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TEMPERATURE REGULATION IN LAYSAN AND BLACK-FOOTED ALBATROSSES

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This paper represents part of a more extensive study on the thermoregulatory responses of nesting sea birds to naturally occurring environmental conditions. Sea birds are especially suitable for such investigations as they may be found nesting in large concentrations in sites that are often fully exposed to the impact of the environment. Numerous procellariiform species offer such advantages for study, but there are relatively few data on thermoregulation in members of that order. Farner (1956) and Farner and Serventy (1959) have provided summaries of the pertinent literature. Our studies were conducted on Midway Island, latitude 28° 13′N and longitude 177° 23′W, in the Leeward Chain of the Hawaiian Islands. Midway is a coral atoll consisting of two small islands—Sand and Eastern islands—and a fringing reef. It is a major nesting site for pelagic birds of three avian orders, and most of the species are present in great numbers. Furthermore, they exhibit to a marked degree the well-known tameness of birds that breed on remote oceanic islands. In consequence, one can obtain in rapid succession a series of measurements from large numbers of individuals exposed to virtually identical environmental conditions. As Midway has served as a cable station and as a naval base for many years, numerous observers have recorded much useful data on the breeding cycles and general natural history of the avifauna (see Bailey, 1952 and 1956, for recent summaries). All of these factors combine to make Midway a uniquely favorable place for studies such as the present one.

ENVIRONMENTAL CONDITIONS

The macroclimate of Midway Island is remarkably equable. Weather data from the navy meteorological station for the months pertinent to our observations are given in table 1; the air temperatures were taken at a height of 21 meters. The climate in January and February is the coolest to which the young birds are exposed; June and July cover the hottest period for juveniles still on land. The absence of stressful temperatures in January and February is noteworthy, as is the almost continuous wind during the warmer part of the year. Air temperatures taken at a height of 21 meters, however, are not always indicative of conditions in locations on or near the ground. In January and February the air temperatures we recorded at the nest sites of albatrosses were not notably different from those of the weather station. In June and July, however, in areas where juvenal birds were numerous, soil temperatures as high as 40°C. and black-bulb temperatures of almost 50°C. were recorded. Air temperatures above the maxima recorded at the weather station were noted almost daily.

The mean annual precipitation is 106 cm., and rainfall may occasionally be so heavy as to cause flooding and destruction of nests. Sandstorms caused by violent winds sometimes occur in winter and may destroy nests situated in exposed locations.

TABLE 1

SUMMARY OF WEATHER STATION DATA DURING WINTER AND SUMMER, RECORDED ON SAND ISLAND AT A HEIGHT OF 21 METERS*

Month	Maximum	Minimum	Mean high	Mean low	Mean wind velocity	Per cent calm
January	24.5	13.0	21.0	17.0	12.8	3.5
February	24.5	12.0	21.0	15.0	12.2	3.0
June	30.5	18.5	28.0	21.0	8.7	2.7
July	31.0	19.5	28.5	23.0	9.3	2.5

*Air temperatures in °C.; wind velocity in knots.

MATERIALS AND METHODS

All measurements were made on unconfined birds under natural conditions. Temperatures were measured by means of a portable, battery-powered, multi-channel 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 sixty feet 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 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 unpipped 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. Temperatures of pipped eggs were measured by introducing the thermister through the punctured shell and pressing it firmly against the surface of the unhatched chick.

The albatrosses can be seized when on land without 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.

LAYSAN ALBATROSS

The Laysan Albatross (*Diomedea immutabilis*) breeds primarily on islands of the Leeward Chain and ranges widely over the Pacific Ocean in the northern hemisphere. This species arrives on Midway about the first of November. Courtship and nest building begin, and eggs are present by the end of that month. The first young are hatched in late January, and they are constantly brooded by the adults for about two weeks. Feeding of the juveniles continues until July and August, when the young birds are finally able to fly. Both parents have an incubation patch and both participate in incubation, brooding, and feeding.

During our visit to Midway in January and February, 1960, we observed the late stages of incubation and the hatching and brooding of young birds. In June and July, 1959 and 1960, we observed full-grown juveniles not yet able to fly. At these times the young birds were unattended except for the feeding visits of the adults.

The Laysan Albatross is extremely numerous and widely distributed on both Sand and Eastern islands. It rarely nests on open, wind-swept sand but is partial to vegetated areas such as *Casuarina* groves and *Scaveola* thickets. This species also nests abundantly among the buildings of the naval installations on the island. The nest is a raised bowl of sand about three to six inches high and includes bits of vegetation (fig. 1). The single egg or young chick is continuously brooded, and the parent may sit on the nest for many days before being relieved by its mate.

