

BODY TEMPERATURE AND THE ONTOGENY OF THERMOREGULATION IN THE SLENDER-BILLED SHEARWATER

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Although a fairly substantial amount of information has been accumulated on body temperatures and thermoregulation in birds, our knowledge of the Procellariiformes in this respect is meager (Farner, 1956). Consequently it appears desirable to present an analysis of a series of data obtained on the Slender-billed Shearwater (*Puffinus tenuirostris*) from some of the nesting colonies on islands in Bass Strait, Australia.

Among previous investigations of the Procellariiformes only those of Folk (1949, 1951) on the Leach Petrel (*Oceanodroma leucorhoa*) and Farner (1956) on the Fairy Prion (*Pachyptila turtur*) are statistically useful and relate body temperature to state of activity. The data of Roberts (1940) on the Wilson Petrel (*Oceanites oceanicus*) give a good indication of the ontogeny of thermoregulation in this species. The older investigations of Eydoux (1838), Martins (1856a, 1856b, 1858), Brown-Séguard (1858), and Simpson (1912) serve primarily to confirm that the body temperatures of active petrels and albatrosses in general are of the order of 38° to 41°C. Prévost (1953) has recorded the cloacal temperature of four breeding Fulmars (*Fulmarus glacialisoides*) at 38.6° to 39.2°C.

PROCUREMENT OF DATA

The investigations reported in this paper were conducted on the islands of the Furneaux group in eastern Bass Strait. Most of the data were obtained at the field station of the Commonwealth Scientific and Industrial Research Organization on Fisher Island at latitude 40° 10' S, longitude 148° 16' E, and adjacent islets. Further data were obtained at Babel Island, latitude 39° 54' S, longitude 148° 20' E (Serventy, 1958:165).

Body temperature was measured by use of calibrated mercury thermometers inserted 1.5 cm. into the cloaca for one minute (Farner, 1956). To reduce thermogenic effects of excitement to a minimum, birds were captured from the surface of the ground or removed from burrows quickly and with minimum struggle. It should be noted that the birds (adults and chicks) removed from the burrows had been considerably conditioned to such manipulation by previous removals for other observations. The entire procedure from beginning of capture or removal from burrow to completion of measurement of temperature was such as to require no more than two minutes. Admittedly this type of measurement of temperature involves bias (Udvardy, 1953) which could be eliminated by the use of permanently installed thermocouples (Bartholomew and Dawson, 1954a); however, such a procedure was not possible in these studies. Moreover, it should be emphasized that our observations on *Puffinus tenuirostris* indicate that the "handling" bias is similar to that for *Pachyptila turtur*. This indicates that the measured temperature is in all probability within 0.2°C. of the temperature of the bird at the time capture or removal from the burrow was begun. Our experience with petrels (Farner, 1956) is somewhat different from that of Baldwin and Kendeigh (1932) with several passerine species; in these it was noted that there was frequently a decline in body temperature while the bird was held in the hand. Possibly the difference is the result of a relatively greater amount of thermogenic muscular activity in passerine birds during the process of capture with a consequent dissipation of the heat load while the bird is held quietly in the hand.

For purposes of this paper body temperature is defined as that temperature which is measured with a mercury thermometer inserted 1.5 cm. into the cloaca for one minute.

The temperatures of unoccupied burrows were measured with maximum-minimum

thermometers which were read and reset daily. The temperatures of occupied burrows were taken with an ordinary laboratory thermometer laid in the burrow while the occupant was removed temporarily for examination.

BODY TEMPERATURE OF ADULTS

The sex of many of the birds included in this study was unknown. However, a comparison of the sexes was possible on the basis of a sample of 32 birds taken from the surface of the rookeries early in the morning. The mean temperature for 15 males was $40.8^{\circ}\pm 0.25^{\circ}\text{C}.$; for 17 females it was $41.0^{\circ}\pm 0.17^{\circ}\text{C}.$ Since the difference between these means is not statistically significant, we have concluded there is no important difference between the sexes and have therefore not separated them, even when possible, in our analyses.

Table 1

Cloacal Temperature in Adult *Puffinus tenuirostris* in Various States of Activity

Group	Description	No.	Mean cloacal temperature ¹ °C.	Standard deviation of sample °C.
A	On surface after landing in evening	55	39.9 ± 0.13	± 0.97
B	On surface before flight in morning	37	40.9 ± 0.13	± 0.79
C	In burrow with chick	8	38.7 ± 0.20	± 0.33
D	In empty burrow	17	37.9 ± 0.09	± 0.35
E	In burrow with egg (incubating)	18	38.0 ± 0.19	± 0.83
F	In burrow feeding young	3	41.5 ± 0.41	± 0.70

¹ \pm Standard error of mean.

