

Sources of Heat for Nests of *Paleosuchus trigonatus* and a Review of Crocodilian Nest Temperatures

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ABSTRACT.—All species of crocodilian that have been studied normally incubate their eggs at temperatures above 27°C. Stable temperatures above 27°C are not naturally available in the tropical-rainforest habitat of *Paleosuchus trigonatus*, and our investigations indicate that its nests are not warmed by the processes that have been suggested for nests of other species: insolation, rotting vegetation, and metabolic heat of embryos. Most nests of *P. trigonatus* are placed at the side of, or on top of, termite mounds. Heat from the termite mound and insulation by the nest material maintain the eggs at about 30°C (28.4–32.1°C).

Crocodilians construct two basic types of nest (Greer, 1970, 1971; Campbell, 1972). Some species lay their eggs in holes in open areas, such as beaches. Temperatures are maintained relatively stable by insolation and the moderating effect of the overburden of sand. Modha (1967) suggested that metabolic heat generated by embryos might also contribute to nest temperatures. Other species construct mounds of vegetation to incubate their eggs. Those nests are also affected by insolation and possibly metabolic heat of embryos (Webb et al., 1983b), but significant amounts of heat are produced by rotting vegetation within nests (Lang (cited by Schmidt, 1919); Smith, 1931; McIlhenny, 1934; Neill, 1946; Lebuff, 1957; Chabreck, 1973; Tansey, 1973; Staton and Dixon, 1977; Goodwin and Marion, 1978; Magnusson, 1979).

Three species of crocodilian are thought to inhabit small forest streams in undisturbed tropical rainforest: *Paleosuchus trigonatus*, *P. palpebrosus*, and *Osteolaemus tetraspis*. These are among the least studied of the crocodilia and there are published observations on less than three nests for each of the species (Bates, 1864; Medem, 1971, 1972, 1981, 1983; Dubost (cited by Knoepfner, 1974); Dixon and Soini, 1977; Ruesta, 1981). No

details of the factors affecting temperatures in those nests were given.

In this paper we present observations and experiments on nests of *Paleosuchus trigonatus* designed to answer the following questions:

1. What are the major external sources of heat for nests?
2. Does metabolic heat produced by embryos contribute significantly to nest temperatures?
3. Does decomposition of nest materials contribute significantly to nest temperatures?
4. What effect do ambient temperatures have on nest temperatures?
5. How do temperatures within nests of *P. trigonatus* compare to temperatures recorded from nests of other species of crocodilians?

METHODS

The study was conducted in Reserva Florestal Ducke, 25 km east of Manaus, Amazonas, Brazil. Additional observations and reports on nests were made in other areas within 100 km of Manaus. Reserva Ducke is an area of relatively undisturbed (some selective logging was carried out about 20 years before the study) tropical rainforest. Most nests were situated around Igará-

pé (creek) Acará, an area remote from most research activity within the reserve.

Nests were located by searching the banks of streams for nests and searching the streams for groups of hatchlings which could indicate a nest in the vicinity. Nests are mounds of loosely compacted leaf litter about 60 cm high and 150 cm in diameter, similar to the nest of *P. palpebrosus* figured by Medem (1981:116). Two nests from the 1983/84 season (approx. Aug.-Jan.), 6 from the 1982/83 season, and 5 nests from previous seasons were located. Two nests from the 1982/83 and 2 nests from the 1983/84 season still had incubating eggs when first found. Nine of the nests had been built against or on top of large (approx. 60 cm dia., 60 cm high) mounds of the termite *Neocapritermes braziliensis*. One of the 1982/83 nests and two of the older nests had diffuse termite workings throughout them, but whether the termites were there when the nest was built could not be determined. One nest from the 1982/83 season (not found until Oct. 1983) was built against the leaf bases of a sessile plant and had no evidence of termite workings.

