# EGG TEMPERATURES AND PARENTAL BEHAVIOR DURING THE TRANSITION FROM INCUBATION TO BROODING IN THE AMERICAN WHITE PELICAN

ROGER M. EVANS

*Department of Zoology, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada*

ABSTRACT.—I monitored incubation behavior and egg temperatures ($T_e$) recorded with agar-filled eggs before and during hatching in American White Pelicans (*Pelecanus erythrorhynchos*) to determine if embryos were subject to more extreme temperature conditions at this critical period than at other stages of development. Before pipping, mean $T_e$ was 35.2°C. It did not change significantly in the presence of a pipped egg or newly hatched young. Diurnal variations in $T_e$ were absent prior to hatching, despite a slight but significant correlation between $T_e$ and ambient temperature ($T_a$). A small drop in $T_e$ (about 2°C) occurred in early morning at nests containing one newly hatched young. $T_e$ minima at these nests correlated significantly with $T_a$. Range and variance in $T_e$ increased with onset of pipping and again when the first young hatched. Increasing variability in $T_e$ was associated with progressive changes in relevant incubation behaviors. Eggs exposed by the removal of foot webs at the onset of pipping were subject to cooling when the parent raised to preen or settled with an egg protruding from the nest. The embryos were exposed to greater temperature extremes during the pipped-egg stage than in other stages. By calling when cold, embryos in pipped eggs may influence parental behavior and hence their own thermal environment. *Received 1 March 1988, accepted 29 July 1988.*

NEST and egg temperatures during incubation have been examined in a wide range of species (Drent 1973, Webb 1987). Recent studies (e.g. Grant 1982, Zerba and Morton 1983, Morton and Pereyra 1985) have provided detailed egg temperature data from continuous or frequent recordings within eggs throughout the 24-h day and, in some studies, over most of the incubation period. In the Pelecaniformes, egg temperatures have been recorded for two tropical species, the Red-tailed Tropicbird (*Phaethon rubricauda*) and Red-footed Booby (*Sula sula*) (Howell and Bartholomew 1962, Whittow and Grant 1985) and data have been obtained for a temperate population of the Double-crested Cormorant (*Phalacrocorax auritus*) (Van Scheik 1985). Apparently nothing has been reported on egg temperatures for the American White Pelican (*Pelecanus erythrorhynchos*).

Most studies of egg temperatures have been confined to the prehatching stages of incubation. Less is known about temperatures subsequent to the onset of pipping (Webb 1987). The period between pipping and hatching is particularly important and is associated with a range of changes in gaseous exchange and metabolic rate (Vleck et al. 1980, Whittow 1980). In the altricial White Pelican, as in many precocial species, this period also marks the onset of embryonic vocalizations, which make it possible for the embryo, still confined within the egg, to influence its own environment through the incubation behavior of the parent (Evans 1988, in press).

A potentially adaptive function of communication between embryo and parent during the transition from incubation to brooding is to ensure the parent maintains suitable incubation temperatures for the pipped egg(s). In the White Pelican, cooling of a pipped egg is a potent stimulus that elicits embryonic calls. In the laboratory I found that pelican embryos could thermoregulate behaviorally (by calling when cold) for periods of up to 5 h of otherwise continuous cold stress (Evans in press). Cooling of the pipped eggs from 38 to 37°C was sufficient to initiate calling, which then increased as cooling continued down to 33°C. Calling normally ceased in under 1 min when warmth was reapplied, regardless of the temperature reached by the cooled egg. This degree of behavioral sensitivity to temperature coupled with the long persistence of the reaction suggests that the pelican embryo is well-equipped after pipping to regulate its thermal environment by communication with the incubating parent.

An obvious objection to the hypothesis that communication from embryos influences the

incubation environment during the pipped egg stage is that, prior to pipping, parents evidently incubate the eggs adequately without recourse to specific vocal communication from the embryos. For the embryonic communication hypothesis to have any biological relevance, it is necessary to show that incubation behavior and thermal or other relevant conditions at the nest normally change as pipping and hatching proceed. In particular, I will show that pipped eggs become exposed to a range of temperatures below those normally experienced prior to pipping, and that these temperatures are at least as low as those known from laboratory work to elicit a strong level of calling. Evidence for the occurrence of low incubation temperatures during the pipped-egg stage is scant. At the onset of pipping in some Charadriiformes, however, changes in incubation behavior which can lead to partial neglect and lower temperatures of the last-hatched egg have been documented (Beer 1962, Drent 1970, Norton 1972). In the Herring Gull (*Larus argentatus*), hatching of the first 2 eggs can result in a decrease in parental incubation attentiveness and a drop in temperature of the remaining pipped egg by as much as 12°C (S. Lee pers. comm.).