Fig. 1. Laysan Albatross (*Diomedea immutabilis*) with recently hatched chick.

We recorded body, incubation patch, and foot temperatures of brooding adults during the day and body temperatures at night. We also recorded under a variety of conditions the temperatures of eggs, recently hatched chicks, and large juveniles. The results are summarized in figure 2; noteworthy points are as follows:

1. Daytime body temperatures of brooding adults (mean 37.5°C.) average almost 1°C. higher than nocturnal temperatures, and the difference is statistically significant. The range of individual variation in body temperature is remarkably slight, and the means are lower than those usually reported for nonincubating individuals of other species.

2. Incubation patch temperatures (mean 36.7°C.) are significantly lower than body temperatures and much higher than foot temperatures (mean 26.9°C.) of adults. The feet clearly do not contribute to incubation heat in this species.

3. The temperatures of advanced brooded eggs (mean 36.0°C.) are not significantly different from incubation patch temperatures.

4. The temperatures of brooded, recently hatched young (mean 38.9°C.) are significantly higher than either incubation patch temperatures or body temperatures of brooding adults.

5. The body temperatures of large juveniles (mean 39.3°C.) exposed to intense solar radiation are much higher than the daytime body temperatures of unstressed brooding adults but lower than those of adults that have been active in full sun (mean 40.5°C.).

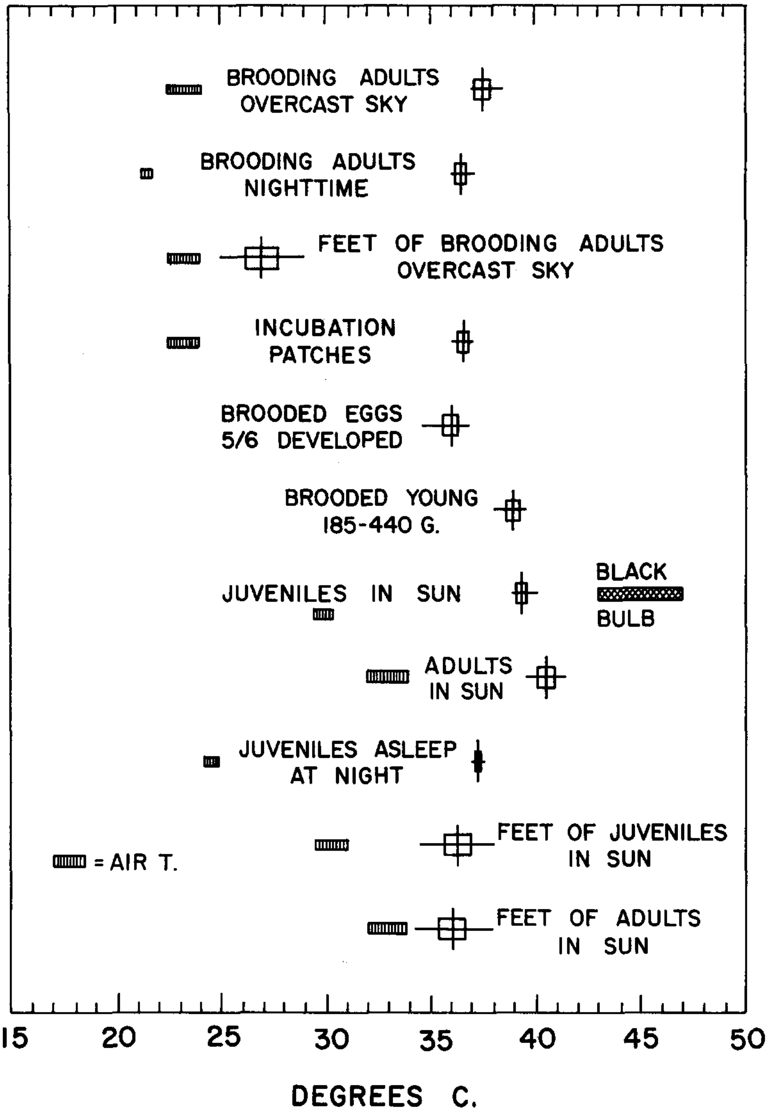

Fig. 2. Summary of temperature data for the Laysan Albatross. Horizontal lines indicate the range; vertical lines indicate the means (M); rectangles indicate the interval M + $2\sigma_M$ to M — $2\sigma_M$. In all cases sample size is 10.

