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Avian Incubation

Interactions among behavior, environment, nest, and eggs result in regulation of egg temperature.

Fred N. White and James L. Kinney

"The stable, warm temperature for early avian development is common to all climates, and is maintained through an equally common prescription for temperature regulation by parental behavior" (*1*). We will consider herein the nature of some major ingredients which are formulated into this "common prescription" for incubation of the avian egg.

The importance of regulating the thermal environment of the developing embryo has been emphasized by studies on the domestic fowl by Lundy (*2*). He found that the optimal temperature for embryonic development in temperature-controlled cabinets was between 37° and 38°C, and that no embryos survived continuous incubation above 40.5°C or below 35°C. Similar results for domestic fowl, pheasant, duck, and quail were reported by Romanoff and Romanoff (*3*). It is generally recognized that 25° to 27°C is a temperature range below which no development occurs, this being the so-called physiological zero temperature. Incubation for any protracted period between physiological zero and the optimum range results in various developmental anomalies. However, maintenance in suspended development below physiological zero for moderate periods is compatible with later development at appropriate temperatures. This correlates with the observed delay in incubation which may occur between the laying of the first egg and the completion of the full clutch. These results emphasize the scope of the task faced by incubating parents in providing a thermal environment that will ensure successful embryonic development and hatching.

With rare exceptions (*4, 5*), the avian embryo is incubated by an attending adult transferring its body heat to the egg. The mean egg temperature is an approximation of the proper developmental temperature. Huggins (*6*) reported a mean egg temperature of 34.0°C ± 2.38° standard deviation (S.D.) for 37 species representing 11 orders. An extensive study of the house wren, *Troglodytes aedon*, revealed mean egg temperatures well within this range (*7*) while other reports have indicated a range of 34° to 36°C for various species (*8, 9*). The narrow range of mean egg temperatures achieved by diverse species suggests that the thermal requirements for successful development are similar for most if not all birds. This requirement must be met through incubation strategies that compensate for fluctuations in environmental temperature and that allow the attending parents to acquire sufficient food to support metabolism.

The relative responsibilities of parent birds varies from mutualistic sharing of the task to total involvement by one parent for the entire incubation

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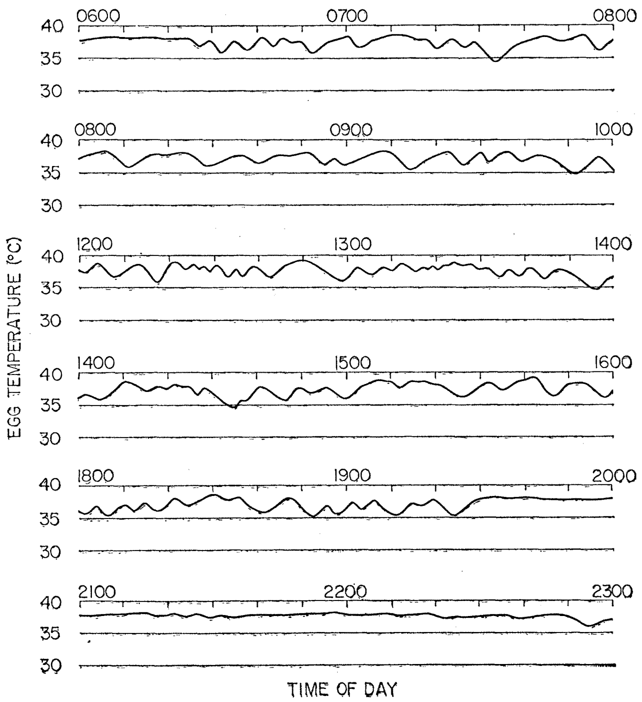

Fig. 1. Portions of a 24-hour record of the egg temperature of the village weaverbird, *Ploceus cucullatus*. Note the contrast between the relatively stable nighttime temperatures and those of the daytime hours when the female alternates between attentiveness and activities away from the nest. Variations in nighttime egg temperature are caused by changes in the contact relationship between the brood patch and the egg (adjustments in tightness of sit). Mean nighttime egg temperature is higher than that for the intermittent incubation pattern associated with the daylight hours.

period. The former, bisexual incubation (primary mode) is exemplified by most marine birds, by many nonpasserine birds in various orders, and by most of the more primitive groups and some advanced taxa within the order Passeriformes. Generally, the eggs of such birds are attended at virtually all times by one or the other parent. Exceptions to constant attentiveness during mild weather have been reported among toucans, puffbirds, barbets, ovenbirds, and some antbirds (*5*). Others engage in single sex intermittent incubation (secondary mode), a strategy in which a single parent, most often the female, divides the time between attentiveness and food gathering, somehow adjusting attentiveness against fluctuations in environmental temperature to regulate egg temperature. House wrens and certain weaver finches are examples of this category. Between these two strategies there exist a number of intermediate situations which we shall refer to as the "intermediate mode." For birds of this category the nonincubating member of the pair may feed the attending mate to a varying extent, depending on the species.

A survey by Van Tyne and Berger (*10*) revealed that, for some 20 families, there appears to be no reliable information on the sex of the parent that incubates the eggs. In 54 percent of the remaining families incubation is performed by both sexes; in 25 percent, by the female alone; in 6 percent, by the male alone; and in 15 percent by the female, the male, or both. Skutch (*5*) has reviewed extensively the division of labor between the sexes during incubation.

The bisexual incubation pattern appears to be the primary or primitive mode from which intermittency has been derived. The intermittent pattern is common among passerines, but members of this group which are considered to be more primitive (*5*) tend to conform to the bisexual pattern. For intermittent incubators there is usually a nest structure of some complexity, while many bisexual incubators may lay eggs in little more than a slight concavity in the substrate. Adoption of the intermittent strategy appears to be coupled with increasing nest complexity, although exceptions exist. The presence of the bisexual mode among the more primitive members of a recent group, the passerines, while intermittency characterizes more modern representatives which have derived varying degrees of nest complexity, strongly supports the contention that the bisexual mode is the more primitive of the two strategies. It is apparent that the intermittent scheme has been adopted a number of times in avian evolution since it occurs in a variety of groups which are not closely related.

