INCUBATION AND BODY TEMPERATURES IN THE YELLOW-EYED PENGUIN

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Although the ornithological literature now contains a substantial body of information on body temperatures and incubation temperatures, our knowledge of these for the penguins remains rather limited. Because of the divergent systematic position of this group, such data have considerable intrinsic value and interest. Of interest beyond this is the behavior of the body temperature during the protracted molt of several weeks during which there is no intake of food and water, and during incubation when there may be appreciable periods (one to five days in the Yellow-eyed Penguin) without food or water. Also of interest is the relation of the incubation temperature to the relatively long incubation periods of penguins, particularly in light of the very high degree of attentiveness.

During the spring and summer of 1953–54 I was able to obtain a series of data on the incubation and body temperatures of Yellow-eyed Penguins (*Megadyptes antipodes*) mostly in a breeding colony at Sandfly Bay on the Otago Peninsula of the South Island of New Zealand. Supplementary investigations were made at two colonies in the Catlins area, also on the South Island. The breeding colonies of this species occur on the relatively steep coastal slopes, usually within 100 meters of the shore line. The cover may vary from relatively dense bush to more open grassy slopes with clumps of New Zealand flax (*Phormium tenax*). The climate is definitely temperate, the mean temperatures for the breeding season being of the order 50–58° F. Mean rainfall is two to three inches per month during the breeding season. The life history and behavior of the Yellow-eyed Penguin have been described extensively and ably by Richdale (1941, 1949, 1951).

My data contain information on the normal range of daytime body temperature for birds ashore, the body temperature of molting birds, incubation temperature in relation to body temperature, and incubation

Yellow-eyed Penguins *(Megadyptes antipodes)* at their nest. The male is covering two chicks three days old. Otago Peninsula, New Zealand, Nov. 24, 1937. Photo by L. E. Richdale.

temperature as a function of the time of incubation. It had been hoped also that information might be obtained on the behavior of incubation temperature during periods in which a single bird incubates for several days without relief. This, however, was unsuccessful since, as Richdale (1951: 226) has previously indicated, periods of more than two days on the nest are relatively infrequent. The data which were obtained for two-day periods give no reason to suspect that there is any change under such circumstances.

PROCEDURES AND METHODS

Measurements of body temperature were made with previously standardized self-registering mercury thermometers. To obtain a measurement the bird was held by the legs and extended ventral side down on the ground by an assistant; the thermometer was then inserted through the cloaca to a depth of 60 mm. Although there was generally little change in the mercury column after 30 seconds, standard procedure was to maintain the insertion for one minute. The thermometer was inserted initially within 10 seconds after capture. Body temperature is here defined simply as that temperature indicated after one minute by the mercury thermometer with the bulb inserted 60 mm. through the cloaca. Obviously, as Kallir (1930) has shown so well, "body temperature" must be some such arbitrary designation.

Measurements of incubation temperature were made in eight different nests. The measurements were effected with iron-constantan thermo-couples fabricated from well-insulated wire of one millimeter diameter.
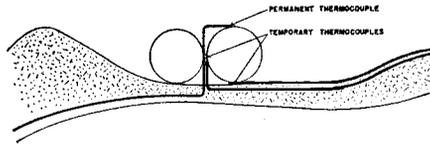

FIGURE 1. Arrangement of thermocouples and thermocouple leads for measuring incubation temperature.

One thermocouple was installed permanently in each of the nests with the leads extending to a site where the potentiometer could be attached and operated unobserved by the incubating bird. The permanent thermocouple was adjusted to a position between the uppermost surface of the egg and the ventral surface of the incubating bird. In principle, this scheme was similar to that of Barth (1949). On several occasions one or two additional temporary thermocouples were installed in order to ascertain the gradient in temperature between the upper and lower surfaces of the eggs (Fig. 1). Since the studies were being conducted

on a bird sanctuary, it was not possible to install thermocouples within eggs.

