THE RESPONSES OF INCUBATING RINGED TURTLE DOVES (*STREPTOPELIA RISORIA*) TO MANIPULATED EGG TEMPERATURES

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Much research on the incubation behavior of birds (*e.g.*, Kirkman, 1937; Tinbergen, 1951; Beer, 1961) has been concerned with how a bird responds to its clutch (size, shape, color, position, or number of eggs). Although the temperature of the eggs may be one of the most important qualities of the clutch affecting the incubating bird (Baerends, 1959), little research has been published on the responses of incubating birds to egg temperature. The lack of published information has led to speculation. For example, Lehrman (1955) theorized that broody doves, whose well-vascularized brood patches may be a peripheral source of irritation, may incubate eggs because the cool, smooth surface of the eggs reduces the irritation. In this paper I shall discuss how incubating Ringed Turtle Doves (*Streptopelia risoria*) respond to a wide variety of egg temperatures.

MATERIALS AND METHODS

My investigation involved the replacement of the doves' two-egg clutch with a pair of artificial eggs. Rubber tubing connected the watertight artificial eggs to temperature-controlled water baths, and thermocouples detecting the temperature on the surface of the eggs were connected to a recording potentiometer. While a small pump forced temperature-controlled water through the eggs, I recorded the activities of the incubating bird as well as the egg temperature and other independent variables (time, sex, breeding experience, and so on). The data were then examined through an analysis of covariance.

The Ringed Turtle Doves in this study consisted of two random-bred adult pairs and one sibling pair of their offspring. Each adult pair, purchased from Ronson Farms, RFD 2, Westerville, Ohio, had raised at least two successful clutches prior to this study, whereas the young pair was involved with its first clutch. The data were gathered from October to December 1964. The doves bred readily during this period since they were caged in a heated laboratory and subject to the natural daylength at Columbus, Ohio.

Each pair of birds was kept in a poultry wire cage measuring 50 cm on each edge and containing a nest box and one perch. The nest box was about 106 mm square and 31 mm deep, and was elevated on short legs to allow rubber tubing, thermocouple wires, and artificial eggs to pass beneath and through a hole drilled in the floor of the nest box. A nest of oat straw was provided for each clutch.

Artificial eggs, through which water could be pumped, were constructed by copper-plating real eggs of the species, a process similar to the bronzing of baby shoes. The copper replicas were then fitted with an inlet and outlet and dipped in Dean and Barry white alkyd flat interior wall finish, which nearly matched the color and texture of the natural eggs (fig. 1). The egg construction process is described more fully in an earlier paper (Franks, 1966).

The temperature of the eggs during incubation was controlled by water circulated through them from separate thermostatted baths containing water of the desired temperature. A small pulse-pump forced 500–1000 ml of temperature-controlled water per minute through well-insulated 6.4 mm latex tubing to the eggs 6.5 m from the baths. In order to supply both eggs of the clutch, the water flow was divided near the nest with a glass Y, the flow then continuing to the eggs via latex tubing of only 3 mm diameter to allow increased movability of the eggs.

Six fine-gauge thermocouples were glued to the surface of the eggs. With so many thermocouples, the eggs could be rotated in any position, yet at least one thermocouple would provide a measure of the temperature at the interface between the egg and the skin of the bird. The potentiometer recorded the temperature of all the thermocouples every eight minutes, and the