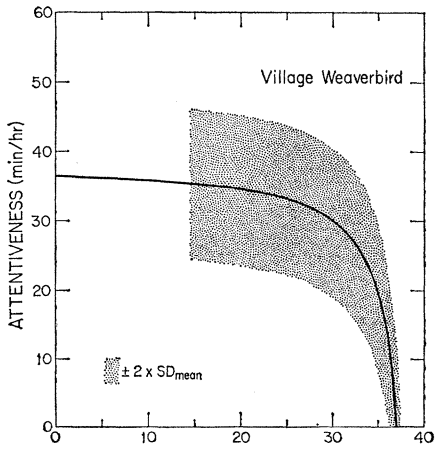

Fig. 2. Relationship of attentiveness and ambient temperature for an aviary-housed colony of village weaverbirds [for derivation of data points, see (*14*)]. There is a large adjustment in attentiveness over the warm range of ambient temperatures but this becomes progressively limited with declining temperature. The attentive curve is described by the equation $Y = (81.8/X - 39) + 38.7$.

One generalization about birds becomes apparent to those who attempt to divide avian behavior into neat categories: there are almost always exceptions. Such are the unusual strategies of the Megapodidae in which nonmetabolic heat sources are utilized for incubation; the emperor penguin, a species in which the male assumes a sole and constant physical association with the egg for the whole incubation period, relying on stored energy while supporting the egg between the foot webbing and the brood patch; and the peculiar hole nesting of the hornbills in which the female is imprisoned behind a mud wall with her eggs where she is periodically fed by the male through a small opening in her cell. Except for the Megapodidae, the relatively few species of birds that show exceptional incubating behavior probably share a fundamental similarity with other birds regarding the basic mechanisms used in the control of egg temperature.

For single sex intermittent incubation, the task of adjusting incubation time against fluctuations in environmental temperature appears to be met by lengthening the periods of attentiveness (time spent on the eggs per unit time) as ambient temperature declines; however, the precise relationship between attentiveness and environmental temperature has remained unclear. Kendeigh (*11*) reported that at an air temperature of 15°C attentive periods of the female house wren averaged 14 minutes, while at 30°C these periods were reduced to 7.5 minutes. Inattentive periods were approximately the same at all but high temperatures, at which they were lengthened. Qualitatively similar observations have been made for the Holarctic wren, *Troglodytes troglodytes* (*12*). Several reports suggest that at air temperatures near the mean egg temperatures reported by Huggins (*6*), attending birds cease to incubate (*9, 13*). For some birds, attentiveness at high temperatures may take on the form of postural shading of the eggs to prevent overheating (*9*).

In this article we consider experimental evidence which elucidates the relationship between attentiveness and ambient temperature in a single sex intermittent incubator, the village weaverbird (*Ploceus cucullatus*). During incubation the female is neither assisted nor fed by the male. Our study, done in an aviary in Los Angeles, afforded us the opportunity of providing the birds with easily accessible food at all times, so that we could control, to some degree, variations in flight distance and food abundance which might affect sortie time, the amount of time spent away from the nest. We also consider the role of nest insulation as a determinant of attentiveness. Implications concerning sensory perception of egg and ambient temperatures are derived from experiments in which sensory receptor mechanisms have been modified by the application of a local anesthetic. By comparing our data with the available data for other species we obtain a generalized scheme for avian incubation from which we can derive information concerning the zoogeographic distribution of breeding birds.

Attentiveness and Environmental Temperature

The efficacy of incubation was assessed through constant monitoring of the temperature of one of the eggs in a clutch (Fig. 1). Such data also yielded information on the division of time between incubation and activities outside the nest (*14*). Typically, the female enters the nest near sunset and remains with her eggs throughout the night. Nocturnal variations in egg temperature reflect adjustments in her "tightness of sit," specifically the physical relationship between the vascular hot spot on her belly, the brood patch (*15*), and the egg; the mean temperature for the eggs is higher and the variation less at night than during the day (*16*). The intermittent pattern of incubation commences with emergence in the morning. By comparing the attentiveness, expressed as minutes per hour, with the shaded air temperature, we observed that attentiveness was related to environmental temperature as previously suggested (*7, 11, 12*). The form of this relationship is by no means a simple one, and we found that the data conformed most closely to the equation $Y - A = B/(X - C)$, where Y is attentiveness in minutes per hour, A is the horizontal asymptote of the curve, X is shaded air temperature, C is the vertical asymptote, and B relates to the curvature of the relationship. The equation describes a rectangular hyperbola (*17*) (Fig. 2). We analyzed our data to discover whether there was a relationship between frequency of attentive bouts and environmental temperature and found none, except at the warm extreme of the curve where there was a sharp reduction in attentiveness. We further analyzed the relationship of egg temperature to attentiveness and frequency for an environmental temperature range of −10° to 40°C (*18*). The degree to which egg temperature varied was highly dependent upon the attentive frequency and the temperature gradient between egg and environment; however, the mean egg temperature depended almost entirely upon attentiveness.

The attentive curve intersects the temperature axis near 37°C where attentiveness becomes essentially nil, a relationship in harmony with several observations from the field for various species (*9, 13*). The range of adjustment in attentiveness is comparatively