In pelicans, as in gannets and boobies (Nelson 1978), parents normally incubate by placing the eggs under the inner webs of their feet. With the onset of pipping of the first egg, there is an abrupt change in incubation mode. Parents elevate the feet and shift both eggs back between the legs where incubation is completed and brooding of the newly hatched young begun (Evans 1988). Details of other relevant changes in incubation or associated behavior of pelicans at this stage, and any effects of the changing mode of incubation on the temperature of unhatched eggs at the nest, are unknown.

## METHODS

Egg temperature ($T_e$) and parental behavior associated with the transition from incubation to brooding were monitored in a colony of >1,000 nests located on islands in East Shoal Lake, Manitoba, Canada (see Evans 1972, O'Malley and Evans 1980, for further description and history of the pelican colony at East Shoal Lake). Hatching dates of nesting subcolonies were estimated (±2 days) from observations of courtship flights over the colony in mid-April (Evans and Cash 1985).

*Egg temperature.*—Egg temperatures throughout the transition period were taken as the temperature of an artificial egg within the nest, which ruled out variation due to embryonic calling or metabolic heat. Artificial eggs were made by strengthening previously collected pelican eggs from which all yolk and albumin contents had been removed. The small end of each egg was removed with the aid of a fine-toothed hacksaw and razor blade (Van Sheik 1985) and the remaining contents removed. Strips of fiberglass fabric ca. 1-cm wide were inserted longitudinally throughout the inside of the egg and cap, then solidified into place by adding sufficient fiberglass resin and hardener to soak the fabric. After the fiberglass had hardened, a small hole was drilled through the egg ca. 2 cm from the center of the large end. A metallic thermistor probe (2 × 50 mm, Grant Instruments, Cambridge, England) was inserted through the hole and positioned along the central longitudinal axis. The egg, with probe in place, and the egg cap were then filled with agar (1.5%; Van Scheik 1985). When the agar had cooled, the cap was placed back on the egg and the joint sealed with epoxy resin.

Thermal characteristics of artificial eggs were examined in the laboratory by shifting them for periods of 3 h between an incubator set at 48°C and a refrigerator set at 8°C. $T_e$ was recorded every 5 min during both heating and cooling periods. Response time of the large probe was examined by comparing 2 pairs of pelican eggs in which one member of each pair was fitted with a small (1-mm diameter) glass bead probe. Over the temperature range of relevance to this study (27–38°C), the 50-mm metallic probes always responded more rapidly (11–22%) than the small bead probes. Presumably the rapidly conducting metal tip of the larger probe was closer to the egg surface than was the centrally positioned bead. Differences between probes diminished as temperatures stabilized.

The joint effects of fiberglass and agar treatments were assessed by comparing 6 pairs of artificial and fresh chicken eggs equipped with centrally positioned bead probes. In 8 of the 12 tests (heating and cooling combined) no time difference (±5 min) occurred between fresh and artificial eggs. Overall, artificial eggs responded 3% (heating) and 3.3% (cooling) slower than fresh eggs. Masses of 5 artificial eggs averaged 4.2% greater than 5 fresh eggs selected at random from the same food-store carton. In summary, the artificial eggs were essentially normal in appearance, with mass and thermal characteristics that approximated fresh eggs. The fiberglass coating on the interior of the egg added appreciably to its strength and virtually eliminated evaporation of the agar. Agar soon evaporates in an untreated egg, cooling the egg and leaving it partially hollow and structurally weakened. The thermal properties are altered. Placement of the thermistor probe ensured that comparable temperature readings from the central axis of the egg would always be obtained no matter which side of

the egg was uppermost in the nest. Incubating parents accepted the eggs without hesitation and appeared to incubate and move them about in the nest normally.

To monitor temperatures at the nest, one egg from a normal two-egg clutch was removed and replaced with an instrumented artificial egg. The wire lead from the egg was led down and outwards, under the lip of the shallow nest cup, and then over the ground surface to a remotely positioned automatic Grant Instruments temperature recorder, calibrated and set to take hourly readings to the nearest 0.5°C.