Spot temperatures were taken with a thermistor thermometer ("CMS digital") from among the eggs and the surfaces of 4 nests. Temperatures at various points within and around 3 nests were taken at hourly intervals over 24 consecutive hours with a thermistor thermometer ("YSI Tele-Thermometer series 400") with 5 separate probes.

To evaluate the contribution of rotting vegetation to nest temperatures, 4 mounds of leaf litter similar in density and size to nests were constructed near natural nests and the temperatures in them recorded at irregular intervals over the following 6 weeks.

The eggs in one nest were moved from their original position at the side of a termite mound to a cooler position at the same depth in the center of the mound of leaf litter, 35 cm from the termite mound. The temperature among

the eggs before and after the move was monitored to determine whether metabolic heat from the embryos could raise the temperature of the eggs above that of the leaf litter. The embryos in the eggs were near full term (stage 15 of Magnusson and Taylor, 1980).

To determine whether the metabolic heat generated by an embryo was capable of raising the temperature of an egg when it had much better insulation than that provided within a nest, a single egg at the same stage of development was taken to the laboratory and allowed to equilibrate with air temperature (23°C). We then wrapped it in a layer of polystyrene 3 mm thick and placed it in a polystyrene box 10 × 10 × 8 cm, with 1 cm thick walls. A thermistor in a hypodermic syringe (YSI Telethermometer model 507) was inserted through the polystyrene and positioned to touch the egg shell at about the middle of its long axis. Another thermistor measured air temperature at the surface of the box. The temperature of the air and the egg were monitored over the following 19 h. The egg was opened at the conclusion of the experiment to verify that the embryo was alive and healthy. Porosity and imperfections in the polystyrene allowed diffusion of gases. Although we did not measure PO₂ at the egg surface we believe it was at least as high as in a natural nest.

We surveyed the literature in an attempt to obtain nest temperatures for as many other species of crocodylians as possible. For some species such as *Alligator mississippiensis* and *Crocodylus porosus* fairly detailed studies are available, but for some species only general statements as to the most common temperatures or the range of temperatures from an unspecified number of nests were given. We included such data if no other were available.

We used parabolic regressions to describe relationships between nest surface and egg cavity temperatures as part of a parabola approximates many other

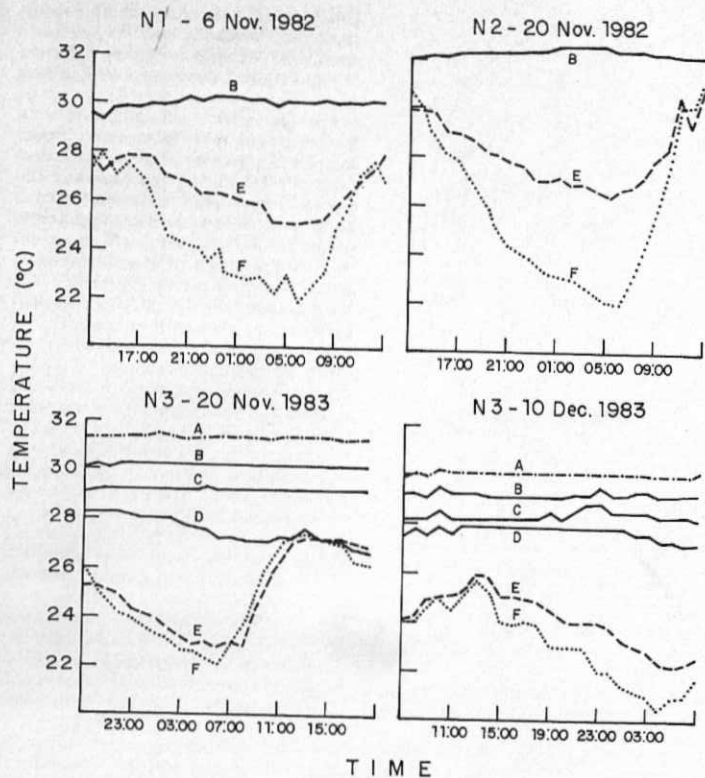


FIG. 1. Temperatures in 3 nests (N1, N2, and N3) of *P. trigonatus* over 24 h periods. A—15 cm into the associated termite mound at the level of the eggs. B—row of eggs closest to the termite mound. C—row of eggs furthest from the termite mound. D—midway between the eggs and the nest surface. E—surface of nest. F—air 1 m from the nest, 30 cm above ground level.

