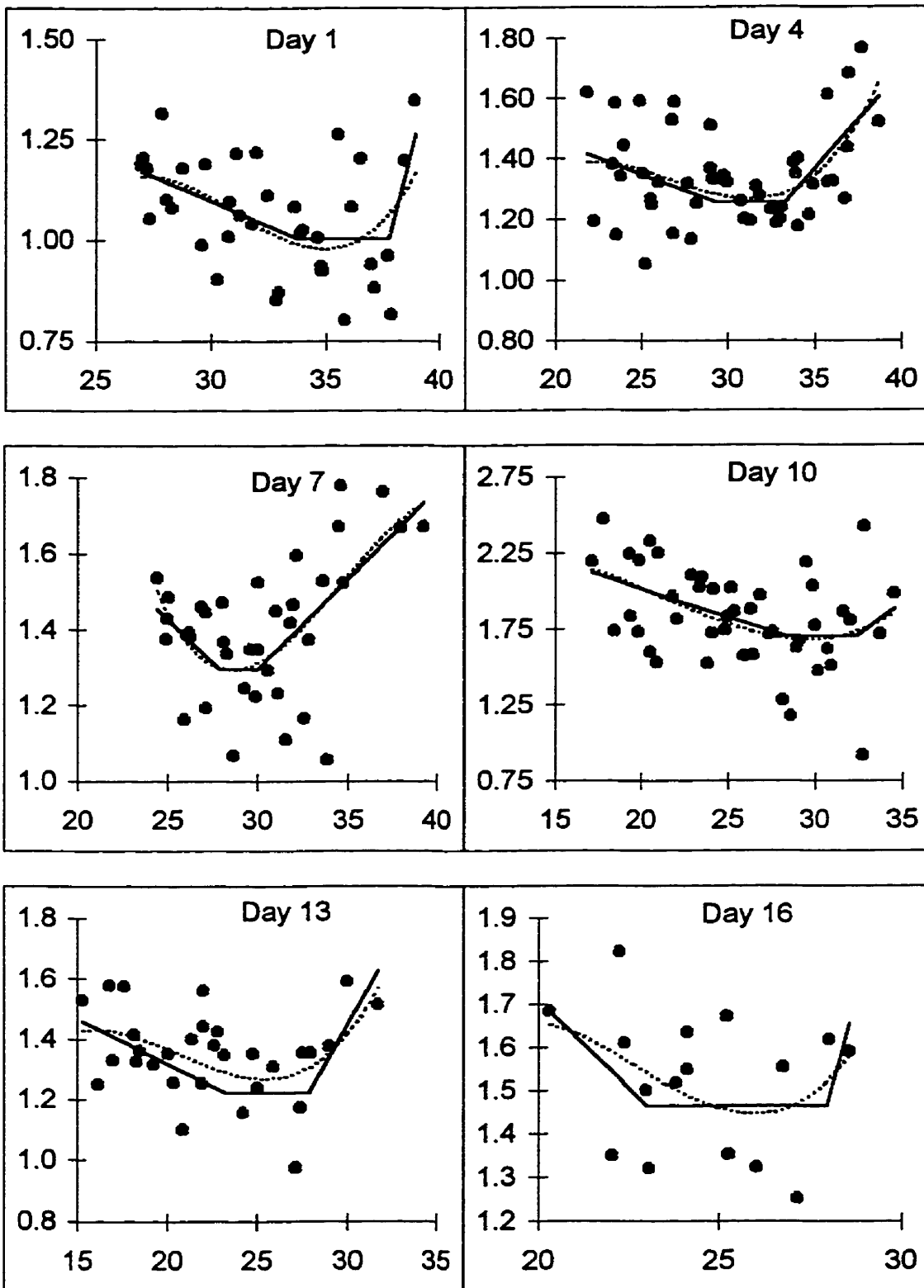


Figure 1-6. The relationship of mass-specific metabolic rate to ambient temperature of 1- to 16-day-old pelican chicks. The solid lines represent the calculated regression lines (lines of best fit) of metabolism in relation to ambient temperature. The dashed lines represent third-order polynomial curves fit to the data. Note the different scales on the x- and y-axes.

$\dot{V}O_2$ (ml·g⁻¹·hr⁻¹)

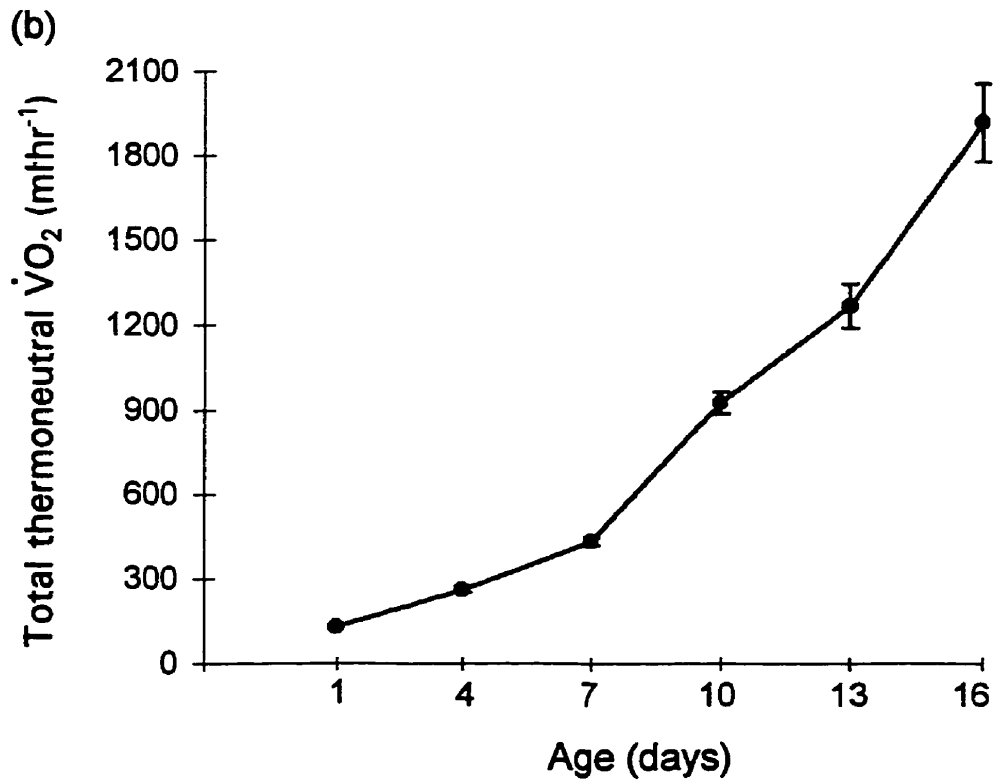
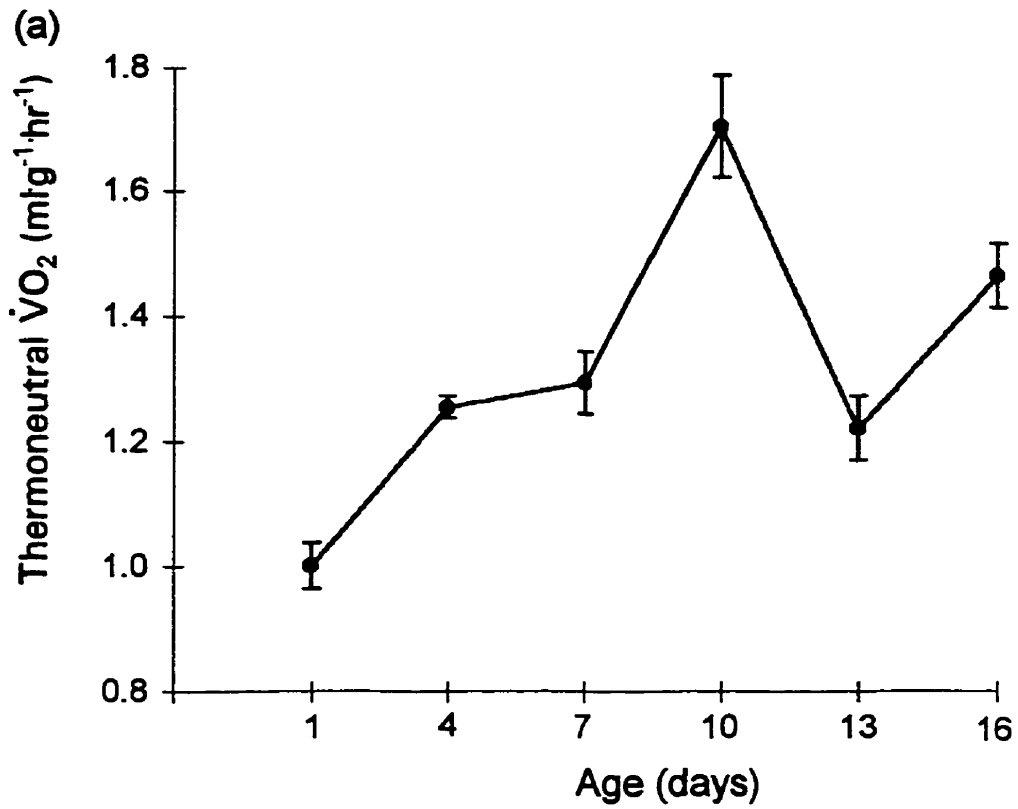


Ambient temperature (°C)

Table 1-1. The calculated lower critical temperatures (LCT) and upper critical temperatures (UCT) and width of the thermoneutral zone (TNZ, derived from the calculated inflection points illustrated in Fig. 1-6), and inflection temperatures calculated for whole-body conductance (C, as illustrated in Fig. 1-8). 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)	C 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	—	—

Figure 1-7. Mean \pm SE (a) mass-specific and (b) mass-independent thermoneutral metabolic rates of 1- to 16-day-old pelican chicks ($n = 12$ at each age).



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 $0.41 \text{ ml}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$), with chicks at day 10 having the highest MR_{TN} of all ages tested. MR_{TN} showed an absolute decrease of $0.48 \text{ ml}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$ 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 $\text{ml}\cdot\text{hr}^{-1}$) was calculated for all thermoneutral measures. MR_{total} increased significantly from days 1 to 16 ($t_1 = 7.1$, $P < 0.01$; Fig. 1-7b). 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 ($t_1 = 60.7$, $P = 0.01$).

Effects of Age and Ambient Temperature on Conductance Whole-body conductance (C) was defined as (McNab 1980):

$$(2) C = \dot{V}O_2 / (T_d - T_a)$$

where $\dot{V}O_2$ = average metabolic rate ($\text{ml}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$), T_d = 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. 1-8). In all cases, C_{\min} was significantly greater than zero (one-sample t -tests, all $t \geq 8.13$, $df \geq 22$, $P < 0.001$), 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} , calculated for all ambient temperatures tested) declined significantly from days 1 to 16 ($t_{20} = 3.0$, $P < 0.01$; Fig. 1-9). The largest absolute incremental decrease in C_{ave} occurred from days 4 to 7 (decrease of $0.15 \text{ ml}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}\cdot\text{°C}^{-1}$), although this was not significant ($t_{43} = 0.9$, $P = 0.34$). C_{ave} showed an absolute increase of $0.13 \text{ ml}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}\cdot\text{°C}^{-1}$ 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. 1-9). 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

Figure 1-8. Whole body conductance of 1- to 16-day-old pelican chicks. The solid lines represent the calculated regression lines of conductance in relation to ambient temperature ($n = 12$ at each age). Note the different scales on the x- and y-axes.

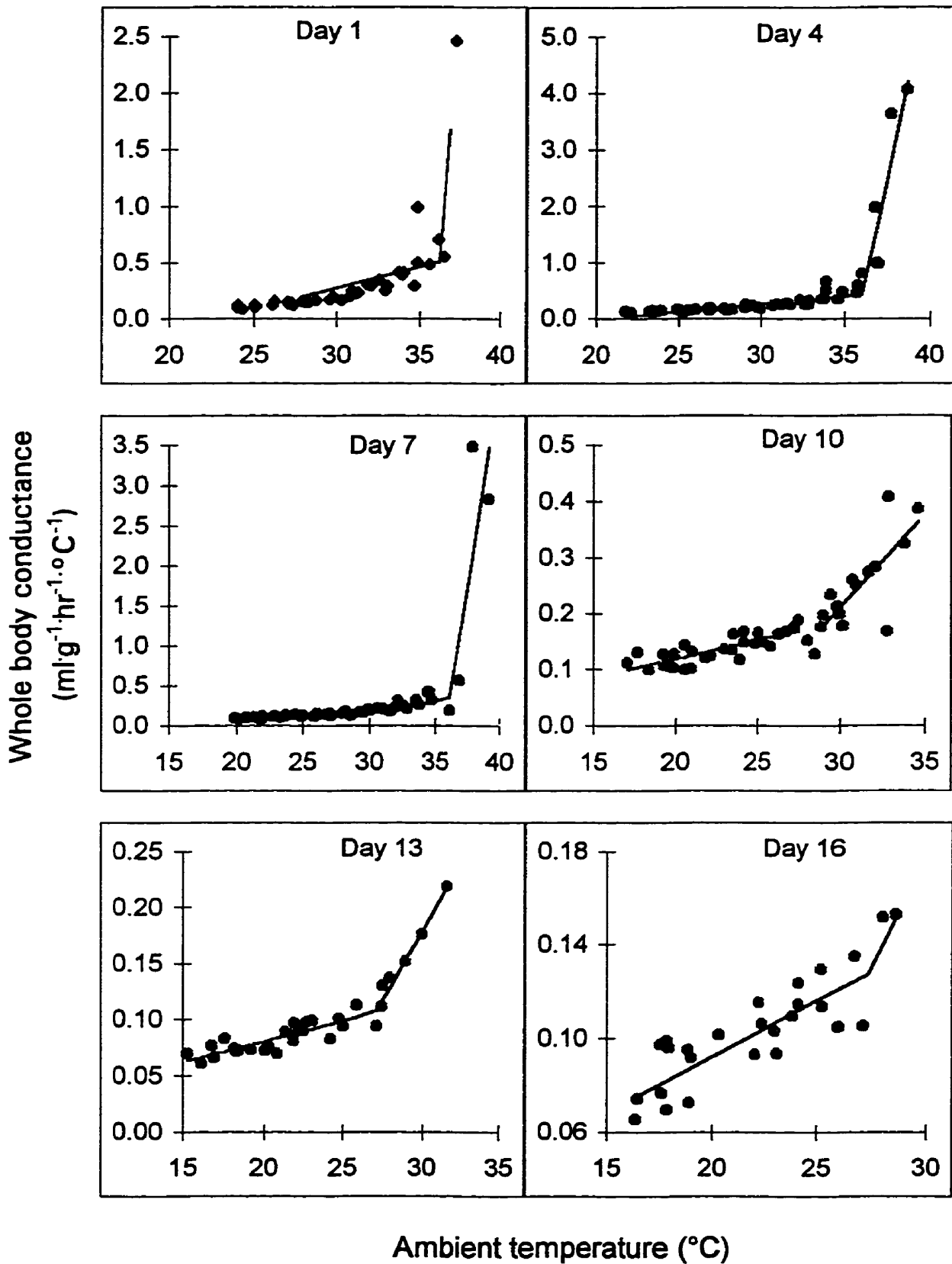
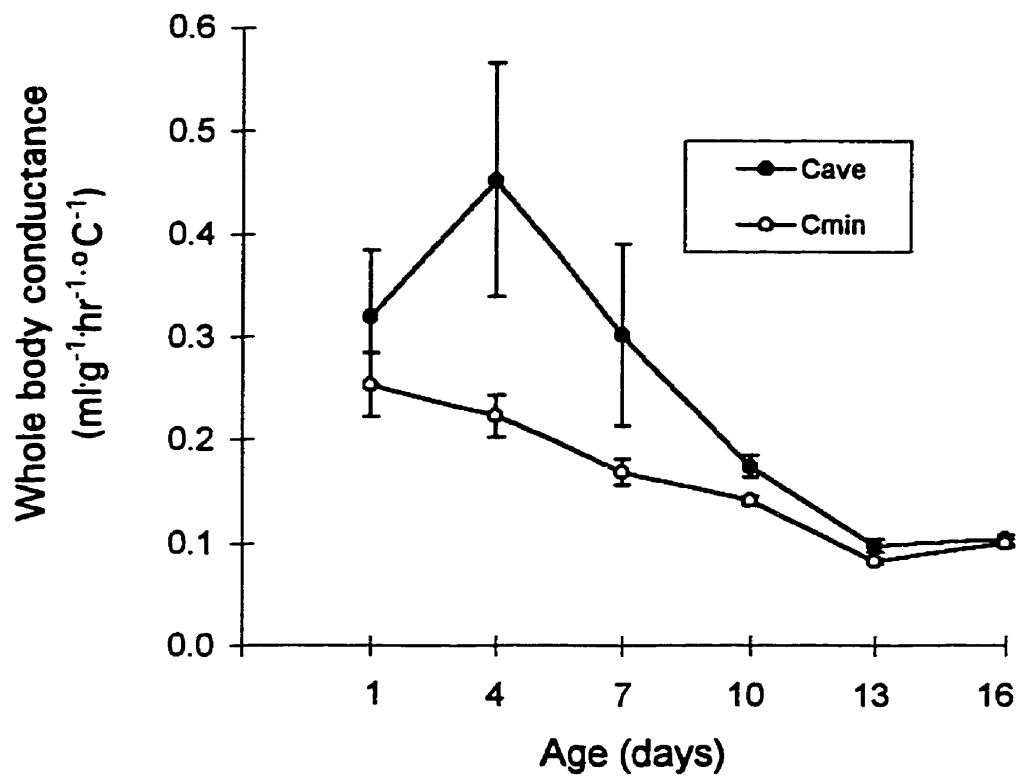