Egg temperatures were recorded at 3 successive stages: unpipped eggs at the nest; one pipped egg and one unpipped egg in the nest; and one young and one egg, either pipped or unpipped, in the nest. In the first 2 stages, an unpipped egg was removed from the nest and replaced with an artificial egg. During the third stage, the egg, whether pipped or unpipped, was replaced. Contents of the nests during temperature recording were thus the same as in natural nests except that nests in the last stage (1 pipped egg and 1 young) would be represented by an unpipped (artificial) egg and the natural young. The latter nests thus provided information on the effects on $T_e$ of a young in the nest, but not for any additional effects that might arise from the presence of a pipped egg at this stage.

Inspection of $T_e$ records indicated that the eggs reached stable temperature levels 2–3 h after being placed in the nests. Data for the first 3 h were not used in the analyses. For the long-lasting first and third stages, the immediately following 24 hourly readings were used to assess $T_e$. Observations within the colony indicated that an egg required approximately 1 day to hatch after the onset of pipping. It was therefore not possible to obtain a complete sequence of 24 hourly readings at nests with a pipped egg. I arbitrarily selected 12 successive hourly readings to analyze for this stage. Twelve nests for each of the three stages were measured. Where possible, nests representing all 3 stages were recorded simultaneously from the same subcolony. Ambient temperature ($T_a$) was recorded simultaneously with $T_e$.

*Parental behavior.*—About 1 week before hatching began, a blind was positioned adjacent to a large subcolony located well away from the nests being used to monitor egg temperatures. Observations were begun with the first onset of pipping, when most nests in the subcolony contained only unpipped eggs. Focal nests were marked daily with small flags, color coded according to nest contents. I began to observe from the blind only after the birds to be sampled incubated or brooded normally. As in the Great White Pelican (*P. onocrotalus;* Brown and Urban 1969), the American White Pelican exhibits enhanced site tenacity at and around the time of hatching. My activities at that time did not appear to adversely affect the birds under observation.

Behaviors recorded during incubation and brood-ing were selected from those described by Schaller (1964) and Evans (1988a). Preening, listed by Schaller as the most prevalent self-care behavior of incubating pelicans, was subdivided into 2 categories, *preening while sitting* and *preening while raised.* During raised preening, the tarso-metatarsi typically remained flat on the nest as in the normal sitting posture, but the body was raised up at the front at an oblique angle. This posture completely exposed the foot webs when these were over the (unpipped) eggs, and commonly exposed eggs or young lying between the anterior portions of the legs from pipping onwards.

*Shuffles* (Evans 1988) occurred during egg turning sequences (Schaller 1964) and both during and after removal of the foot webs from over newly pipped eggs. The shuffling bird shifted its weight from side to side, slightly lifting one leg, then the other.

Shuffling was commonly associated with *turning* on the nest, and with *billing* the eggs or young. Turning appeared to facilitate the shifting of the eggs or young to their normal postpipping position between the parent's legs (Evans 1988). Billing the eggs or young included instances where the parent merely touched or nibbled nest contents and instances where the parent physically pushed back the eggs and, on occasion, even a new young.

All of the above activity, with the probable exception of preening while sitting, appeared to have potentially important implications for the amount or effectiveness of temperature regulation applied to the eggs or young by the parent. One additional behavior, *manipulation of nest material*, was also recorded. White Pelican nests are typically shallow with a poorly defined nest cup. Nest material applied to the nest cup could presumably have some effect both on its insulation capacity and its capacity as a barrier to prevent dislodged eggs from rolling away from the area of optimal thermoregulation under the sitting parent.

Ten nests at each of the following chronological stages were monitored for 1 h per nest: 2 unpipped eggs, 1 unpipped and 1 pipped egg, 1 unpipped egg and 1 young, 1 pipped egg and 1 young, and 2 young. Because I took nests for the first stage (2 unpipped eggs) from the same subcolonies as the nests used in the later stages, they were late in the incubation period when observed. At all nests observed, the second, or b-egg, was not yet pipped when the a-egg hatched; hence the third stage listed above, consisting of 1 unpipped egg and 1 young, was typical of natural two-egg clutches.