Only the actual thermocouple junction and a few millimeters of the separate wires, a total of about 15 millimeters, were uninsulated. The length of the iron and constantan leads was about eight meters. Since the use of an ice-bath reference junction proved to be impractical under field conditions, an insulated brass reference-temperature block was used (Fig. 2). Careful testing under a variety of laboratory conditions demonstrated this to be a reliable procedure. In field practice then the block temperature was recorded at the time of each measurement of potential difference. The true temperature at the site of the thermocouple was then obtained by adding the temperature indicated by the measured difference in potential to the temperature of the reference block at the time of measurement. All thermocouples were calibrated individually against a standard thermometer. Differences in potential were measured with a Leeds and Northrup portable potentiometer (No. 8667).
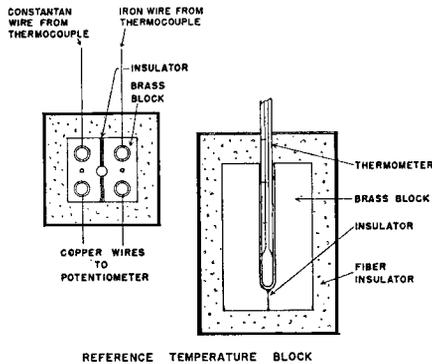

FIGURE 2. Reference temperature unit for use with thermocouples in the field.

The time of the beginning of incubation was estimated from our first observation of an incubating bird or, as was necessary in two cases, from the date of hatching. Most of the estimates are correct within two days; all are probably correct within five days. Young were hatched in three of the nests studied. No significant differences in the temperature at the interface of the egg and body surface of the incubating bird could be detected between birds incubating eggs which subsequently hatched and those with eggs which failed to hatch.

Even a most casual perusal of the literature will lead to the conclusion that the term *incubation temperature* has no uniform usage. This is to be expected since in incubation the egg has a thermal gradient between the upper surface which is in contact with the heating surface of the body of the bird and the lower surface which is in contact with the floor of the nest. This gradient is apparently in the order of 5–10° C. in several species. Naturally the important datum is the temperature of the

embryo itself (Baldwin and Kendeigh, 1932). However, there must also
be a temperature gradient within the embryo as soon as it develops to
an appreciable thickness. Since thermocouples could not be inserted
into the eggs, the basic data obtained were measurements of the tempera-
ture at the interface of the incubating bird and the egg. It is assumed
that the relation between this measurement and the actual temperatures
of the embryo, or a given point within the embryo, is roughly linear,
recognizing, of course, the complications of the increased size and
thermogenesis of the embryo in the later stages of incubation. In this
paper, *incubation temperature*, is designated as the temperature at the
interface between the top surface of the egg and surface of the incubation
strip of the bird.

Measurements of incubation temperature were made at intervals
of two to seven days depending on weather conditions and the availa-
bility of assistance. In most instances, the incubating bird was first
removed from the nest, its body temperature recorded, the permanent
thermocouple adjusted, and sometimes one or two temporary thermo-
couples installed. The difference in electromotive force and the
temperature of the reference block was recorded at intervals of two or
three minutes until the temperature of the thermocouple junctions
remained reasonably constant. These temperatures were then regarded
as characteristic for the particular day. Once the temperature was
elevated to this maximum, there was little tendency for it to change
except briefly when the bird changed position. At the conclusion of a
series of measurements the thermocouples were checked with respect
to their positions and the temporary units removed. Usually the body
temperature of the incubating bird was measured again at this time.

RESULTS AND DISCUSSION

Body Temperatures

A series of daytime body temperatures was obtained from *non-molting,
non-incubating penguins* ashore in the Sandfly Bay and Catlins colonies.
Only birds which could be captured without pursuit have been included
in this series. These were primarily unemployed birds in the sense
of Richdale (1951: 7). The mean for this series is 37.8° C. (Table 1).
The importance of excluding birds obtained by pursuit is emphasized by
three particular cases. On 24 March 1954 at Jack's Bay in the Catlins
area, I pursued a non-molting bird for about 10 minutes. During this
period, it climbed upward about 150 feet over a very steep grassy slope.
The body temperature recorded immediately thereafter was 40.4° C.
Another penguin taken after an upward pursuit involving 120 feet in