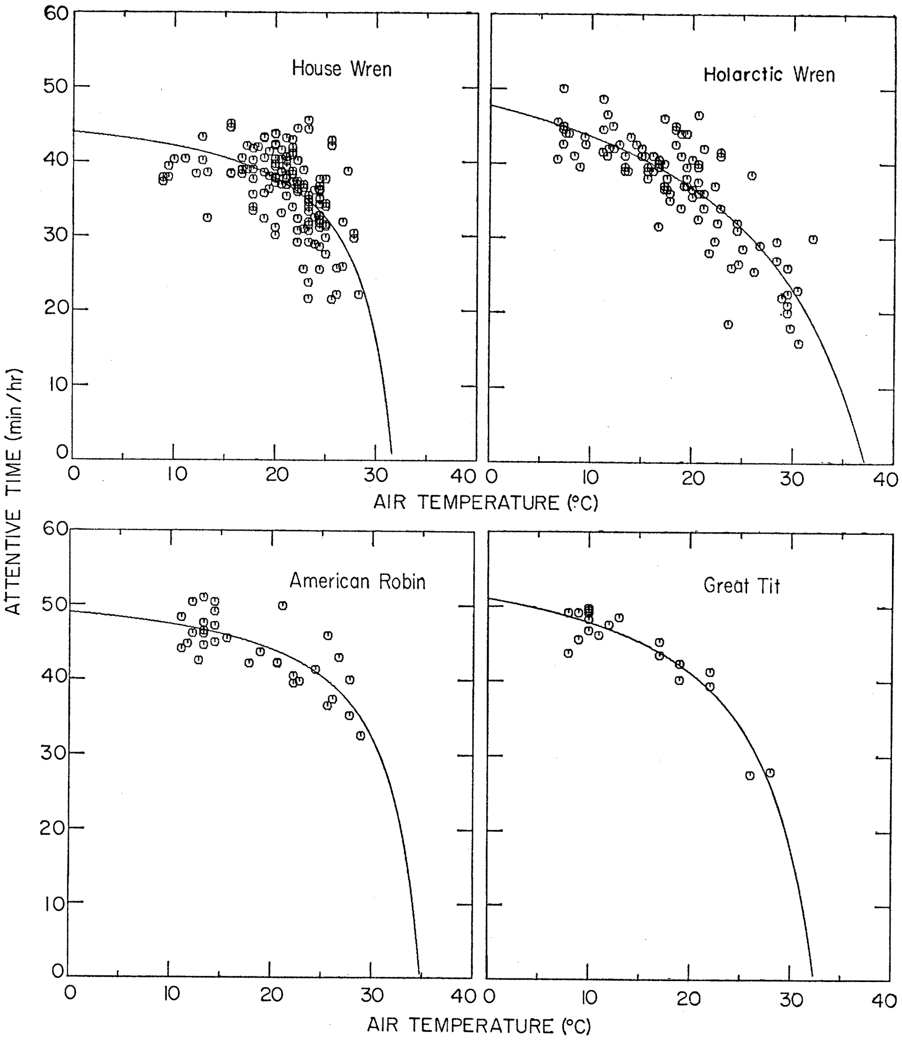

Fig. 3. Attentive behavior of four species of birds in which only the females incubate the eggs (single sex intermittent incubation). Data derived from the house wren (*11*), Holarctic wren (*12*), American robin (*11*), and great tit (*36*). The female great tit may be fed, to a moderate degree, by the male. Values for B, γ, α, A, and C are: house wren, 162, 8.5, 22, 48.6, 35; Holarctic wren, 826, −0.3, 21, 64.2, 50; American robin, 170, 8.3, 25, 535, 38; and great tit, 338, 0.7, 19.7, 60, 38.

large at the warmer end of the curve but becomes increasingly limited at temperatures below that corresponding to the point of maximum curvature (30.1°C) which we have designated α. Thus, as temperature declines, there is a progressive decrease in the time available during a given sortie for activities other than food gathering.

Data on attentiveness as it relates to environmental temperature have been extracted from the literature for four species in which only the females of each pair incubate the eggs intermittently. These data were analyzed by the same method as was described for the village weaverbird. Figure 3 illustrates the basic similarity in the attentive curves for these species, the intercepts on the temperature axis suggesting that "recognition" of a critical temperature for cessation of attentiveness is a common phenomenon. However, these data must be viewed against the different methods used by the investigators. Numerous data were collected for the house wren (*11*), for example, but the ambient temperatures were derived from the mean daily temperatures at a weather station somewhat removed from the study site. For the Holarctic wren (*12*), the temperature data were more satisfactory, representing hourly means at the site, but only a single individual was studied. Thus, high reliance on the precise form of these curves and their intersects is not warranted.

The more extensive data on the village weaverbird permit a useful comparison of the intercept temperature for zero attentiveness with egg temperatures both during the day and the night. The intercept of 37.0°C (95 percent confidence interval, 1.2°C) for our group coincides closely with the mean maximum daytime egg temperature of 36.7°C ± 1.5° (S.D.) and the mean maximum nighttime egg temperature of 36.7°C ± 1.4° (S.D.). The standard deviations reflect more the variations in the maximum egg temperatures among the animals (*19*) than great variation for given individuals. There is close coincidence of the peak egg temperatures and the environmental temperature at which attentiveness ceases. This suggests that the sensory mechanisms utilized in reducing attentiveness as the egg reaches a "release" temperature may also be employed in the assessment of the external thermal environment.

Nest Insulation and Attentiveness

The cooling rates of the eggs within different nests provide us with a useful index of nest insulation (*20*). Among our weaver finches, we found a variety of cooling rates and we have normalized the attentiveness for these birds at 25°C, the mean daytime temperature for our study (*21*). By plotting cooling rate against the attentiveness at 25°C we obtained a relationship (Fig. 4A) which points up a role for insulation as a determinant of attentiveness. Birds with nests that were relatively well insulated exhibited less attentiveness, and had greater time available for both food acquisition and activities unrelated to food gathering than did birds with less insulated nests. Insulation may well be a manipulatable factor through which breeding range can be extended altitudinally or into colder climates, other critical factors being equal. The variability in the insulation of our weaverbird nests suggests that a range of nest construction potentialities are available for natural selection.

That birds utilizing well-insulated nests spend less time incubating their eggs than do those whose nests are not so well insulated indicates that the mean attentive curve which we have derived (Fig. 2) is in reality a composite of several attentive curves having similar intercepts but different curvatures. The asymptotes of the attentive curve serve to locate the curve, while the *B* value dictates the curvature. The insulative component is reflected by *B*, large *B* values (*22*) being associated with high indices of insulation (Fig. 4B).