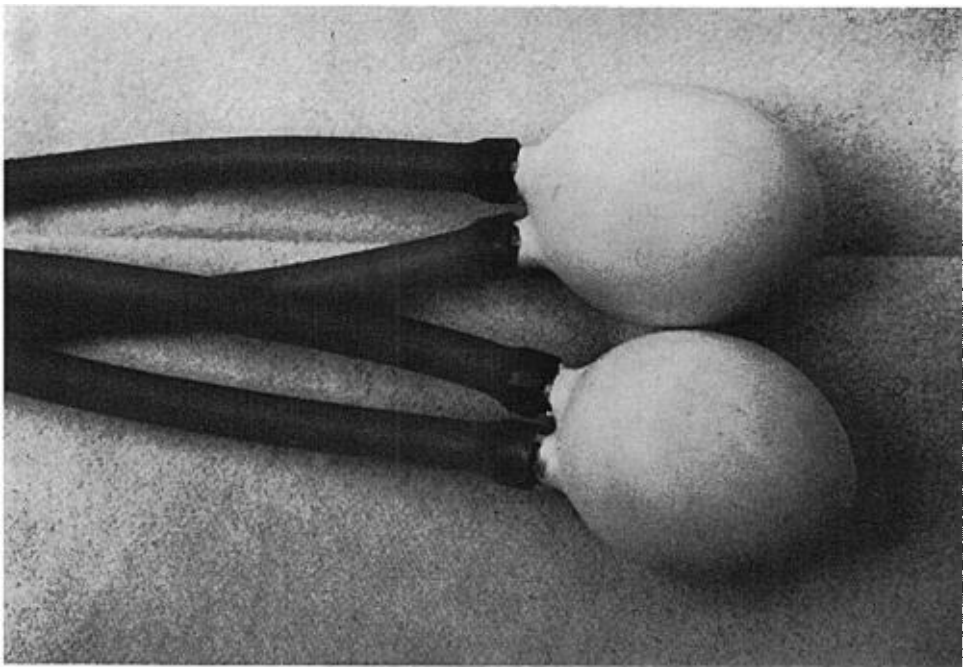

Figure 1. Artificial eggs equipped with rubber tubing.

one reading nearest the normal body temperature indicated the true egg temperature affecting the incubating bird.

The egg temperatures to which the doves were subjected ranged from –4° C (with alcohol added to the cold-water bath) to 62° C. In most tests a given abnormal egg temperature was maintained for less than one hour, during which detailed observations were recorded every minute. On one occasion, however, near-freezing solution was circulated through the eggs for over 39 hours; on another occasion an egg temperature of 46° C (7°–8° C above normal) was maintained for 13 days.

During detailed observations, I recorded the independent variables and, for each minute, which of 20 different activities occurred during that minute. If the incubating bird demonstrated a number of different activities during a minute, all were recorded; but if only one were manifest, only that one was credited to that minute. The activities were defined so that at least one would be occurring at any time. The following activities or conditions were studied.

Building. The pulling, pushing, or manipulating of straws in the nest or within the reach of the incubating bird.

Cooing. The perch *coo*, described by Miller and Miller (1958). It may be paraphrased "Coot, cooteroo-oo."

Eyes-open-but-no-other-activity. A tranquil staring into space. It precludes the occurrence at the same time of any other activity except the condition of feathers-elevated.

Eyes-shut. At least one eye is closed for one second. This may be concurrent with other activities.

Feathers-elevated. By appearance (not necessarily by function), equivalent to the condition described by Morris (1956) as "ruffled," *i.e.*, feathers are fully erected, giving the bird a round but ragged shape (fig. 2).

Footwork. The moving of the feet without turning the body, in an apparent attempt to roll the eggs.