TABLE 1

COMPARISON OF DAYTIME BODY TEMPERATURES OF MOLTING, INCUBATING AND
NON-MOLTING NON-INCUBATING YELLOW-EYED PENGUINS

Group	Number of Birds	Number of Measurements	Mean °C	Standard Deviation °C
Non-incubating non-molting	13	13	37.8[3]	±0.43
Molting	10	20	38.6[3]	±0.43
Incubating[1]	11	41	37.7[4]	±0.56
Incubating[2]	10	21	38.1[4]	±0.53

[1] Temperature measurement completed within 2 minutes after coming in sight of the bird. [2] Temperature measurement made after measurement of incubation temperature, 25–120 minutes after first coming in sight of the bird. [3] Mean 38.6° is significantly greater ($P < 0.01$) than 37.8°. [4] Mean 38.1° is significantly greater ($P < 0.02$) than 37.7°.

about 12 minutes had a body temperature of 40.2° C. On 8 April 1954 in the same locality a molting individual had a body temperature of 40.0° C. after a vigorous chase for about one minute. These differences of an order of 2° C. are consistent with differences between exercise and rest observed in other species by Baldwin and Kendeigh (1932), Udvardy (1953), Irving and Krog (1954), and Farner (1956).

This raises also the question of the effect of handling on body temperature of birds. There was actually no certain way in which this could be ascertained under the conditions of our investigations. However a brief series of data bearing on the matter should be presented. On eight occasions, involving four incubating birds, measurements were obtained beginning at the usual interval of 10 seconds or less after capture; and the birds were held then for a period sufficiently long for two additional measurements at approximately two-minute intervals. In other words measurements were completed at intervals of approximately one, three, and five minutes after capture. After holding for about three minutes, five were found to have an increased body temperature, one was unchanged, and two had lower body temperatures; the mean change was +0.1° C. which is not statistically significant. After five minutes of holding, however, the mean change was +0.7° C. although in two cases the body temperature was lower than the initial measurement. Nevertheless the difference of +0.7° C. proves to be statistically significant ($P < 0.02$). Although these observations are fragmentary they appear to indicate that exercise and handling tend to elevate body temperature. They also suggest that the temperature measurement completed approximately one minute after capture is probably very close to the body temperature at the time of capture, since during an additional two minutes of holding there is on the average only a slight, statistically insignificant increase. It seems reasonable to conclude that the normal daytime body temperature for non-molting non-incubating birds ashore is very close to 37.8° C.

The data on the body temperature of *molting birds* also involves only individuals which could be captured without pursuit and for which the temperature measurement could be begun within ten seconds after

capture. Notations were recorded with respect to the stage of molt for each temperature measurement. However, the data do not appear to indicate any definite trend in body temperature during the course of the molt although the series is deficient with respect to the very early and terminal parts of the molt. A statistical analysis of the data (Table 1) reveals that the higher mean body temperature of the molting birds (38.6° C., compared to 37.8° C. for non-incubating, non-molting birds, and 37.7° C. for incubating birds) is statistically highly significant ($P < 0.01$) and therefore in all probability represents a true physiologic difference. Initially this appears somewhat surprising in view of the nature of the activity of the penguin during the molt period. For this period of about 24 days (Richdale, 1949:20) the bird apparently remains restricted to an area of a few square feet, unless disturbed, and obtains neither food nor water. However, this is a period of intense metabolic activity in which approximately 45% of the body weight is lost (Richdale, 1951: 284).

In obtaining data on the body temperature of *incubating birds*, there was of course the question of the effect of the activity of the investigators in setting up and adjusting the apparatus for measurement of incubation temperature. In order to ascertain the effect of this, on 16 occasions, involving 10 different incubating birds, measurements of body temperature were made immediately after first coming into sight of the incubating bird, and then again after the completion of the measurements of incubation temperature. The time period separating the two measurements varied from 25 minutes to 117 minutes. On 13 occasions there was an increase in body temperature, in one case no change, and in two cases a decrease. The mean change was +0.49° C. which, on statistical analysis, proves to be significant ($P < 0.01$). A further comparison (Table 1) of all measurements made immediately after coming into sight of the experimental bird with measurements made after the measurement of incubation temperatures shows a similar difference of +0.4° C. and a similar statistical significance. There can be little doubt that the activity of the investigators about the nest has the effect of causing an elevation of the body temperature of the incubating bird, a point to be borne in mind in considering the data on incubation temperatures. It appears reasonable to conclude that the daytime body temperature of the incubating Yellow-eyed Penguin is about 37.7° C. and is actually no different than that of a non-molting, non-incubating bird ashore. In this respect it should be noted that Kossack's (1947) observations on Canada Geese (*Branta canadensis*) suggest that the incubating bird may have a lower body temperature (mean for two birds, 40.6° C.) than birds after incubation (mean for three, 41.6°) and non-breeders (mean for four,

