TEMPERATURE REGULATION IN NESTING BONIN ISLAND PETRELS, WEDGE-TAILED SHEARWATERS, AND CHRISTMAS ISLAND SHEARWATERS

THOMAS R. HOWELL AND GEORGE A. BARTHOLOMEW

THIS paper represents part of a study on the thermoregulatory responses of nesting sea birds to natural environmental conditions. The investigations were conducted on Midway Island, a coral atoll located at latitude 28° 13′ N. and longitude 177° 23′ W. in the Leeward Chain of the Hawaiian Islands. A previous publication (Howell and Bartholomew, 1961) dealt with the two species of albatrosses that breed on Midway, and the present study concerns the other three procellariiform species that regularly nest on the island. Bailey (1956) has summarized much of the natural history information on the avifauna of Midway Island, and Farner and Serventy (1959) include references to most of the pertinent literature on thermoregulation in procellariiform birds.

ENVIRONMENTAL CONDITIONS

Data from the Navy meteorological station show that the macroclimate of Midway Island is remarkably equable. In January and February, the mean low is 15° C and the mean high is 21° C (extremes, 12° to 24.5° C). In June and July, the mean low is 21° C and the mean high is 28.5° C (extremes, 18.5° to 31° C). However, these temperatures were taken at a height of 21 meters above ground; the microclimates to which the nesting birds are exposed are more variable and are discussed below in the accounts for each species.

MATERIALS AND METHODS

All measurements were made on unconfined birds under natural conditions. Temperatures were measured by means of a portable, battery-powered, multichannel thermister thermometer manufactured by the Yellow Springs Instrument Company, Yellow Springs, Ohio. We used a variety of probes and leads that enabled us to measure temperatures with the sensing element as far as 20 meters from the indicating meter. All thermisters were calibrated with a Bureau of Standards thermometer. Temperatures were read to the nearest 0.1° C. By using several sensing elements in different channels of the instrument, we were able to obtain essentially simultaneous determinations of black-bulb, air, substratum, and body temperatures. Deep body (core) temperature was measured by gently inserting a steel-sheathed thermister

Figure 1. Bonin Island Petrel taken from its nesting burrow on Midway Island in January 1960. Note the distinctive underwing pattern.

probe down the esophagus to or into the stomach. Foot temperatures were obtained by enclosing a "banjo tip" surface-temperature-indicating thermister in a fold of the webbing. The same thermister was used in taking incubation patch temperatures by pressing the flat tip of the probe against the bare skin. Temperatures of eggs were obtained by slipping a vinyl-sheathed probe 3 mm. in diameter through a small hole bored in the shell; care was taken to place the thermister element in the approximate center of the egg.

The species studied can be seized when on land without much difficulty, and temperatures were recorded within 15 or 20 seconds after grasping the birds. It is highly improbable that any significant elevation of temperature due to struggle or excitement would occur in this brief interval.

Pterodroma hypoleuca hypoleuca

The form known as the Bonin Island Petrel (Figure 1) breeds in the Bonin Islands and the Leeward Chain of the Hawaiian Islands and ranges widely over the tropical and temperate parts of the Pacific. These petrels are probably the most abundant nesting species on Midway; they nest in burrows in the coral sand and are strictly nocturnal. They are found on Midway during fall, winter, and spring, but are scarce or completely absent during summer. Because they are nocturnal and nest in deep burrows, these birds are not exposed to the heat stress imposed on surface nesters. During January and February 1960 all of the burrows that we dug out contained single eggs, and one or both parents were in attendance.

Our observations on the temperatures of these birds are summarized in Table 1. The daytime temperatures were obtained by digging the petrels out of their burrows and taking measurements as soon as we could reach the birds. Nocturnal temperatures were obtained by picking up birds on the ground as they returned to their burrows after feeding at sea. Nocturnal body temperatures average 1.4° C higher

TABLE 1

TEMPERATURES (°C) OF THE BONIN ISLAND PETREL

	Time	*Mean*	*No. of birds*	σ	*Range*	*Air T.*	
Daytime	1345–1530	38.5	10	0.47	37.4–39.2	23.0–23.8	(in burrows)
Nighttime	2130–2206	39.9	10	0.51	39.1–41.0	22.5	(in open)

Figure 2. Wedge-tailed Shearwaters at a fully exposed surface nest on Midway Island, June 1959.

than the daytime temperatures, and the difference is statistically significant. In fact, there was practically no overlap between the maximum daytime (resting) temperature and the minimum nocturnal (active) temperature, although environmental temperatures were virtually the same under both circumstances.