The massive amounts of data on the regulated mean egg temperatures for various species (*6–9*), and the observations that some species cease to incubate at or near this temperature (*9, 13*), make us confident that the intercept on the temperature axis is not a significant major variable. Food abundance and availability have been controlled in our aviary study; however, one can appreciate that variation in the flight distance to food, or in food density, would strongly affect the parent's ability to provide an attentive relationship appropriate to successful incubation. Long flight distance to a poor food source and relatively poor nest insulation would rapidly become incompatible as ambient temperature declined. A comparison of nest materials utilized by *Ploceus cucullatus cucullatus* and its relative, *P. c. graueri*, that lives at a higher altitude, revealed that the nests of *P. c. graueri* contained a much thicker and better insulated lining (*23*). Similarly, the high-altitude hummingbirds, *Oreotrochilus chimborazo* and *O. estella*, appear to build nests of greater bulk than do their low-altitude relatives (*24*). The difference between the attentive curves for the wrens, *Troglodytes aedon* and *T. troglodytes* (Fig. 3), may be attributable to nest insulation rather than inherent differences in attentive behavior. The extraordinarily high *B* value for the Holarctic wren should be indicative of a well-insulated nest. In their description of the nest of the individual utilized in their study, Whitehouse and Armstrong (*12*) stated that the nest was built "on the disused nest of a robin in a cycle saddle-bag hanging on a nail in a summer-house," a description compatible with the high *B* value characterizing the attentive curve.

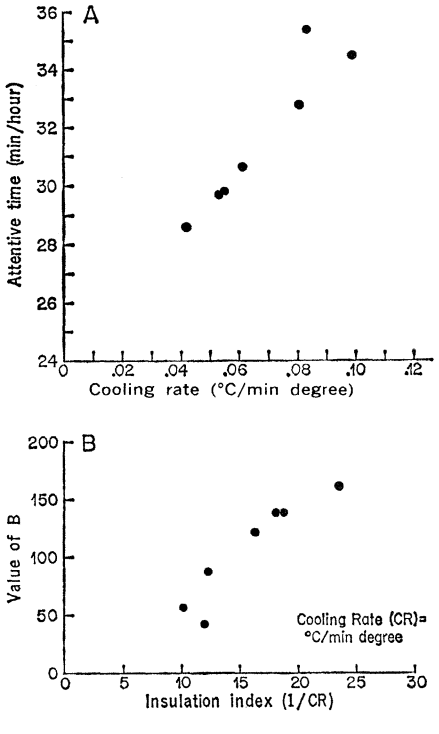

Fig. 4. (A) Relationship of attentiveness to the cooling rates of eggs in nests with different insulative properties among village weaverbirds. Data were normalized to the mean daytime temperature of the study, that is, 25°C. (B) Relation of the *B* value in the equation describing attentiveness $[Y - A = B/(X - C)]$ to the index of insulation for the various nests.

Mean Egg Temperature and Embryonic Heat Production

Empirically determined rates for heating and cooling of individual nest-egg complexes, and records of egg and environmental temperatures, were utilized to obtain the maximum, minimum, and mean egg temperatures characteristic of the birds in our study (*25*). The mean egg temperature was determined from predicted values for egg temperature based on a few critical values for each cycle. The close correlation between our predicted values and the actual record is shown in Fig. 5. The 24-hour mean egg temperature for the village weaverbird was 35.9°C ± 1.5° (S.D.). During the nighttime, mean egg temperature was 36.5°C ± 1.5° (S.D.) while the daytime mean was 35.3°C ± 1.6° (S.D.). The higher egg temperatures at night are associated with the constant physical relationship of the parent with the eggs during this period. Our data suggest that the mean egg temperature of 34°C ± 2.38° (S.D.) reported by Huggins (*6*) is an underestimate of the 24-hour mean egg temperature for the series of birds in his study. It seems likely that two complications contributed to this underestimate; first, the measurements were made during daylight hours, and, second, some cooling of the eggs may have occurred between the departure of the attending parent and measurement of the egg temperature. Our daytime mean egg temperature of 35.3°C corresponds rather closely to the figure of 35°C which Kendeigh has suggested as characteristic of passerine species (*26*). Dual sex incubators presumably maintain the eggs at a higher temperature by virtue of their essentially constant attentiveness. A temperature of 37.5°C appears to characterize the herring gull egg (*27*).

Upon examination of our data on mean egg temperature it became apparent that, at the higher range of ambient temperatures (30°C and above), the sample size was too small for us to evaluate the exact nature of the curve. To better appreciate this relationship, we determined the mean heating and cooling rates of eggs and calculated the effect of the observed mean attentiveness on egg temperature over a wide range of environmental temperatures (*18*). This curve revealed that mean egg temperature should be relatively stable at 37°C between point α and the intercept of attentiveness and ambient temperature (31° and 37°C, respectively). We have designated this zone as the zone of stable regulation (Fig. 6). Above an ambient temperature of 37°C, ambient and egg temperatures are coincident when incubation ceases. The predicted mean egg temperature for the zone of stable regulation and the mean egg temperature observed were 37°C and 36.9°C, respectively. At ambient

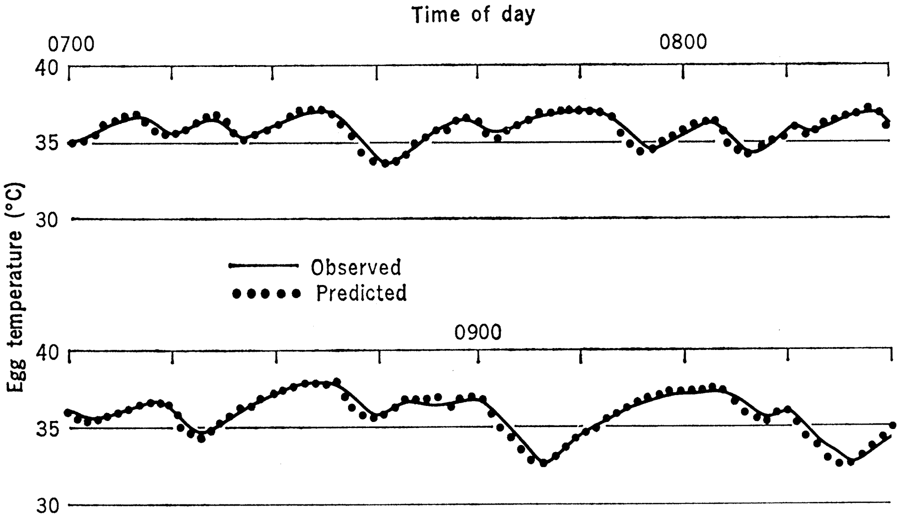

Fig. 5. Comparison of empirically determined egg temperature with that predicted from the mean heating and cooling rates of the egg, ambient temperature, and attentiveness (*25*).