Table 2

Comparisons of Significances of Differences Among Means

Group Mean, °C.	F 41.5	B 40.9	A 39.9	C 38.7	E 38.0	D 37.9
D	1.0 per cent	1.0 per cent	n.s.	n.s.	n.s.	
E	0.1	0.1	0.1 per cent	5.0 per cent		
C	0.1	0.1	1.0			
A	1.0	0.1				
B	n.s.					

1 per cent indicates that the means for the pair of groups indicated are significantly different at the 1 per cent level, etc.; n.s. indicates that they are not different at the 5 per cent level ($P > 0.05$) of probability.

The data on body temperatures of adults in various stages of activity have been summarized in table 1; the significances of the differences among means, as indicated by an analysis of variance, are given in table 2. Of particular interest is the mean temperature of incubating birds ($38.0^{\circ}\pm 0.19^{\circ}\text{C}.$) which is significantly lower than that of active birds on the surface of the ground immediately after landing in the evening (Group A, $39.9^{\circ}\pm 0.13^{\circ}\text{C}.$) and before takeoff in the morning (Group B, $40.9^{\circ}\pm 0.13^{\circ}\text{C}.$), and it is also lower than that of active birds in the burrows (Group F, $41.5^{\circ}\pm 0.41^{\circ}\text{C}.$). This lower temperature in incubating petrels is similar to that observed by Farner (1956) in *Pachyptila turtur*, and by Folk (1949, 1951) in *Oceanodroma leucorhoa*. Thus the situation in these three species of petrels appears to differ from that of the Yellow-eyed Penguin, *Megadyptes antipodes* (Farner, 1958), in which there appears to be no difference in body temperature between incubating birds and nonincubating, nonmolting birds. Few data are available for other species. However, in the Canada Goose (*Branta*

canadensis) it appears possible that the temperature of incubating birds is lower than that of nonincubating birds (Kossack, 1947). The similarity of the means for birds (groups C, D, E) in burrows, except those feeding young, suggests that the accompanying inactivity has a temperature-depressing effect similar to that noted for *Oceanodroma leucorhoa* (Folk, 1949, 1951) and *Pachyptila turtur* (Farner, 1956) and that the lower body temperature of incubating petrels is the result of the temperature-reducing effect of burrow life rather than any peculiarity associated with incubation *per se*. Birds coming in at night to feed young are in quite a different category from adults spending a prolonged period in the burrows (such as groups C, D, and E in table 1); they remain in the burrow for comparatively short periods. It should be noted also that a similar difference in body temperature exists between chicks on the surface and chicks in the burrow (table 4). In comparison with the smaller *Pachyptila turtur* a striking difference is to be noted in *Puffinus tenuirostris* with respect to body temperature immediately after the incoming flight. In *Pachyptila turtur* the incoming birds have markedly higher temperatures than the active birds on the surface of the ground at night. This difference is lacking in *Puffinus tenuirostris*; indeed the body temperature appears to be higher in the morning before takeoff (Group B, $40.9^{\circ} \pm 0.13^{\circ}\text{C}.$) than after landing in the evening (Group A, $39.9^{\circ} \pm 0.013^{\circ}\text{C}.$). There is no apparent explanation for this difference; possibly the body temperature in flight is not as high in *Puffinus tenuirostris* as it is in *Pachyptila turtur*.

BODY TEMPERATURE AND THERMOREGULATION IN CHICKS

It is obvious (table 3 and fig. 1) that within the first day or two the chicks have sufficiently adequate thermoregulation to maintain essentially adult temperatures in the burrow environment of about $22^{\circ}\text{C}.$ (fig. 2), an environment whose maximum daily fluctuation in temperature is less than $5^{\circ}\text{C}.$ Although the improvement in thermoregulation and the increase in body temperature after hatching appear to be rather slight, an analysis of variance of cloacal temperature of 15 chicks for the first 6 days after hatching reveals that individual chicks tend to have their own characteristic body tem-

Table 3

Cloacal Temperature in *Puffinus tenuirostris* Chicks in Relation to Age and Burrow Temperature.
Data for Selected Intervals