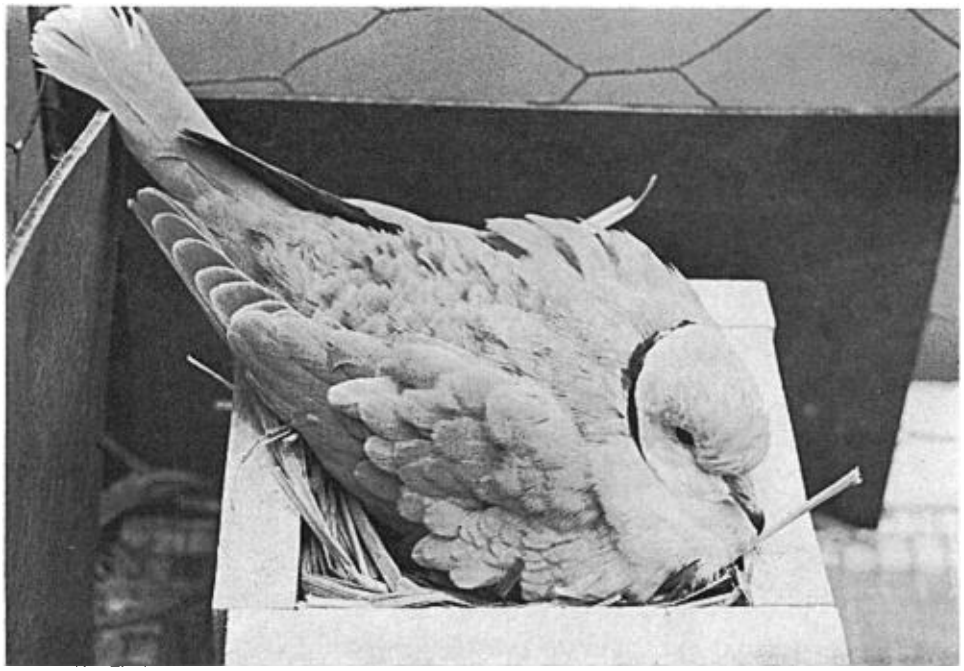

Figure 2. Feathers-elevated with neck shortened, both typical reactions to cold eggs.

Gular-flutter. A rhythmic pulsation of the anterior portion of the throat, accompanied by a slightly opened bill (fig. 3).

Nest-change. The replacement of the incubating bird by its mate, either by the sitter deserting or by the mate forcefully evicting the sitter.

Pecking-at-eggs. A gentle tapping on the eggs, accompanied by a slight standing in the nest.

Pecking-at-nest-box-edge. The idle pecking at bits of dirt on the edge of the nest box.

Preening. The "homopreening" of Miller and Miller (1958), in which the feathers of the body are rapidly manipulated with the bill.

Questioning-bill. A brief period of rapid chewing while the mouth is empty.

Rapid-peering. The active tilting or "searching" movements by the head on an elongated neck.

Scratching-head. A brief series of head-scratching strokes by the toes.

Settling. The rocking of the body from side to side, the degree of tilting decreasing progressively during a period of about a second until the body becomes stationary and usually lower in the nest.

Shaking-head. A brief, rapid, rotating vibration of the head.

Shifting. The hooking of the bill over an egg in an apparent attempt to roll the egg toward the bird.

Shivering. Evidenced by the sustained rapid vibration of the feathers of the wing or body.

Turning. The changing of the bird's directional orientation in the nest.

Yawning. The brief, wide opening of the bill.

To determine whether these 20 activities (dependent variables) were significantly affected by the egg temperature or by other independent variables, an analysis of covariance in a multiple regression program was applied. Therefore, the data were quantified. With two exceptions, the activities were given a numerical value according to the number of minutes in which each occurred during each eight-minute period. That period length was selected because once every eight minutes I could determine the temperature of the egg next to the skin of the bird. The two ac-