curves and is useful when the exact relationship is not known. Also, parabolic regression does not require transformation of the dependent variable and so does not create heteroscedasticity. However, the regressions do not model any underlying biological or physical processes and should be considered purely descriptive.

RESULTS

External Sources of Heat for Nests.—Temperatures among eggs were relatively stable and always much higher than nest surface and air temperatures (Fig. 1). In nest 3 (N3) the temperature of the eggs was intermediate between that 15 cm inside the termite mound (A)

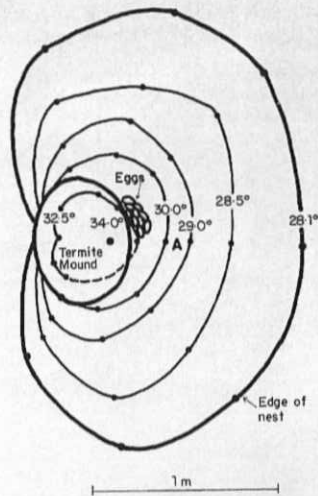


FIG. 2. Temperature profile through Nest 1 and its associated termite mound at the level of the eggs.

and midway to the surface of the nest (D, Fig. 1, lower). All temperatures were lower on 10 Dec., than 20 Nov., but the difference between the row of eggs closest to the termite mound (B) and the row furthest from the mound (C) was about 1°C on both days.

The source of heat leading to egg temperatures higher than those at the nest surface in N3 was the termite mound (Fig. 1) and this can also be seen in a horizontal temperature profile (15 cm depth) through N1 and its associated termite mound (Fig. 2).

Metabolic Heat Production by Embryos.—When the 15 eggs in N1 were moved from their original position (Fig. 2) to the center of the mound of leaf litter (Fig. 2A) the cavity where the eggs had been maintained its temperature (29.8°C), but the eggs equilibrated with the temperature at their new site

(26.2°C) and maintained temperatures similar to that of the leaf litter over the next 24 h. The eggs were then returned to the original cavity to avoid killing the embryos.

The egg insulated by polystyrene in the air-conditioned room followed room temperature (which rose to 29.2°C and fell to 24.2°C during the course of the experiment), with a delay of about 1 h because of the insulating effect of the polystyrene. That range of temperatures is similar to that of soil in the forest and the polystyrene is probably better insulation than could be provided by a natural nest so it seems unlikely that the amount of metabolic heat produced by the embryos could be significant in raising nest temperatures.

Effect of Heat of Decomposition.—The mounds of leaf litter we constructed to mimic nests were not placed near termite mounds, and their temperatures rarely rose above 26.0°C. The maximum recorded was 27.1°C and the maximum temperature we recorded from a natural accumulation of litter, some of which was as large and as compacted as crocodilian nests, was 26.6°C.

One nest was built at the side of a large, decomposing trunk of a tree. The stump was full of termite workings but they appeared to have been abandoned. The nest had been opened by an adult and the young released shortly before we found it. However, when we reconstructed the nest and left it to equilibrate for 24 h, the temperature at the site of the egg cavity was 28.8°C and the temperature 20 cm further from the trunk 26.0°C. While we cannot be sure that the higher temperature was not being maintained by a termite colony deep within the trunk we believe it most likely that the heat came from decomposition of the stump.