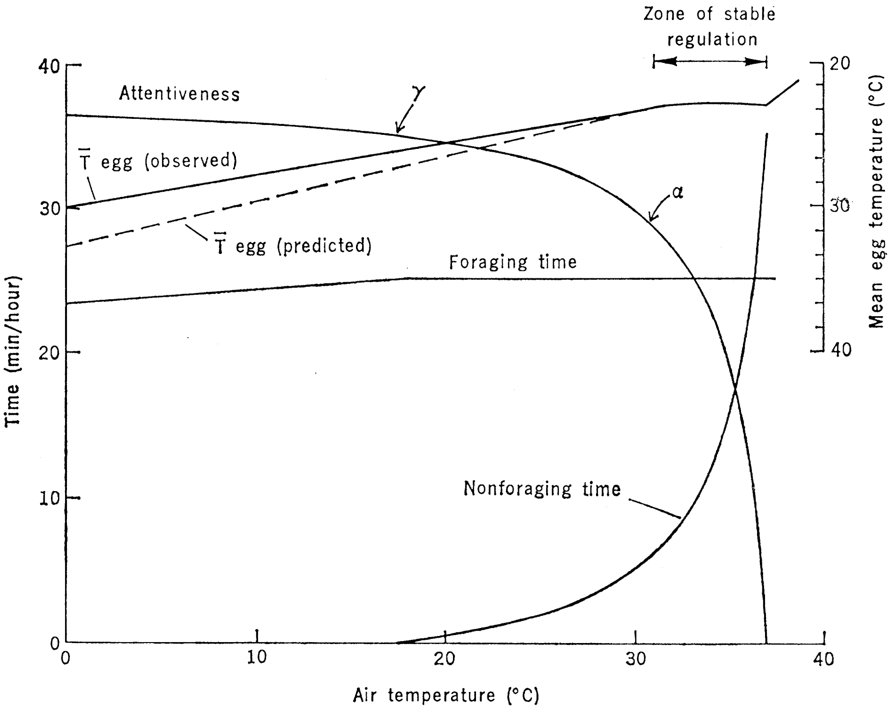

Fig. 6. The mean attentive curve for a village weaverbird colony. The point of greatest curvature, α, corresponds to the lower ambient temperature for stable regulation of egg temperature; γ is the point on the attentive curve at which the mean egg temperature is 34°C. Maintenance below this temperature for a protracted period of time is likely to be incompatible with normal embryonic development. Derivation of the division of nonattentive time as a function of ambient temperature reveals that nonforaging time is adjusted, as a reserve, in favor of stable foraging time and increasing attentiveness at ambient temperatures above γ. Below γ a progressive recruitment from foraging time is mandatory if the attentive relationship is to be maintained.

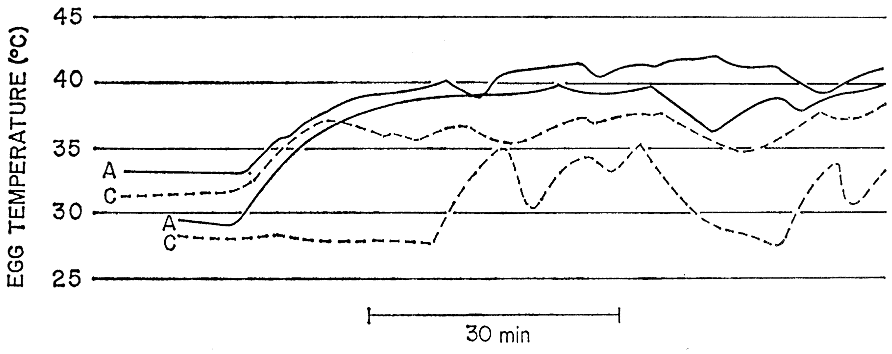

Fig. 7. Effect of injecting the brood patch with a local anesthetic (*A*) on attentiveness and egg temperature. Injection of saline, as a control (*C*), was followed by resumption of a pattern of incubation more characteristic of undisturbed birds. The experiment suggests that a low level of discharge from receptors located in the skin covering the belly intensifies attentiveness and elevates egg temperature.

temperatures below 31°C the predicted mean egg temperature was slightly less than that observed.

Drent (*27*) demonstrated for the herring gull egg that heat production is positively correlated with the weight of the developing embryo. At an incubation temperature of 38°C, heat production exceeded heat loss after day 13, and by day 27 a gradient of + 2.69°C was evident. Qualitatively similar results for the duck egg were obtained by Khaskin (*28*). Thus, embryonic heat production facilitates heating and retards cooling. As a result, the release temperature (the temperature at which the bird can leave the nest) should be reached progressively faster as embryonic development proceeds. This effect probably causes a progressive decrease in attentiveness over the incubation period. Embryonic heat production ought to have an effect similar to an increase in insulation: hence, the *B* value for the attentive curve should increase. The magnitude of this effect on attentiveness is unknown; however, in late embryonic development, it may be sufficient to provide a significant increment in foraging time.

Adjustments in Attentiveness with Environmental Temperature

Nonattentive behavior may be divided into two categories: foraging (behavior related to food acquisition) and nonforaging (social interaction, preening, for example). It is apparent that the time available for nonforaging behavior is maximized at temperatures requiring a minimum of attentiveness. As temperature declines, the ratio of foraging to nonforaging must increase if metabolism is to be maintained, while attentiveness increases in support of the regulation of egg temperature. This effect of low ambient temperature is inferred from observations made on the Alaska wren when it was incubating at low ambient temperatures and high latitudes (*29*). A high degree of precision in the timing of feeding sorties of 2 to 5 minutes' duration was reported while attentive periods exceeded 20 minutes. Flight was said to be direct. Predictable food supply and good nest insulation may conjoin to allow energetic balance when foraging time is limited.

Birds do not appear to increase their heat production to support incubation except at temperatures which induce shivering thermogenesis (*30*). Rather, it is the percentage of time spent on the eggs that is adjusted. By recruiting time for incubation from nonforaging activities, a bird may adjust attentiveness with no decrement in foraging activities as long as a reserve of nonforaging time remains available. As ambient temperature falls, this reserve must, of necessity, decrease.

