



INCUBATION TEMPERATURE OF THE PIGEON EMBRYO (*COLUMBA LIVIA*)

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Abstract—This study compared the growth and development of pigeon embryos raised in the nest under normal parental care to that of eggs from the same clutch incubated in an incubator. The average daily temperatures of both environments (nest and incubator) were the same, but the hourly average temperatures and patterns of temperature fluctuations of these environments differed. Our results indicate that the small temperature fluctuations experienced by pigeon eggs in the nest under parental incubation may be the optimal thermal environment for *in ovo* growth and development. © 1998 Elsevier Science Ltd. All rights reserved

Key Word Index: Incubation temperature; pigeons; growth and development

INTRODUCTION

Early definitions of incubation described it as the process by which the heat necessary for embryonic development is transferred to an egg after it has been laid (Beer, 1964). Modern definitions of incubation recognize that heat transfer is not the only factor involved in influencing the growth and development of avian embryos and therefore describe incubation as the process by which thermal environment, humidity, gaseous environment, egg turning and other physical factors are regulated to influence embryonic development (Drent, 1975; Wilson, 1991). In spite of this expanded definition there is little doubt that the incubation temperature plays a crucial role in the growth and development of avian embryos.

Over the past 50 years there has been considerable research to determine the optimal incubation temperatures of various domestic and wild bird species. Most studies of this nature were conducted by incubating eggs under artificial conditions. For example, Lundy (1969), as cited in White and Kinney, (1974) determined that the optimal incubation temperature for domestic fowl is between 37 and 38°C, and that death occurs at temperatures above 40.5 and below 35°C. The temperature range of 25–27°C was defined as the physiological zero temperature, the incubation temperature under which

no development occurs (Romanoff and Romanoff, 1972). White and Kinney (1974) concluded that the mean incubation temperature of avian eggs must be close to the optimal temperature for their development.

Unlike studies on avian eggs in artificial incubators, the incubation temperature of eggs in a natural environment varies according to parental attentiveness. Birds share incubation responsibilities in several different ways. In some species only one parent, usually the female, is the sole incubator of the eggs. In other species both sexes share the incubation responsibility. Under the dual parental care system the single incubating parent splits its days between sitting on the eggs and foraging for food. The result is intermittent incubation for the eggs, causing significant fluctuations in temperature, mirroring the periods of attentiveness and inattentiveness (White and Kinney, 1974).

Pigeons utilize bisexual incubation. One parent, the female, remains in the nest for the bulk portion of the incubation period, switching incubation responsibilities with her partner several times a day. During the entire incubation, the eggs are seldom left unexposed (Vatnick, Morrone and Davis unpublished). Therefore, one would not expect to observe a large variation in embryonic temperature throughout the entire *in ovo* development. This study was designed to determine the natural variation of the thermal environment that pigeon embryos experience throughout incubation.

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METHODS AND MATERIALS

A flock of seven mated domestic pigeons (*Columba livia*) was purchased from a local breeder who has kept the same breeding flock for over 30 years. The pigeons were kept in a coop (2.4 m × 2.4 m × 3.25 m) housed on the roof of Kirkbride Hall (Widener University, Chester, PA). Eggs were collected from January through to September 1994. A total of 13 eggs from two-egg clutches were used in this experiment. Eggs were given identification marks within 6 hr of being laid. The day on which the egg was laid was considered day 0 chronological age. The first day of incubation was considered the day that the second egg was laid.

The first laid egg was left in the nest to be incubated by its parents. The second egg was removed from the nest on the day after it was laid and placed in an Hova-Bator Incubator (G. Q. F. Manufacturing Co., Savannah, GA) kept at approximately 36.9°C for the entire incubation period. This method was chosen in order to allow the pigeons to establish incubation, as taking the first egg would have impeded the process. The incubator was equipped with an automatic egg-turner to prevent membranes from adhering to the shell. The second egg was replaced in the nest by a water-filled dummy egg instrumented with a thermocouple connected to a CR7 Measurement and Control System data logger. A similar dummy egg was also placed in the incubator to monitor the incubation environment of the incubator eggs.