Puffinus pacificus

This species breeds at many locations in the Indian and Pacific oceans within about 30° of the equator. On Midway it is abundant in spring and summer. Although at many localities within their range these shearwaters nest in burrows, on Midway they commonly nest in shallow depressions in the sand. The nest is usually in at least partial shade, but in rare instances nests were placed completely in the open (Figure 2). One egg constitutes the usual clutch, but occasionally we found a bird incubating two eggs. In mid-June 1959 these birds were in the early stages of incubation, for numerous eggs examined in connection with temperature measurements had no visible embryos and we found no nestlings. Both parents participate in incubation and both have an incubation patch; often both birds are present at the nest site.

Data on temperature of the environment, the internal temperature of brooded eggs, and temperatures of relevant parts of the body are summarized in Figure 3. Noteworthy points are as follows:

1. The mean diurnal body temperature (39.5° C) is significantly higher than the mean nocturnal body temperature (37.7° C).
2. Daytime incubation patch temperatures (mean 37.8° C) average 1.7° C lower than daytime body temperatures.
3. Internal egg temperatures (mean 34.3° C), although taken within 30 seconds after removal from under the incubating bird, average 3.5° C lower than incubation patch temperatures.
4. Eggs left exposed in full sun have internal temperatures (mean 40.2° C) that are essentially the same as that of the substratum and average over 6° C higher than the incubated eggs and 2.4° C above the incubation patch.
5. Foot temperatures (mean 33.6° C) average lower than egg temperatures and incubation patch temperatures but are higher than air temperature; foot temperatures are also highly variable.

The diurnal cycle of body temperature in this species is considered in the general discussion in comparison with other species. The difference between incubation patch temperature and internal egg temperature merits comment here. None of the eggs had visible embryos, and

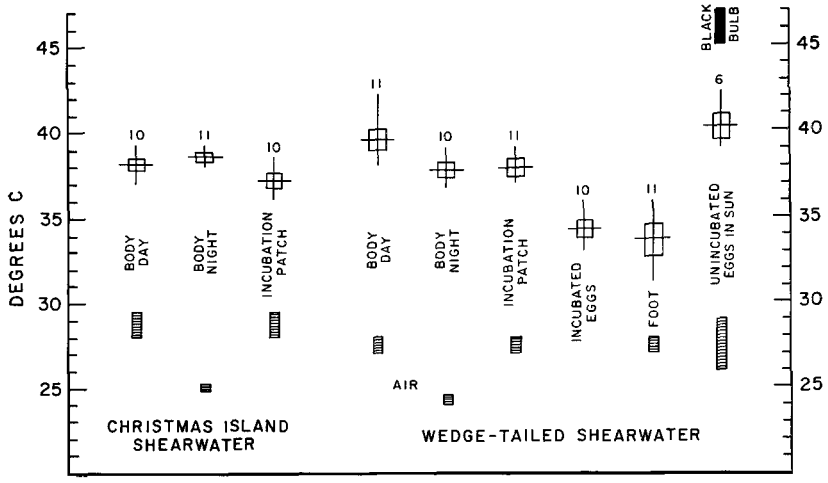

Figure 3. Summary of temperature data for Christmas Island and Wedge-tailed Shearwaters. Horizontal lines indicate the means (M); vertical lines indicate the range. Rectangles indicate the interval M + 2 σ_M to M − 2 σ_M. Numbers indicate the sample size. Cross-hatched symbols show the range of air temperatures during the period when body temperatures were being measured.

heat production within the egg must have been negligible. The internal egg temperature, then, presumably represents an equilibrium between the slightly warmer skin of the incubation patch and the cooler substratum. The range of variability of egg and incubation patch temperatures is almost identical, indicating the extent to which the patch controls the egg temperature.