Figure 1-9. Average and minimum conductances (mean \pm SE) of 1- to 16-day-old pelican chicks ($n = 12$ at each age).



increased with each age increment, with the largest increase occurring between days 4 and 7 (Fig. 1-4). 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. My measure of average TC differs from Dunn's (1975) index of homeothermy in that my age-specific mean values of TC incorporate ambient temperatures between 20 and 25°C, whereas Dunn only used data between 15 and 25°C. Pelican chicks were close to a 75% level of average TC on day 7 (Fig. 1-4). Average cooling rates also declined with each age increment, with the largest decrease occurring between days 1 and 4 (Fig. 1-5).

My 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 Manitoba 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. 1-6, Table 1-1). 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 1-1), and gular fluttering was only observed at ambient temperatures above the calculated upper critical temperatures (Table 1-1). 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. 1-7a). 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. 1-7a), 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 1-1). 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 behavioural 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 (Fig. 1-8), 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 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, it has been shown that 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 mass, all between 16 and 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 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). I have used the same terminology for these stages as 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 to 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 behaviour in order to forage, thus leaving chicks unattended for prolonged periods of time.

My 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).

Chapter 2: Honest Signalling of Anticipated Thermal Need in Young American White Pelicans

Introduction

Godfray's (1991) model of honest signalling predicts that the level of offspring solicitation will be a true reflection of its needs as long as solicitation is costly and any benefits of resources received increase with need of the offspring. Offspring are predicted to signal at a higher rate as condition worsens, and parents are predicted to allocate resources to offspring using the signal level as an accurate indicator of the offspring's needs. Young pelicans make use of a strategy of behavioural thermoregulation (vocal heat solicitation) until they are capable of physiological thermoregulation (Evans 1992), which appears to be largely developed by 16 days post-hatch (Evans 1984a). If brooding behaviour is energetically costly (Haftorn and Reinertsen 1985) for parent pelicans, and if vocalizations given by young pelicans to solicit brooding warmth care are costly as well, then conditions for conflict may arise, and an honest signalling resolution of this conflict can be evolutionarily stable (Godfray 1991).

The assumptions and predictions of Godfray's model have not yet been tested for vocal responses to anticipated offspring need, as opposed to real need. An anticipatory response to thermal need can be described as the vocal response of

young, primarily ectothermic pelicans due to any ambient thermal challenge, where body temperature remains close to brooding body temperature. This usage corresponds to control theory analysis (McFarland 1985), where a system disturbance (cold challenge) is detected and corrective action is taken before the regulated variable (body temperature) is affected significantly. Indeed, previous work on the costs of vocal heat solicitation calls given by ectothermic white pelican embryos supports this view (Abraham and Evans 1999); pelican embryos vocalized, with low costs, in response to acute chilling but where body temperature remained close to natural brooding temperature.

The aim of the present study was to test for the presence and magnitude of the metabolic costs associated with vocal heat solicitation calls given by young pelicans in response to anticipated thermal need during the period before endothermy is fully functional. From Godfray's (1991) model, I predicted that the metabolic costs associated with calling would increase with anticipated need for heat, and that costs would decline with age and endothermic development, as the need for external heat is declining. I also predicted that the rate of heat solicitation calls given during cold trials would remain relatively constant with age, as chicks were experiencing a consistent ambient gradient below the lower critical temperature. I measured anticipated thermal need as the magnitude of ambient temperature deficit relative to the age-specific lower critical temperature, but where body temperature during testing remained close to brooding body temperature. My approach was to expose each chick to two

temperatures; mid-thermoneutral levels (warm, thermal need absent), and ambient temperatures approximately 5°C below thermoneutral (cold, representing anticipated thermal need). As predation, which occurs rarely, is unrelated to chicks vocalizations (Evans and Knopf 1993), the chief costs of signalling are likely energetic.

Methods

Subjects and Apparatus

I collected 9 pelican eggs, one per two-egg clutch (to minimize effects on productivity), from a colony at East Shoal Lake, in June of 1998. At the time of collection, eggs were externally pipped, or approximately 24 hours prior to hatching. Eggs were hatched in a commercial poultry incubator set at $37.8 \pm 0.5^\circ\text{C}$. On day 1 (where day 0 = day of hatch), I transferred chicks to a small brooder held at the same temperature. On day 4 I transferred chicks to larger brooding cages (46 x 41 x 61 cm) in a controlled environment room with ambient temperature controlled by heat lamps and monitored with a thermostat placed near the front of the cages. I 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 from front to back of the cages. I held ambient brooding temperature at mid-thermoneutral levels (Table 1-1), declining from 32°C at day 4 to 26°C at day 13. I 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. I housed chicks in this fashion for the remainder of the study. I 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 remained relatively consistent for each age, ranging from 38.2°C at day 1 to 38.5°C at day 13.

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

I 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 13). I painted the insides of the chambers flat black to minimize radiative heat transfer. The removable lids had several openings to accommodate thermocouples, 2 microphones to monitor vocalizations and incurrent and excurrent air ports positioned at opposite ends of each lid. A small fan inside the chamber assisted in air circulation. I installed a coil of copper tubing (6.5 mm outside diameter) in each chamber that 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. Chamber ambient temperature was controlled by circulating water from a temperature-regulated water bath through the coil (see figure 1 in Evans 1990).

I monitored cloacal temperature during testing with a 30-gauge thermocouple inserted 1 cm into the cloacal opening, and the recorded values represented core body temperature. I monitored the ambient temperature of the chamber with the same type of thermocouple taped to the plastic mesh separating the chick from the surrounding ring of copper coil.

I monitored vocalizations continuously using a sound-operated relay and an Esterline Angus event recorder. In addition, a second microphone placed in the chamber lid allowed for continuous, live broadcast of events inside the chamber during trials. Mean call rates were taken as the number of vocal heat solicitation calls given per minute for the duration of each trial.

I made metabolic measurements using a single channel, open-flow respirometry system (after figure 4c in Stack and Rossi 1988). Flow rates ranged from 435 to 1794 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). I monitored flow rates < 800 ml·min⁻¹ with an AMETEK R-1 flowmeter calibrated according to the bubble flow method (Levy 1964). I 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 H₂O and CO₂ (using Drierite, soda lime and Drierite again), then was drawn through the oxygen sensor and flow meter. I monitored the fractional oxygen content of chamber excurrent air with an AMETEK S-3A oxygen analyzer equipped with an N-22M sensor. I recorded fractional O₂, ambient temperature and cloacal temperature every 5 s using a Sable System data acquisition and analysis program (DATACAN V). This program simultaneously recorded all temperatures to 0.1°C.

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

Procedure

For each age class, I measured call rates and metabolic rates during exposure to each of two relatively constant ambient temperatures, chosen in random order; mid-thermoneutral (warm) and about 5°C below thermoneutral (cold) (Chapter 1, Table 1-1). The warm ambient test temperatures were close to brooding ambient temperatures for each age class. During each test, I placed individual chicks in the metabolic chamber where they were immediately exposed

to a specified test ambient temperature. I terminated tests after 30 min or when cloacal temperature fell by more than 2°C below brooding cloacal temperature. This protocol ensured that chicks had sufficient time to rest and return to brooding cloacal temperature before further testing, and that the cold test ambient temperature likely represented anticipated (rather than real) need for heat. I tested individual chicks twice daily (once under each temperature regime) at each age. Between tests, I returned chicks to their cages to rest, rewarm and feed. I weighed chicks immediately before and after each test and calculated their mean mass. I averaged the masses of all chicks tested at each age to obtain a mean daily mass.

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 I was interested in measures of $\dot{V}O_2$ during calling and silent periods. Under these conditions, short-term (approaching 'instantaneous') measures are more appropriate (Bartholomew et al. 1981). When actual oxygen uptake changes, for example due to the onset of calling or silence, O_2 levels in the excurrent air stream change exponentially, only gradually approaching a new equilibrium. I 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.

I calculated mass-specific $\dot{V}O_2$, corrected to STP, using equation 4a of Withers (1977) and expressed $\text{ml}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$. Validation of the accuracy of these calculations for this system was obtained by calculating $\dot{V}O_2$ over successive 5 s 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 $\leq 0.011 \pm 0.384 \text{ ml}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$) during washout measurement (no live animal in the chamber).

I analysed $\dot{V}O_2$ during periods of silence and calling for each test temperature regime (warm, cold). Differences in mean $\dot{V}O_2$ measured during silence and calling were then compared to detect any metabolic response to ambient cooling, under conditions when cloacal temperature during testing remained close to brooding cloacal temperature.

I performed statistical analyses using S.P.S.S. (version 7.5). MANOVAs incorporated a repeated measures design (Winer 1971) for age, test temperature and silence versus calling (a significance level of $\alpha = 0.05$ was used for all MANOVAs). Post-hoc paired *t*-tests (one-tailed) were used to make comparisons within and between ages. A significance level of $\alpha = 0.01$ was used for all paired *t*-tests (Bonferroni correction).

Results

Patterns of Growth

Chick mass increased 10-fold from days 1 to 13 ($F_4 = 2420.41$, $P < 0.001$) with the largest absolute increase (442.7 g) occurring from days 10 to 13 (Fig. 2-1). Chick masses observed in this study were not significantly different than those reported by Evans (1997) for wild pelican chicks reared without sibling competition on days 1 and 4 (one-sample t -tests, all $t \leq 1.609$ $df \geq 16$, $P \geq 0.126$), were slightly but significantly lower (7%) on day 7 ($t_{11} = 3.036$, $P = 0.008$), and were slightly but significantly higher than wild pelican chicks on days 10 (6%) and 13 (13%) (one-sample t -tests, all $t \geq 3.128$, $df \geq 9$, $P \leq 0.012$).

Effects of Ambient Temperature on Cloacal Temperature

During the periods when $\dot{V}O_2$ was measured, cloacal temperature remained close to brooding cloacal temperature (within approximately 1.5°C) at all ages. However, there was a significant main effect of test temperature on mean cloacal temperatures during $\dot{V}O_2$ measurement ($F_{1,6} = 167.024$, $P < 0.001$; Fig. 2-2). For all ages tested, cloacal temperatures during warm trials were significantly greater than those during cold trials (all $t \geq 5.591$, $df \geq 7$, $P \leq 0.0001$), and were not significantly different from brooding cloacal temperature (all $t \leq 1.722$, $df \geq 7$, $P \geq 0.106$), with the exceptions of day 1 ($t_{16} = 2.938$, $P = 0.01$) and day 13 ($t_9 = 2.801$,

Figure 2-1. Mean \pm SE daily mass of lab-reared pelican chicks at each age tested ($n = 5-9$ individuals per age) and mass of wild pelican chicks reported by Evans (1997).