Because the greatest fluctuations in egg temperature occur during the daytime in single sex intermittent incubators, it is reasonable to assume that the daytime mean egg temperatures, observed under natural conditions, should represent temperatures compatible with successful development. From available data on daytime mean egg temperatures of passerine birds, 34°C appears to represent a temperature approaching the lower limit for successful hatching. Data on mean egg temperature and attentiveness are available only for the village weaverbird and the house wren. We have located a point, γ, on the attentive curves for these birds, which corresponds to a mean egg temperature of 34°C (see Fig. 6). At ambient temperatures below this point, the attentive curve is essentially linear. This apparent linearity suggests that the influence of multiple factors as determinants of nonattentiveness has effectively disappeared. The second derivative of the weaverbird attentive curve at γ is -0.015. For the house wren this value is -0.009. We think that, in the absence of data on mean egg temperatures, the locus of the second derivative of the attentive curve corresponding to the mean value of -0.012 should approximate an environmental temperature at which the mean egg temperature is 34°C. This value should become increasingly refined as more data become available for species in which only one sex incubates the eggs intermittently. Therefore, successful incubation should be limited to geographic areas in which the mean daytime temperature exceeds that for γ.

It is reasonable to assume that the nonattentive activities at temperatures below γ are devoted to foraging behavior, because the attentive curve approaches linearity at temperatures below γ and it is unlikely that foraging would be sacrificed in favor of activities not related to the acquiring of energy. For heuristic reasons we have assumed that nonforaging activities have become nil at this temperature. We also assume that foraging time is relatively stable and is sufficient to maintain metabolism over the temperature range in which nonforaging behavior occurs. With this in mind we have calculated the division of time spent in foraging and nonforaging activities at various environmental temperatures (Fig. 6). Over the zone of stable temperature regulation the strategy is to draw heavily on nonessential activities in favor of attentiveness. At temperatures below α, most of the nonforaging time has been utilized and attentiveness is adjusted less and less with declining temperature. This results in a decline in mean egg temperature. Since we have deduced that nonforaging time is nil at γ, any increment in attentiveness at lower temperatures must be gained at the expense of foraging time. The strategy of compromising both attentiveness and foraging time at such temperatures is indicated. These considerations suggest that there is a critical range of temperatures below γ, and that within this temperature range, the energy stores of the attending bird must be utilized if the attentive relationship is to be maintained. A single sex intermittent incubator attending its eggs for a protracted period of time at temperatures below γ would be expected to lose weight, extend the incubation period, or fail to provide the thermal conditions necessary for a successful hatch. For several domestic species, prolonged incubation below 35°C is incompatible with the hatching of viable young. When the zebra finch, *Taeniopygia castonotis*, incubated eggs at an environmental temperature of 14.5°C, all the embryos died. The birds were unable to acquire sufficient energy for the maintenance of the eggs at the temperature appropriate to successful development (*31*).

Sensory Receptors and Attentiveness

The body heat of an attending parent is transferred to its eggs by way of the brood patch. Drent *et al.* (*32*) observed that herring gulls adjusted their contact with artificially heated or chilled eggs, while we observed adjustments in tightness of sit during the nighttime sessions. These observations suggest that the brood patch may contain sensory receptors that provide the parent bird with information concerning egg temperature. We investigated this possibility by anesthetizing the skin of the brood patch, by topical application or subcutaneous injection of 2 percent Xylocaine (Astra). To control for the disturbing influence of capturing the birds and applying the anesthetic, we injected the brood patches of two incubating birds with saline in an identical manner. As shown in Fig. 7, birds with anesthetized brood patches incubated their eggs more intensely than control birds, and their eggs reached the highest temperatures which we have observed. Such birds appeared to spend unusually little time away from the eggs. Although our data are somewhat limited, we conclude that sensory receptors that influence attentiveness reside in the skin of the brood patch, and that a low frequency of discharge in these receptors encourages attentiveness. Whether these same receptors are responsive to the thermal environment when the parent is away from the nest is not known.

Modulation of Attentiveness: A Summary

We have summarized the probable interactants determining attentiveness for both dual sex (primary mode) and single sex intermittent (secondary mode) incubators in Fig. 8. Cases in which the female incubates the eggs but is periodically fed at the nest by the male, or in which the fat reserves of the attending parent are sufficient to allow protracted incubation, constitute an intermediate mode of incubation.

In the primary mode the principal means of regulating egg temperature is through adjusting tightness of sit. Such adjustments appear to involve detection, through brood patch receptors, of differences between a reference temperature near that of the core of the adult and the surface temperature of the egg. Release from incubation depends upon the intensity of factors competing with the incubation drive. The most important of these competing factors are hunger, the presence and behavior of the relieving parent, or both.

The secondary mode, during nighttime periods, resembles the incubation pattern of primary mode birds in that it is the tightness of sit which is adjusted during this period of protracted attentiveness. The photic environment appears to induce the parent to enter the nest at night. In order to maintain metabolism, a single sex intermittent incubator must spend periods away from the nest during the day when foraging is possible. Other drives, such as social interaction, preening, and so forth, may also be present. Like Baerends (*33*), we view these drives as factors of varying intensity which compete with attentiveness. Hence, satisfaction of these drives favors the expression of attentiveness. The intermediate mode of incubation, in which attentiveness is relatively protracted, appears to depend upon the amelioration of hunger through utilization of fat stores or feeding of the attending bird by a mate. In this situation the dependency of attentiveness on ambient temperature decreases, and in some cases may show little or no relationship with ambient conditions. Regulation of egg temperature, although provided by one parent, may resemble the pattern of dual sex incubators in which tightness of sit determines egg temperature. Thus, although there is a considerable range of incubating patterns among birds, all species are likely to share common sensory mechanisms for regulating physical contact with eggs.