6. Body temperatures of large juveniles asleep at night (mean 37.2°C.) are slightly higher than nighttime temperatures of brooding adults that are awake (mean 36.6°C.).

The foot temperatures of large juveniles require extended comment. During the summer months solar radiation may be intense, and the birds are often fully exposed to this stress. Under these conditions, body temperatures of juveniles are elevated about 2°C. above those of unstressed adults, but foot temperatures of juveniles are about 10°C. higher than those of unstressed adults (fig. 2).

Juveniles in the sun characteristically sit balanced on their heels with the webbed

Fig. 3. Juvenal Laysan Albatross resting on its heels. For photographic clarity the bird was induced to turn so that the feet were in the sun; the feet are usually kept in the shade of the body.

feet spread and held in the air (fig. 3). The birds almost always orient themselves with their backs to the sun so that their feet are in the shade of their bodies, even if this means facing away from the prevailing winds. Temperatures of feet held off the ground, as well as temperatures of the body, the air, and the substratum in the sun are given in table 2. The foot temperatures are always higher than those of the surrounding air but lower than those of the substratum. It follows that heat is lost from the feet by radiation and convection to the cooler air, whereas heat would be gained by conduction were the feet rested on the hot substratum.

TABLE 2

RELATION OF FOOT TEMPERATURES OF JUVENAL LAYSAN ALBATROSSES, EXPOSED TO INTENSE SOLAR RADIATION, TO TEMPERATURES OF AIR AND SUBSTRATUM*

	Birds balanced on heels with feet in air	Birds crouched on soil with feet underneath body
Air	29.4–31.0	31.0
Substratum	39.5–40.2	31.0–36.1
Foot	36.3±1.1	36.9±0.6
Body	39.3±0.8	39.3±0.8

*Data from 11 birds with feet exposed and 10 birds with feet sheltered. Temperatures in °C.

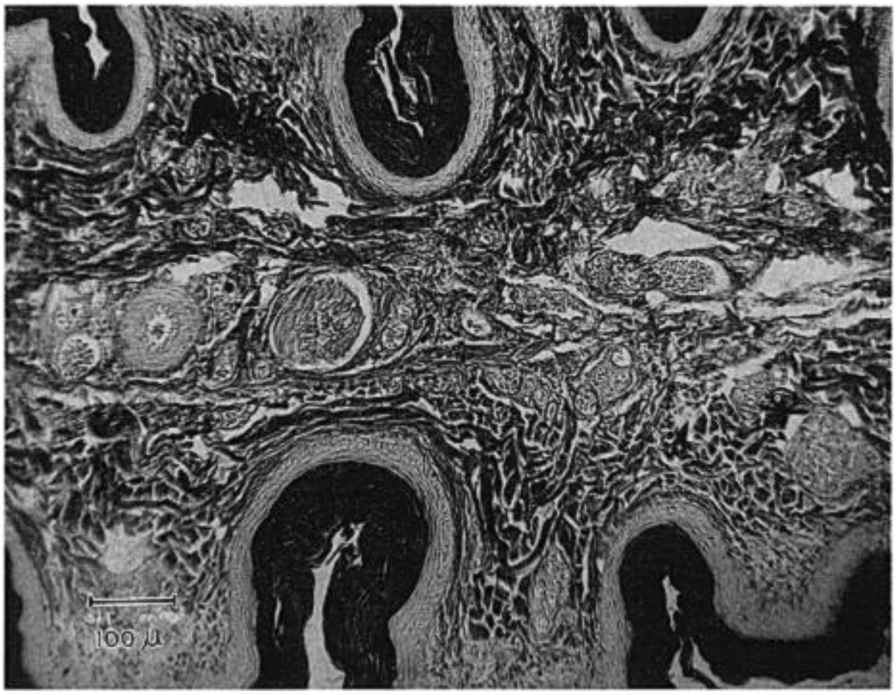

Fig. 4. Photomicrograph of foot webbing of juvenal Laysan Albatross, showing heavy vascularization. Mallory Azan stain was used.

In some cases, juvenal birds exposed to intense solar radiation remained crouched on the substratum with the feet kept under the body. Temperatures of the feet and the shaded substratum under such birds are given in table 2. The foot temperatures are about the same as those of birds with feet exposed, but the substratum temperature is always lower than that of the feet. Hence, heat is lost by conduction from the feet to the cooler substratum.