42.1° C.).   Certainly this is different from the situation in Yellow-eyed Penguins.   It should be noted, however, that Bernard *et al.* (1944) found the mean body temperature of 11 non-incubating Canada Geese to be 39.8° C.

Comparison of the body temperature of the Yellow-eyed Penguin with those of other penguins can be made only with considerable caution in view of the above-described influence of excitment and struggling. Unfortunately publications of investigations rarely include the methods by which the data were obtained.   For the Adelie Penguin (*Pygoscelis adeliae*), a somewhat smaller species, Eklund (1942) found a mean temperature (thermometer inserted 76 mm. through the cloaca) of 39.9° C.   Further reports for this species include those of Valette (1906), 40.5° C.; Andersson (1908) 37.9–40.5° C.; and Gain (1914) 39.2–39.3° C. Sapin-Jaloustre (1955) found that thermoregulation became established 15 days after hatching and that at this time the body temperature was 39.7–40.0° C.   For the small Little Blue Penguin (*Eudyptula minor*), mean body temperatures of 38.5° C. and 39.0° C. have been reported by Morgan (1916).   A body temperature of 38.2° C. for the large Emperor Penguin (*Aptenodytes forsteri*) has been reported by Wilson (1907) for a single bird which was pithed after catching, the body temperature being measured immediately thereafter.

Incubation Temperature

A striking aspect of the data on incubation temperature is the time required to attain the characteristic maximum of about 38° C.   This is illustrated in Figure 3.   It was either observed or assumed that the incubation period begins after the laying of the second egg, although Richdale (1951: 226) indicates that this is not necessarily the case. Since no significant differences could be noted among the data obtained from the eight nests they have been treated as a single sample.   It appears probable that the relatively long "warm-up" period of about two weeks may, at least in part, account for the long incubation period (about 42 days) in this species.   Although several factors may enter into this gradual development of the incubation temperature, it appears likely that most important is the increase in vascularization of the incubation patch, or more descriptively, the incubation strip.   At the beginning of incubation the incubation strip is yellowish orange; thereafter it changes gradually to a reddish purple at about the end of the second week and retains this color for the remainder of the incubation period.   It is true also that the birds appeared not to settle on the eggs as soon after release during the first two weeks as during the latter part of the incubation period.   Since measurements were continued in each

case until a maximum sustained reading was attained, this is not likely a factor in the curve in Figure 3. Furthermore it is unlikely that this relationship can be in anyway a function of the metabolic activity of the developing embryo, for the curve for nests with eggs which failed to develop differed in no appreciable way from the curve for successful
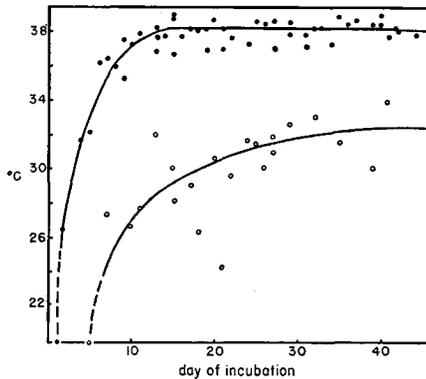

FIGURE 3. Incubation temperature through the course of the incubation period. Incubation was either observed or assumed to have begun after the laying of the second egg. Closed circles indicate the temperatures at the interface between the top of the egg and the surface of the body. Open circles represent the temperatures at the interface between the bottom of the egg and the surface of the nest. The data are from eight different nests and are treated as a single sample since no significant difference could be observed among them.

nests. Furthermore if, as in all probability it is, the pattern of increasing metabolic activity is similar to that of the developing chick embryo (Hasselbalch, 1902; Bohr, 1903; Romijn and Lokhorst, 1951), one would expect the increase in temperature much later in the incubation period. It should be noted (Fig. 4) that through the course of the incubation period the bird becomes more efficient at bringing the eggs back to normal temperature on returning to the nest. This doubtless involves, among other factors, the tendency to settle on the eggs sooner and the development of the elongated brood patch.