Day of Life	Adult present			Adult absent			Difference between chick and burrow temperature		
	No. ¹	Mean cloacal temperature ² °C.	Standard deviation of sample °C.	No.	Mean cloacal temperature ¹ °C.	Standard deviation of sample °C.	No.	Mean difference ¹ °C.	Standard deviation of sample °C.
1	14	37.9 ± 0.12	± 0.36	1	37.7	15	14.6 ± 0.48	± 1.86
2	10	38.2 ± 0.22	± 0.70	5	38.4 ± 0.27	± 0.61	15	15.1 ± 0.49	± 1.89
3	5	38.8 ± 0.33	± 0.74	10	38.3 ± 0.09	± 0.30	15	16.3 ± 0.48	± 1.85
4	4	38.5 ± 0.22	± 0.41	11	38.7 ± 0.13	± 0.41
5	2	38.4 ± 0.15	± 0.21	13	38.4 ± 0.17	± 0.65	15	17.2 ± 0.31	± 1.20
6	1	38.9	14	38.3 ± 0.22	± 0.82
7	2	39.0 ± 0.20	± 0.28	12	38.4 ± 0.16	± 0.56
10	6	38.3 ± 0.28	± 0.68	6	16.5 ± 0.30	± 0.75
33-45	17	38.6 ± 0.08	± 0.33	17	19.9 ± 0.33	± 1.35
88-98	17	38.4 ± 0.15	± 0.63	17	21.4 ± 0.18	± 0.75

¹ The data for days 1 through 10 all are from the same group of 15 chicks. The data for 33-45 and 88-98 days are from another group of 17 chicks.

² \pm Standard error of the mean.

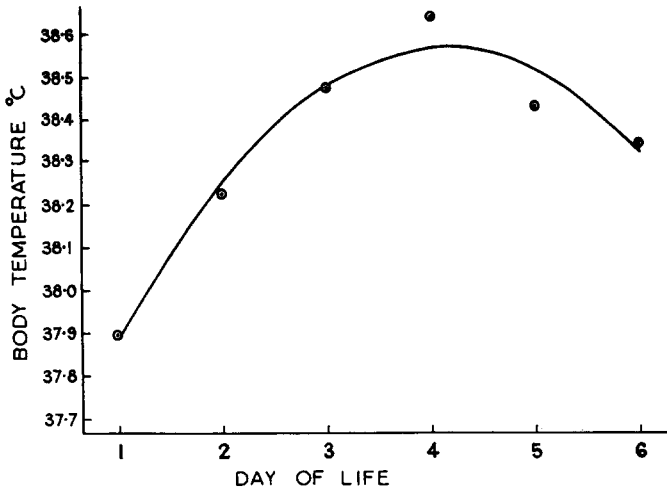


Fig. 1. Body temperature in *Puffinus tenuirostris* during the first six days after hatching. The plotted points are means for 15 chicks. See text for calculation of curve.

perature and, more importantly, that the increase in body temperature from day 1 to day 4 is very significant ($P < 0.01$). A quadratic regression of cloacal temperature (y) on days (x) accounted for practically all the variability between day means, both regression coefficients being highly significant ($P < 0.001$) and the residual on 3 degrees of freedom being negligible and not significant. The curve relating body temperature as a function of time after hatching may be represented by:

$$y = 38.538 + 0.0867x - 0.0698x^2$$

where x is the day of life - 3.5, and y is body temperature. Equating the differential of this equation to zero indicates that the maximum temperature (about 38.6°C .) is attained during the fourth day. The subsequent history of body temperature of chicks after the sixth day does not lend itself to useful analysis with the data available. Apparently it is one of a slight and uneven downward trend toward the typical body temperatures of quiet adults in burrows. On the basis of information available, we cannot offer a suggestion of the biological significance of the surpassing of the adult levels beginning about the second day of life.