These dummy eggs were prepared using recently-laid eggs which were emptied by making a small hole in one end and injecting air into them. Eggs were rinsed, air-dried and a thermal couple was inserted and held in place with silicon adhesive and the entire egg was sealed by dipping in clear nail polish. The eggs were then filled with water to simulate the

contents of fertile eggs. In order to allow for parental manipulation similar to living eggs, the dummy eggs were not secured at the bottom of the nest. The data logger recorded the temperature of the dummy eggs every 5 min throughout incubation.

For each nest and incubator egg, an average temperature was calculated for every hour of incubation. Each hourly average corresponded to a specific hour of a 24 h day (e.g. 2400 h) for each incubation day, from day 0 to day 18. There were approximately 16–18 hourly temperature measurements for each time corresponding the same number of incubation days. These measurements were averaged to yield a 24 h pattern of incubation temperature for each individual nest. The data from all nests were then averaged to yield the overall 24 h pattern of incubation for all nests. Daily temperature averages for each nest were calculated by averaging all 288 temperature measurements for (egg temperatures were recorded every 5 min, i.e. 12/h or 288/day) a particular day. The daily averages of all nests were then averaged to yield an average daily pattern of incubation for each of the 18 days of incubation. Data taken from the incubator dummy eggs were compiled in exactly the same manner.

RESULTS

Average daily incubation temperature pattern

Incubator embryos experienced a daily average incubation temperature of $36.9 \pm 0.2^\circ\text{C}$ from days 1–18 of incubation (Fig. 1). Embryos in the nest experience lower daily incubation temperatures in their first 2 days of life. The average daily temperature at day 0 (chronological age), before incubation commenced, was 35.3°C for nest embryos, almost 2° lower ($P < 0.5$) than the average day 0

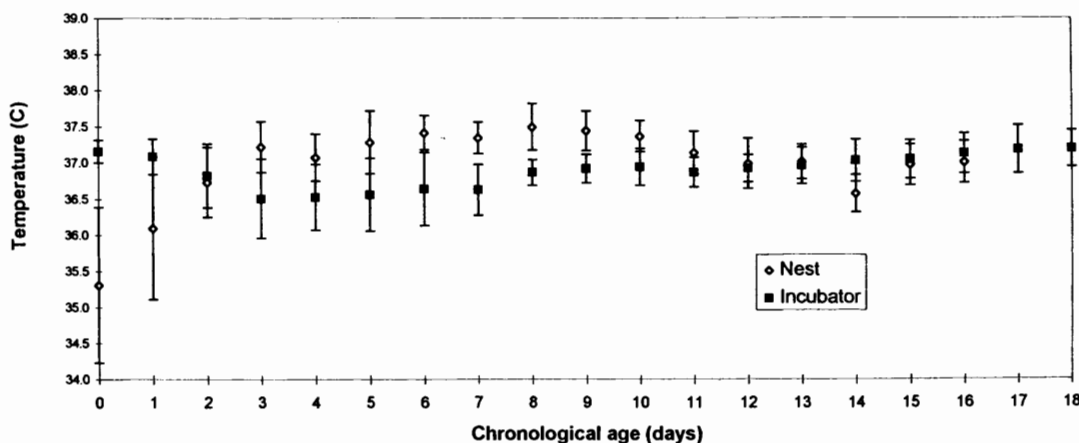


Fig. 1. Average daily incubation temperatures of pigeon embryos raised in nests and in an incubator (mean \pm standard error).