Effect of Ambient Temperatures.—One nest (N1) from the 1982/83 season and one (N3) from the 1983/84 season had been constructed at the side of termite mounds. The eggs were covered by 15

cm and 25 cm of well compacted leaf litter, respectively. One nest (N2) from the 1982/83 season, and one (N4) from the 1983/84 season had been constructed on top of termite mounds. N2 completely covered the termite mound but the eggs were placed high on the mound and were covered by only 10 cm of loose leaf litter. To us, N4 appeared to have been very poorly built. The eggs were placed in a cavity near the top of the termite mound, but half the eggs were subsequently dug up as the adult remodelled the nest. The eggs in the original cavity, both before and after the remodelling were covered by 10 cm of dirt and sticks.

The regression describing the relationship between spot nest-surface temperatures and temperatures among eggs in N1 and N3 was significantly different to that describing the same relationship for N2 and N4 (Analysis of Covariance, $F_{3,15} = 7.8$, $P < 0.003$). We attribute the difference to differences in insulation. The nests with thin cover of leaf litter are affected more by intermediate ambient temperatures (causing nest surface temperatures 26–28°C) than nests with thicker cover of leaf litter, though there does not appear to be much difference between nests at the highest and lowest recorded ambient temperatures (Fig. 3).

The insulative effect of the nest material can also be seen in Fig. 2. The 32.5°C isotherm indents away from the exposed side of the termite mound, but extends out of the mound on the side covered by the nest.

Comparison with Other Crocodilians.—The mean temperatures of the four nests of *P. trigonatus* studied in detail are close to the temperatures recorded for *Paleosuchus* species in other studies, and close to the median temperature for most other species of crocodilian (Fig. 4). However, the ranges and standard deviations are lower than one would expect considering the variability within and between nests of other species.

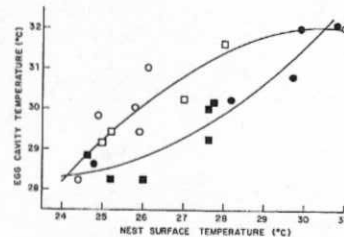


FIG. 3. Relationships between nest-surface and egg-cavity temperatures in nests N1 (○), N2 (●), N3 (□) and N4 (■). N1 and N3 had >15 cm of leaf litter covering the eggs. N2 and N4 had <10 cm of leaf litter covering the eggs.

DISCUSSION

The major sources of heat causing egg temperatures to be higher than the greater part of the nest material of the four nests we studied in detail were termite mounds. As 9 of 13 nests we located were associated with large termite mounds it seems that termite mounds are significant sources of heat for most nests of *P. trigonatus* in the area. Another nest, located by World Wildlife Fund staff, 90 km from Manaus was also reported to be associated with a large termite mound. Elevated temperatures have been reported for mounds of many species of termites. Fungus gardens within nests of some species may elevate temperatures, but according to Noirot (1970) "it is the metabolism of the insects which plays the essential role in the elevation of the temperature within the nest."

A ball of termite (*Nasutitermes similis*) workings only 10 cm in diameter in an abandoned nest had a temperature of 28.9°C when the rest of the nest had a temperature of 26.7°C. Medem (1971) wrote of eggs of *P. palpebrosus* that "older ones are always covered by a thick black layer formed by debris and the excrement of the abundant ground termites," and Chirivi-Gallego (1973) commented that the interior of nests of *Cai-*

