BODY TEMPERATURES OF PETRELS

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During the course of a study of the development rates of albatrosses, shearwaters, and other petrels (Warham MS), the existing data on body temperatures of birds in the order Procellariiformes were examined. These suggested that petrels have unusually low body temperatures and that these might provide clues to the birds' unusually long incubation and nestling periods. Subsequently it became possible to extend the data to cover a much wider range of species during visits to the Campbell, Antipodes, and Snares Islands, south of New Zealand. Figures for 31 species are now available.

Determinations were made with mercury-in-glass thermometers calibrated to 0.1°C and inserted at least 2.5 cm into the rectum for at least 1 min. Clinical thermometers were used for the smaller species. The instruments were checked at intervals against thermometers of known accuracy. Rectal temperatures were also checked in some instances by insertion of the thermometers deep into the proventriculus through the mouth but no significant differences between the two values were revealed. Whenever possible, measurements were made immediately after the capture of birds from their nests but some readings were taken on birds brought to earth with the help of a spotlight. The body temperatures of such active birds might therefore be expected to be higher than those of resting or incubating individuals of the same species as shown by Farner (1956) and Farner and Serventy (1959) for *Pachyptila turtur* and *Puffinus tenuirostris*. However, the inclusion of any such higher readings does not invalidate the main findings of the present paper.

RESULTS

The known data on body temperatures in Procellariiformes are given in table 1 where my own figures are listed together with those of previous workers. Birds measured by me were not sexed and the body weights are mean values for samples composed of both sexes. The weights and temperatures are not necessarily based on the same individuals but the weights given are those for the correct subspecies where substantial differences exist between populations. For example, McNab (1966) used Prévost's (1964) data for body temperature for *Pagodroma nivea* but linked these with body weights evidently taken from Maher (1962) for a sample from a population composed of much smaller birds. Where possible the weights are based on determinations of birds not carrying heavy reserves of subdermal fat.

In discussing early work on body temperatures, Simpson (1912) pointed out that measurements made on birds dragged on board at the end of fishing lines were likely to be abnormal because protracted struggles involve heat production. Nonetheless the data he obtained by these methods do not show any dramatic increases of temperature compared with those in table 1. For example, two specimens of *Procellaria aequinoctialis* had rectal temperatures of 40.8 and 39.7°C, five of *Daption capensis* averaged 40.7°C, two of *Procellaria cinerea*, 39.6°C, two of *Macronectes*, 39.7°C, while nine specimens of *Diomedea exulans* and *D. chlororhynchos* had mean temperatures of 39.8°C. Eydoux and Souleyet's (1838) value of 39.6°C for 11 *Diomedea exulans*, probably of the race *chionoptera*, mean weight, 8677 g (Tickell 1968), also agrees well with my figure for birds of the smaller race *exulans*.

The grand mean and SE for the 31 species of adult petrels listed in table 1 is 38.78 ± 0.17°C, and the sample means have an approximately normal distribution. The highest temperature I recorded was 41.3°C for a Black-bellied Storm Petrel *Fregetta tropica* freshly caught on the wing, and the lowest, 37.3°C, for specimens of *Diomedea epomophora* and *Puffinus huttoni* measured at rest.

The values are clearly low and would be expected to be even lower had all the birds been truly at rest when measured. The only groups known to have similarly low temperatures are the ratites and penguins. McNab (1966) lists mean body temperatures for penguins of six species from various sources ranging from 39.0 to 37.7°C, and figures for four species of *Eudyptes* I measured also fall within this range.