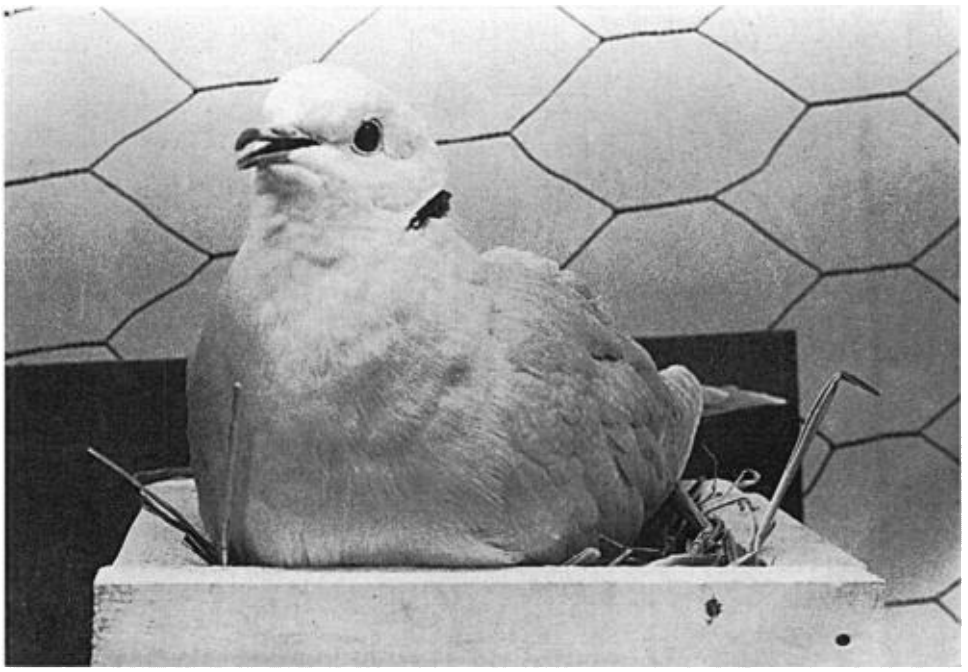

Figure 3. A dove incubating hot eggs. Though the motion of gular-flutter is not shown in this photograph, the concomitant slightly opened bill is apparent. Note that the neck is extended and the feathers are not elevated.

tivities not scored on that basis were feathers-elevated, rated on the estimated degree of elevation (0, 1, or 2), and nest-change, scored on the percentage of minutes of occurrence per experimental period. The independent variables were the day of the season (beginning 1 October), hour of the day, sex, previous nesting experience, number of days since the clutch was laid, the egg temperature, the previous manipulated egg temperature, and the length of time continuously subject to a given egg temperature.

RESULTS

The statistical analysis of detailed data from 380 eight-minute periods of observation showed that the frequencies of 14 of the 20 defined activities were influenced

TABLE 1

NUMBER OF MINUTES OF OBSERVATION INCLUDED FOR EACH TEMPERATURE RANGE

Temperature range °C	Total minutes of observation
−4 to 9	360
10 to 19	280
20 to 29	256
30 to 37	184
38 to 39	1024
40 to 49	800
50 to 62	136

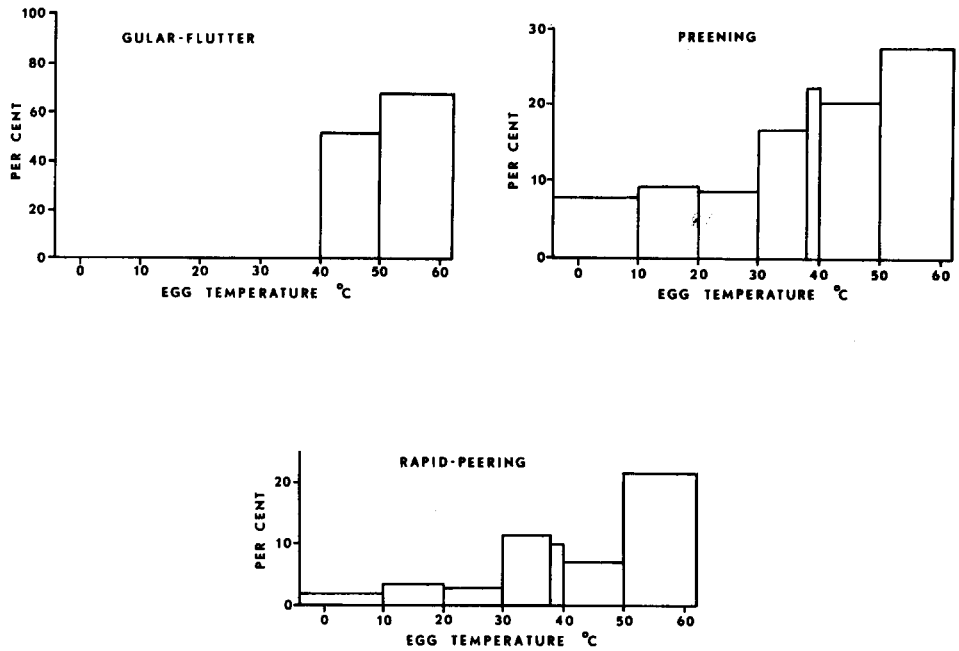

Figure 4. The mean percentage of minutes of occurrence per temperature range for activities associated primarily with high egg temperatures.

significantly ($P < 0.05$) by the egg temperature. For those 14 activities, the graphs in figures 4 to 7 show the mean percentage of minutes in which each activity occurred for seven temperature ranges. The total minutes of observation included in the analysis for each temperature range is shown in table 1.