*Statistical analyses.*—For egg temperatures, descriptive statistics were first applied to the data set from each nest. Means, variances and ranges obtained in this way were then subjected to second-order analyses; parametric ANOVAS where second-order variances were homogeneous ($F_{max}$ test) and Kruskal-Wallace ANOVAS where they were not. Significant ANOVAS were followed by pairwise comparisons (Duncan's multiple range test or Mann-Whitney
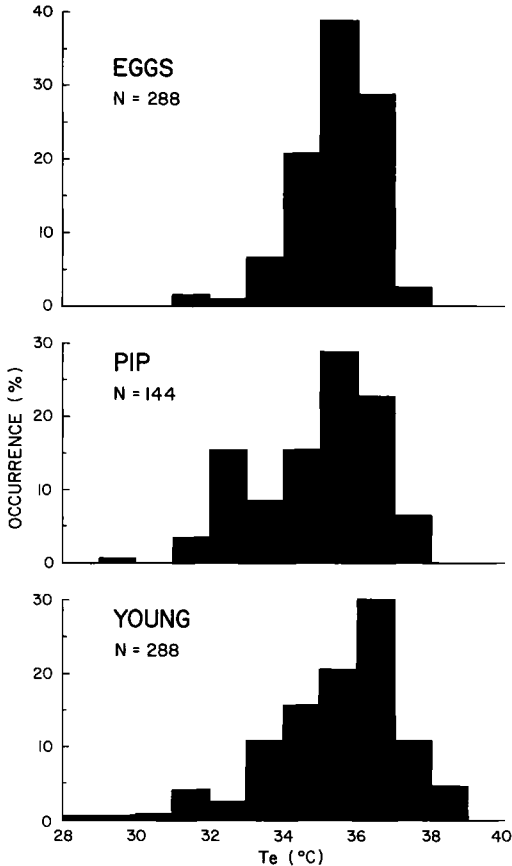
Fig. 1. Percentage occurrence of egg temperatures ($T_e$) at nests containing one artificial egg and one unpipped egg (top), one pipped egg (middle), or one newly hatched young (bottom). N is the number of hourly readings for each stage.

TABLE 1. Average values for mean, variance, and range in egg temperature ($T_e$) at nests containing one artificial egg and one unpipped egg, one pipped egg, or one young.

|  | Mean $T_e$ | Variance in $T_e$ | Range in $T_e$ |
|---|---|---|---|
| Unpipped egg | 35.2°C | 0.38°C | 2.26°C |
| Pipped egg | 34.7°C | 1.33°C | 3.14°C |
| Young | 35.2°C | 1.95°C | 4.72°C |
| Statistic | $F = 1.1$ | $H = 13.2$[a] | $F = 7.3$ |
| df | 2, 33 | 2 | 2, 33 |
| P | NS[b] | <0.01 | <0.01 |

[a] $H$ = Kruskal-Wallace statistic distributed as $\chi^2$.
[b] Not significantly different ($P > 0.05$).

1). The presence of a pipped egg resulted in a shift towards more temperatures as low as 32°C. When a young was present, the range was extended further in both the upper and lower directions. Despite the occurrence of temperatures well below average in nests with 1 young, the modal temperature actually increased to between 36 and 37°C.

In the absence of significant differences in mean $T_e$, I used variances, rather than coefficients of variation, along with range to assess differences in variation between stages. Average variance and range in $T_e$ both exhibited significant increases with incubation stage (Table 1). Pairwise comparisons indicated that average variance increased more than threefold between nests with unpipped eggs and nests with one pipped egg ($U = 31$, $P < 0.02$), and more than fourfold between nests with unpipped eggs and nests with one young ($U = 11.5$, $P < 0.002$). Differences between nests with a pipped egg and young were not significant ($P > 0.05$). Average range in $T_e$ for nests with pipped eggs did not differ significantly from average range in nests with eggs only ($P > 0.05$). Nests with young had significantly greater ranges than nests with unpipped eggs ($P < 0.001$) or nests with a pipped egg ($P < 0.05$).