The above mean body temperature of 38.78°C for the 31 petrels has been compared with those of the non-procellariiform birds

TABLE 1. Mean body weights and body temperatures in petrels.*

Species	Body weight		Body temperature		Reference[a]
	g	*n*	°C	*n*	
Diomedeidae					
Diomedea epomophora[b]	8728	18	38.7	4	
Diomedea exulans[c]	6636	14	39.2	10	
Diomedea melanophrys[d]					
adults	3015	20	38.7	5	
chicks[e]	2420	5	39.0	5	
Diomedea chrysostoma	3312	20	39.7	8	
Diomedea bulleri	3012	31	39.5	3	
Diomedea nigripes	3148	306	38.1	10	Frings and Frings 1961 (w) Howell and Bartholomew 1961a (t)
Diomedea immutabilis	2853	134	37.5	10	Frings and Frings 1961 (w) Howell and Bartholomew 1961a (t)
Procellariidae					
Fulmarus glacialis	793	35	38.8	41	Dunnet and Anderson 1961 (w) Mougin 1967 (t)
Fulmarus glacialoides	739	18	38.8	23	Prévost 1964
Daption capensis	424	9	39.1	29	Prévost 1964
Pagodroma nivea	377	14	38.7	26	Prévost 1964
Pterodroma lessoni	585	13	38.9	3	
Pterodroma mollis	274	8	39.0	7	
Pterodroma hypoleuca	180	144	38.2	10	Fisher 1961 (w) Udvardy 1963 (t)
Pachyptila desolata	159	124	40.3	46	Tickell 1962
Pachyptila turtur[f]	132	100	38.6	43	Richdale 1965b (w) Farner 1956 (t)
Bulweria bulwerii			37.8	10	Udvardy 1963
Procellaria aequinoctialis	1129	11	39.7	2	
Procellaria cinerea	1035	15	38.1	2	
Puffinus pacificus	358	9	39.5	11	Howell and Bartholomew 1961b
Puffinus griseus	787	100	37.8	3	Richdale 1963 (w)
Puffinus tenuirostris	543	25	40.9	37	Serventy *in* Palmer 1962 (w) Farner and Serventy 1959 (t)
Puffinus nativitatis			38.1	10	Howell and Bartholomew 1961b
Puffinus puffinus			37.0	4	Howell and Bartholomew 1961b
Puffinus huttoni	364	17	37.3	2	Harrow, pers. comm. (w)
Puffinus assimilis	238	5	38.6	4	
Hydrobatidae					
Oceanites oceanicus	34	10	38.8	10	Roberts 1940
Garrodia nereis	32	10	40.7	3	
Fregetta tropica	55	9	39.8	2	
Oceanodroma leucorhoa	48	66	37.2	14	Palmer 1962 (w) Folk 1951 (t)
Pelecanoididae					
Pelecanoides urinatrix	124	100	39.1	6	Richdale 1965a (w)

[a] Sources of weight data only are indicated by (w); sources of temperature data only, by (t).

[b] Sub-species *epomophora*.

[c] Sub-species *exulans*.

[d] Sub-species *impavida*.

[e] Downy chicks that had attained homeothermy.

[f] McNab's (1966) figure of 470 g is an error.

* Since this article was written, body temperatures for *Pterodroma breviostris* have been given by Mougin (Oiseau 39:58–81, 1969). The mean value was 36.6°C and the range, 36.0–37.6°C.

listed by King and Farner (1961, table 8), mean value, 40.02 ± 0.13°C for 28 species; King and Farner (1961, table 9), mean, 41.25 ± 0.14°C for 70 species; and McNab (1966, table 1), mean, 40.82 ± 0.16°C for 81 species. As the raw data are not given for many of the published figures I have used the mean values for each species so that the above figures are the grand means for each table. Standard error tests of the differences of these grand means, and non-parametric Mann-Whitney *U* tests, using the species' means, all indicate that the differences between the petrel data and those of the other three samples are significant, with $P < 0.001$ in each case.

DISCUSSION

Long ago Bergtold (1917) suggested that the body temperature of the parent bird was the most important factor controlling incubation time. He attempted to show that large birds have lower body temperatures than small ones and that members of the more highly evolved groups have higher body temperatures than do those belonging to more primitive groups. Kendeigh (1940), who used rates of gaseous exchange of the eggs to measure rates of growth of their embryos, investigated the effects of temperature on the development of the House Wren (*Troglodytes aedon*). He suggested that inter-specific differences in incubation temperatures might affect the lengths of incubation periods even though different species might be adjusted to particular incubation temperatures.