The frequency of gular-flutter was increased more than the frequency of any other activity by high egg temperatures (fig. 4). It did not occur when the egg temperatures were normal (38°–39° C) or lower, but occurred in two-thirds of the minutes when the eggs were between 50° and 62° C. Usually it did not begin until several minutes after the egg temperature was increased. Preening also became more frequent at higher egg temperatures, its frequency of occurrence rising from 8 per cent of the minutes at the lowest range to 27 per cent at the highest range. The frequency distribution of rapid-peering was similar, although somewhat more erratic. In contrast to these activities which became more frequent at higher egg temperatures, four others became generally more prevalent as the egg temperatures decreased (fig. 5). Most striking were shivering and feathers-elevated, although the direction of the trend in the distributions of eyes-shut and shaking-head is also obvious. Like gular-flutter, shivering and feathers-elevated were delayed responses. The frequencies of footwork, turning, shifting, and nest-change (fig. 6) all show a sudden increase at the highest egg temperatures and a secondary increase as egg temperatures drop below normal. Building activity (fig. 7) was most frequent at egg temperatures just below normal, and questioning-bill had a peak in the 40°–49° C range, but otherwise showed a gradual decrease in frequency as the eggs progressed from cold to hot. Eyes-open-but-no-other-activity was infrequent at the extreme temperatures, indicating the

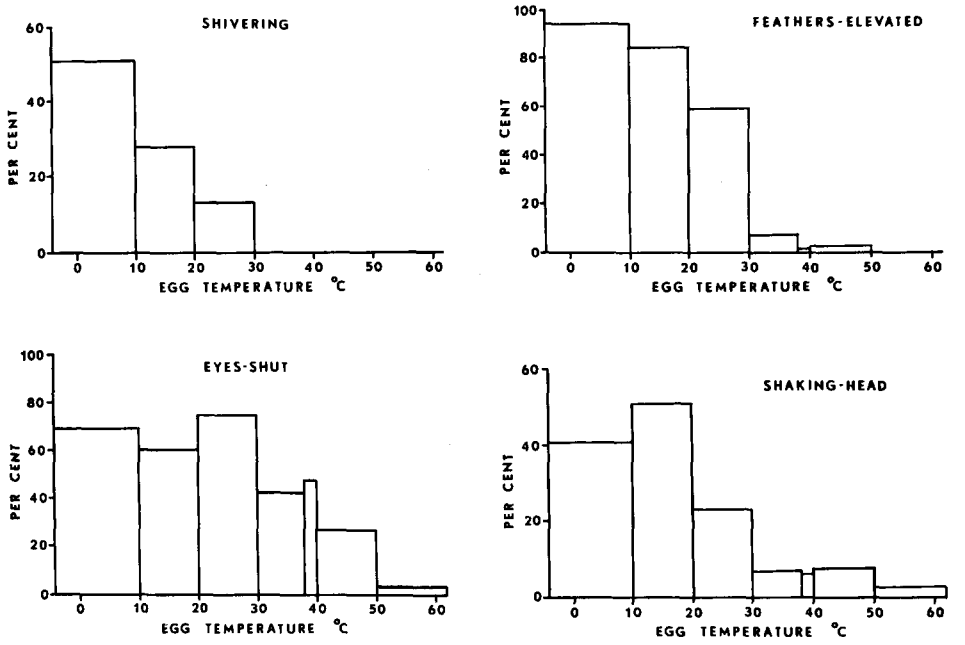

Figure 5. The mean percentage of minutes of occurrence per temperature range for activities associated with low egg temperatures.

increased occurrence of other activities in those ranges. The activities defined previously but not graphed in figures 4–7 (cooing, pecking-at-eggs, pecking-at-nest-box-edge, scratching-head, settling, and yawning) were not significantly influenced by the egg temperature.

The tests in which the eggs were maintained continuously at –3° to 8° C for 39 hours and at 46° C for the first 13 days of incubation showed that the doves incubated with generally the same activities and tenacity during these tests as they did in the routine short-term experiments of similar temperatures.