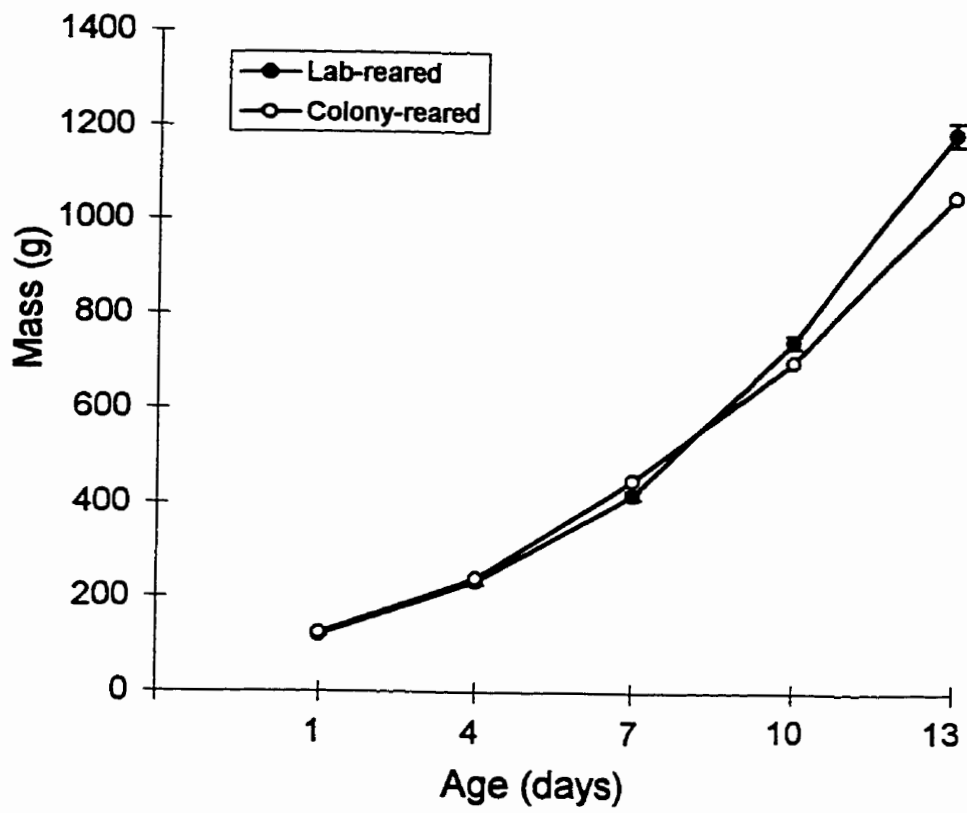
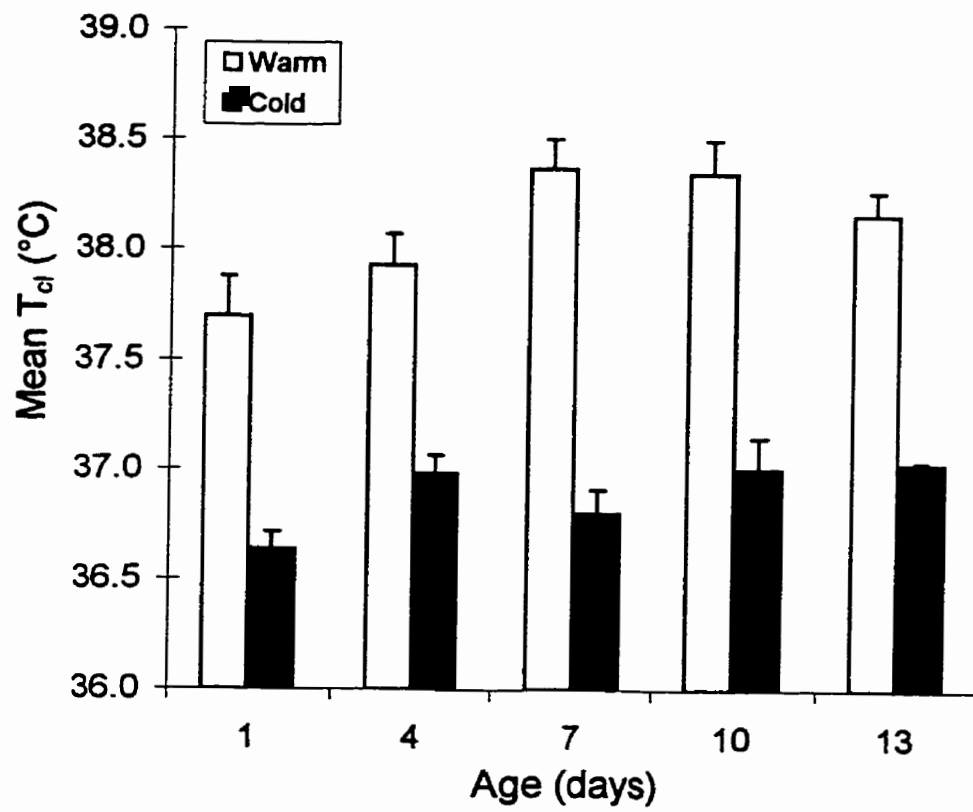


Figure 2-2. Mean (+ SE) cloacal temperature of pelicans chicks during the period of $\dot{V}O_2$ measurement ($n = 5-9$ individuals per age).



$P = 0.021$). Cloacal temperatures during cold trials were significantly lower than brooding cloacal temperatures for all ages (all $t \geq 9.223$, $df \geq 6$, $P \leq 0.0001$).

For cold trials which were terminated before 30 min, I calculated the final cloacal temperatures as if trials had been allowed to continue for the entire 30 min period given a linear rate of body cooling (Fig. 2-3); for cold trials which lasted 30 min the actual final cloacal temperatures were used. These values were compared to the actual to the actual final cloacal temperatures of the warm trials. There was a significant main effect of test temperature on final cloacal temperature ($F_{1,3} = 77.110$, $P=0.003$). Final cloacal temperatures were significantly lower in the cold than in the warm trials at all ages (all $t \geq 4.038$, $df \geq 3$, $P \leq 0.008$).

Rates of Calling

There was a significant main effect of test temperature on call rate ($F_{1,3} = 54.765$, $P=0.005$; Fig. 2-4). Call rates during warm trials increased with each age increment between days 1 and 13 ($t_6 = 3.83$, $P = 0.0095$). During cold trials, there were no significant incremental changes in call rates with age ($\alpha=0.01$, all $t \leq 2.642$, $df \geq 3$, $P \geq 0.023$). Call rates during cold trials were significantly greater than those during warm trials for days 4 through 13 (all $t \geq 3.922$, $df \geq 4$, $P \leq 0.0085$). Call rate during cold trials at day 1 were greater than those during warm trials, but the effect was only approaching significance ($t_6 = 2.681$, $P = 0.018$).

Figure 2-3. Final cloacal temperature (mean + SE) for cold and warm trials ($n = 5-9$ individuals per age).

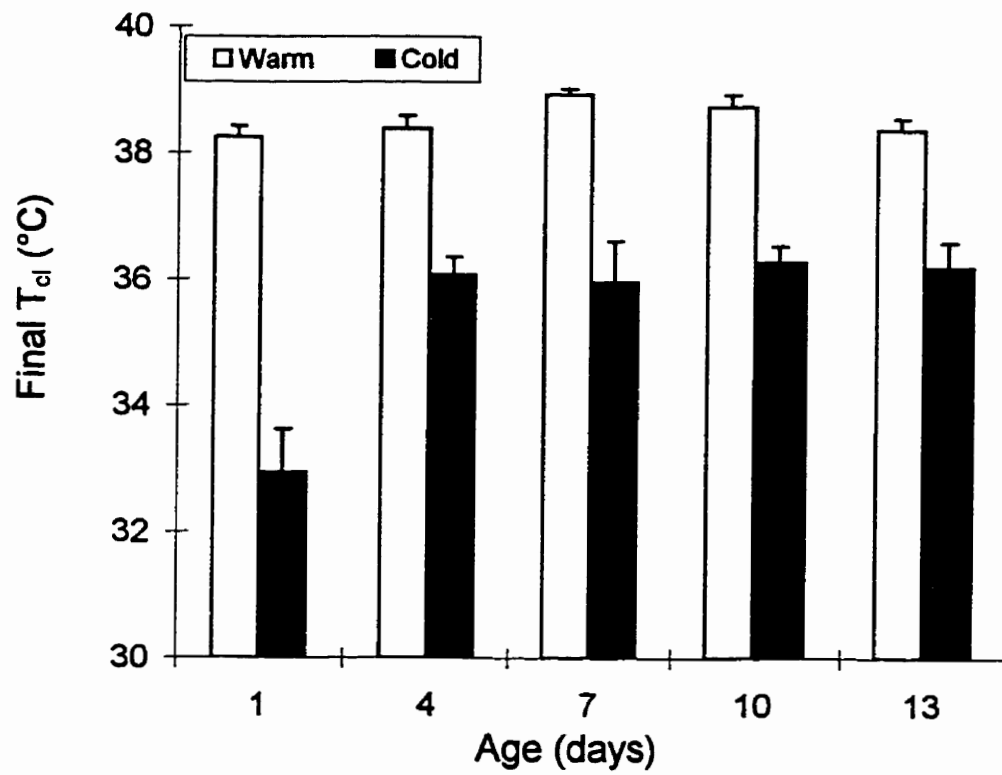
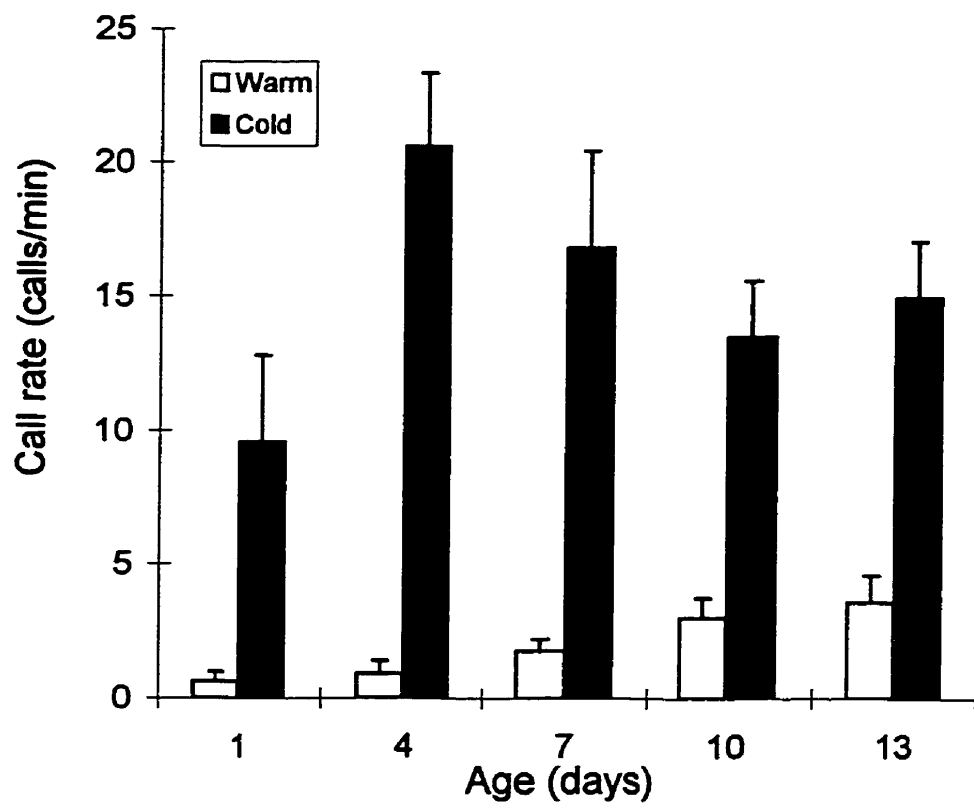


Figure 2-4. Call rates (mean + SE) given by pelican chicks at each test ambient temperature ($n = 5-9$ individuals per age).



Metabolic Costs Associated with Calling

At each age and test temperature, $\dot{V}O_2$ during calling was greater than that during each corresponding period of silence (Fig. 2-5), although this trend was significant only for warm trials at day 4 ($t_7 = 5.916$, $P = 0.0005$) and cold trials at days 4 and 7 ($t \geq 3.467$, $df \geq 5$, $P \leq 0.009$).

I calculated the absolute metabolic costs associated with calling at each test temperature as the $\dot{V}O_2$ during periods of calling (total $\dot{V}O_2$ associated with calling) minus the $\dot{V}O_2$ during corresponding silent periods. There was no significant main effect of temperature on absolute costs ($F_{1,2} = 3.279$, $P = 0.212$; Fig. 2-6a), although the power of this test was low (power = 0.019). However, absolute costs during cold trials tended to be greater than those in warm trials from days 1 to 10, while the reverse trend was seen at day 13. There were also no significant differences in absolute costs for warm or cold trials across age increments (all $t \leq 2.227$, $df \geq 3$, $P \geq 0.045$).

I also calculated the relative metabolic costs associated with calling at each test temperature ($\dot{V}O_2$ during calling divided by the $\dot{V}O_2$ during corresponding silent periods). There was no significant main effect of temperature on relative costs ($F_{1,2} = 3.77$, $P = 0.192$; Fig. 2-6b), although the power of this test was low (power = 0.209). Again, relative costs during cold trials tended to be greater than those in warm trials from days 1 to 10, while the reverse trend was seen at day 13. There were also no significant differences for warm or cold trials across age

Figure 2-5. Mass-specific $\dot{V}O_2$ (mean + SE) during periods of silence and calling at each test ambient temperature ($n = 5-9$ individuals per age).

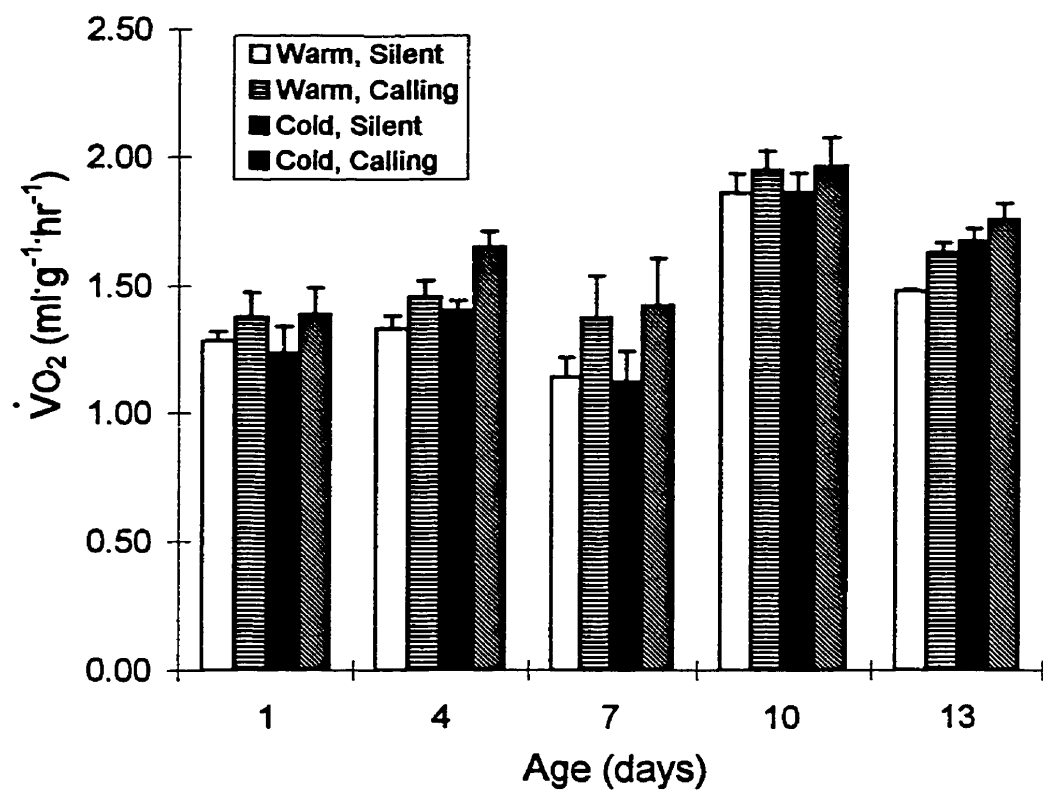
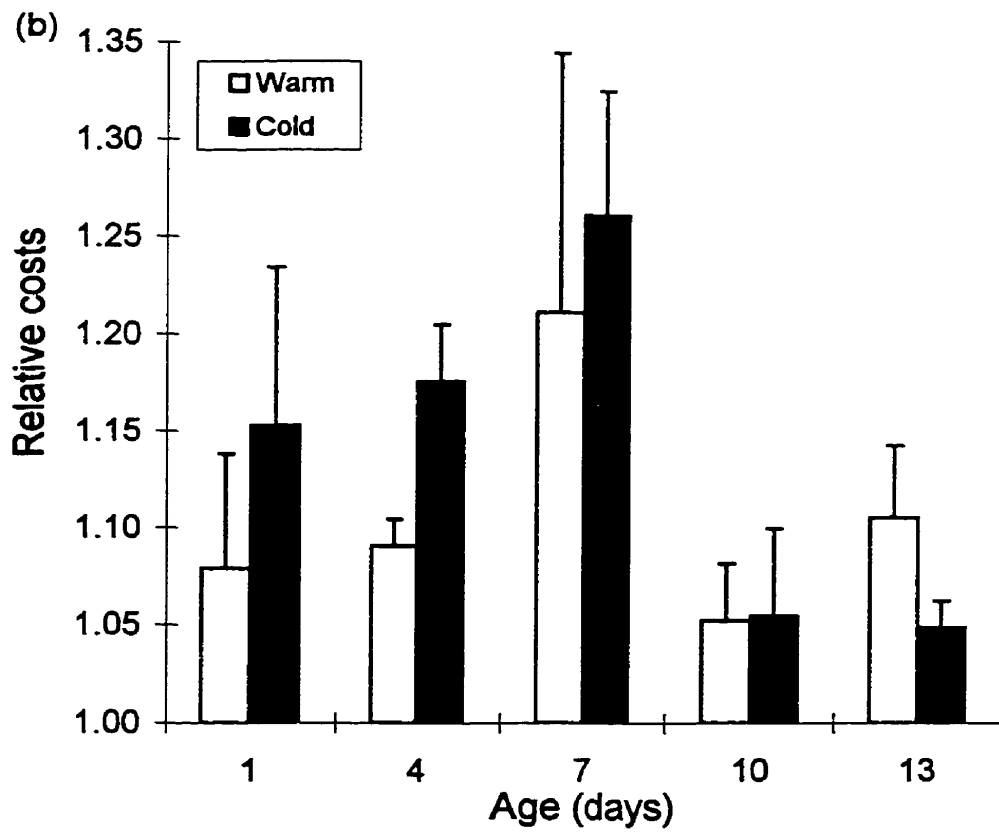
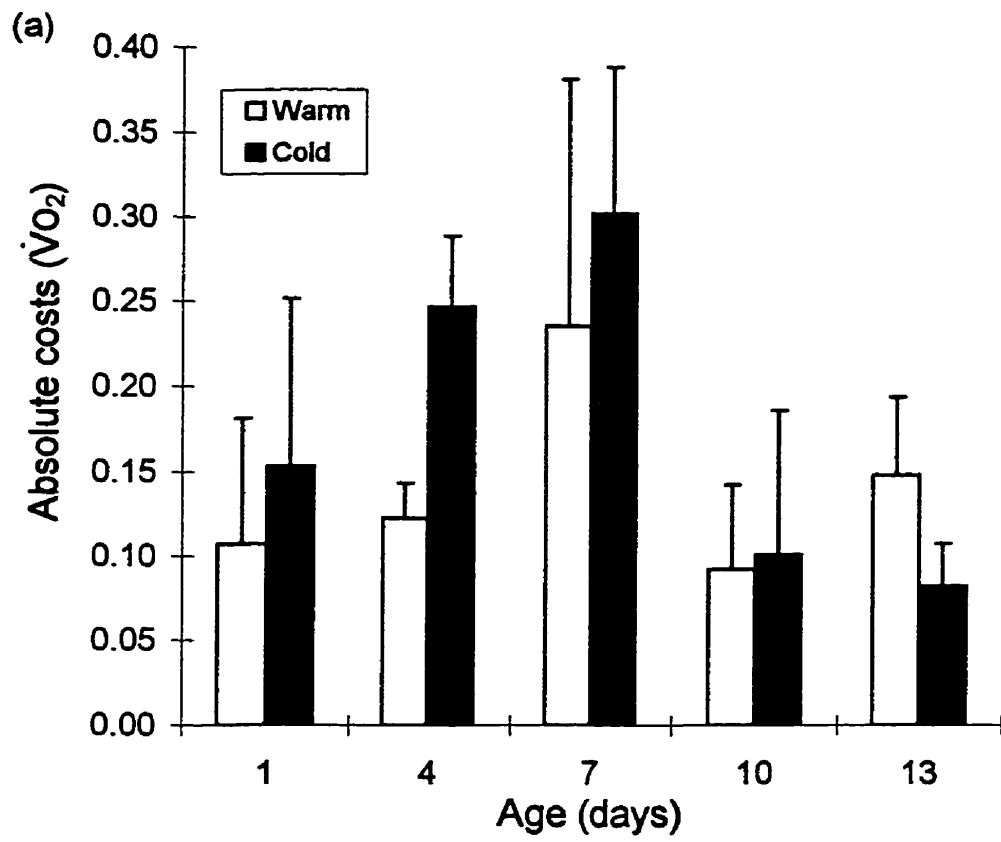