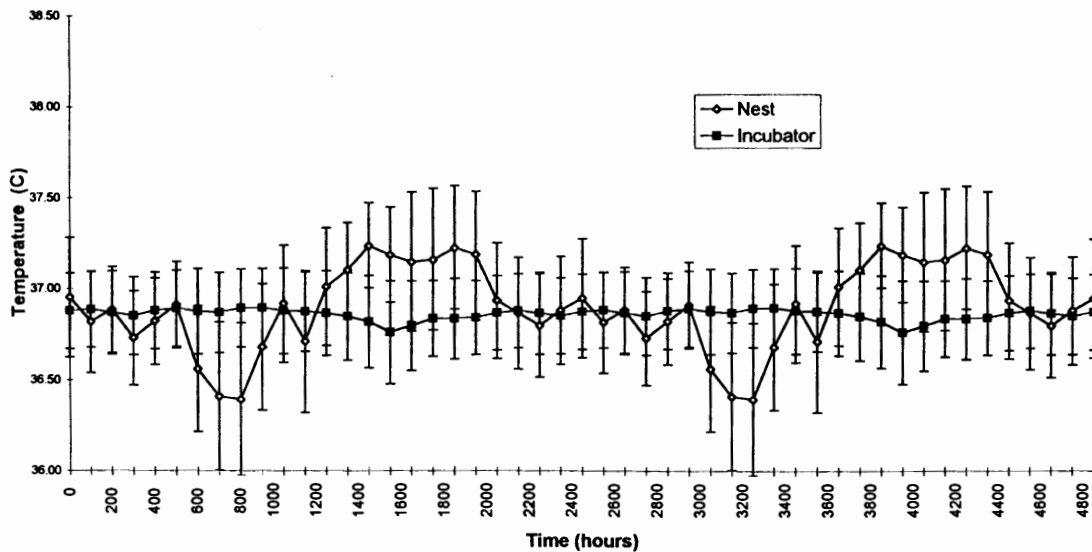


Fig. 2. Average hourly incubation temperatures of pigeon embryos raised in nests and in an incubator (mean \pm standard error).

(chronological age) temperature for incubator embryos. By day 2 (chronological age), when incubation commenced there was no difference between the average daily incubation temperatures of both treatments (approx. 36.9°C; Fig. 2). This temperature remained the same for the rest of the experiment.

Average hourly incubation temperature pattern

Embryos in the incubator were exposed to an average hourly temperature of $36.9 \pm 0.2^\circ\text{C}$ that varied very little throughout incubation (about 0.2°C), while the average hourly incubation temperature in the nest exhibited a diurnal pattern (Fig. 2). An average high temperature of 37.2°C was reached in the late afternoon between 1400 and 1800 h. An average low temperature of 36.5°C occurred in the morning between 0600 and 0900 h.

DISCUSSION

Direct measurement of internal egg temperature is difficult and can result in embryo mortality. A variety of indirect measurements have been taken by different investigators to better assess the thermal environment experienced by living embryos. Different studies measured various variables such as air, parent's body, and brood patch temperature in addition to making several temperature measurements (e.g. top, bottom and core) of non-viable eggs instrumented with thermocouples. For example, Lennerstedt (1966) looked at internal egg temperature and air temperature in his study of Capercaillie (*Tetrao urogallus L.*). Bergstrom (1989), studying Wilson's Plover (*Charadrius wilsonia*) and Killdeer

(*C. vociferus*), measured internal egg, nest bottom and shaded air temperatures. Russell (1969) and Purdue (1976) added an extra variable, brood patch temperature, in their study of white-winged doves (*Zenaida asiatica*) and Snowy Plovers (*Charadrius alexandrinus*), respectively. Measurements of air and parent body temperature were taken in addition to internal egg temperature in a study of rock pigeons (*Columba livia*) conducted by Marder and Gavrieli-Levin (1986).