We endeavored to obtain continuous figures on the incubation temperature by implanting a thermister probe inside an incubated egg and replacing it under the bird. The probe was flexible, and presumably its tip was located under the upper surface of the egg and thus very close to the incubation patch. A continuous record of incubation temperature for three hours varied only from 36 to 36.6° C, which is at the upper limit of the range of temperatures taken in the center of incubated eggs.

The moderate air temperature in the shade on Midway in the summer should present no heat stress for unbrooded eggs in sheltered locations. The relatively few shearwaters that nest in the open sun, however, face a formidable intensity of solar radiation as black bulb temperatures are often above 45° C. The parents at these nests left the eggs from midmorning to midafternoon, presumably because the

heat was too great for the birds. The egg temperatures reached levels that are known to be detrimental to development in other species (Baerends, 1959:357), and we doubt that these fully exposed shearwater nests were successful.

The Wedge-tailed Shearwater has pale foot webbing in which blood vessels are clearly visible, and we took foot temperatures to see if there was any indication that the vascular webbing contributed to the heat of incubation. The variability of foot temperature, and especially the low mean, shows that this is not the case.

We obtained weights of 19 eggs without visible embryos, and the weights proved quite variable. The range was 52-67 g., with a mean of 59.5±4.2 g.

Puffinus nativitatis

The Christmas Island Shearwater breeds on many Pacific islands within 30° of the equator. On Midway this species is less frequently seen in the daytime than the Wedge-tailed Shearwater, but at dusk and at night the two forms appear to be equally numerous. Nests of *P. nativitatis* were usually shallow depressions in the sand in *Scaveola* thickets, but the nests tended to be farther inside the thickets and in deeper shade than those of *P. pacificus*. Most of the nests that we found contained single eggs, but two nests had recently hatched young. Adults of both sexes have an incubation patch, and both were often present together at the nest.

Data on body and incubation patch temperatures are summarized in Figure 3. Noteworthy points are as follows:

1. There is no significant difference between diurnal (mean 38.1° C) and nocturnal (mean 38.6° C) body temperatures, although the latter average slightly higher.

2. Under a given set of conditions, body temperatures are strikingly uniform.

3. Daytime incubation patch temperatures (mean 37.2° C) average almost 1° C lower than daytime body temperatures.

The only two nestlings that we found were discovered on 20 June. One had just hatched, and the other was a 61-g. chick that was being closely brooded. Both were covered with sooty black down. On 22 June their weights were, respectively, 40 g. and 84 g. They were taken from under the brooding parents on that day and placed in the open in direct sunlight; the results are shown in Figure 4. Both the nestlings began to pant within 10 minutes of the start of their exposure. The temperature of the younger chick rose steadily, and the bird died