Figure 2-6. (a) Absolute and (b) relative metabolic costs (mean + SE) associated with calling at each test ambient temperature ($n = 5-9$ individuals per age).

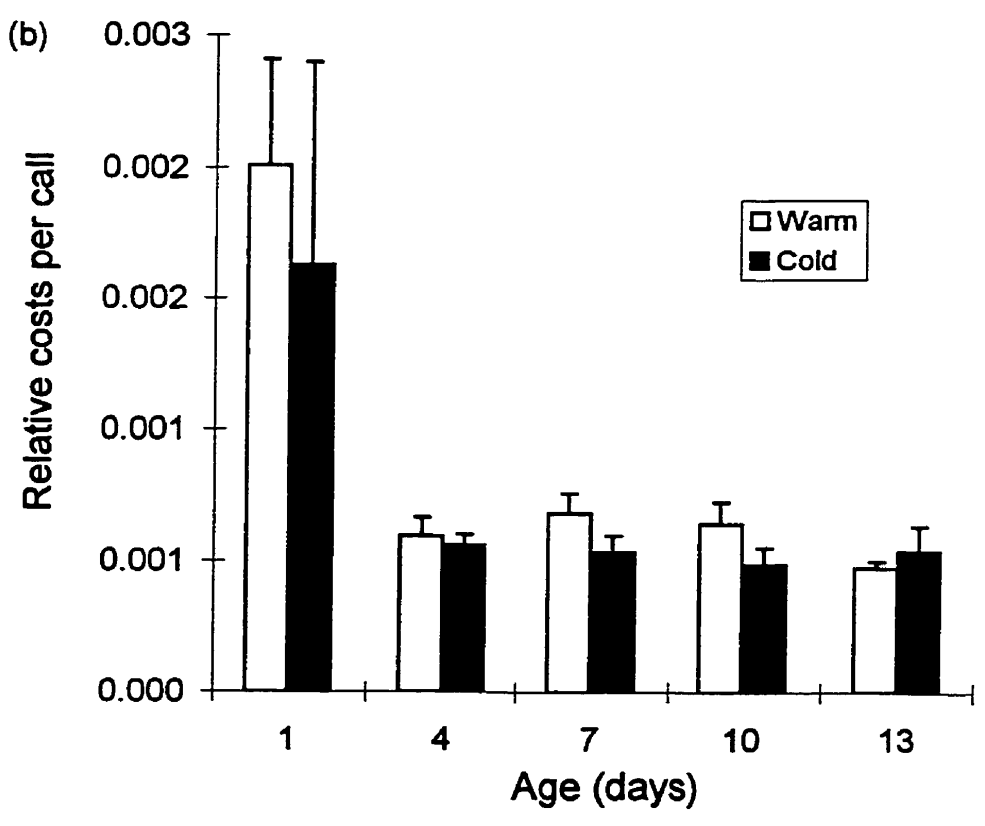
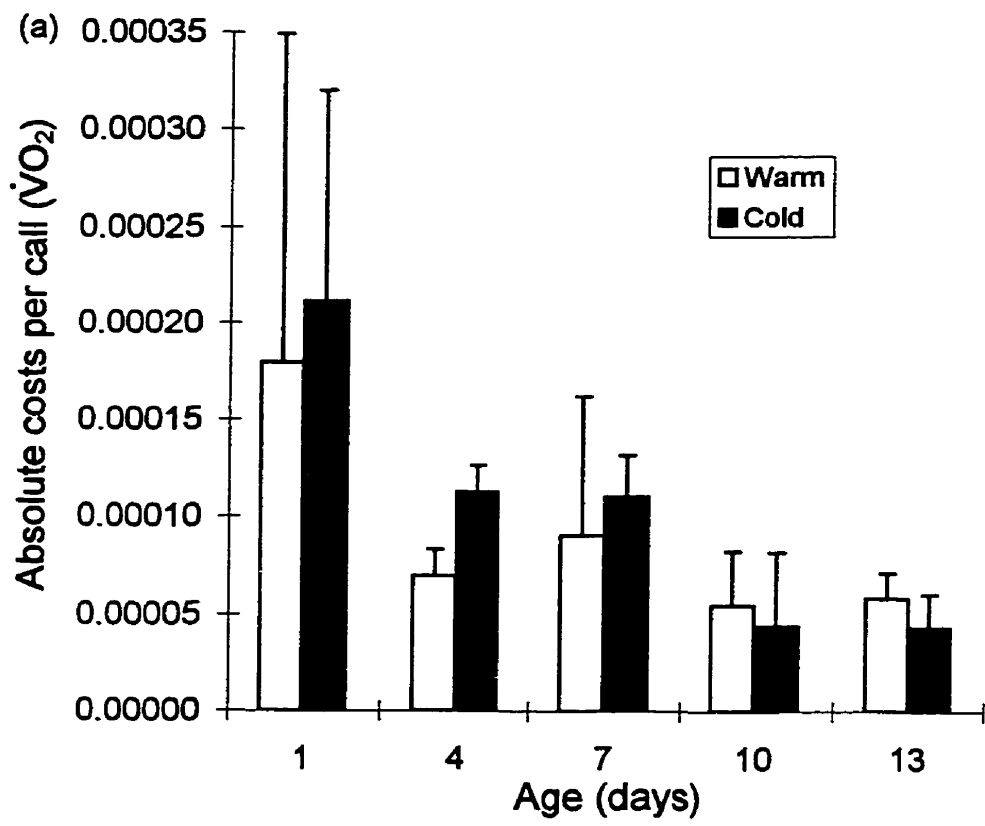


increments (all $t \leq 1.242$, $df \geq 3$, $P \geq 0.141$), with the exception that relative costs during cold trials decreased significantly from days 7 to 10 ($t_4 = 3.633$, $P = 0.01$).

I calculated the absolute metabolic costs per call as the absolute costs (in $\text{ml}\cdot\text{g}^{-1}$) during each period of calling divided by the absolute number of calls given (Abraham and Evans 1999). There was no significant main effect of test temperature on absolute costs per call ($F_{1,2} = 0.178$, $P=0.714$; Fig. 2-7a), although the power of this test was low (power = 0.058). Absolute costs per call during cold trials tended to be greater than those in warm trials from days 1 to 7, while the reverse trend was seen on days 10 and 13. There were also no significant differences in absolute costs per call for warm or cold trials across age increments (all $t \leq 2.608$, $df \geq 3$, $P \geq 0.03$), with the exception of a significant decline during cold trials between days 1 and 13 ($t_4 = 4.857$, $P = 0.0085$).

I calculated the relative metabolic costs per call as the relative costs (in $\text{ml}\cdot\text{g}^{-1}$) during periods of calling divided by the absolute number of calls given during the period when $\dot{V}\text{O}_2$ was measured. There was no significant effect of test temperature on relative costs per call ($F_{1,2} = 3.245$, $P=0.213$; Fig. 2-7b), although the power of this test was low (power = 0.189). Relative costs per call during warm trials were greater, although not significantly, than those in cold trials from days 1 to 10, while the reverse trend (also not significant) was seen at day 13. There were no significant incremental changes in relative costs per call for either warm or cold trials across age (all $t \leq 3.612$, $df \geq 3$, $P \geq 0.015$).

Figure 2-7. (a) Absolute and (b) relative metabolic costs per call (mean + SE) at each test ambient temperature ($n = 5-9$ individuals per age).



Discussion

Anticipated versus Real Need for Heat

I was interested in vocal heat solicitation calls given by primarily ectothermic pelican chicks in response to anticipated (rather than real or significant) thermal need. An anticipatory response to thermal need can be described as the vocal response of young pelicans due to any ambient thermal challenge, but where body temperature remains close to brooding temperature. This usage corresponds to control theory analysis (McFarland 1985), where a system disturbance (cold challenge) is detected, in this case presumably by peripheral (skin) temperature receptors, and corrective action (vocal heat solicitation) is taken before the regulated variable (deep body temperature) is affected significantly. During the period before endothermy is fully functional, such uncorrected chilling would inevitably lead to a reduced body temperature and real need for heat (Evans 1984).

Although cloacal temperatures during cold trials were lower than in the warm trials (Fig. 2-2), it is unlikely that those chicks were experiencing real thermal need. Colony-reared pelicans (Evans 1984) were found to have mean \pm SE cloacal temperatures of $31.6 \pm 1.00^{\circ}\text{C}$ on day 6, $33.3 \pm 0.86^{\circ}\text{C}$ on day 9, and $34.7 \pm 0.64^{\circ}\text{C}$ on day 12. However, these values are likely to be slight underestimates of actual cloacal temperature due to some body cooling of chicks caused by their removal from the nest for measurement. Since cloacal temperatures during cold trials (Fig. 2-2) were greater

than those observed in the field and remained close to (within about 1.5°C) brooding cloacal temperatures in this study, I assume that significant need for heat was absent. However, if chilling were left uncorrected for a prolonged period, there would likely be a further reduction in body temperature, eventually resulting in real need for heat.

Vocal Heat Solicitation: Call Rates

Call rates during cold trials were greater than those during warm trials for all ages tested (Fig. 2-4), although this was significant only for days 4 through 13. Call rates during warm trials increased slightly but consistently with age. This increase may be due in part to older chicks becoming increasingly intolerant of being confined in the metabolic chamber. Call rates during cold trials increased dramatically between days 1 and 4, possibly due in part to a combination of an increase in thermal competence (Fig. 1-4) and an overall improvement in vocal responsiveness to cool ambient temperatures on day 4 (pers. observ.). Call rates during cold trials declined between days 4 and 10, corresponding to a period of increased endothermic development (Evans 1984), and finally increased slightly between days 10 and 13. These results are consistent with a previous study on white pelican embryos (Evans 1990) which reported an increase in call rate in response to relatively short-term cooling episodes. With the exception of an increase between days 1 and 4, call rates during cold trials remained relatively consistent with age, perhaps owing to the fact that, although real need for heat

was absent, the gradient of the cold test temperature to the lower critical temperature (5°C gradient) remained constant for each age. Therefore, although the endothermic development of chicks increased with age, they would still be incapable of effectively defending body temperature at the cold (sub-thermoneutral) test temperature.

Metabolic Costs Associated with Calling

The overall trend of metabolic rates observed during warm trials (Fig. 2-5) is similar to the trend for thermoneutral metabolic rates of pelican chicks tested at the same ages (Fig. 1-7a). There was a gradual increase in $\dot{V}O_2$ between days 1 and 10, followed by a decline in $\dot{V}O_2$ between days 10 and 13. In all cases, $\dot{V}O_2$ was greater during periods of calling than during corresponding silent periods.

For all ages, absolute and relative increases in metabolic rate associated with anticipated thermal need were modest and consistently insignificant (Figs 2-6a, b). There was a reversal (not significant) in both absolute and relative costs at day 13, with costs during warm trials greater than those during cold trials. Relative cost increments during periods of anticipated thermal need ranged from 1.05 to 1.26 times the corresponding periods of silence. Absolute and relative costs did not decline over the range of ages tested as predicted (Figs 2-6a, b). Both absolute and relative costs during cold trials increased incrementally from days 1 through 7, declined to day 10 and remained relatively consistent to day 13. The

decrease in costs from days 7 to 10 may be due in part to a combination of a significant increase in downy plumage cover after day 7 (Daniels 1997), an improved ability to shiver after day 7 (Evans 1994), and a rapid increase in mass (Fig. 2-1).