While some species do seem to be incubated naturally at a constant temperature, Huggins (1941) found that "in natural incubation there is no one egg temperature, but a range of temperatures through which an egg can develop normally and the young can hatch". Many investigators have measured egg temperatures throughout the incubation period of numerous species. Caldwell and Cornwell (1975) determined the average egg temperature for Mallards (*Anas platyrhynchos*) to be 36.3°C for the entire 24 days of incubation. Egg temperature slowly increased over a 7°C range ($T_{\text{max}} = 41.5^\circ\text{C}$) during incubation until hatching. They determined that "embryo temperatures of about 38.0°C are more constant than their data indicates" due to the difficulties of estimating embryo temperatures from probes placed in the egg air cell. The incubation temperature of Goldencrest *Regulus regulus* is held constant over the entire incubation period, independent of time of day (Haftorn, 1978).

In this study the daily average temperatures of nest eggs increased during the first 4 days of life and leveled off thereafter. The daily average egg temperature from day 5 until the end of incubation

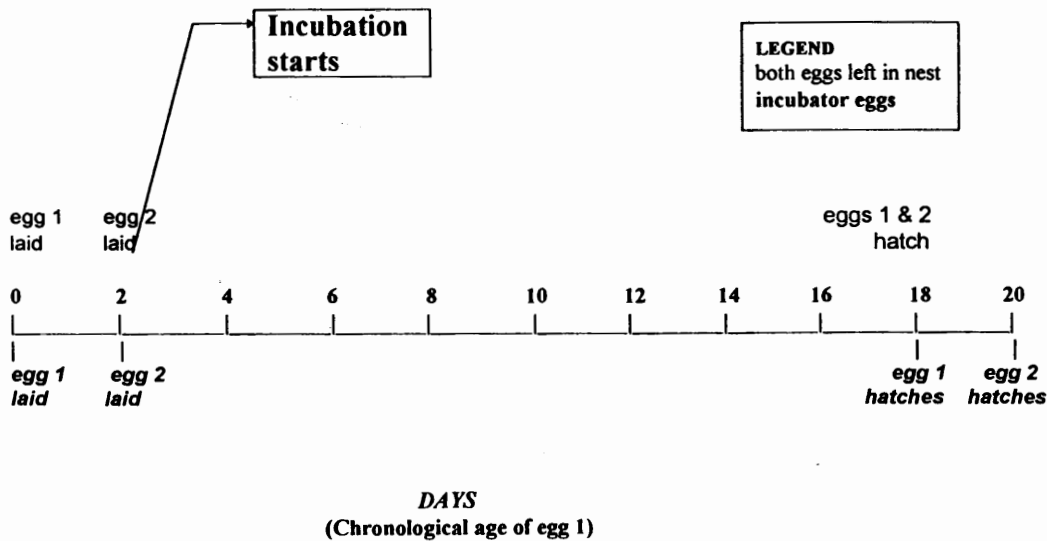


Fig. 3. Timeline of incubation. The control timeline is a result of previous observations of the incubation length of pigeons in our flock. When both eggs are left in the nest, they hatch within a few hours of each other 18 days after the first egg is laid. In this experiment, the nest eggs followed the normal incubation period, while the incubator eggs (2nd eggs) hatched 2 days later on day 20 (chronological age).

was remarkably constant (Fig. 2). Pigeons do not begin incubation of their eggs until the clutch is complete, roughly 48 h after the first egg was laid. After that time, eggs are attended by both sexes and are left unattended less than 1% of the time (Vatnick, Morrone and Davis unpublished). Therefore, one should expect that pigeon eggs experience very little fluctuation in their temperatures when incubation is well established.

A large portion of the studies of incubation temperatures of eggs of several domestic (e.g. Martin and Insko, 1935, turkeys; Lundy, 1956, domestic fowl) and wild species (e.g. Morton and Pereyra, 1985, dusky flycatchers; Lennerstedt, 1966, Capercaillie) reported mean daily temperatures. It may be that the *hourly fluctuations* in incubation temperatures throughout a given day are as important in determining growth and development of birds embryos as the average *daily temperature* which they experience. Looking at average hourly temperature, Haftorn (1983) found that the Great Tit (*Parus major*) experiences an incubation temperature range of 34.0–36.2°C ($X = 35.4^\circ\text{C}$), high temperatures occurring from 0600 to 1600 h, and low temperatures from 0500 to 1800 h.