Mean $T_e$ prior to the onset of pipping showed little variability throughout the 24-h day (Fig. 2, top curve) and provided no evidence that variation was related to time of day (Fig. 2, bottom curve). In contrast, nests with a young present showed a drop of almost 2°C in mean $T_e$ during the early hours of the morning (Fig. 2, middle curve). $T_e$ for nests with a pipped egg were not obtained throughout an entire 24-h day, but a sequence of 11 h (1600–0200) was obtained for 11 of the nests at this stage. For
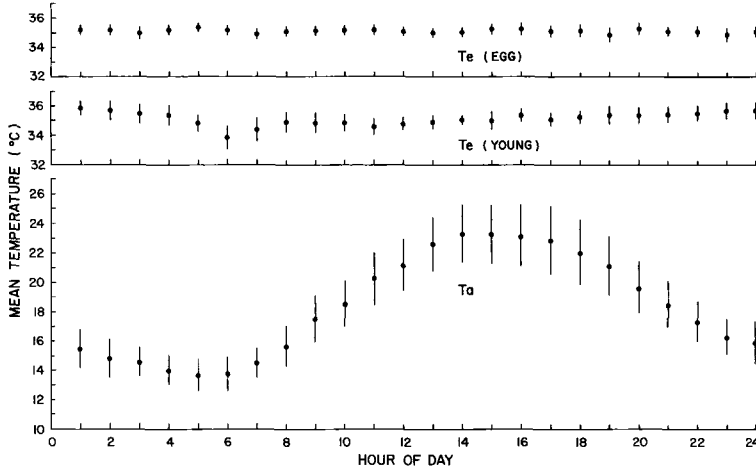
$U$-test). I predicted a priori that any correlations between $T_a$ and $T_e$ would be positive, hence one-tailed tests for positive correlations were employed. Data for incubation was typically not normally distributed and variances were unequal. Only nonparametric Kruskal-Wallace ANOVAS and Mann-Whitney $U$-tests were used for these data.

## RESULTS

*Egg temperature.*—Before pipping, most egg temperatures were clustered around the modal value of 35–36°C, with few readings below 34 or above 37°C (Fig. 1). Mean $T_e$ at nests with unpipped eggs was 35.2°C. Mean $T_e$ was not significantly affected ($P > 0.05$; Table 1) by the progression of the hatch, but temperatures became progressively more variable (Fig. 1; Table

Fig. 2. Hourly means (solid circles) and one SE (vertical lines) for egg temperatures ($T_e$) at nests with one artificial egg and one unpipped egg (top) or one young (middle). Ambient temperature ($T_a$) is given at bottom.

these nests, the mean $T_e$ remained essentially constant. For each of the 3 chronological stages, there was a significant correlation between $T_a$ and $T_e$ (unpipped eggs: $r = 0.19$, $P < 0.01$; pipped egg: $r = 0.17$, $P < 0.01$; young: $r = 0.14$, $P < 0.01$).

Maximum and minimum $T_e$ at individual nests occurred more or less indiscriminately throughout the day (Fig. 3). Maximum egg temperatures were not correlated with $T_a$ ($r = 0.09$ for unpipped eggs, $r = 0.12$ for 1 pipped egg, $r = 0.13$ for 1 young, $P > 0.05$). Minimum $T_e$ for nests with unpipped eggs was lowest in early evening and early morning (Fig. 3), but were not correlated significantly with $T_a$ ($r = 0.14$, $P > 0.05$). The correlation for pipped egg minima was greater, but not significant ($r = 0.27$, $P >$

$0.05$). A stronger effect of $T_a$ was exhibited for minimum $T_e$ at nests with 1 young (Fig. 3, open triangles). The lowest $T_e$ occurred in the cool morning hours, and once near midnight. These minima correlated significantly with $T_a$ ($r = 0.53$, $P < 0.05$).

*Parental behavior.*—The most common behavior of pelicans during the late incubation stage was simply to sit on the nest with foot webs over the eggs. Often the head was tucked under a wing in a sleeping posture. Various behaviors were superimposed on this general inactivity. Preening was present throughout the period from before pipping until after hatching (Table 2). Preens while sitting were less frequent at all stages than were preens while the front part of the body was raised ($\chi^2 = 24.14$, $P < 0.001$, all
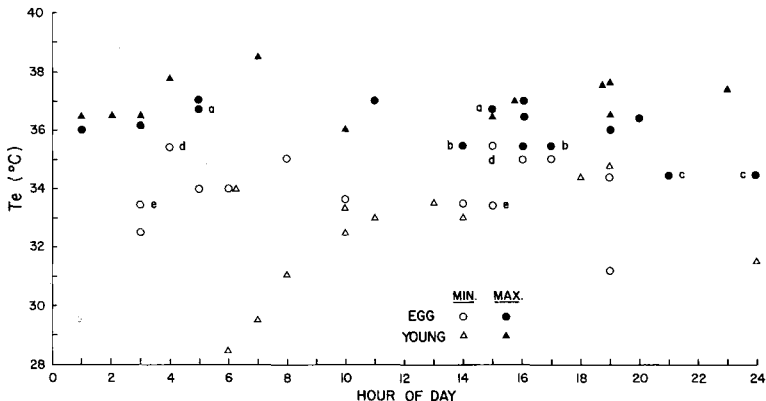


Fig. 3. Time of day when maximum and minimum egg temperatures ($T_e$) occurred for individual nests containing one artificial egg and one unpipped egg (circles, $n = 12$ nests) or one young (triangles, $n = 12$ nests). Plotted values beside same letter represent tied maximum or minimum values for a particular nest.