Unfortunately there are no comparable series of data for other species of petrels. The limited series of observations by Roberts (1940) on the chicks of *Oceanites oceanicus* lead him to the conclusion that they pass through a semi-poikilothermal stage, since, at the ages of one and two days the body temperature is 30°C . or less; between the fourth and seventh days it apparently stabilizes at 36.5° to 37.5°C . where it remains at least until the 40th day. Although comparisons must be made cautiously, it would appear then that in both *Puffinus tenuirostris* and *Oceanites oceanicus* there is an improvement in thermoregulation and an increase in body temperature during the first few days after hatching. The increase in body temperature is rather slight in *Puffinus tenuirostris* whose burrows have a mean temperature of about 22°C . whereas it is quite pronounced in *Oceanites oceanicus* where the mean temperature of the burrows is of the order of 0° to 5°C . Because of this difference in burrow temperatures, it should not be assumed by any means that the thermoregulatory ability of the chicks of *Puffinus tenuirostris* is necessarily superior to that of the chicks of *Oceanites oceanicus*. Our observations suggest

that the early development of adult body temperatures in *Puffinus* represents an adaptation which permits the chicks to be left unattended in a relatively cool environment. Ordinarily the chick is attended by the parents only for two days after hatching, but it may be alone in the burrow even on the first day (table 3). The same adaptation may well exist in *Oceanites oceanicus* except that it does not compensate completely for the much lower burrow temperatures. The ability of the chicks of *Puffinus tenuirostris* to maintain an essentially adult body temperature in an environment 15° lower is quite remarkable.

It is of interest to compare the thermoregulatory ability of the chicks of *Puffinus tenuirostris* with those of other precocial species. It appears that it is quite comparable with that of the chicks of the Common Eider (*Somateria mollissima*) in which thermoregulation becomes well established at 2 to 7 hours after hatching (Rolnik, 1948). Ap-

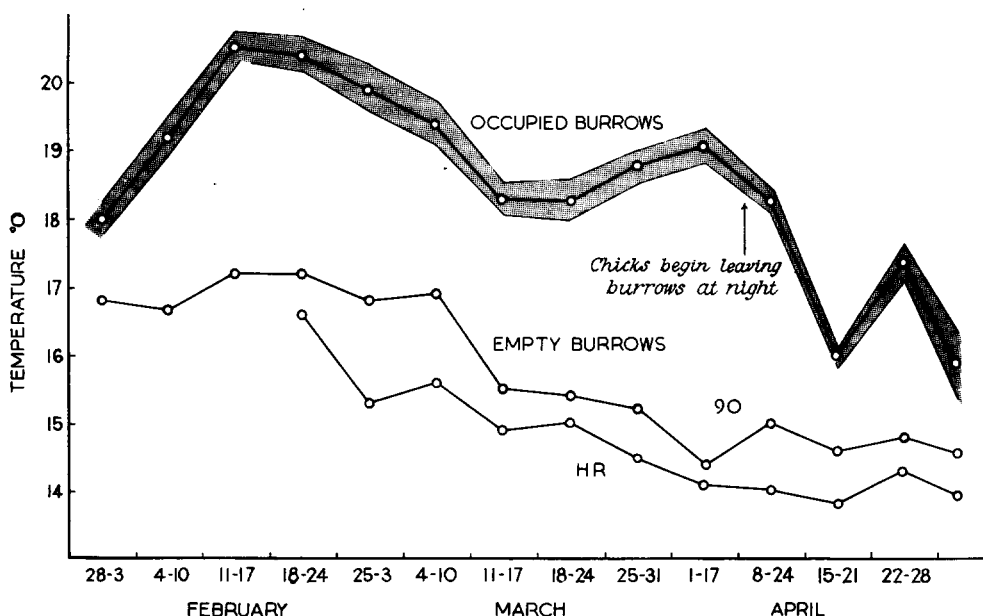


Fig. 2. Temperatures in the burrows of *Puffinus tenuirostris* during the breeding season. Plotted points for occupied burrows are weekly means for about 20 burrows. Shaded area includes ± 2 standard errors of the mean. Plotted points for empty burrows are weekly means for single burrows.

parently thermoregulation develops earlier in *Puffinus tenuirostris* than in the chicks of such galliform species as the domestic fowl (Randall, 1943), the quail, *Coturnix coturnix* (Böni, 1942), and the Ring-necked Pheasant, *Phasianus colchicus* (Ryser and Morrison, 1954). According to the excellent series of observations by Barth (1951) the chicks of the Mew Gull (*Larus canus*), the Herring Gull (*Larus argentatus*), the Lesser Black-backed Gull (*Larus fuscus*), and the Great Black-backed Gull (*Larus marinus*) develop fairly good thermoregulation by the end of the first day and after three days can maintain near-adult thermoregulation except under very severe conditions. This is consistent with the observations of Rolnik (*op. cit.*) who concluded that thermoregulation is well established between the second and third day after hatching in *Larus canus* and between one and one-half and two days in *Larus argentatus*. The observations of Bar-