Huggins (1941) determined the egg temperatures under natural conditions of 37 species belonging to 11 orders of birds. No significant differences were found in the average temperatures from order to order. The mean figure of 34.0°C had a SD of 2.28°C. He concluded that there could be little difference in the average body temperatures of the incubating birds and that other factors must control the lengths of the incubation periods. Irving and Krog (1956) found no significant difference in egg temperatures among seven species of Arctic birds from those determined by Huggins, and they noted the low variability in resting body temperature among the 29 Alaskan birds they studied.

Unfortunately there is little quantitative data on the effects of differing temperature regimes on incubation periods and none for petrels. Kendeigh (1940) calculated that for a House Wren, whose eggs are normally hatched at 35°C in 13 days, the incubation period at 32.2°C and 37.8°C would be 18 and 10 days respectively; that is, a fall and rise of 2.8°C would lead to alterations of +40 per cent and –23 per cent in incubation period. Frith (in Nice 1962) provides an example of the effect of temperature on incubation in the megapode *Leipoa ocellata*, whose eggs are laid in a mound of decaying vegetation. They hatched in summer after about 57 days at 33°C, required as many as 90 days in late autumn, but in an incubator at 37.7°C hatched in 44 days, though prematurely and with their yolk sacs still attached. Frith (1959) ascribed such differences in incubation periods to the differences in temperature levels within the mounds. These data from two very dissimilar species suggest that quite small changes in egg temperature may result in substantial changes in incubation periods.

Incubation periods in petrels are species-specific and vary from 79 days for *Diomedea epomophora sanfordi* (Richdale 1952) to about 40 days for *Hydrobates pelagicus* (Davis 1957) and are highly correlated with egg weight and female body weight except that the fulmars *Fulmarus glacialis*, *F. glacialoides*, *Macronectes*, *Daption*, and *Pagodroma* have significantly shorter incubation and nestling periods than other petrels of equivalent size (Warham MS). Incubation periods are also long in penguins, varying according to species from 33 to 64 days. In ratites they vary from 30 to 77 days.

The analysis of table 1 indicates that, apart from penguins and ratites, petrels do have lower body temperatures when at rest than other birds so far studied. For all these birds, Bergtold's hypothesis that body temperature is an important factor controlling incubation periods seems to require further investigation. Nice (1962), using data from fewer petrels than are now available, also commented on the association of protracted incubation periods with low body temperature, while Brown-Séquard (1858) drew attention to the temperatures of petrels captured off the Cape of Good Hope which he thought surprisingly low in view of their active habits.

Unfortunately few figures for the temperatures at which petrel eggs are incubated are available. Howell and Bartholomew (1961a) gave values of 36.4 and 36.0°C for eggs of *Diomedea nigripes* and *D. immutabilis*, respectively; Etchécopar and Prévost (1954) gave 29.3°C for eggs of *F. glacialoides*; Prévost (1964), 29.6 and 26.0°C for *Daption* and *Pagodroma*; Howell and Bartholomew (1961b), 34.3°C for *Puffinus pacificus*; and Folk (1951), 22.5°C for *Oceanodroma leucohroa.*

The determinations reported by Etchécopar and Prévost (1954), Prévost (1964), and Folk (1949, 1951) suggest that the egg temperatures of petrels may be considerably lower than those of the species studied by Huggins (1941). Among Prévost's birds, all Antarctic species, the ranges of egg temperatures were wide (21.4–31.6°C for *Pagodroma*, 22.9–33.6°C for *Daption*, and 27.2–33.0°C for *Fulmarus glacialoides*). These were much greater than the ranges of the body temperatures and suggest that the eggs were cooling shortly before measurements were taken, perhaps as a result of human interference. The ambient temperatures were slightly below zero and the wind strengths about 6–8 m/sec, so that cooling effects could have been highly important and, in conjunction with difficult field conditions, may explain the variations and low figures obtained.