For most of the analyzed activities, there were significant interactions between sex and egg temperature, indicating that some certain combination of the two produced a frequency of an activity different from that predicted on the basis of simple additive effects. Scheffé (1959) stated, "The interpretation of an analysis of variance is much simpler when we decide (on statistical or other grounds) that there are no interactions." With interactions present in the biological situation, the possibility exists in the mathematical model that the significance of the measured results could be due to the interactions rather than to the additivity of the main effects.

DISCUSSION

The frequency distribution of activities significantly affected by egg temperature is shown in figures 4–7. In spite of high egg temperatures, the birds persisted in incubating the eggs. At the highest egg temperatures (60°–62° C) the birds would settle on the eggs, in several seconds rise up slightly, engage in footwork or shifting,

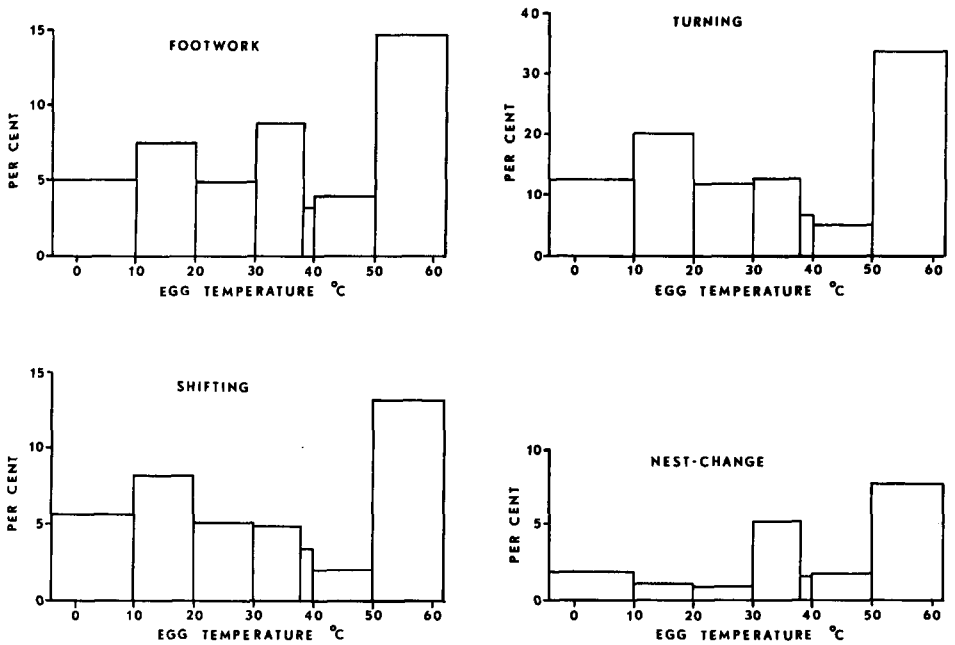

Figure 6. The mean percentage of minutes of occurrence per temperature range for activities showing a sudden increase in frequency at the highest temperature range.

turn a little, and settle again, temporarily. Finally, nest-change may occur. This pattern of response, evident from figure 6, is apparently due to the discomfort of sitting on hot eggs.

Baerends (1959) and Baerends, Posthuma, and Joustra (1960) found that Herring Gulls (*Larus argentatus*) responded to egg temperatures in the 45°–50° C range by ruffling the plumage, increasing the body surface, and increasing the incidence of panting, settling, shifting, building, preening, and standing up. The caged Ringed Turtle Doves did not show feather elevation in response to warm eggs, although an elongation of the neck and rapid peering were evident (figures 3 and 4). Gular-flutter, a mechanical aid to evaporative cooling found in Columbiformes and others (Lasiewski and Bartholomew, 1966), was obvious at high egg temperatures (fig. 4), but true panting was not noted. The other responses by the gulls to warm eggs were shared by the doves except building, which in the doves was decidedly most frequent at subnormal temperatures.