The gradual increase in temperature is similar to that observed by Holstein (1942, 1944, 1950) for the Goshawk (*Accipiter gentilis*), the European Sparrow Hawk (*Accipiter nisus*), and the Honey Buzzard (*Pernis apivorus*). In the case of the Goshawk, whose incubation period he found to be 41–43 days, the incubation temperature (top of the egg) was found to reach its maximum (about 41° C.) at about the 22nd day. Similarly for the Sparrow Hawk (incubation period, 39–42 days) the maximum incubation temperature (37.5° C.) was attained about the

22nd day, whereas in the Honey Buzzard (incubation period, 37–38 days) the maximum incubation temperature (39° C.) was reached about the 11th day. These data, in addition to observations on the rate of development of the embryo, lead Holstein to the conclusion that the relatively long incubation periods of these species are the result of these preliminary periods of relatively ineffective incubation temperatures. Another case involving a gradual development of incubation temperature, according to observations of Bergman (1946), appears to be that of the Turnstone (*Arenaria interpres*). In this species (incubation period 23–26 days) incubation temperatures were found to increase from about 30° C. initially to a maximum of 38–40° C. on the 18th day.

Actually there are surprisingly few observations of incubation tem-
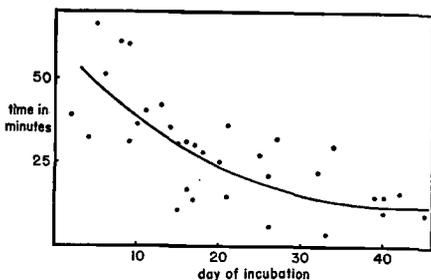
FIGURE 4. Time required to return eggs to normal incubation temperature as a function of the day of incubation. The period off the eggs in each case was between one and two minutes.

perature as a function of time during the incubation period. In the domestic fowl Burke (1925) found only very slight fluctuations (39.0–39.2) during the period between the 2nd and 20th days of incubation. An earlier series of observations by Eycleshymer (1907) indicated a mean range of 39.7–40.5° C. for the same period. Martin and Insko (1935) found, with developing domestic turkey embryos, that the temperature of the dorsal surface of the embryo fluctuated only from 36.5° C. on the first to 39.7° C. on the 27th day. A similar situation was observed by Kossack (1947) with Canada Geese, the incubation temperature (top of the egg) increasing from 36.5° C. in the 2nd day to about 39° C. at the end of incubation.

The House Wren (*Troglodytes aedon*) is also a species in which there is apparently little change in incubation temperature through the course of the incubation period (Baldwin and Kendeigh, 1932). The temperature at the surface of the incubation patch is about 41° C. This temperature may be attained as early as the night following the laying

of the second egg although it is more generally attained during the night following the laying of the fourth egg of the clutch (Kendeigh, 1952). Thus the "warm-up" period which occurs during the first third of the incubation period of the Yellow-eyed Penguin (Fig. 3) has its obvious counterpart during the laying period of the House Wren. In both species the effective attentiveness (total incubation time per day) apparently remains unchanged during the course of the incubation period. However, in the case of the Yellow-eyed Penguin the effective attentiveness is greater and involves both sexes.

An obviously important variable in incubation, as shown so well by Baldwin and Kendeigh (1932) and Barth (1949), is the degree of attentiveness. In the case of the Yellow-eyed Penguin, my rather brief observations indicate that the eggs are left uncovered only for a few minutes at most, at the change of incubating birds which occurs at intervals of one to five days (Richdale, 1951). On the basis of much more extensive observations Richdale, (1941: 276) has noted that ". . . when a bird does return a change in guard occurs immediately . . ." Since effective attentiveness appears to be nearly maximum, it appears that the time required during the incubation period to attain maximum or near-maximum incubation temperature must be a primary factor in fixing the duration of the incubation period. Furthermore the available information indicates that this relationship is probably broadly applicable in birds and may well account for many of the striking differences in incubation periods.