leaf - 0 (fl) leave
lit on side of mound

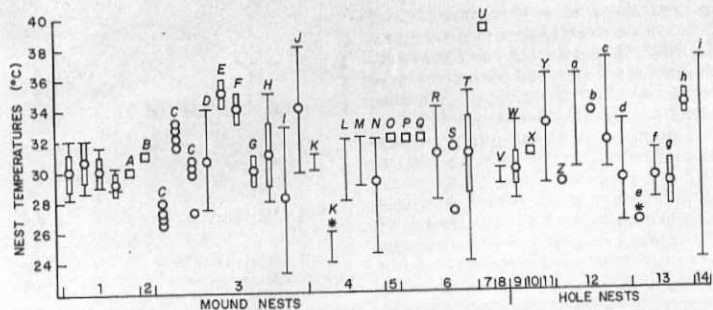


FIG. 4. Temperatures of crocodilian nests. Open circle—mean, vertical bar—standard deviation, vertical line—range, square—single observation. 1—*Paleosuchus trigonatus*, 2—*P. palpebrosus*, 3—*Alligator mississippiensis*, 4—*Caiman crocodilus*, 5—*C. latirostris*, 6—*Crocodylus porosus*, 7—*C. novaeguinae*, 8—*C. moreleti*, 9—*C. palustris*, 10—*C. intermedius*, 11—*C. niloticus*, 12—*C. acutus*, 13—*C. johnstoni*, 14—*Gavialis gangeticus*. Sources (number following date is the number of nests in the sample): A—Ruesta, 1981 (1); B—Medem, 1971 (1); C—Chabreck, 1973 (means of 4 periods for each nest); D—Deitz and Hines, 1980 (24); E—Ferguson and Joanen, 1982 (2 levee nests); F—*Ibid.* (2 dry-marsh nests); G—*Ibid.* (2 wet-marsh nests); H—Goodwin and Marion, 1978 (14); I—Joanen, 1969 (11); J—McIlhenny, 1934 (1); K—Blohm, 1928; L—Medem, 1973 (a general statement, and *temperatures of a nest that produced no living young); M—Medem, 1983 (a general statement); N—Staton and Dixon, 1977 (not given, but from their table 3 at least 39); O—Crawshaw and Schaller, 1980 (not given but mean based on 71 measurements and they investigated more than that number of nests of *Caiman crocodilus yacare*); P—Vaz-Ferreira and Achaval, cited by Medem, 1983 (1); Q—Deraniyagala, 1939 (1); R—Kopstein, 1929 (1); S—Magnusson, 1979 (11); T—Webb et al., 1977 (means of 2 nests); U—Webb et al. 1983b (39); V—Neill 1946 (1); W—Alvarez del Toro, 1974 (a general statement); X—Whitaker and Whitaker, 1978 (1); Y—Medem, 1958 (1); Z—Toro, 1974 (a general statement); a—Alvarez del Toro, 1974 (1); a—Dunbar-Cooper and Lutz, 1981 (not given); b—Modha, 1967 (28); c—Alvarez del Toro, 1974 (1); c—Lutz and Dunbar-Cooper, 1982 (8); d—Ogden, 1978 (9); e—Compton, Inchaustegue et al., 1980 (103); f—Webb et al. 1983a (6); g—Webb et al. 1983a (51 nests measured within a week of laying); h—Webb et al. 1983a (5 nests measured after about 60 days of incubation); i—Singh, 1978 (a general statement).

man crocodilus he studied were always infested with termites. Termites may also affect the temperatures in nests of other neotropical crocodilians.

All nests associated with termites in this study were excavated by an adult or showed evidence of having been excavated. The only nest not associated with termite workings showed no evidence of having been excavated, but as there were only fragments of shells left in the nest when it was found we do not know the fate of the embryos. The temperature of the nest, which was constructed almost entirely of sandy soil, was 26.0°C when it was found. Similar temperatures result in total loss of embryos in nests of *A. mississippiensis* (Cha-

breck, 1972; Ferguson and Joanen, 1982), *Caiman crocodilus* (Blohm, 1973), *Crocodylus novaeguinae* (Bustard 1971), and *Crocodylus johnstoni* (Compton, 1981; Webb et al., 1983a). In fact, no species of crocodilian appears to have eggs that normally develop below 27°C (Fig. 4).

One nest in this study, although associated with termite workings, we believe gained most of its heat from a decomposing stump. However, such stumps are rare in the area. We found 6 other, superficially similar, but slightly smaller, rotting trunks. They had core temperatures ranging from 24.3 to 25.8°C. Why mounds of litter do not produce significant amounts of heat in the forest is not clear. It may be that

ambient temperatures are too low to start decomposition and/or it may be because litter dropped by rainforest trees in Amazonia is very resistant to degradation by microorganisms (Howard-Williams, 1974).