It seems probable, therefore, that the true egg temperatures for these three species when undisturbed were closer to the maxima recorded by the French workers. This belief is reinforced by the albatross and shearwater figures given by Howell and Bartholomew (1961a, b) who found that egg temperatures were not significantly different from those of the incubation patches.

If egg temperatures of the order given by Folk (1951) and by Etchécopar and Prévost (1954) are really typical of petrels, then the whole question of the temperature range within which petrel eggs develop calls for investigation, for these temperatures are close to the physiological zero of 26.7°C given for the domestic hen by Funk and Biellier (1944).

Data on the Antarctic Skua (*Stercorarius skua maccormicki*), a bird that also incubates at low ambient temperatures, are perhaps relevant here. The birds had a mean body temperature of 41.2°C and their eggs a mean temperature of 35.9°C at Wilkes Station, Antarctica. That is, the eggs were only about 5.3°C below that of the body temperature of the incubating bird (Eklund and Charlton 1959). The range in temperature of the skua eggs was quite wide, some 16.5°C, which the authors ascribed to the frequent changes of the adults on the eggs, i.e., to cooling by the ambient air.

Unfortunately the petrel egg temperature figures are somewhat ambiguous. Even if those of Folk and Prévost are too low it will be seen that the temperatures of the eggs of the two tropical albatrosses are above that of 34.0°C determined by Huggins for birds in general. Yet for a third species, *Puffinus pacificus*, breeding on the same island as the albatrosses, the egg temperature was 2° lower. The anomaly may be more apparent than real. The albatross eggs were well incubated so that their embryos may have been producing a considerable amount of metabolic heat and it is suggestive that the body temperatures of brooded, recently hatched young were significantly higher than those of the brooding adults (Howell and Bartholomew 1961b). The shearwater egg measurements were made on eggs lacking visible embryos; this may explain their markedly lower temperatures.

Furthermore, even if the mean egg temperatures for petrels were significantly lower than the mean egg temperatures for other birds, this would not enable a meaningful comparison to be made because with most of the birds studied by Huggins, the eggs were subjected to a fluctuating temperature regime as were those of the Antarctic Skua already discussed. These conditions are quite different from those under which the petrel egg develops. Petrels sit very tightly and incubation is continuous. Howell and Bartholomew (1961b), for instance, found that the eggs of *Puffinus pacificus* varied by only 0.6°C in 3 hr continuous recording. Thus a comparison of the effect of temperature on incubation between petrels and other birds would involve comparing fluctuating with steady states. Furthermore, due to the increasing liberation of metabolic heat by the embryo, the temperature of the egg tends to rise throughout incubation (Eycleshymer 1907 in Needham 1963; Kendeigh 1940) and petrels, unlike some other birds, do not seem to apply themselves any less closely to their eggs in the later stages of incubation than they do at the start of this process. Clearly a continuous study of body and egg temperatures of petrels throughout incubation, combined with artificial incubation of eggs at different temperatures, would be well worth attempting.

Recently McNab (1966) revived the idea that small birds have higher basal metabolic rates and temperatures than large ones and modified King and Farner's (1961) equation relating basal metabolism to body weight, to one relating body weight and body temperature. The data in table 1, however, do not support the view that smaller petrels have higher resting temperatures than large ones ($r = -0.055$, $P > 0.1$), although any such tendency might be expected to show particularly clearly in a group with so wide a range of body size. This does not, of course, invalidate McNab's hypothesis with respect to other birds.

McNab points out that body temperatures of birds depend on rates of metabolism and rates of heat loss, low body temperatures being a consequence of low metabolic rates and high conductances or both. Although no data for heat conductances in petrels are available, the dense waterproof plumage of these birds indicates that conductances are low, so that their low body temperatures imply low basal metabolic rates. A similar reasoning would apply to penguins. Petrels and penguins are generally considered to have been derived from a common ancestor and their low body temperatures may also have been inherited from this ancestor. Whether these low temperatures are truly primitive and have been retained for adaptive reasons, or have been evolved from the more normal avian condition is problematical. Nevertheless, if rates of metabolism are low this must be an important factor affecting their biology and may help explain their slow growth rates, long periods of immaturity, low annual mortality and high longevity.