My results are consistent with those reported for ectothermic pelican embryos at the pipped-egg stage (Abraham and Evans 1999). Pelican embryos are faced with a continuously depleting energy reserve while within the egg and incur modest absolute and relative costs associated with calling in response to anticipated thermal need, and greater absolute and relative costs only in the presence of real thermal need at low body temperatures. It is therefore possible that significant absolute and relative metabolic costs associated with vocal heat solicitation calls given by young pelican chicks may be directly associated with the presence of real thermal need, as measured by a suboptimal body temperature (Abraham and Evans 1999). Any reallocation of energy from maintenance functions or growth to behavioural thermoregulation (Vleck and Vleck 1996) may or may not have a significant impact on energy reserves in young pelicans. If begging costs are substantial, critical energy may be diverted from growth, development or maintenance, ultimately affecting survival. Wild pelican chicks are fed up to 4 times daily (Evans and Knopf 1993), and thus obtain access to a frequently renewed supply of energy. Therefore, significant costs associated with calling may also be realized only when food is short.

It is important to note that there may also be significant costs associated with not calling for warmth. Young pelicans reared at suboptimal ambient temperatures (simulating conditions if young failed to solicit parents for heat) beg less for food and have lower masses than those reared under thermoneutral conditions (Safiniuk and Evans unpubl. data). Particularly during the period when endothermy is still developing, maintaining a warm body temperature should facilitate any future energy gains, which may compensate for the costs of vocal thermoregulation. Thus, any food that a chick may receive would be more efficiently assimilated, resulting in a net energy gain. In addition, warm body temperatures may also facilitate eating and begging for food (Choi and Bakken 1990), which would further increase a chick's chances of getting fed.

Consistent with my prediction, both absolute and relative costs per call in both warm and cold trials declined with age and endothermic development. As external need for heat declines during the period of increased endothermic development, pelican chicks should expend less energy soliciting a resource they can, in part, provide for themselves. Absolute costs per call showed a more gradual decline with age, while relative costs per call showed a dramatic decline from days 1 to 4, and remained relatively consistent to day 13.

The relative metabolic costs associated with vocal heat solicitation obtained in this study are within the range of those reported in other studies on avian vocal energetics, although their interpretations have been variable. Leech and Leonard

(1996) reported a 28% increase in metabolic costs of begging in tree swallows, and suggested that such costs could have a significant impact on energy expenditure of individual nestlings. Horn et al. (1995) found a 15% increase in metabolic costs of rooster calling (above resting metabolic rate), and deemed these to be energetically inexpensive. McCarty (1996) found that relative increases in the metabolic costs of begging by young songbirds varied from negligible up to 27%, and also concluded that such begging was not energetically costly. Bachman and Chappell (1998) reported relative costs calling in house wrens of 27% above resting, and again, suggest that energy costs of begging were insubstantial. Vocal heat solicitation calls given by young pelicans in response to anticipated thermal need also appear to be relatively inexpensive to produce. However, it remains possible that the energy increments of from about 1.05 to 1.26 times the corresponding periods of silence may have biologically significant fitness consequences.

Implications for Honest Signalling Theory

A key assumption of Godfray's (1991) game-theoretic honest signalling model is that fitness benefits to the offspring will increase with need, given that some characteristic of the signal increases with need. For the signalling system to remain evolutionarily stable, the model also requires that any increments in offspring benefit be balanced by a corresponding increase in cost (Godfray 1995).

It follows that signalling costs should also increase with need (Johnstone 1997). It is unlikely, however, that pelican chicks in our study were experiencing real need, as cloacal temperatures during testing remained close to brooding cloacal temperatures. Because anticipated need, if uncorrected, will eventually translate into real need (low body temperature) we can assume that investigating the costs associated with the vocal response to perceived or anticipated thermal need in the context of his model is valid.

Whether or not parental brooding/incubation behaviour of pelicans and the vocal signals produced by pelican chicks are to be considered 'costly' enough to constitute conflict, as assumed by honest signalling models (Godfray 1991, 1995) remains somewhat arbitrary. If, in fact, brooding behaviour is not costly for parent pelicans, then conditions for conflict dissolve. It is possible that the production of vocal heat solicitation calls involves at least some energetic expenditure, even in the absence of selection for reliability (Kilner and Johnstone 1997), possibly accounting for a portion of the costs observed in this study. Honest signalling models simply predict that a conflict of interest between parents and offspring will favor more costly signals than would otherwise be the case. In the absence of conflict, the signal costs observed in this study may be considered low, but may still reflect anticipated offspring need. It is also possible that the costs associated with anticipated thermal need reported here are due in part to changes in signal quality (call intensity and duration; Abraham and Evans 1999) with need. Even if

this is the case, parents may still use these changes in signal quality as an accurate assessment of anticipated offspring need for heat. If parents and young are in agreement about the amount of heat that the young require (Evans et al. 1995), relatively low-cost signals may still be honest (Kilner and Johnstone 1997). Under these conditions, parents and offspring would be expected to cooperate via reliable, efficient signals, without exaggerated costs (Johnstone 1997).

Although costs associated with calling were relatively small, my results lend some support to the prediction that fitness costs of vocal signalling should increase with anticipated thermal need. Call rates during cold trials were greater than those during warm trials at each age. There were greater (although not significant) absolute energy costs at all suboptimal ambient temperatures where anticipated thermal need was present, than during warm trials where need was absent. Further support was provided by relative costs (although not significant), which increased with decreasing ambient temperature and increasing anticipated thermal need. Absolute and relative costs per call declined with age and improved endothermic development. My results suggest that pelican chicks are willing to pay additional metabolic costs in the presence of anticipated thermal need in order to honestly communicate their needs to an attending parent, and that these costs decrease as the need for external heat declines with age. Consistent with results reported for ectothermic pelican embryos (Abraham and Evans 1999), the vocal response of young pelicans to acute chilling while body temperature is still high

appears to be an example of an anticipatory response to cooling, providing accurate (honest) information to a parent. An accurate but energetically inexpensive anticipatory vocal response to cooling could be of significant adaptive value for pelican chicks during the period when endothermy is developing, initiating an early corrective parental brooding response and thereby minimizing costs relative to that required if body temperature were allowed to fall significantly before calling began.

Chapter 3: Metabolic Costs associated with Vocal Thermoregulation in Young American White Pelicans

Introduction

Pelican chicks employ a strategy of behavioural thermoregulation by vocally soliciting brooding warmth from a parent to maintain a warm body temperature during the period before endothermy is fully functional (Evans 1992). During approximately the first 2 weeks after hatching, pelican chicks are constantly attended to at the nest by a parent. Under natural conditions, young pelicans call, and the attending parent responds quickly by increased brooding (Evans 1992, 1994). By about day 16, parents cease constant brooding behaviour, which corresponds to the age at which pelican chicks attain physiological endothermy (Evans 1984, Chapter 1).

Young pelicans are effective at vocally regulating their body temperature provided that a parent or surrogate responds appropriately by providing additional brooding warmth (Evans 1994). This behavioural thermoregulation is especially important during the early development of young altricial pelicans, where a combination of small size, incompletely formed insulative covering, and limited endothermic capabilities combine to limit the young's ability to thermoregulate by physiological means alone. Evans (1994) tested the honesty of these signals and

concluded that vocal heat solicitation calls given by young pelicans provide the parent with accurate information regarding the offspring's thermal needs and condition. These vocal heat solicitation calls appear to be energetically inexpensive to produce as long as body temperature remains close to optimal brooding body temperature (Chapter 2). However, any costs incurred as the result of calling for heat may be more than offset by the benefits associated with the higher metabolic rate that accompanies the maintenance of a high body temperature.

Godfray's (1991) model of honest signalling predicts that, as offspring need for resources increases (condition worsens), the level of offspring solicitation should increase. Because costs are directly proportional to the level of offspring signalling, it follows that costs of signalling should also increase with increasing need. Although the costs of vocal heat solicitation calls given by young pelicans were relatively small, costs did increase as the degree of ambient cooling increased (Chapter 2).

The main objective of this study was to assess the overall metabolic costs and benefits associated with vocal thermoregulation and the maintenance of a high body temperature in young, cold-challenged pelicans during the period before endothermy is fully functional. My approach was to measure the metabolic rates of chicks that were given the opportunity to vocally thermoregulate via a sound-operated relay that shifts ambient ('brooding') temperature upwards towards

thermoneutral levels. This vocal thermoregulation group will be compared to two control groups: (1) warm-only controls, where ambient temperature is held within the thermoneutral zone (Table 1-1), and (2) cold-only controls, where ambient temperature is held 5°C below the thermoneutral zone. Based on Godfray's (1991) model, chicks in the vocal thermoregulation group are predicted to maintain their body temperature close to brooding body temperature by signalling rapidly in response to a cold challenge, with minimal metabolic costs, but with costs above the warm-only controls owing to some chilling and resultant calling. Cold-only controls are predicted initially to experience both a lower metabolic rate and body temperature as in typical ectotherms, with both metabolic rate and body temperature increasing as endothermy develops with age.

Methods

Subjects and Apparatus

I collected a total of 9 pelican eggs, one per two-egg clutch (to minimize effects on productivity), from a colony at East Shoal Lake, Manitoba, in June of 1998. At the time of collection, eggs were externally pipped, or approximately 24 hours prior to hatching. Eggs were hatched in a commercial poultry incubator set at $37.8 \pm 0.5^\circ\text{C}$. On day 1 (where day 0 = day of hatch), I transferred chicks to a small brooder held at the same temperature. On day 4 I transferred chicks to larger

brooding cages (46 x 41 x 61 cm) in a controlled environment room with ambient temperature controlled by heat lamps and monitored with a thermostat placed near the front of the cages. I 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). Throughout the study, I held ambient brooding temperature at mid-thermoneutral levels (Table 1-1), ranging from 32°C at day 4 to 26°C at day 13. A small fan placed inside the room provided air circulation. By day 4, chicks were sufficiently mobile to select an area of the cage that was thermally comfortable. I housed chicks in this fashion for the remainder of the study. Cloacal temperature was monitored in the incubator and brooding cages for about 10 min prior to testing to determine body temperature during brooding. Brooding cloacal temperature remained relatively consistent across ages, ranging from 38.25°C at day 1 to 38.26°C at day 13.

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

I 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). I painted the insides of the chambers flat black to minimize radiative heat transfer. The removable lids had several openings to accommodate thermocouples, microphones to monitor vocalizations and incurrent and excurrent air ports positioned at opposite ends of each lid. A small fan inside the chamber assisted in air circulation. I installed a coil of copper tubing (6.5 mm outside diameter) in each chamber, surrounding 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. I controlled chamber ambient temperature by circulating water from a temperature-regulated water bath through the coil (see figure 1 in Evans 1990).

I monitored cloacal temperature during testing with a 30-gauge thermocouple inserted about 1-2 cm into the cloacal opening, and assumed this value represented core body temperature. I 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.

I monitored vocalizations continuously using a sound-operated relay and an Esterline Angus event recorder. A second microphone placed in the chamber lid allowed for continuous live broadcast of vocal behaviour inside the chamber.

Mean call rates were taken as the number of vocal heat solicitation calls given per minute for the duration of each trial.

I made metabolic measurements using a single channel, open-flow respirometry system (after figure 4c in Stack and Rossi 1988). Flow rates ranged from 435 to 1794 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). I monitored flow rates < 800 ml·min⁻¹ with an AMETEK R-1 flowmeter calibrated according to the bubble flow method (Levy 1964). I 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 H₂O and CO₂ (using Drierite, soda lime and Drierite again), then was drawn through the oxygen sensor and flow meter. I monitored the fractional oxygen content of chamber excurrent air with an AMETEK S-3A oxygen analyzer equipped with an N-22M sensor. I recorded fractional O₂, ambient temperature and cloacal temperature every 5 s using a Sable System data acquisition and analysis program (DATACAN V). This program simultaneously recorded all temperatures to 0.1°C.

I 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.

Procedure

I measured body temperatures, call rates and metabolic rates of pelican chicks during exposure to three treatments. In the warm trials, I held each chick at a relatively constant mid-thermoneutral ambient temperature, which varied with age (Table 1-1). In the cold trials, I held each chick at an ambient temperature that was about 5°C below the lower critical temperature (LCT), representing a constant cold challenge. During the warm and cold trials, individual chicks were placed into the metabolic chamber where they were immediately exposed to a given, relatively constant test temperature. In the vocal thermoregulation trials, chicks were given the opportunity to vocally thermoregulate via a sound-operated relay that shifts ambient chamber ('brooding') temperature from a cold default temperature upwards towards thermoneutral levels (Evans 1990). Vocal thermoregulation trials began with an initial 5 min period of warmth (thermoneutral temperature), followed by a period of chilling using the cold (below LCT) ambient temperature for a period of time to be determined by the chick. I manually controlled a pump assembly that changed the water circulating through the coil, and thus chamber temperature, from cold to warm for a preselected period of 3 min in response to 5 vocal heat solicitation calls (given by chicks in response to ambient cooling). During the

periods of chilling, I counted the 5 calls using the event recorder and the live broadcast as a backup. At the end of each vocally induced 3 min period of rewarming, chamber temperature was manually reverted back to the cold temperature. Chilling thus represented the default condition that was maintained except when punctuated by periods of vocally induced rewarming. Rewarming ambient temperature must be slightly higher than mid-thermoneutral so that the overall mean ambient temperature during the vocal thermoregulation trials will be similar to the mean ambient temperature during the warm controls (Bugden 1996). By adjusting the latency to begin calling when chilled, chicks could control the ratio of chilling to rewarming time, and in this way regulate their own body temperature.

I terminated tests after 30 min or when cloacal temperature fell by more than 2°C below brooding cloacal temperature. This protocol ensured that chicks had sufficient time to rest and return to brooding body temperature before further testing. I tested individual chicks three times daily (once for each temperature regime, chosen in random order) at each age. Between tests, I returned chicks to their cages to rest, rewarm and be fed. I weighed chicks immediately before and after each test, and recorded the mean. I averaged masses for all chicks tested at each age to obtain a mean daily mass.

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 I was interested in measures of $\dot{V}O_2$ during calling and intervening silent periods. Under these conditions, short-term (approaching 'instantaneous') measures are more appropriate (Bartholomew et al. 1981). When actual oxygen uptake changes, for example due to the onset of calling or silence, O_2 levels in the excurrent air stream change exponentially, only gradually approaching a new equilibrium. I 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), as incorporated into the DATACAN V software analysis package.

I calculated mass-specific $\dot{V}O_2$, corrected to STP, using equation 4a of Withers (1977) and expressed as $ml \cdot g^{-1} \cdot hr^{-1}$. Validation of the accuracy of these calculations for this system was obtained by calculating $\dot{V}O_2$ over successive 5 s 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 $\leq 0.011 \pm 0.384 ml \cdot g^{-1} \cdot hr^{-1}$) during washout measurement (no live animal in the chamber).

I took mean $\dot{V}O_2$, cloacal temperature and ambient temperature per trial as the mean of all 5 s recordings during each trial. I compared differences in mean

$\dot{V}O_2$ measured for cold, warm and vocal thermoregulation trials to detect any metabolic response to the specified treatments.