In this study the average daily temperature of nest eggs after the third day of life varied less than 0.5°C. The hourly average temperature of nest eggs in this study exhibited a discernible diurnal pattern with lows in the early morning (0600–0800 h, Fig. 2) and highs in the early afternoon (approx. 1400 h, Fig. 2). The differences between the high and low tempera-

tures were also remarkably small (about 0.7°C). In contrast, the average hourly temperature of incubator eggs was constant throughout the day and did not vary by more than 0.2°C. Perhaps the diurnal pattern of nest-egg temperature is a reflection of the daily fluctuations in the parent's body or brood patch temperature. It may be that this diurnal pattern in incubation temperature changes the rate of growth and development of pigeon embryos, contributing to the difference in the incubation length between the treatments (Fig. 3). Future studies could mimic, with the use of an incubator, the small hourly fluctuations in the incubation temperatures that pigeon eggs experience under natural incubation and examine the effect on incubation length of eggs subjected to this treatment.

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REFERENCES

- Beer, C. G. (1964) Incubation. In *A New Dictionary of Birds*, ed. A. L. Thomson, pp. 396–398. Nelson, London.
- Bergstrom, P. W. (1989) Incubation temperatures of Wilson's Plovers and Kildeers. *Condor*, **91**, 634–641.
- Caldwell, P. J. and Cornwell, G. W. (1975) Incubation behavior and temperatures of the Mallard Duck. *Auk*, **92**, 706–731.
- Drent, R. H. (1975) Incubation. In *Avian Biology*, Vol. 5, pp. 333–420. Academic Press, New York.
- Haftorn, S. (1978) Egg-laying and regulation of egg temperature during incubation in the Goldcrest. *Ornis Scand.* **9**, 2–21.

- Haftorn, S. (1983) Egg temperature during incubation in the Great Tit *Parus Major*, in relation to ambient temperature, time of day, and other factors. *Fauna Norv. Ser. C6*, 22–38.
- Huggins, R. A. (1941) Egg temperature of wild birds under natural conditions. *Ecology* **22**, 148–157.
- Lennerstedt, I. (1966) Egg temperature and incubation rhythm of a Capercaillie in Swedish Lapland. *Oikos* **17**, 169–174.
- Lundy, H. (1969) *The fertility and hatchability of the hen's egg*. Oliver and Boyd, Edinburgh.
- Marder, J. and Gavrieli-Levin, I. (1986) Body and egg temperature regulation in incubating pigeons exposed to heat stress: the role of skin evaporation. *Physiol. Zool.* **59**, 532–538.
- Martin, J. J. and Insko, W. M. (1935) Incubation experiments with turkey eggs. *Bull. Ky. Ag. Exp. Sta.* **259**, 151–177.
- Morton, M. L. and Pereyra, M. E. (1985) The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher. *Auk*. **102**, 25–37.
- Purdue, J. R. (1976) Thermal environment of the nest and related parental behavior in Snowy Plovers. *Condor*. **78**, 180–185.
- Romanoff, A. L. and Romanoff, A. J. (1972) *Pathogenesis of the avian embryo*. John Wiley and Sons, New York.
- Russell, S. M. (1969) Regulation of egg temperature by incubating White-winged Doves. In *Physiological systems in semi-arid environments*, pp. 107–112. Univ. New Mexico Press, Albuquerque.
- White, F. N. and Kinney, J. L. (1974) Avian incubation. *Science* **186**, 107–115.
- Wilson, H. R. (1991) Physiological requirements of the developing embryo; temperature and turning. In *Avian Incubation*, pp. 145–156. Butterworth-Heinemann, London.