It is tempting to speculate further that low metabolic rates may have been important in pre-adapting the petrels for a pelagic existence where a capacity for sustained fasting enabled penetration to areas where birds with higher energy requirements were unable to survive. Many present-day members of the order are exploiting niches where food is scattered and highly patchy so that they appear to have to withstand long periods between meals, rather as they do when ashore incubating their eggs or guarding their chicks. And although there are no figures for the temperatures of petrels in flight, the differences found between active and inactive birds by Farner (1956) and Farner and Serventy (1959) are not very great, amounting to about 2°C. An adult *Diomedea exulans* which I chased, although obviously under some stress when captured, proved to have a cloacal temperature of 40.0°C, only 1.2°C above the mean value for 10 birds caught from their nests. As many petrels (not only the albatrosses and other large forms) economize on energy expenditure by sailing the winds, it would be surprising if their body temperatures when cruising in search of food are greatly elevated above those of their resting states. McNab (1966) proposed a similar explanation for the low metabolic rate and low body temperature of the Turkey Vulture (*Cathartes aura*) as being an adaptation to an undependable food supply, permitting the bird to tolerate prolonged periods of fasting.

SUMMARY

The body temperatures of 31 species of petrel have a mean and SE of 38.78 ± 0.17°C. This is significantly lower than mean values for non-procellariiform birds hitherto published. Other birds that have similarly low temperatures are the penguins and the ratites. Members of all these groups have long incubation periods and it is suggested that the low body temperatures of petrels may supply an important reason for their slow rates of development, that the birds' basal metabolic rates are also low, a condition advantageous for energy conservation where food is in erratic supply and fasting is necessary during, and probably out of, the breeding season.

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LITERATURE CITED

BERGTOLD, W. H. 1917. A study of the incubation periods of birds. Kendrick-Bellamy, Denver.

BROWN-SÉQUARD, E. 1858. Note sur la basse température de quelques Palmipèdes longipennes. J. Physiol. l'homme animaux 1:42–46.

DAVIS, P. 1957. The breeding of the Storm Petrel. Brit. Birds 50:85–101, 371–384.

DUNNET, G. M., AND A. ANDERSON. 1961. A method for sexing living Fulmars in the hand. Bird Study 8:119–126.

EKLUND, C. R., AND F. E. CHARLTON. 1959. Measuring the temperatures of incubating penguin eggs. Amer. Sci. 47:80–86.

ETCHÉCOPAR, R. D., AND J. PRÉVOST. 1954. Données oologiques sur l'avifaune de Terre Adélie. Oiseaux 24:227–247.

EYDOUX, F., AND A. SOULEYET. 1838. Sur la température de l'homme et des oiseaux. C. R. Acad. Sci. Paris 6:456–458.

FARNER, D. S. 1956. Body temperatures of the Fairy Prion (*Pachyptila turtur*) in flight and at rest. J. Appl. Physiol. 8:546–548.

FARNER, D. S., AND D. L. SERVENTY. 1959. Body temperature and thermoregulation in the Slender-billed Shearwater. Condor 61:426–433.

FISHER, H. I. 1961. Weights and measurements of organs of Bonin Island Petrels *Pterodroma leucoptera hypoleuca*. Auk 78:269–271.

FOLK, G. E. 1949. Body temperatures of Leach's Petrel. Anat. Rec. 105:590.

FOLK, G. E. 1951. Observations of the body temperature of Leach's Petrel. Anat. Rec. 111:541–542.

FRINGS, H., AND M. FRINGS. 1961. Some biometric studies on the albatrosses of Midway Island. Condor 63:304–312.