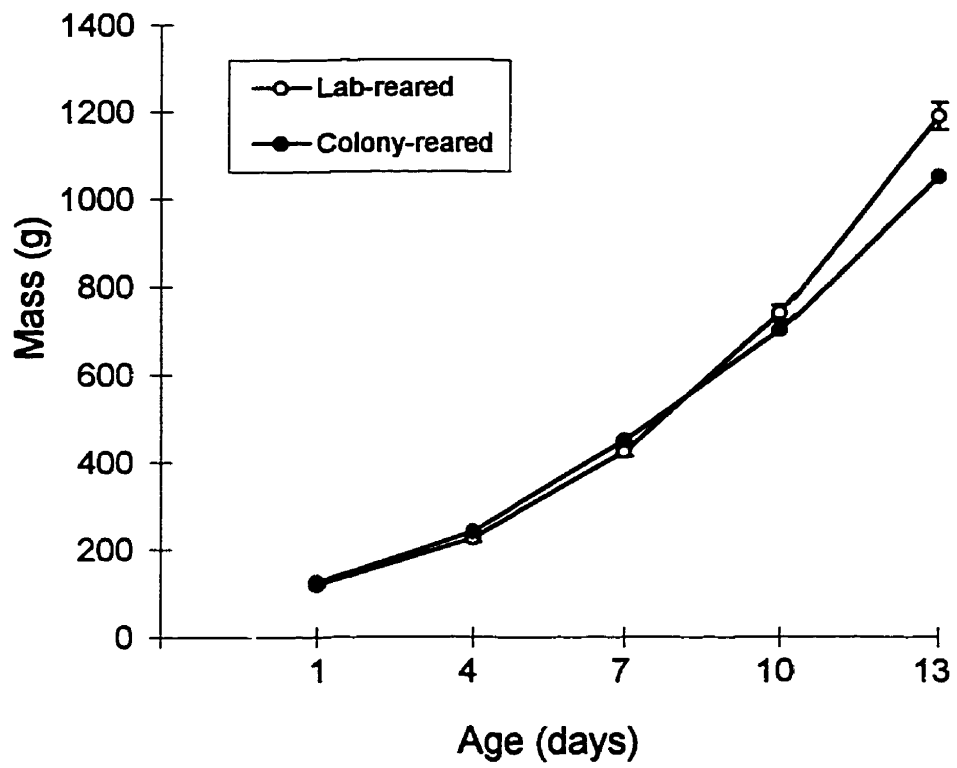
I performed statistical analyses using S.P.S.S. (version 7.5). ANOVAs incorporated a repeated measures design (Winer 1971) for age and ambient condition (a significance level of $\alpha = 0.05$ was used for all ANOVAs). Post-hoc paired *t*-tests (one-tailed) were used to make comparisons within and between ages. A significance level of $\alpha = 0.01$ was used for all paired *t*-tests (Bonferroni correction).

Results

Patterns of Growth

Chick mass increased significantly with age ($F_{4,16} = 928.87$, $P=0.0000$; Fig. 3-1), by about 9.5 fold from days 1 to 13. The largest absolute increase in mass occurred from days 10 to 13 (increase of 448.7 g). Chick masses observed in this study were not significantly different from those reported by Evans (1997) for wild pelican chicks reared without sibling competition on days 1 and 4 (one-sample *t*-tests, all $t \leq 1.499$, $df \geq 8$, $P \geq 0.086$), were slightly, but significantly lower (6%) on day 7 ($t_5 = 2.633$, $P = 0.023$), and were slightly but significantly higher than wild pelican chicks on days 10 (5.4%) and 13 (13%) (one-sample *t*-tests, all $t \geq 2.198$, $df \geq 4$, $P \leq 0.0465$).

Figure 3-1. Mean \pm SE daily mass of lab-reared pelican chicks at each age tested ($n = 5-9$ individuals per age) and mass of wild pelican chicks reported by Evans (1997).



Effects of Ambient Temperature on Body Temperature

At all ages, mean ambient temperatures during cold trials were significantly lower than during both warm and vocal thermoregulation trials (all $t \geq 8.571$, $df \geq 3$, $P \leq 0.0005$; Fig. 3-2). Mean ambient temperatures during vocal thermoregulation trials were significantly lower than during warm trials only at day 1 ($t_8 = 5.351$, $P = 0.0005$); at all other ages, ambient temperatures during thermoregulation and warm trials were not significantly different (all $t \leq 2.279$, $df \geq 4$, $P \geq 0.0425$).

There was a significant main effect of ambient temperature on mean cloacal temperature ($F_{2,6} = 56.5675$, $P = 0.0000$; Fig. 3-3). Mean cloacal temperatures during cold trials were lower than during warm trials at all ages, but this was significantly different only from days 1 to 10 (all $t \geq 4.317$, $df \geq 3$, $P \leq 0.004$). Cloacal temperatures during cold trials were lower than during vocal thermoregulation trials at all ages, although this was significant only on days 4, 7 and 13 (all $t \geq 3.785$, $df \geq 4$, $P \leq 0.0095$). Cloacal temperatures during vocal thermoregulation trials were slightly lower but not significantly different than during warm trials at all ages (all $t \leq 2.452$, $df \geq 4$, $P \geq 0.02$).

Mean cloacal temperatures during cold trials were significantly lower than mean brooding cloacal temperatures at all ages (one-sample t -tests, all $t \geq 6.127$, $df \geq 3$, $P \leq 0.002$). Mean cloacal temperatures during both warm trials and vocal thermoregulation trials were not significantly different from mean brooding cloacal temperatures at all ages (all $t \leq 2.121$, $df \geq 4$, $P \geq 0.065$), with the exception of

Figure 3-2. Mean + SE ambient temperatures during cold, vocal thermoregulation and warm trials ($n = 5-9$ individuals per age).

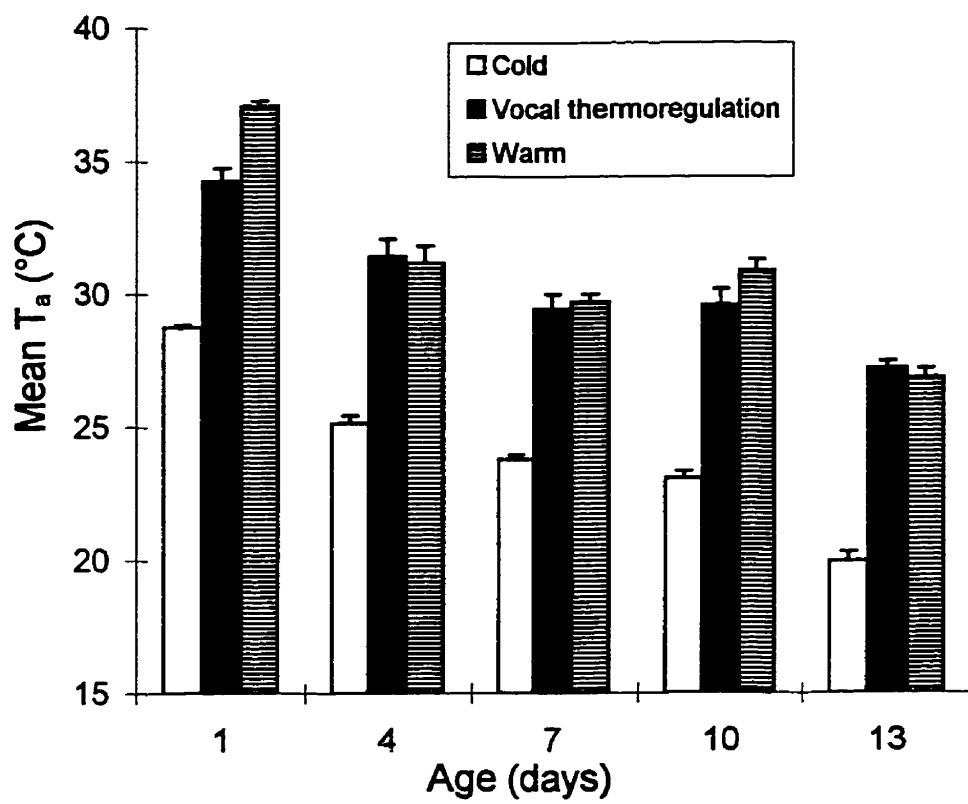
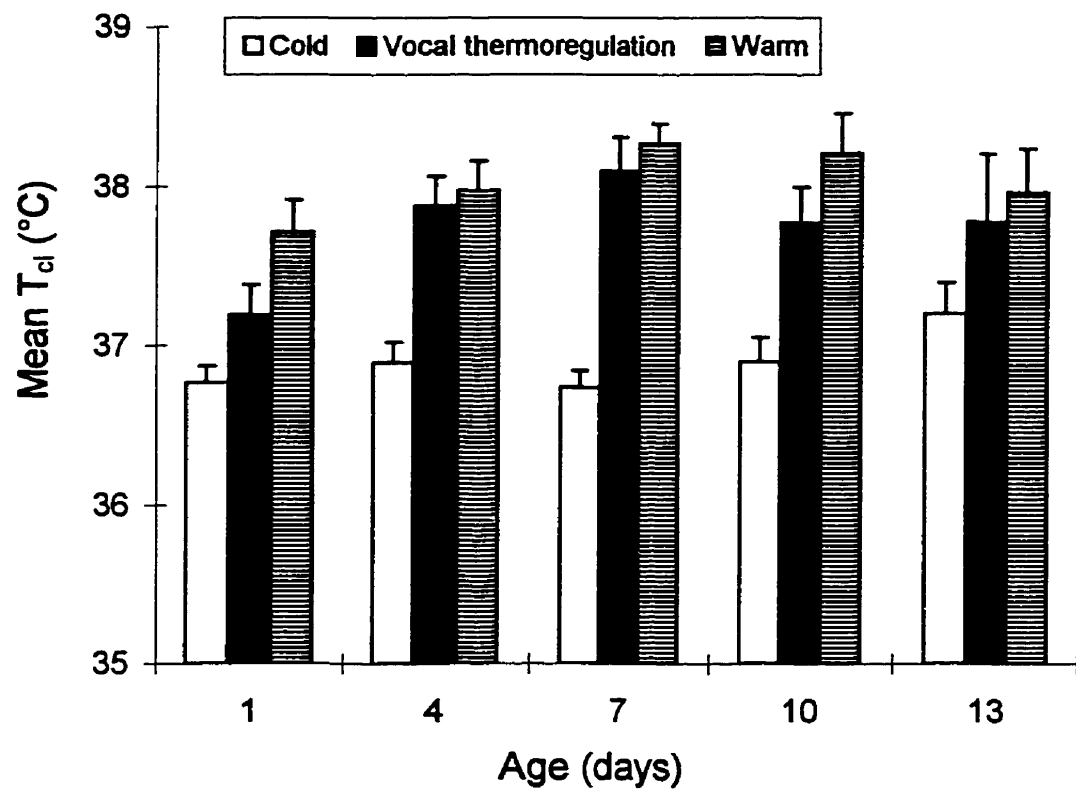


Figure 3-3. Mean + SE cloacal temperature of pelicans chicks during cold, vocal thermoregulation and warm trials ($n = 5-9$ individuals per age).

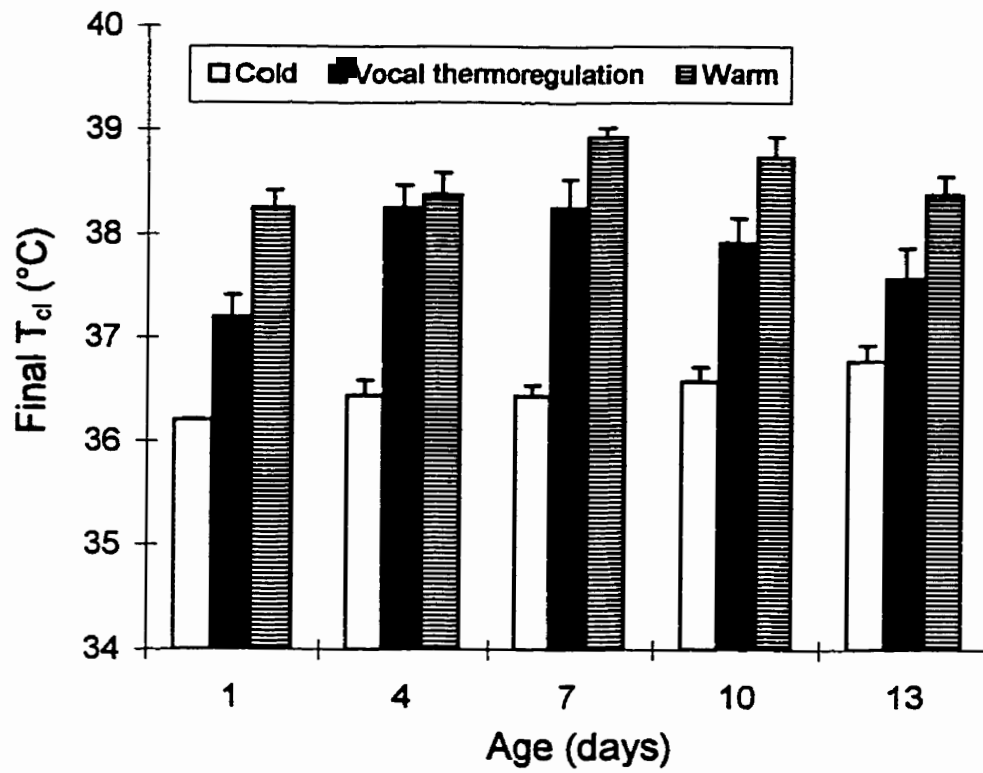


mean cloacal temperatures during both trials on day 1 (all $t \geq 2.625$, $df \geq 4$, $P \leq 0.015$).

For cold trials which were terminated before 30 min, I calculated the final cloacal temperatures as if trials had been allowed to continue for the entire 30 min period given a linear rate of body cooling (Fig. 3-4); for cold trials which lasted 30 min the actual final cloacal temperatures were used. These values were compared to the actual to the actual final cloacal temperatures of the warm and vocal thermoregulation trials. There was a significant main effect of ambient temperature on final cloacal temperature ($F_{2,6} = 65.732$, $P = 0.0000$; Fig. 3-4). Final cloacal temperatures during cold trials were significantly lower than during warm trials at all ages (all $t \geq 7.903$, $df \geq 3$, $P \leq 0.0015$). Final cloacal temperatures during cold trials were lower than during vocal thermoregulation trials at all ages, although this was significant only on days 1, 4 and 7 (all $t \geq 3.724$, $df \geq 5$, $P \leq 0.0005$). Final cloacal temperatures during vocal thermoregulation trials were slightly lower than during warm trials at all ages, although this was significant only on days 1 and 13 (all $t \geq 4.665$, $df \geq 4$, $P \leq 0.005$).

Final cloacal temperatures during cold trials were significantly lower than mean brooding cloacal temperatures at all ages (one-sample t -tests, all $t \geq 10.443$, $df \geq 3$, $P \leq 0.0005$). Final cloacal temperatures during warm trials were not significantly different from mean brooding cloacal temperatures on days 1, 4, 10 and 13 (all $t \leq 2.37$, $df \geq 4$, $P \geq 0.077$), but were significantly greater than mean

Figure 3-4. Final cloacal temperature (mean + SE) of pelicans chicks at the end of cold, vocal thermoregulation and warm trials ($n = 5-9$ individuals per age).



brooding cloacal temperatures on day 7 ($t_5 = 5.983$, $P = 0.001$). Final cloacal temperatures during vocal thermoregulation trials were significantly lower than mean brooding cloacal temperatures only on day 1 ($t_8 = 4.929$, $P = 0.0005$).