TABLE 2. Average frequency per hour of seven parental behaviors during the transition from incubating eggs to brooding the young. Values are means ± SE ($n = 10$ nests at each stage of the hatching sequence).

| Behavior | Nest contents[a] | | | | | $H$[b] | $P$ |
|---|---|---|---|---|---|---|---|
| | e/e | e/p | e/y | p/y | y/y | | |
| Preens raised | 5.1 ± 1.2 | 8.6 ± 1.2 | 7.4 ± 1.7 | 10.1 ± 1.3 | 10.8 ± 1.9 | 10.93 | <0.05 |
| Preens sitting | 1.1 ± 0.5 | 3.1 ± 1.2 | 2.5 ± 1.2 | 4.2 ± 1.9 | 4.1 ± 1.0 | 5.92 | NS[c] |
| Shuffles[d] | 2.0 ± 0.7 | 8.5 ± 1.3 | 9.7 ± 1.7 | 11.9 ± 1.5 | 9.3 ± 2.2 | 17.47 | <0.01 |
| Turns | 0.8 ± 0.2 | 1.5 ± 0.5 | 1.7 ± 0.6 | 1.7 ± 0.5 | 1.9 ± 0.9 | 1.56 | NS |
| Bills e/y[a] | 0.4 ± 0.2 | 1.3 ± 0.3 | 5.0 ± 1.1 | 6.6 ± 1.5 | 4.0 ± 1.1 | 27.76 | <0.001 |
| Manipulates nest material | 0.8 ± 0.2 | 1.1 ± 0.4 | 0.7 ± 0.5 | 1.4 ± 0.7 | 3.2 ± 0.7 | 11.80 | <0.02 |
| Egg exposed[e] | nil | 2 | 5 | 3 | NA | — | — |

[a] e = unpipped egg; p = pipped egg; y = newly hatched young.
[b] Kruskal-Wallace 1-way ANOVA by ranks. df = 4.
[c] NS = Not Significant ($P > 0.05$).
[d] See text for description.
[e] Number out of 10 nests where an egg was exposed while parent sitting.

stages combined). Preens while sitting showed a slight but not significant increase in frequency as hatching progressed. In contrast, preens while raised increased significantly over time; the main increase occurred with the onset of pipping of the a-egg ($U = 9.0$, $P < 0.002$).

Shuffles increased markedly with the onset of pipping of the a-egg ($U = 7$, $P < 0.002$) and exhibited a significant overall increase with incubation stage (Table 2). Billing the eggs or young also increased significantly with incubation stage; the main increase occurred with the hatching of the a-egg ($U = 14$, $P < 0.02$). Manipulation of nest material increased with incubation stage, but mainly only after both young hatched. Turns on the nest occurred at a low but steady rate throughout all stages and were not affected by pipping or hatching of the eggs (Table 1).

Unpipped eggs under the foot webs were often partially visible at the front of the nest. After the webs were removed with the onset of pipping, eggs were usually either fully covered where they lay between the parent's legs or were exposed briefly when the parent stood to preen. On occasion, eggs at this stage of incubation protruded from the front of the sitting adult. This form of egg exposure was not seen prior to pipping, but occurred at all stages thereafter (Table 2).

## DISCUSSION

The egg temperatures measured with agar-filled eggs represent $T_e$ in the absence of embryonic calls or metabolism. Metabolic rate increases appreciably in pelicans as incubation progresses (Bartholomew and Goldstein 1984).

However, Howell and Bartholomew (1962) found no correlation between internal egg temperature and degree of embryonic development over a span of from ¼ to ⅞ of total prehatch development. Embryonic heat is evidently not a significant variable influencing $T_e$ in altricial passerines (Webb and King 1983), but the larger size of White Pelican eggs means that embryonic heat cannot at this time be eliminated, especially during the pipped-egg stage when metabolic rate should be maximal (Whittow 1980).