Because they lay their eggs, birds must behave in such a way that they maintain the eggs at a temperature compatible with embryonic development. When eggs are incubated by both members of the pair bond, the egg temperature in regulated within a rela-

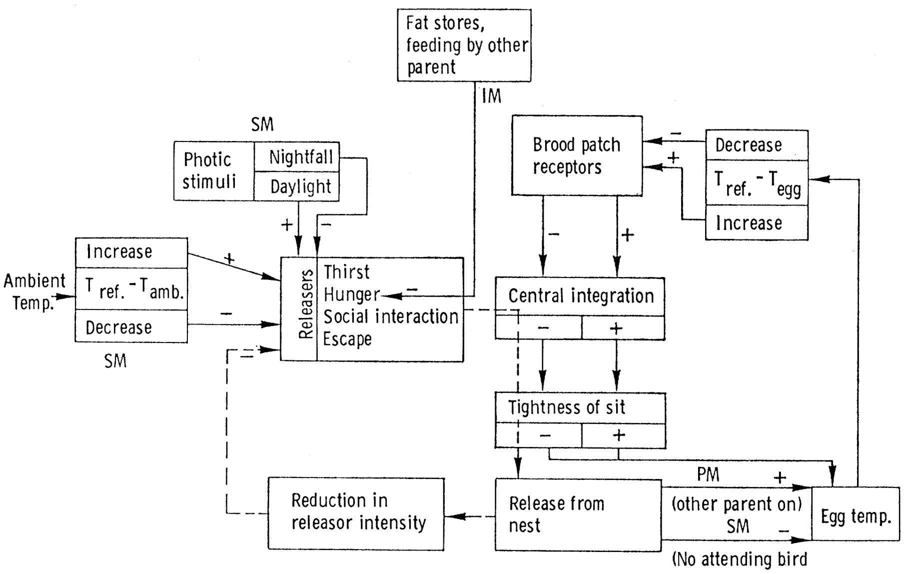

Fig. 8. A generalized scheme for avian incubation. The scheme emphasizes the role of competitive interplay among centrally integrated information related to egg temperature and releasers favoring nonattentiveness. *PM*, *SM*, and *IM* indicate aspects applying specifically to primary mode, secondary mode, and intermediate mode patterns of incubation.

tively narrow range. Overheating or underheating is prevented by central neural modulation of the tightness of sit. The almost constant attentiveness to the eggs provided by bisexual incubation has certain obvious advantages. Among these is the protection against predation of the eggs by other species or by members of the same species. Further, the constant attentiveness of parents effectively ameliorates the influence of fluctuations in environmental conditions. This is especially important for marine birds which must often forage at great distance from their nesting grounds.

The adoption of the single sex intermittent, or secondary mode of incubation, requires of the attending parent periodic foraging excursions away from the eggs. While unattended, the eggs tend to equilibrate with the environmental temperature, at a rate depending upon the heat-retaining capacity of the egg-nest complex; an attending bird must therefore adjust attentiveness in accordance with the temperatures of its habitat and the degree to which it has insulated its nest. The contribution of nest insulation is best expressed by the value B which reflects the curvature of the hyperbolic attentive curve (Fig. 4B). Eggs may be regulated at relatively constant mean temperatures over a rather limited range of warm environmental temperatures by the parent adjusting the time it uses for nonforaging behavior while it is away from the nest. At ambient temperatures below α (see Fig. 6), the mean egg temperature declines because the reserve of nonforaging time has been largely exhausted. At environmental temperatures below γ (Fig. 6), the foraging time must be sacrificed if the attentive relationship is to be maintained. Periodically, environmental temperatures may fall below γ and development will not be affected; however, geographic zones characterized by daily mean temperatures below that indicated by γ are likely to mitigate against successful reproduction. The position of γ is suggested as a means of approximating the lower mean daytime temperature compatible with hatching of the clutch. Furthermore, in the absence of data on the egg temperature, a line projected from a mean egg temperature of 34°C located at γ to 37°C located at α should provide a reasonable estimate of mean egg temperature at any environmental temperature below that corresponding to α.

Other ecological factors being equal, species engaging in single sex intermittent incubation could use several temperature related strategies to extend their breeding ranges into cooler climates. Examples of such strategies are as follows: (i) Nest insulation could be augmented through the use of more or different materials; this would result in a greater B value for the attentive curve and a concomitant shift to cooler areas of the curve of both α and γ. (ii) Nesting sites could be selected in close proximity to a predictable supply of food; this would allow closer adherence, by the attending parent, to the attentive relationship necessary for achieving a successful hatch. (iii) The male could become a provider of food for the incubating female or, as in the case of high-altitude hummingbirds in South America, the species could revert to a dual sex mode of incubation (*34*).

Birds engaging in the intermediate modes of incubation may rely upon large fat stores for support of metabolism so that a single parent may indulge in constant attentiveness throughout the entire incubation period. The male emperor penguin is the classic example of this pattern. Pheasants and chickens rely heavily upon their capacity to fast for periods far in excess of that tolerable for small passerine birds. With the exception of infrequent periods away from the clutch for feeding, their pattern of incubation is similar to that seen in bisexual incubators. As with single sex intermittent incubators at night, or bisexual incubators at all periods, adjustments in tightness of sit characterize the way in which egg temperature is regulated. In other species, the nonincubating member of the pair bond may feed the incubating parent. The necessity for foraging is thus reduced to the extent that the energy requirements of the attending bird are met by a helpful mate. The pattern of egg temperatures for such birds should resemble those of bisexual incubators in that the variations around the mean temperature should be slight in comparison to single sex intermittent incubators.

The evolution of nest complexity, although undoubtedly related to the protection of eggs from such factors as wind, rain, and predation, also appears to be related to selective pressures favoring the augmentation of insulation. In addition to attenuating changes in egg temperature while the attending birds are foraging, the nest structure provides an environment in which the energy reserves of the incubating bird may be conserved at ambient temperatures below the thermoneutral zone (*35*). This factor is critical for small passerine birds which must fast overnight within the nest when the external temperatures reach their minima. In the population of weaverbirds that we studied, the range of cooling rates of eggs in different nests suggests that these birds possess a spectrum of nest building potentialities which influence insulation. This variation is available for natural selection and indeed appears to have been one of the factors allowing for altitudinal extension of the breeding range for *Ploceus cucullatus graueri* and some Peruvian hummingbirds. The insulation of the giant nest of the sociable weaverbird appears to be a critical factor in allowing opportunistic breeding during the cold winter of the Kalahari desert (*35*).