Call Rates and Latencies

There was a significant main effect of ambient temperature on call rate ($F_{2,6} = 57.879$, $P = 0.0000$; Fig. 3-5). Call rates during cold trials were consistently greater than during both warm and vocal thermoregulation trials at all ages, although this was significant only from days 4 to 13 (all $t \geq 3.922$, $df \geq 4$, $P \leq 0.0085$). With the exception of day 13, call rates during vocal thermoregulation trials were slightly greater than during warm trials from days 1 to 10, although this was significant only on day 4 ($t_7 = 4.072$, $P = 0.0025$). Although call rates during warm trials were slightly greater than during vocal thermoregulation trials at day 13, this difference was not significant ($t_4 = 0.311$, $P = 0.3855$).

During vocal thermoregulation trials, latency to start calling was measured as the time (s) it took for chicks to vocally respond to the default cold stimulus (Fig. 3-6). There was a significant main effect of age on latency to begin calling ($F_{4,16} = 1.881$, $P = 0.0163$). Latency to begin calling declined dramatically from days 1 to 4, then remained relatively consistent to day 13. Latency to stop calling was measured as the time (s) it took for chicks to cease calling once rewarming had been initiated (Fig. 3-6). There was no significant main effect of age on

Figure 3-5. Call rates (mean + SE) given by pelican chicks during cold, vocal thermoregulation and warm trials ($n = 5-9$ individuals per age).

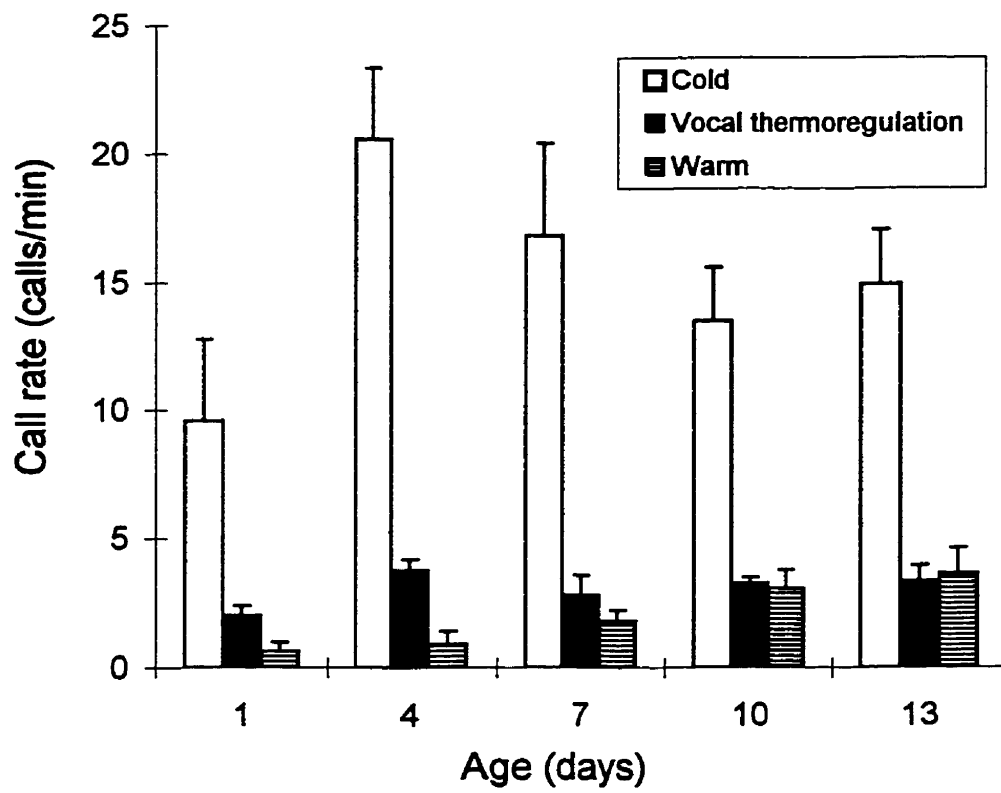
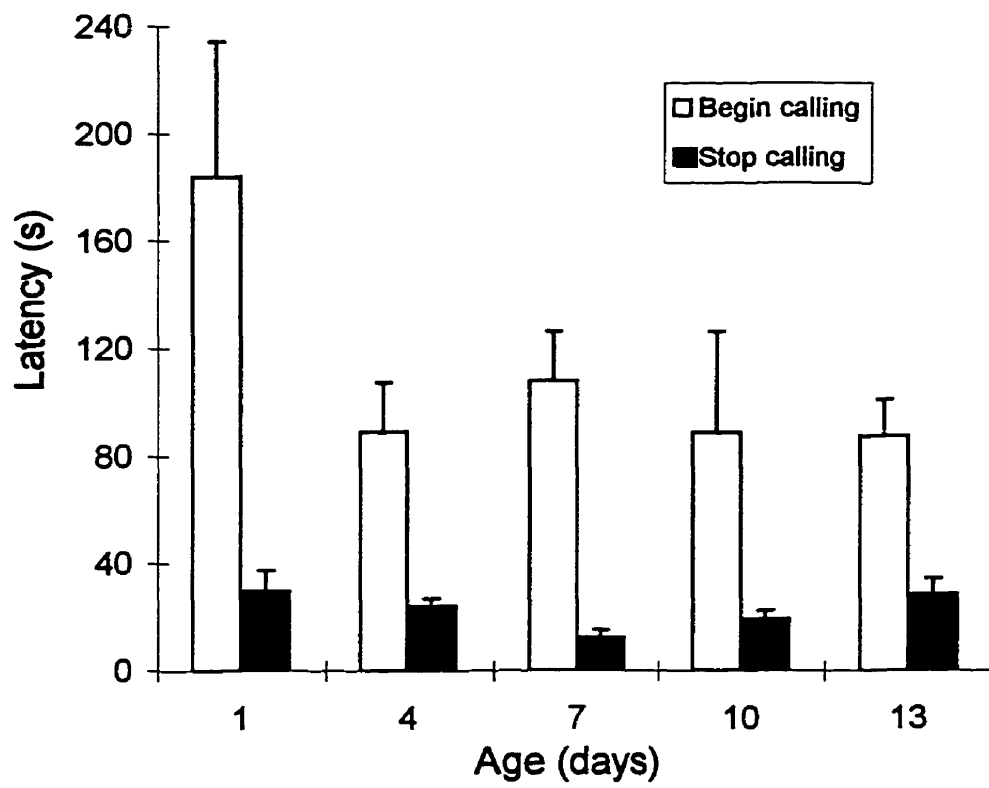


Figure 3-6. Mean + SE latencies of pelican chicks to start calling in response to a cold stimulus and to stop calling in response to the onset of rewarming during vocal thermoregulation trials ($n = 5-9$ individuals per age).



latency to stop calling ($F_{4,16} = 2.595$, $P = 0.076$), although the power of this test was low (power = 0.591). Latency to stop calling remained relatively consistent with age.

Metabolic Costs Associated with Temperature and Vocal Thermoregulation

There was no significant main effect of treatment on $\dot{V}O_2$ ($F_{2,6} = 2.085$, $P = 0.205$; Fig. 3-7), although the power of this test was low (power = 0.278). With the exception of day 1, $\dot{V}O_2$ was highest during cold trials and lowest during warm trials. $\dot{V}O_2$ during cold trials was significantly greater than during warm trials only on day 4 ($t_7 = 6.617$, $P = 0.0000$), and was significantly greater than during vocal thermoregulation trials only on day 10 ($t_4 = 5.497$, $P = 0.0025$). $\dot{V}O_2$ during warm trials was not significantly different than during vocal thermoregulation trials at all ages (all $t \leq 2.466$, $df \geq 4$, $P \geq 0.0215$).

I calculated the absolute metabolic costs associated with the presence of vocal thermoregulation at each age (mean $\dot{V}O_2$ during thermoregulation trials minus the mean $\dot{V}O_2$ during corresponding warm trials). I also calculated the absolute metabolic costs associated with the absence of vocal thermoregulation at each age (mean $\dot{V}O_2$ during cold trials minus the mean $\dot{V}O_2$ during corresponding thermoregulation trials). There was no significant main effect of age on absolute costs ($F_{4,12} = 1.36$, $P = 0.305$; Fig. 3-8), although the power of this test was low

Figure 3-7. Mean + SE $\dot{V}O_2$ during cold, vocal thermoregulation and warm trials
($n = 5-9$ individuals per age).

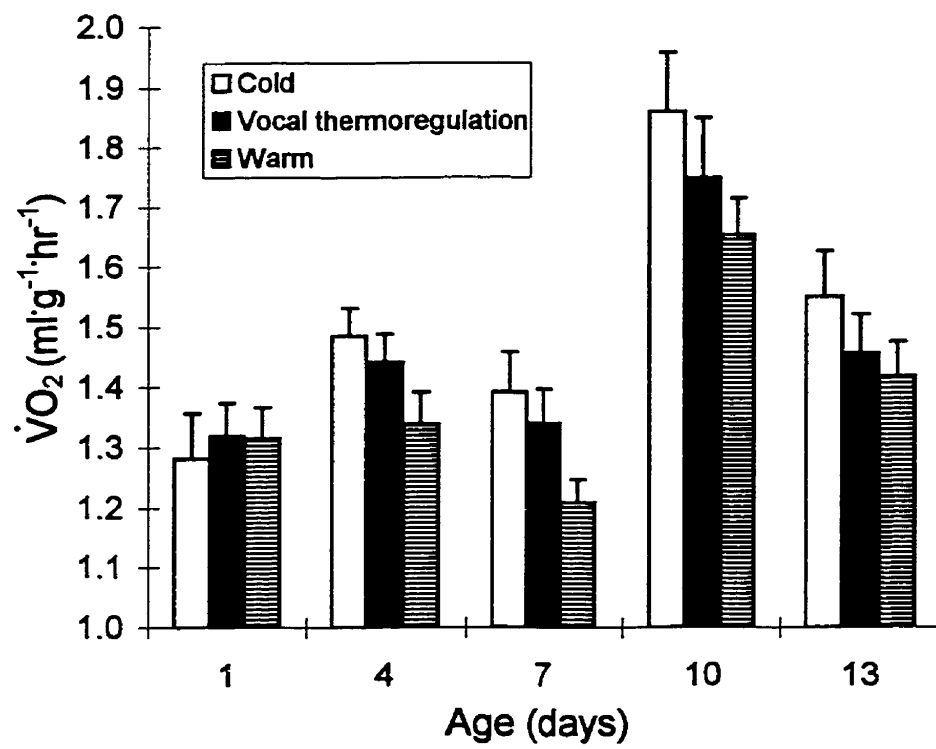
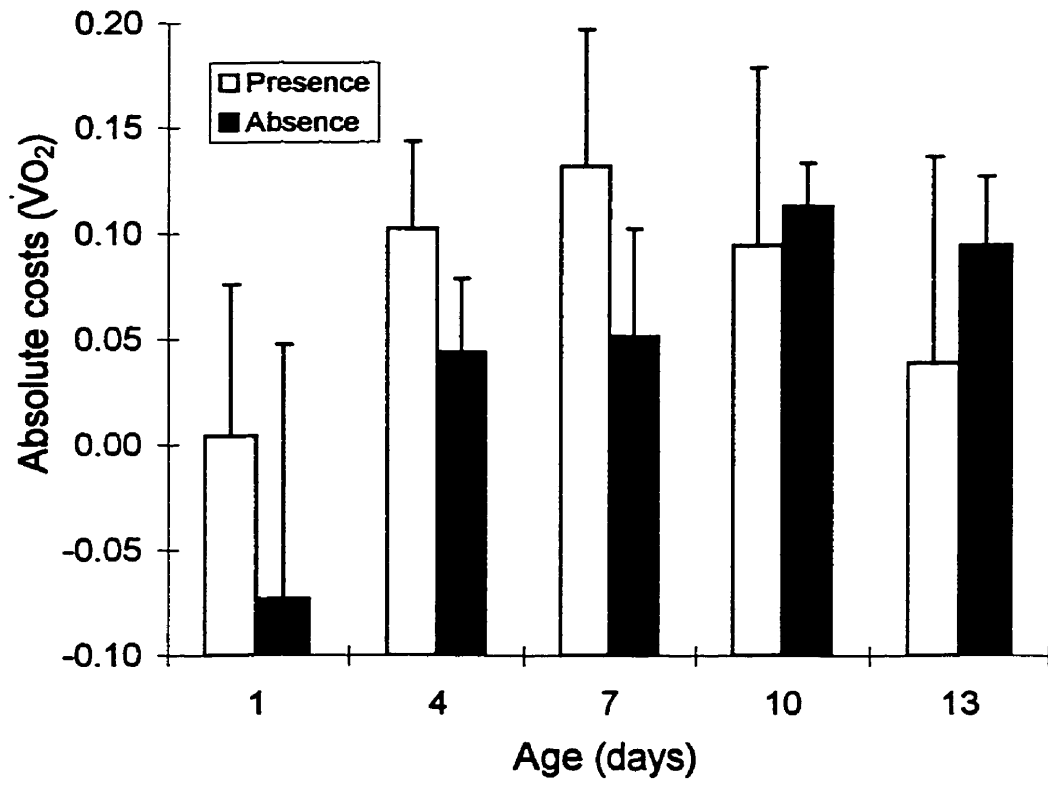


Figure 3-8. Absolute metabolic costs (mean + SE) associated with the presence and absence of vocal thermoregulation ($n = 5-9$ individuals per age).



(power = 0.302). There was also no significant main effect of the presence or absence of vocal thermoregulation on absolute costs ($F_{1,3} = 0.079$, $P = 0.797$; Fig. 3-8), although again, the power of this test was low (power = 0.055). Absolute costs associated with the presence of vocal thermoregulation increased incrementally from days 1 to 7, then declined incrementally to day 13. Absolute costs associated with the absence of vocal thermoregulation increased incrementally from days 1 to 10, then declined to day 13. Absolute costs associated with the presence of vocal thermoregulation were greater than those associated with the absence of vocal thermoregulation from days 1 to 7, with the reverse trend seen on days 10 and 13 (Fig. 3-8), although none of these differences were significant.

Discussion

Effects of Ambient Temperature on Body Temperature

Consistent with the results of a previous study (Evans 1994), my results suggest that pelican chicks at all ages tested were capable, at least to some degree, of effectively vocally regulating their body temperature close to optimal brooding body temperature, provided that a parent or surrogate responds appropriately to vocal heat solicitation calls by providing brooding warmth (Figs 3-3, 3-4). However, in the absence of vocal thermoregulation (cold trials), pelican

chicks were unable to maintain body temperature near brooding body temperature solely by facultative thermogenesis. The low final cloacal temperatures observed in the cold trials illustrates how quickly body temperature can decrease (about a 1.5°C decline in 0.5 hr even at day 13) if pelican chicks are left unattended at the nest. If chicks are left unattended for long periods of time, they may become comatose and die if not rewarmed (Evans and Knopf 1993).