Examination of Figure 3 shows that the incubation temperature of the Yellow-eyed Penguin is strikingly similar to actual body temperature. The data include 15 measurements after the 15th day of incubation in which body temperature was measured immediately after the measurement of incubation temperature. For these cases the mean difference between incubation and body temperature was $-0.2°$ C., a difference with no statistical significance. Baldwin and Kendeigh (1932) found the temperature of the brood patch in contact with the eggs to be about $0.7°$ lower than body temperature in the female House Wren (*Troglodytes aedon*). The data of Kossack (1947) suggest a difference in the Canada Goose of about $1°$ C. at end of incubation. In the domestic goose the temperature at the interface between the surface of the bird and the egg was found to be $39.7°$ C. (Koch and Steinke, 1944) as compared to a body temperature of 40.2–$40.7°$ C. (Löer, 1909, 1910; Hari, 1917; Fronda, 1921). The maximum temperatures at the interface of egg and body surface given by Barth (1949) for Willow Ptarmigan (*Lagopus lagopus*), Red-breasted Merganser (*Mergus serrator*), Lesser Black-backed Gull (*Larus fuscus*), Mew (Common) Gull (*Larus canus*), and Common Tern

(*Sterna hirundo*), and by Holstein (1950) for the Goshawk must be very close to actual body temperatures. It must be emphasized however (Baldwin and Kendeigh, 1932; Huggins, 1941) that the actual temperature of the embryo is somewhat lower.

From the comparisons cited above it appears that the incubation of the Yellow-eyed Penguin, in relation to body temperature, is not strikingly different from other species. I am unable to find in the literature any comparable data for other species of penguins. For the Emperor Penguin, the mean egg temperatures of 26.6–33.9° C. reported by Etchécopar and Prévost (1954) (see also Prévost, 1955) were obtained by inserting thermometers into the eggs. There appears to be no way of effecting a useful comparison between their data and mine.

It is of interest to compare the temperature gradient between the top and bottom of the egg in various species when the incubating bird is maintaining maximum or near maximum incubation temperature. In the Yellow-eyed Penguin (Fig. 3) this gradient appears to decrease through the course of the incubation period being in the order of 5–8° during the last half of the period. In the domestic fowl (Burke, 1925) the gradient is of the order 7–9° C., the smaller gradient occurring during the latter half of the period. Koch and Steinke (1944) have reported an 8° C. gradient for the domestic goose, whereas Barth's (1949) data indicated 9° C. for the Willow Ptarmigan (*Lagopus lagopus*), 9° C. for the Lesser Black-backed Gull (*Larus fuscus*), and 14° for the Common Tern (*Sterna hirundo*). The data of Baldwin and Kendeigh (1932) suggest that the gradient is about 9° C. for the House Wren. Here again the Yellow-eyed Penguin, although attaining a low gradient in the latter part of the incubation period, does not differ substantially from other species.

SUMMARY

1. Body temperatures of Yellow-eyed Penguins were measured by insertion of a self-recording thermometer 60 mm. through cloaca for one minute. The mean body temperature for non-incubating non-molting birds ashore was found to be about 37.8° C. (100.0° F.). The temperature for molting birds (38.6° C., 101.5° F.) was significantly higher. The body temperature of previously undisturbed incubating birds (37.7° C., 99.8° F.) is not significantly different from that of non-molting non-incubating birds. The presence of a person near the nest causes a significant increase (about 0.4° C., 0.7° F.) in the body temperature of the incubating bird.

2. Incubation temperature (*i.e.* the temperature at the interface between the incubation strip and the surface of the egg), as measured with iron-constantan thermocouples, increased gradually (Fig. 3) from 20–25° C. (68–77° F.) during the first two days to a maximum of about 38° C. (100.4° F.) at 15 days; this maximum was maintained throughout the remainder of the incubation period. The period of increasing incubation temperature coincides with a period of increased vascularization of the incubation strip.

3. The maximum incubation temperature, which occurred generally from the 15th day to the end of incubation, was found not to differ significantly from the body temperature of the incubating birds.

4. There is a gradual decrease in the gradient between the upper and lower surfaces of the egg to a level of about 5–8° C. (41–46° F.) during latter half of the incubation period (Fig. 3).

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