Although Modha (1967) and Webb et al. (1983b) suggested that metabolic heat contributes significantly to nest temperature within and between nests of *P. trigonatus* investigated in this study was much less than that experienced by other species of crocodilians (Fig. 4). If sex was determined by the same temperatures that determine sex of *A. mississippiensis* (Ferguson and Joanen, 1982) all *P. trigonatus* in our area would be female. Considering the difficulty in tropical rainforest of attaining the high temperatures that result in males in *A. mississippiensis*, it is likely that some males are produced at lower temperatures in *P. trigonatus* as in *C. johnstoni* (Webb et al. 1983a). The temperature difference between *P. trigonatus* eggs closest to termite mounds and those furthest away potentially could result in both sexes being produced in the same nest. However, we could not test this as we did not wish to kill embryos before hatching and the hatchlings dispersed or died soon after hatching.

It is strange that crocodilians have not evolved to incubate their eggs at lower temperatures like the majority of reptiles. There is little difference in incubation temperatures among *Gavialis gangeticus* which live in Himalayan mountain streams (Fig. 4i), *A. mississippiensis* which live in temperate swamps (Fig. 4c–j), *Caiman crocodilus* in tropical savannas (Fig. 4K–N) and species of *Paleosuchus* that live in tropical rainforest (this study; Fig. 4A, B). Adults of those species resist very different temperature regimes, but the eggs of all species must incubate at similar temperatures. As insolation, decomposition of nest materials, and embryonic heat, which have been suggested as sources of heat for other species of crocodilians, do not appear to be viable alternatives in trop-

ically caused by rain. *Paleosuchus trigonatus* near Manaus construct nests between August and September (the end of the dry season) and hatching occurs from November to January (wet season). Therefore, nests probably maintain higher temperatures at the beginning of incubation than towards the end. However, the variation in temperature within and between nests of *P. trigonatus* investigated in this study was much less than that experienced by other species of crocodilians (Fig. 4). If sex was determined by the same temperatures that determine sex of *A. mississippiensis* (Ferguson and Joanen, 1982) all *P. trigonatus* in our area would be female. Considering the difficulty in tropical rainforest of attaining the high temperatures that result in males in *A. mississippiensis*, it is likely that some males are produced at lower temperatures in *P. trigonatus* as in *C. johnstoni* (Webb et al. 1983a). The temperature difference between *P. trigonatus* eggs closest to termite mounds and those furthest away potentially could result in both sexes being produced in the same nest. However, we could not test this as we did not wish to kill embryos before hatching and the hatchlings dispersed or died soon after hatching.

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Stumps rotting (modha)

ical rainforest, *P. trigonatus* has little alternative to the use of termite mounds if it is to maintain warm temperatures within its nests.

Oviposition in nests of ants is common among South American reptiles (Vaz-Ferreira et al., 1970), but the use of termite mounds by *P. trigonatus* is somewhat more complex as a *P. trigonatus* cannot enter a termite mound, and the temperature of the surface of the mound is close to ambient. The termite mound serves as an incubator only in conjunction with a mound of leaves. Porter and Tracy (1983) commented: "The interaction between (1) potential nest environments and (2) adaptations such as viviparity, delayed oviposition, and nest site selection are obviously more important than previously appreciated in population studies of reptiles." That comment seems especially applicable to rainforest crocodylians. Logical questions are: Do *P. palpebrosus* and *O. tetraspis* breed along the small forest streams in which they are often found, and, if so, how do they maintain nest temperatures?

Acknowledgments.—We thank Terzinha Tesche and Mike Roberts for help with temperature recording, Jorge Dácio for preparing the figures, Ademar Bandeira for identifying the termites, and Maria de Nazaré Góes Ribeiro for administrative support. Hygia Pimenta Carmo typed the manuscript. Part of this study was financed by a research grant from the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico to W. E. Magnusson.

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