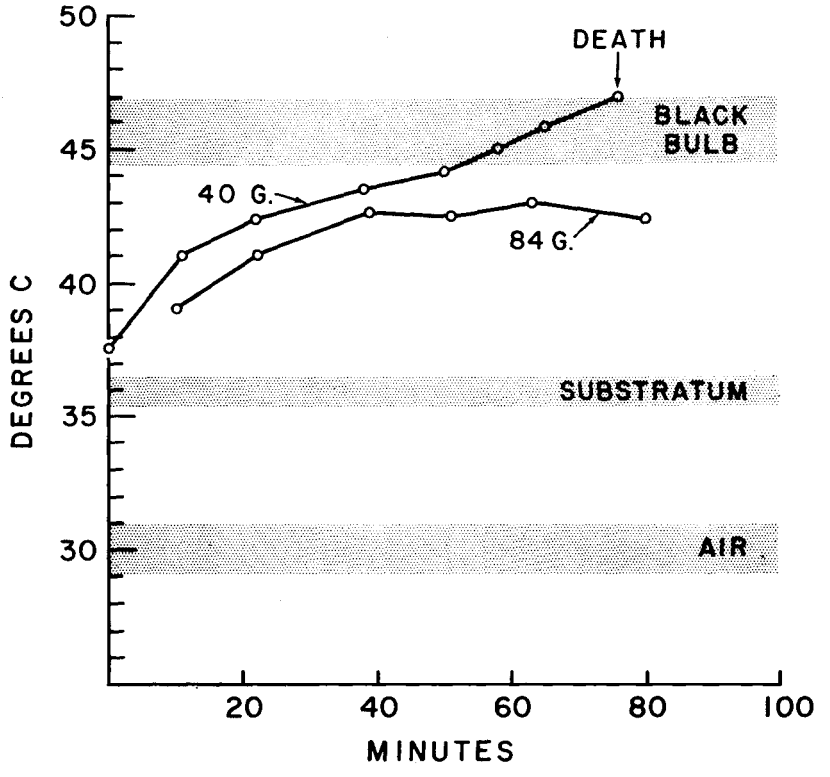

Figure 4. The course of body temperature of two downy nestlings of the Christmas Island Shearwater removed from the nests and placed in direct sun.

at a body temperature of 47° C. The dead nestling was left in the sun; after 50 minutes the body temperature was 44° C—essentially the same as the black bulb temperature at the time the measurement was made. The body temperature of the older nestling rose initially and then stabilized between 42 and 43° C; the bird remained in excellent condition to the end of the experiment. It was returned to its nest, and when examined on subsequent days it appeared to be in good health and to be growing well.

DISCUSSION

It was not possible to distinguish externally between the sexes of the three procellarids that we studied. In each species both sexes have incubation patches and appear to participate in nest activities. We

assume that in these species as in *P. tenuirostris* (Farner and Serventy, 1959) there is no sexual difference in body temperature.

Daily temperature cycles. Farner (1956) has shown that in a southern hemisphere procellarid, the Fairy Prion *(Pachyptila turtur)*, body temperatures of active birds on the ground at night average about 1.3° C higher than those of birds incubating in burrows during the day. Our data for the Bonin Island Petrel show a similar situation; body temperatures of birds active on the ground at night averaged 1.4° C higher than those of incubating birds in burrows during the day. The mean body temperature of incubating Bonin Island Petrels (38.5° C) is almost identical to that of the Fairy Prion (38.6° C) but considerably higher than the mean of 37.2° C reported by Folk (1951) for incubating Leach's Petrels, *Oceanodroma leucorhoa* (Hydrobatidae). Environmental temperatures were about 23° C for the Bonin Island Petrel and 11.6° C for Leach's Petrel; Farner did not indicate environmental temperatures in his study.

Although not as strictly nocturnal as the Bonin Island Petrel, the Christmas Island Shearwater is primarily active at night during the nesting season. The nocturnal body temperatures of this species averaged slightly but not significantly higher than those recorded during the day. The absence of a significant difference probably has several causes. The surface-nesting habits expose the birds to higher air temperatures during the day than would be encountered in burrows; the lack of air movement in the dense *Scaveola* thickets allows air temperature at the nests to reach almost 30° C. The nests are located in the midst of a dense population of active, vocalizing birds of a number of species; this probably keeps the incubating shearwaters more alert than if they nested in burrows, and consequently may contribute to the relatively high level of daytime body temperature. Moreover, the Christmas Island Shearwaters that we studied had lower nighttime temperatures than have been reported for other shearwaters nesting at higher latitudes. For example, the maximum body temperatures (39.3° C) of active *P. nativitatis* caught on the ground at night are not as high as even the mean nocturnal body temperatures (39.9° C) of *Puffinus tenuirostris* measured under similar conditions (Farner and Serventy, 1959). About half of the Christmas Island Shearwaters captured on the ground at night must have recently come in from the sea as they vomited fresh squid when handled, yet these active birds had temperatures in the same range as those sitting quietly on shaded nests during the day. Thus, unexpectedly high daytime body temperatures for the incubating birds overlapped unexpectedly low nighttime temperatures

of the active birds and eliminated any evidence of a clear-cut daily temperature cycle.