The work on the gulls also showed that eggs cooled to 17°–25° C elicited shivering, fluffed plumage, and swaying; and compared with the warm-egg reactions, a smaller increase in settling, shifting, and preening, as much building, and more quivering. Cold eggs under the doves also caused shivering, a contraction of the neck, and very obvious elevation of the feathers. Secondary increases in footwork, shifting, and turning probably indicated that, at these low egg temperatures, the incubating doves frequently adjusted the contact between the eggs and their skin. Eyes-shut, most frequent when the eggs were cold, was probably not a true "sleeping" action but may have indicated a decreased responsiveness to the rest of the immediate environ-

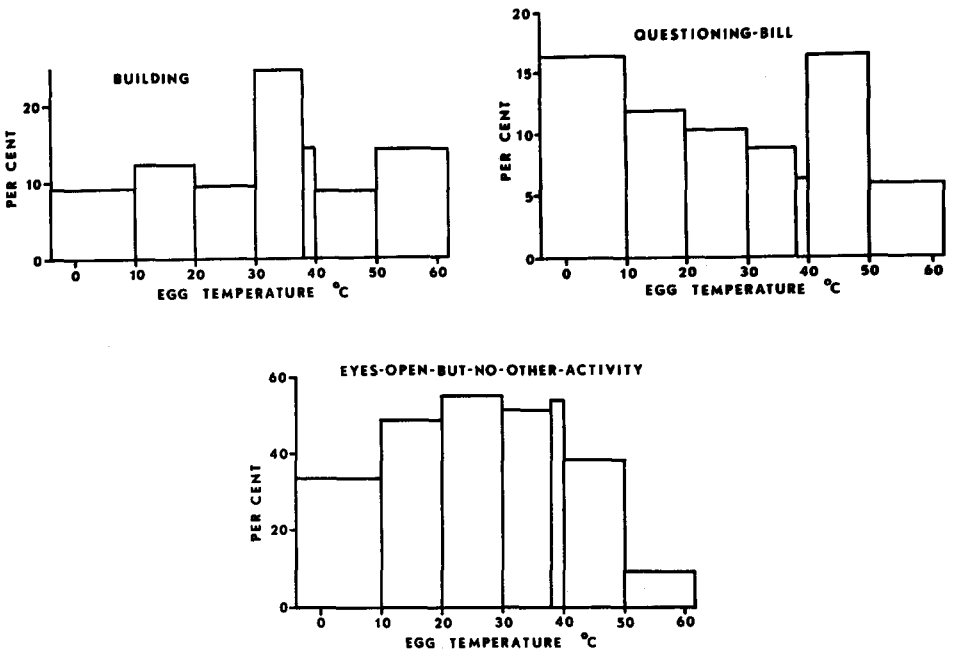

Figure 7. The mean percentage of minutes of occurrence per temperature range for other activities.

ment. Although questioning-bill was frequent in the 40°–49° C range, it was more prevalent at the low temperatures. As suggested by Miller and Miller (1958), this could be a reaction to an unfamiliar situation (thus the term "questioning-bill"). Shaking-head activity was quite pronounced at low egg temperatures. This movement has been called a displacement activity (Moynihan, 1953), and an action to rid the face of foreign objects or a response to psychologically irritating stimuli (Goodwin, 1956). At low egg temperatures, shaking-head activity apparently functioned in shaking the contour feathers free from each other, allowing a greater degree of feather elevation.

SUMMARY

The eggs of caged Ringed Turtle Doves were replaced with artificial eggs through which temperature-controlled water was pumped. Data were gathered on the responses of the incubating doves to the egg temperatures.

The immediate reaction to a newly created abnormal egg temperature is often the adjusting of the contact between the eggs and the skin of the bird. After several minutes gular-flutter may occur if the egg temperature is high, or shivering and elevation of feathers if it is low, indicating that the body temperature has probably been affected by egg temperature. Incubation persisted at all manipulated egg temperatures between −4° and 62° C, even in one instance when the clutch was maintained warmer than body temperature for 13 days and in another when the eggs were near freezing for 39 hours. Therefore, the temperature of the eggs is not an immediate cause of incubation behavior.

ACKNOWLEDGMENTS

The facilities for this research were provided by the Department of Zoology and Entomology at The Ohio State University. Bertram Price arranged the statistical analysis, and computer time was furnished by The Ohio State University Numerical Computation Laboratory. I am indebted to D. E. Davis and L. S. Putnam for critical reading of the manuscript. This paper is condensed from a dissertation presented in 1965 to The Ohio State University in partial fulfillment of the requirements for the Ph.D. degree.

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