The average $T_e$ of 35.2°C at nests that contained only unpipped eggs in the American White Pelican is ca. 1–4°C above the means computed for 5 orders of nonpelecaniform birds (Webb 1987). Mean $T_e$ for pelicans was within the range of $T_e$ reported for other Pelecaniformes: Red-tailed Tropicbirds, 35.0°C (Howell and Bartholomew 1962), 36.0–36.7°C (Whittow and Grant 1985); Red-footed Boobies, 36°C (Howell and Bartholomew 1962), Double-crested Cormorant, 35.6–36.0°C for clutches of 3 and 4 eggs (Van Scheik 1985).

At nests that contained only unpipped eggs, $T_e$ was steady throughout the 24-h day, and most readings clustered within 2°C of the mean (Fig. 1). The correlation between $T_a$ and $T_e$ was evidently too weak to produce a daily $T_e$ cycle. Low variability in $T_e$ of unpipped eggs was also characteristic of tropicbird and booby eggs (Howell and Bartholomew 1962) and of completed 3 and 4 egg clutches of Double-crested Cormorants (Van Scheik 1985). A large proportion of species from other orders exhibit markedly greater variations in $T_e$ (Webb 1987). The relative lack of variability in pelicans is accounted for, at least in part, by their essentially constant in-

cubation attentiveness throughout the day and night.

The main change in $T_e$ during the transition from incubation to hatching was a progressive increase in range and variability. The increase in $T_e$ variability was paralleled by, and presumably caused by, changes in parental incubation behavior. During incubation of unpipped eggs, parents had low levels of behaviors such as raised preening or shuffling that could disrupt normal incubation patterns. With the onset of pipping, raised preening and shuffling increased in frequency and the eggs were shifted from under foot webs to between the legs. These changes in incubation behavior resulted in a lowering of some $T_e$ readings, and also resulted in an elevation in temperature range. Evidently the temperature applied to eggs held between the legs is sometimes higher than earlier when the eggs were held towards the edge of the nest under the webs.

During incubation of unpipped eggs, raising to preen was the most common adult behavior, excluding simple quiet sitting. While raised to preen at this stage, the eggs remained under the foot webs. This presumably shielded the eggs from wind or sun and thereby contributed to thermal stability of the eggs. After pipping, when the webs no longer covered the eggs, the eggs were commonly visible when the parent stood to preen. Eggs also protruded at times from under the adult sitting on the nest. Under these conditions, greater exposure would probably contribute to greater variability in $T_e$, especially during the colder portions of the day. The significant correlation between $T_a$ and the minimum $T_e$ reached at nests with 1 young present suggests that egg exposure arising from changes in incubation behavior was responsible for the lower range of temperatures recorded at that time. Maximum $T_e$ were usually below 38°C (Fig. 3, solid symbols) which implies that overheating due to exposure of eggs to the sun was not a problem (Webb 1987).

Temperature readings below 33°C became more frequent after pipping (Fig. 1). After a young had hatched, $T_e$ fell to below 29°C (see also Fig. 3). These uncommonly low temperatures were well outside the range of temperatures normally experienced when the nest contained only unpipped eggs. Little is known about the effects of cool temperatures during the pipped-egg stage on embryonic development or survival (Webb 1987), but incubation temperatures below 34°C during the final 4 or 5 days of the normal incubation period significantly decrease hatchability and delay hatching times in domestic chickens (Romanoff 1936). Similar trends were found in clutches of Ring-billed Gulls (*Larus delawarensis*) incubated in the laboratory from pipping of the a-egg onwards at 33°C (R. Evans unpubl. data).

Temperatures as low as 33°C elicited persistent calling by pelican embryos when pipped eggs were cooled in the laboratory (Evans in press). Calling by embryos within pipped eggs also occurred under natural conditions in the colony and was especially common when eggs were exposed to cool ambient temperatures (Evans 1988, in press). I suggest that pelican eggs become exposed to increased temperature variation from pipping onwards, and that calling in response to cooling provides a mechanism whereby pipped eggs can potentially influence their own incubation temperature by communicating with the parent. Further examination of this embryonic behavioral temperature regulation hypothesis would appear warranted in other species where embryonic vocalizations are well-developed and the thermal environment at the nest becomes either cooler or more variable during the transition from incubation to brooding.

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