Further studies of the complex interactions among climates, nests, eggs, and parent birds should yield greater insight into the zoogeographic distribution of breeding ranges and provide a more complete appreciation of the "common prescription" for temperature regulation of the avian egg by parental behavior.

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14. Attentive times were determined from temperature recordings from thermistors or thermocouples positioned to measure temperature in the nest cup or implanted near the center of an egg in the nest cup. Attentive intervals were tested against visual records and were found to be accurate within ± 15 to 20 seconds. Values for attentiveness represent the total time "on" for the number of complete "on-off" cycles required to satisfy a minimum time interval of 60 minutes. The ambient temperature reported with each attentive value is the average shaded air temperature during that interval. Because of the nature of the daily temperature fluctuations, it was

judged that the daily mean temperature was not always representative of the ambient conditions to which the animals were exposed. For intervals greater than about 60 minutes, the variance for ambient temperature increased greatly for some intervals. For intervals shorter than about 40 minutes, variation in cycle length greatly increased the scatter for the attentiveness-temperature relation. The 60-minute interval appears to agree with that employed by Whitehouse and Armstrong (*12*).

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16. The mean nighttime temperature for all animals ($N = 13$) was 36.5°C and the standard deviation for individual mean egg temperature ranged from 0.3° to 0.8°C. The mean temperature for each egg was derived from 15 to 36 measurements. Comparable figures for daytime were as follows: when $N = 15$, the mean temperature was 35.3°C and the range of standard deviations was 0.8° to 1.7°C; the means were obtained from 19 to 117 measurements.
17. Data were coded for linear regression where $X = 1/(\text{air temperature} - C)$ and constants, B and A, in the equation $Y = BX + A$ were determined by Bartlett's three-group method for model II regression [R. E. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969), pp. 483–485]. The value of C was determined by a process of reiteration whereby A and B were calculated for each value of C. The constants for the equation of best fit were derived from the values, C, A, and B, which produced the least sum of squares when tested against the uncoded data. For derivation of values for attentiveness (Y) and temperature (X), see (*14*).
18. From the rates of heating and cooling of eggs and from the attentiveness, the minimum, maximum, and mean egg temperatures can be calculated as a function of cycling rate and ambient temperature if brood patch or body temperature can be assessed or estimated (estimated to be 41.5°C). At steady state, the egg must heat as much as it cools. Therefore $T_{E,0}(i) = T_{E,0}(i+1)$, where $T_{E,0}$ is the egg temperature at the start of heating; therefore,

$$T_{E,0} = \frac{T_A + (T_B - T_A)e^{B_c(1-Y)/F} - T_B e^{B_h Y/F + B_c(1-Y)/F}}{1 - e^{B_h Y/F + B_c(1-Y)/F}}$$

where $T_{E,0}(i)$ is the egg temperature at the start of heating for some cycle (i); $T_{E,0}(i+1)$ is the egg temperature at the start of heating for the following cycle ($i+1$); T_A is ambient temperature; T_B is brood patch or body temperature; B_c is the rate of cooling of the nest-egg complex; Y is attentiveness, determined by (minutes on/60 minutes)/60 minutes; F is the cycling rate (expressed as cycles per minute); and B_h is the rate of heating of the nest-egg complex. The mean egg temperature can be found as a quantity: the integral of egg temperature during heating plus the integral of egg temperature during cooling, divided by the time for one cycle. The following equation yields the steady state value for mean egg temperature as a function of ambient temperature and cycling rate:

$$T_E = 1/F\left[\int_0^{Y/F} T_E\,(t) + \int_{Y/F}^{1/F} T_E\,(t - Y/F)\right]$$

$$= T_A + (T_B - T_A)\left[\frac{Y + F\left(1 - e^{B_h Y/F}\right)\left(1 - e^{B_c\,(1-Y/F)}\right)}{\left(1 - e^{B_h Y/F + B_c(1-Y)/F}\right)\left(\dfrac{B_c - B_h}{B_c B_h}\right)}\right]$$

where t is time. At steady state, the maximum egg temperature is given by the equation

$$T_{E,m} = T_B - (T_B - T_{E,0})e^{B_h Y/F}$$

19. A single class analysis of variance showed a significant variation for mean egg temperatures among birds ($P < .001$).
20. We use the term "insulation" loosely to mean the heat-retaining properties of the egg-nest complex.
21. A single class analysis of variance showed a significant difference among cooling rates of eggs ($P < .001$). This finding prompted us to take a closer look at the attentiveness-temperature relationship. Data points for attentiveness were corrected to the mean daytime ambient temperature for our study (25°C) according to the equation: $Y_{\text{corrected}} = Y_{\text{actual}} + B[25 - 1/(T_A - C)]$, where Y_{actual} is the attentive time in minutes per hour and T_A is the corresponding ambient temperature; B is 81.8 and C is 38.7. A one class analysis of variance showed a significant difference for attentive times among animals ($P < .001$).
22. A family of attentiveness-temperature curves was derived for some of the birds in our study for which cooling rates were determined and background disturbances were judged to be minimal. It was not possible to employ the method described in (*17*) to determine the individual attentiveness-temperature curves because the range of ambient temperatures for a given day was usually too small. However, an estimate of the B value of the curve for each animal was found by fixing two points and a limit. One point represented the mean ambient temperature and the mean attentiveness for a given animal for 1 day. The second point represented the X-intercept for our attentiveness-temperature curve which was derived from the pooled data. We think that this value is of biological significance and preferred to use it rather than a limit, the vertical asymptote. On the other hand, the Y-intercept appears to be a point of mathematical convenience, hence we preferred to set the upper limit of the curve by employing the horizontal asymptote calculated for the pooled data. Thus for the equation $Y - A = B/(X - C)$, we estimated B and C for each animal assuming: $A = 38.7$; that at $Y = 0$, $X = 37$; and that at $X =$ mean ambient temperature, $Y =$ mean attentive time for a given animal on a given day. From the family of attentiveness-temperature curves, the attentive time at $T_A = 25$°C was plotted as a function of cooling rate. The product moment of correlation was 0.942 [$R_{(\alpha=0.01)} = 0.917$]. The individual B values were plotted as a function of 1/cooling rate (insulation index), and the corresponding product moment of correlation was 0.937 [$R_{(\alpha=0.01)} = 0.917$].

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