Nesting Wedge-tailed Shearwaters are more active during the day than nesting *P. nativitatis,* but they are still primarily nocturnal. Nevertheless, our data on this species at Midway Island show that daytime body temperatures of incubating birds average significantly higher than those of active birds at night. The causes of this situation are probably similar to those outlined above for *P. nativitatis,* but accentuated. Many nests of the Wedge-tailed Shearwaters are in only partial shade, and solar heat undoubtedly augments the effect of high air temperatures on the body temperatures of incubating birds in the daytime. The body temperatures of four birds incubating in partial sun averaged 40.3° C (39.3-42.1); these figures include the highest temperatures we recorded for this species and account in part for the high mean daytime body temperature.

Farner and Serventy (1959) reported a mean body temperature of 38° C for *P. tenuirostris* incubating in burrows at air temperatures of about 22° C. Bartholomew obtained data on the similarly sized subtropical species, *Puffinus puffinus opisthomelas,* on Guadalupe Island, Baja California, Mexico, on 19 April, 1956. These shearwaters were incubating deep in burrows where the air temperature was 21-21.9° C; the body temperatures of four birds averaged 37° C (36.8-37.2). Thus, the mean daytime body temperatures of both *P. tenuirostris* and *P. puffinus* are lower than the daytime mean (39.5° C) for the surface-nesting *P. pacificus* on Midway.

Nesting temperatures. Farner and Serventy (1959) have pointed out that at burrow temperatures of about 22° C, one- and two-day-old chicks of *Puffinus tenuirostris* have sufficient thermoregulatory ability to keep body temperatures up to the typical adult level. Although our data on thermoregulation in nestlings of *P. nativitatis* are limited, it is apparent that young chicks of this species are unable to keep body temperatures *down* to the typical adult range when exposed to direct solar radiation and moderately high air and soil temperatures (Figure 4). Surface nests of the Christmas Island Shearwater on Midway were always in deep shade, and the attentive parents brooded the nestlings continuously during the day. It is not surprising, in view of the nesting habits of these and most other shearwaters, that thermoregulation of the young under cool conditions is more effective than it is under heat stress.

ACKNOWLEDGMENTS

This study was aided in part by a contract between the Office of Naval Research, Department of the Navy, and the University of California, Nonr 2807(00). We are especially grateful to Cmdr. I. A. Kittel, Commanding Officer, U.S. Naval Air Station, Midway Island, and to Lt. Cmdr. Glenn A. Wilson, Security Officer on Midway, for their many courtesies and invaluable assistance during our visits. Lt. Cmdr. Wilson's personal interest and extensive knowledge of the bird life was particularly important in enabling us to make the best use of our time.

SUMMARY

Thermoregulation was studied in three species of procellarids nesting on Midway Island. The Bonin Island Petrel *(Pterodroma hypoleuca hypoleuca)*, a nocturnal species that nests in burrows, shows a significantly higher mean body temperature when active at night than when incubating during the day (39.1° C as opposed to 37.4° C). The Wedge-tailed Shearwater *(Puffinus pacificus)*, a partly nocturnal species that is primarily a surface nester on Midway, shows a mean daytime body temperature (39.5° C) that is significantly higher than the mean nighttime body temperature (37.7° C). Measurements of egg, incubation patch, and foot temperatures show that the temperatures of incubated eggs without visible embryos average 3.5° C lower than incubation patch temperatures (mean 37.8° C) and that the feet do not contribute to the heat of incubation. The Christmas Island Shearwater *(Puffinus nativitatis)* has habits similar to those of *P. pacificus* but is more nocturnal and locates its surface nests in deeper shade. Daytime (mean 38.1° C), and nighttime (mean 38.6° C) body temperatures of adults do not differ significantly. A two-day-old nestling could not tolerate long exposure to intense solar heat, but an older downy chick regulated body temperature at an elevated but sublethal level (42-43° C) under the same conditions. Ecological implications of the data on all three species are discussed.

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Department of Zoology, University of California, Los Angeles, California.