FRITH, H. J. 1959. Breeding of the Mallee Fowl, *Leipoa ocellata* Gould (Megapodiidae). C.S.I.R.O. Wildlife Res. 4:31–60.

FUNK, E. M., AND H. V. BIELLIER. 1944. The minimum temperature for embryonic development in the domestic fowl (*Gallus domesticus*). Poultry Sci. 23:538–540.

HOWELL, R. T., AND G. A. BARTHOLOMEW. 1961a. Temperature regulation in Laysan and Black-footed Albatrosses. Condor 63:185–197.

HOWELL, R. T., AND G. A. BARTHOLOMEW. 1961b. Temperature regulation in nesting Bonin Island Petrels, Wedge-tailed Shearwaters, and Christmas Island Shearwaters. Auk 78:343–354.

HUGGINS, R. A. 1941. Egg temperatures of wild birds under natural conditions. Ecology 22:148–157.

IRVING, L., AND J. KROG. 1956. Temperatures during the development of birds in Arctic nests. Physiol. Zool. 29:195–205.

KENDEIGH, S. C. 1940. Factors affecting length of incubation. Auk 57:499–513.

KING, J. R., AND D. S. FARNER. 1961. Energy metabolism, thermoregulation and body temperature. *In* A. J. Marshall [ed.] Biology and comparative physiology of birds. Academic Press, London.

MAHER, W. J. 1962. Breeding biology of the Snow Petrel near Cape Hallett, Antarctica. Condor 64:488–499.

MCNAB, B. K. 1966. An analysis of the body temperatures of birds. Condor 68:47–55.

MOUGIN, J. L. 1967. Etude écologique des deux espèces de fulmars le Fulmar Atlantique (*Fulmarus glacialis*) et le Fulmar Antarctique (*Fulmarus glacialoides*). Oiseaux 37:57–103.

NEEDHAM, J. 1963. Chemical embryology. Haffner, New York.

NICE, M. M. 1962. Development of behavior in precocial birds. Trans. Linnaean Soc. New York 4:1–247.

PALMER, R. S. 1962. Handbook of North American birds. Yale Univ. Press, New Haven.

PRÉVOST, J. 1964. Remarques écologiques sur quelques procellariens antarctiques. Oiseaux 34:91–112.

RICHDALE, L. E. 1952. Post-egg period in albatrosses. Biol. Monogr. 4.

RICHDALE, L. E. 1963. Biology of the Sooty Shearwater *Puffinus griseus*. Proc. Zool. Soc. London 141:1–117.

RICHDALE, L. E. 1965a. Biology of birds of Whero Island, New Zealand, with special reference to the Diving Petrel and the White-faced Storm Petrel. Trans. Zool. Soc. London 31:1–86.

RICHDALE, L. E. 1965b. Breeding behaviour of the Narrow-billed Prion and the Broad-billed Prion on Whero Island, New Zealand. Trans. Zool. Soc. London 31:87–155.

ROBERTS, B. 1940. The life cycle of Wilson's Petrel *Oceanites oceanicus* (Kuhl). British Graham Land Expedition 1934–1937. Sci. Rept. 1:141–194.

SIMPSON, S. 1912. Observations on the body temperatures of some diving and swimming birds. Proc. Roy. Soc. Edinburgh 32:19–35.

TICKELL, W. L. N. 1962. The Dove Prion, *Pachyptila desolata* Gmelin. Falkland Islands Dependencies Survey. Sci. Rept. 33.

TICKELL, W. L. N. 1968. The biology of the Great Albatrosses, *Diomedea exulans* and *Diomedea epomophora*. Antarctic Bird Studies 12:1–55. Amer. Geophys. Publ. 1686.

UDVARDY, M. D. F. 1963. Data on the body temperatures of tropical sea and water birds. Auk 80:191–194.

WARHAM, J. 1968. Biometric studies of birds in the order Procellariiformes. M.Sc. Thesis, Univ. Durham, England.

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