Vocal Heat Solicitation: Call Rates and Latencies

Call rates during cold trials were consistently greater than during both warm and vocal thermoregulation trials at all ages (Fig. 3-5). The dramatic increase in call rates during cold trials from days 1 to 4, in concert with the decline in latency to begin calling during vocal thermoregulation trials from days 1 to 4, indicates an overall improvement in the ability of pelican chicks to respond behaviourally to a cold challenge within this age span (Figs 3-5, 3-6). Call rates during cold trials and call latencies (to both start and to stop calling) during vocal thermoregulation trials remained relatively constant from days 4 to 13. This is probably due to the fact that the gradient of ambient cooling during cold trials and the default cold temperature in the vocal thermoregulation trials remained consistent with the age-specific lower critical temperature, thus representing a similar degree of cold challenge. Call rates during vocal thermoregulation trials were slightly greater than during warm trials from days 1 to 10, with the reverse trend seen at day 13. These

results suggest that chicks in the vocal thermoregulation group are not vocalizing much more than necessary in order to maintain a warm stable body temperature. The fact that call rates during warm trials increased slightly with age is probably due in part to pelican chicks becoming increasingly intolerant of being confined in the metabolic chamber as their physical mobility improves, particularly after day 10 (pers. observ.).

Metabolic Costs Associated with Vocal Thermoregulation

My results are consistent with other studies that have reported moderate costs associated with avian vocalizations (Horn et al. 1995; Leech and Leonard 1996; McCarty 1996; Bachman and Chappell 1998). I found only modest relative cost increments of vocal heat solicitation calls given by young pelicans tested at the same ages in response to anticipated thermal need (Chapter 2; Figs 2-6, 2-7), where body temperature remained close to brooding body temperature, and where costs during calling ranged from 1.05 to 1.26 times the corresponding periods of silence. My results are also consistent with those reported for ectothermic pelican embryos at the pipped-egg stage (Abraham and Evans 1999), which incur modest metabolic costs associated with calling in response to anticipated thermal need, and greater costs only in the presence of real thermal need at low body temperatures. It is therefore possible that significant metabolic costs associated with vocal heat solicitation calls given by young pelican chicks may be directly

associated with the presence of real thermal need, as measured by a suboptimal body temperature (Abraham and Evans 1999). Because vocal heat solicitation calls given by pelican chicks appear to be relatively inexpensive to produce provided that body temperature remains high, it follows that the overall costs associated with vocal thermoregulation and the maintenance of a warm body temperature should also be low, as seen in the present study.

The absolute metabolic costs associated with the presence of vocal thermoregulation were greater than the costs associated with the absence of vocal thermoregulation from days 1 to 7, with a reversal on days 10 and 13. It may be noteworthy to discuss additional costs (other than energetic) associated with the absence of vocal thermoregulation. Young pelicans reared at suboptimal ambient temperatures in the lab (simulating conditions if young failed to solicit brooding warmth from parents or if parents failed to respond to offspring vocalizations) beg less for food and have lower masses than those reared under thermoneutral conditions (Safiniuk and Evans unpubl. data). Young pelicans also experience reduced locomotor activity when chilled for extended periods of time (Evans 1984), which may inhibit acquisition and ingestion of food, while even a moderate drop in temperature may inhibit begging for food (Evans 1994). Choi and Bakken (1990) reported that warm body temperatures may also facilitate eating and begging for food in young red-winged blackbirds (*Agelaius phoeniceus*), which would further increase a chick's chances of getting fed. Particularly during the period when

endothermy is still developing, maintaining a warm body temperature should facilitate any future energy gains, which may compensate for the modest costs of vocal thermoregulation. Thus, any food that a chick may receive would be more efficiently assimilated, resulting in a net energy gain and improved physical condition.

Honest signalling

During the vocal thermoregulation trials, the tendency for cold-induced calls to begin soon after the onset of the cold challenge and to cease when corrective rewarming is initiated suggests that these calls normally provide accurate (honest) information, indicating to an attending parent that the offspring is experiencing an anticipated need for warmth (Evans 1990). Particularly during the period before endothermy is fully functional, this anticipated need, if uncorrected, will eventually translate into a real need for warmth, as measured by a suboptimal body temperature. In fact, call rates during vocal thermoregulation trials were only slightly different from those during warm trials at all ages, suggesting that pelican chicks only call as frequently as is necessary to maintain body temperature (Fig. 3-5).

Honest signalling models (Godfray 1991, 1995) predict that the level of offspring solicitation will be a true reflection of its needs as long as solicitation is costly and that any benefits of resources received increases with the need of the

offspring. Although the magnitude of the costs observed in my study may be considered low, they do occur in the direction predicted. The highest metabolic costs, call rates and body temperatures occurred during the cold trials and the lowest metabolic costs, call rates and body temperatures occurred during the warm trials. Therefore, the level of vocal heat solicitation calls and the associated costs increased in a graded fashion relative to potential thermal need. If parents and young are in agreement about the amount of heat that the young require (Evans et al. 1995), relatively low-cost signals may still be honest (Kilner and Johnstone 1997). Under these conditions, parents and offspring would be expected to cooperate via reliable, efficient signals, without exaggerated costs (Johnstone 1997). By maintaining low levels of background calling under thermoneutral conditions, then responding to ambient temperature variation before body temperature is significantly affected and stopping the vocal response when thermoneutral temperatures were reinstated, chicks attain high levels of thermal stability with moderate energetic costs.

General Discussion

Development of Endothermy

My results indicate a development of endothermy in lab-reared pelican chicks. 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). By day 16, chicks are capable of effectively coping with prolonged periods of cooling due to parental absence. The age of endothermy in young pelicans corresponds to the age at which parents begin to terminate continuous brooding behaviour (Evans 1984b). 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 endothermic temperature control is likely energetically efficient. Younger, more ectothermic pelicans presumably are able to save the metabolic costs associated with thermoregulation, and thereby are able to allocate a greater portion of energy resources to growth of body tissue (Weathers 1996).

The results reported in Chapter 1 revealed the limits of the thermoneutral zone (Table 1-1). If exposed to temperatures below the lower critical temperatures, young pelicans will attempt to thermoregulate vocally, but will be successful at

maintaining a warm body temperature only if a parent or surrogate responds appropriately by increased brooding. If a brooding response to vocal heat solicitation is absent, even short-term ambient cooling (anticipated thermal need) will eventually translate into real need for heat, as reflected by a suboptimal body temperature. If young pelicans are left unattended for even short periods of time, they may become comatose and die if not rewarmed (Evans and Knopf 1993). When chilled for extended periods of time, young pelicans also experience reduced locomotor activity (Evans 1984a), which may inhibit acquisition and ingestion of food, while even a moderate drop in temperature may inhibit begging for food (Evans 1994).

Costs and Benefits associated with Vocal Heat Solicitation: Implications for Honest Signalling and Parent Offspring Conflict Theories

Although Eberhardt (1994) reported that singing in Wrens is associated with significant metabolic costs of over two to five times standard metabolism, the methods and interpretations of that study have been strongly criticized (Gaunt et al. 1996). These criticisms do not apply to my study, as there was sufficient mixing of chamber air, I correctly applied instantaneous measures of oxygen consumption, and ambient temperature measurements were recorded every 5 s for the duration of each trial. The relative metabolic costs associated with vocal heat solicitation obtained for young pelicans are within the range of those reported in

other studies on avian vocal energetics, although their interpretations have been variable. Leech and Leonard (1996) reported a 28% increase in metabolic costs of begging in tree swallows, and suggested that such costs could have a significant impact on energy expenditure of individual nestlings. Horn (et al. 1995) found a 15% increase in metabolic costs of rooster calling (above resting metabolic rate), and deemed these to be energetically inexpensive. McCarty (1996) found that relative increases in the metabolic costs of begging by young songbirds varied from negligible up to 27%, and also concluded that such begging was not energetically costly. Abraham and Evans (1999) found that vocal heat solicitation calls given by pelican embryos were not an overwhelmingly costly signal to produce, but concluded that the energy increments of about 1.2 - 2.0 times a silent baseline could well have biologically significant fitness consequences, given the energy-limited condition present within the avian egg prior to hatching.

Indeed, the relative costs associated with vocal heat solicitation in response to anticipated thermal need observed in the study reported in Chapter 2 appear to be relatively low, ranging from 1.01 to 1.26 times the baseline periods. However, Abraham and Evans (1999) suggested that significant metabolic costs associated with vocal heat solicitation calls given by pipped pelican embryos appear in large part to be directly associated with the presence of real thermal need, as reflected by a suboptimal body temperature. This explanation may in part justify the relatively low costs associated with vocal heat solicitation calls given by

pelican chicks in response to ambient cooling, but where body temperature during testing remained close to brooding body temperature. It is possible that greater costs associated with vocal heat solicitation would be observed if pelican chicks were experiencing real thermal need at low body temperatures. In addition, theories which predict that communication requires substantial costs to enforce honesty deal with signals of quality (Zahavi 1975; Grafen 1990). Signals of quality indicate the extent to which the signaller can provide resources and, therefore, the costs which signallers can bear. Because these signallers are indicating the ability to pay costs, it is the costs which determine signal quality. High quality individuals pay lower costs and signal at higher levels than low quality individuals. Honest signals of condition, in contrast, indicate the needs of the signaller; individuals of low condition have higher needs for resources (i.e. heat, food), signal at greater levels and pay greater costs than individuals of high condition. Given that needs are directly proportional to benefits (Godfray 1991, 1995), individuals of low condition would receive large benefits from the resource in question. In the case of offspring solicitation of resources, needy young are indicating the benefits associated with receiving further parental care (i.e. brooding warmth). Costs may be relatively small within such a benefit-moderated system of communication. Provided that costs increase with signal level, honesty and cooperation between parents and offspring can be maintained because it is the benefits which signallers are indicating.

Although several studies have shown that parental incubation/brooding behaviour is metabolically costly (Mertens 1980; Vleck 1981; Walsberg 1983; Haftorn and Reinertsen 1985), others have reported that incubation/brooding costs are negligible (Walsberg and King 1978a, b). No measurements are available to date on the cost of brooding in white pelicans, which typically lay two eggs (Evans and Knopf 1993). However, young pelicans are commonly left exposed for brief periods as parents move about the nest. Chicks then call and parents alter their brooding behaviour (Evans and Knopf 1993); these movement patterns and the resultant losses of body heat to the chicks may represent an energetic cost to the parents. If so, the cost of brooding by parents and the cost of an offspring's solicitation for brooding may generate conditions for conflict between parents and offspring. An honest signalling resolution of this conflict can be evolutionarily stable (Godfray 1991).

Whether or not the parental brooding/incubation behaviour of pelicans and the vocal signals produced by chilled pelican chicks are to be considered costly enough to constitute parent-offspring conflict, as assumed by honest signalling models (Godfray 1991, 1995) remains somewhat arbitrary. Honest signalling models simply predict that a conflict of interest between parents and offspring will favour more costly signals than would otherwise be the case. In the absence of conflict, the signal costs observed in this study may be considered low, but likely still reflect offspring need. Daniels (1997) reported that the frequencies of vocal heat solicitation bouts and call rates given by young colony-reared pelicans

increased during the first two weeks after hatching while parental 'responsiveness' showed a corresponding decline. Daniels concluded that these patterns were consistent with Trivers' (1974) predictions of parent offspring conflict. However, according to Mock and Forbes (1992), behavioural 'squabbles' (intensified offspring signalling) between parents and offspring may not result from genotypic conflict. Greater overall solicitation will be found in circumstances where offspring needs are particularly variable (Godfray 1991), but may still be honest. This may occur towards the end of the period of parental care (brooding) when individuals are beginning to fend for themselves and parents require more information. Therefore, an increase in the level of solicitation at this time may not be an example of 'weaning conflict', but a mutually beneficial communication system.

Most empirical studies to date have focused on the costs, context and potential exaggerated signals of offspring solicitation for food and parental provisioning. There is little evidence to support the prediction that conflict exists between parents and young, as well as conflict or competition between siblings, over parental brooding warmth as a resource (Evans 1990; Evans et al. 1995). The currency of POC is parental investment (PI), defined as any action done by the parent for the offspring that increases the offspring's chance for survival while decreasing the parent's ability to invest in future offspring (Trivers 1974). If a parent must brood its young until they are capable of maintaining a warm body temperature by physiological means (about 16 days for pelicans), it is unlikely that

any additional episodic parental brooding events (solicited by offspring) within this period of time provided to current offspring would result in decreased PI in future offspring. Lazarus and Inglis (1986) defined 'unshared' parental investment as any effort on behalf of the parent in which the total benefit of investment can simultaneously benefit more than one offspring. Unlike vocal solicitation of food, if one offspring vocally solicits brooding warmth from a parent, the parent responds by brooding both offspring by default (unshared PI, both offspring benefit), as both chicks are in close proximity in the nest cup. Thus, it is possible that both chicks receive the total benefit (high body temperature) of parental brooding. Again, unlike parental provisioning of food, pelican chicks are not likely to solicit more brooding warmth than the parent is selected to provide (as assumed by honest signalling and POC models), as there is a threshold level of parental provisioning of warmth; essentially ectothermic chicks cannot increase their body temperature beyond that of the brooding parent. Evans et al. (1995) reported that the parent's and offspring's optimal amount of PI (in terms of brooding warmth) were identical for pipped embryos of herring gulls. Pipped pelican embryos also vocally regulate their body temperature close to the parent's preferred incubation temperature (Evans 1990), again illustrating the lack of conflict. Once young pelicans have reached an optimal developmental temperature, there would be no increase in temperature-related benefit should the parents endeavor to incubate more closely.

The call rates and latencies reported in Chapter 3 (Figs 3-5, 3-6) support the suggestion that pelican chicks are honestly signalling their needs and condition when presented with ambient chilling. Vocally thermoregulating chicks call just enough to initiate rewarming, then quickly cease calling once rewarming has begun. In the studies described in Chapters 2 and 3, call rates were generally highest at the cold ambient test temperatures and lowest at the warm ambient test temperatures. Therefore, the vocal response of young pelicans to ambient cooling occurs in a graded fashion resulting in greater levels of signalling as thermal needs intensify. The fact that young pelicans vocalize in response to acute chilling even when body temperature was still high (see also Evans 1994) poses a potential problem for relating calling to need, in that actual need (low body temperature) was not present when calling began for chicks tested at cold ambient temperatures. However, because young pelicans are ectothermic (particularly during the first week after hatching), such uncorrected chilling would inevitably lead to a reduced body temperature and a real need for heat, as found in the studies reported in Chapters 2 and 3. This vocal response to acute chilling while body temperature is still high thus appears to be an example of a functionally important anticipatory response to cooling, providing accurate 'feed forward' information to a parent (McFarland 1985; Evans 1994).

My results also are generally supportive of the honest signalling prediction that fitness costs associated with vocal signalling should increase in a graded

fashion with anticipated thermal need, particularly during the first week after hatching when young pelicans have a limited thermogenic capacity. The metabolic rates associated with vocal heat solicitation were generally highest for chicks tested at cold ambient temperatures and lowest for chicks tested at warm ambient temperatures. These results suggest that young pelicans are willing to pay additional metabolic costs in the presence of anticipated thermal need in order to honestly communicate their needs and condition to an attending parent. An accurate (honest) but energetically inexpensive anticipatory vocal response to cooling could be of significant adaptive value for young pelicans, initiating an early corrective parental brooding response and thereby minimizing costs relative to that required if body temperature were allowed to fall significantly before calling began.

The results reported in this thesis provide some insight into the evolution and advantages of a system of honest offspring communication of needs and condition to parents. To date, the relatively few studies which have attempted to quantify the costs associated with nestling signals of need have reported highly variable results, were often limited in scope and often used measurement techniques with poor temporal resolution. Additional empirical research, and perhaps some standardized methodology, is almost certainly needed in order to gain a broader understanding of signal evolution and parent-offspring relations.

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