tholomew and Dawson (1952, 1954b) indicate an approximately similar ontogeny of thermoregulation in the Western Gull (*Larus occidentalis*). On the other hand good thermoregulation does not develop in the chicks of the Black-legged Kittiwake (*Rissa tridactyla*) until the sixth or seventh day (Rolnik, *op. cit.*). Rolnik (*op. cit.*) also found that the development of thermoregulation in certain alcids was similar, or perhaps slightly slower, than in *Larus*. Her observations indicate adequate development at about three days in the Common Murre (*Uria aalge*), three to four days in the Razorbill (*Alca torda*), three to four days in the Black Guillemot (*Cepphus grylle*), and six to seven days in the Common Puffin (*Fratercula arctica*). Since the chicks of most of these alcid and larid species are naturally subjected to greater extremes of environmental conditions than those of *Puffinus tenuirostris*, a precise physiologic comparison of their thermoregulatory abilities is not possible without comparably controlled experiments. Related to their own environments, however, there appears to be no doubt that an adequate thermoregulation develops earlier in *Puffinus tenuirostris* than in the gulls and alcids.

Our data for older chicks in the burrows (table 3, 33–45 and 88–98 days) indicate a close similarity with those of Folk (1951) for *Oceanodroma leucorhoa*; nine young birds aged 45 to 65 days had body temperatures ranging from 38.2° to 39.7°C.; a tenth was recorded at 35.0°C. The temperature of the burrows of this species is about 12°C.

BURROW TEMPERATURES

The burrow provides a relatively stable micro-climate. Whereas mean daily air temperatures (in shade) oscillate between 15° and 30°C., the diurnal range in unoccupied burrows is only of the order of 1° to 5°C. (Serventy, 1958). In the occupied burrows the presence of the birds has a warming and stabilizing effect on the temperature (fig. 2).

Table 4

Cloacal Temperatures of Chicks of *Puffinus tenuirostris* for the First Six Days after Hatching
Analysis of Variance

Source	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Individual chicks	14	9.1582	0.6542	2.37 ¹
Days	5	4.9125	0.9825	3.56 ¹
Chicks x days	70	19.3325	0.2762	
Total	89	33.4032		

¹ Highly significant ($P < 0.01$).

Table 5

Cloacal Temperature in Fully Grown Chicks of *Puffinus tenuirostris*
Comparison of Birds in Burrows with Birds on Surface

Group	Description	No.	Mean cloacal temperature ¹ °C.	Standard deviation of sample °C.
C-1	Chicks, 97–106 days old, in burrows	7	38.4 ± 0.41 ²	± 1.16
	Same individuals on surface, same day	7	39.7 ± 0.35 ²	± 0.69
C-2	Chicks, 88–98 days old, in burrows	17	38.4 ± 0.15 ³	± 0.63
C-3	Chicks, 96–106 days old, on surface	53	39.7 ± 0.13 ³	± 0.92

¹ ± Standard error of mean.

² Significantly different at 5 per cent level.

³ Significantly different at 0.1 per cent level.

In both the occupied and unoccupied burrows a maximum level of summer temperature is attained during the latter part of February; thereafter there is a slow decline which is arrested and reversed in the occupied burrows during March and early April by the warming effect of the large rapidly growing chick. The seasonal decline is resumed in late April when the chicks begin to spend a large portion of the night outside of the burrow.

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SUMMARY

The body temperature of adult Slender-billed Shearwaters (*Puffinus tenuirostris*) on the surface of the ground in the nesting colonies is from 40° to 41°C. It is apparently higher in the morning before takeoff (40.9°±0.13°C.) than in the evening after landing (39.9°±0.13°C.). Adults in the burrows, except when feeding chicks, have lower temperatures; in incubating birds and in those in empty burrows the body temperature is about 38°C. The lower temperature of the incubating birds should be regarded as characteristic of quiet burrow life rather than as a functional peculiarity of incubation itself.

The chicks of *Puffinus tenuirostris* at hatching, or within a very few hours thereafter, have sufficient thermoregulatory capacity to maintain adult body temperatures in burrows at temperatures of about 22°C. There is a slight, although very significant, increase in body temperature during the first four days after hatching. Older chicks have a higher temperature on the surface of the ground than in the burrows. The difference is similar to that of the adults.

DEDICATION

This paper is dedicated to Professor Erwin Stresemann on his 70th birthday anniversary.

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