These observations indicate that the feet function in heat loss as follows. Some juveniles do not move from the spot where they roosted at night until many hours after dawn, if at all. The substratum under these birds remains relatively cool as it is shielded from the sun, and as long as the feet are kept on this substratum they will lose heat to it. On the other hand, birds that move away from their roosting place may come to rest on a heated substratum, and when these birds settle down they assume the feet-in-air position. This odd posture has been noted by observers for over half a century (Fisher, 1903:18, pl. 5); it may serve some function in addition to permitting heat loss, but the latter must certainly occur. The foot temperatures of nonbrooding adults in the full sun are approximately the same as those of juveniles under the same conditions, but only one of many thousands of adults which we have observed assumed the feet-in-air posture so typical of the young birds. Presumably the adults need only take to the air to dissipate excess heat.

Samples of foot webbing of large juvenal Laysan Albatrosses were taken for histological examination. As shown in figure 4, there is considerable vascularity in the subepithelial tissue. There are larger vessels in the central part of the webbing and bundles of smaller ones near the surface of each fold of the skin; this arrangement would greatly

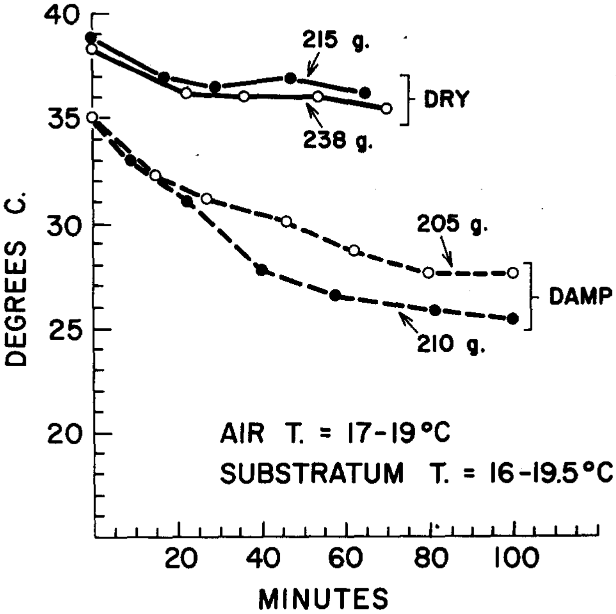

Fig. 5. Temperatures of newly hatched, unbrooded Laysan Albatrosses in shade.

facilitate heat loss to the environment. As expected, there is a high degree of vasomotor control in the foot webbing. When we attempted to obtain blood samples by cuts across visible blood vessels in the foot webs of juvenal albatrosses, we were usually unable to obtain even enough blood for a smear without vigorous "milking" or waiting as long as several minutes for some vasodilatation to occur. No amount of extensive cutting produced a copious flow of blood.

Like many other birds, albatrosses routinely employ evaporative cooling in regulating body temperature. Under conditions of severe heat loading both adults and young pant heavily with mouth open and throat lowered and distended, but they never show the gular fluttering so typical of pelecaniform birds. The panting rate is only moderately high and averages about 160 per minute (range shown by 10 heavily panting large juveniles in full sun, 138 to 198 per minute). When panting, the oral mucosa is conspicuously moist and drops of fluid commonly are visible in the corners of the mouth. Large juveniles often combine panting with the feet-in-air posture when they are exposed to intense solar radiation and little or no air movement.

As previously indicated, recently hatched and brooded young have higher temperatures than either brooded eggs or brooding adults. Obviously, the chicks are producing heat in addition to that provided by the parent. However, their heat-producing capacity is not sufficiently developed to permit the degree of body temperature regulation that is possible at a later stage. Figure 5 presents data on young chicks exposed to ambient temperatures lower than those provided by brooding adults. Two still-damp nestlings showed a steady decline in body temperature, finally leveling off about 10° to 12°C. below the initial brooded temperature and about 6° to 8°C. above the moderate ambient temperature. On the other hand, chicks of similar size but with dry down had a higher initial brooded temperature; after a small decline, they maintained a body temperature only slightly below that of adults under the same conditions. As the damp chicks were

Fig. 6. Black-footed Albatross (*Diomedea nigripes*) and its egg, at edge of *Scaveola* thicket.

only a few hours younger than the dry ones, we interpret the difference in regulatory capacity to be a function of quality of insulation rather than a difference in physiology.

BLACK-FOOTED ALBATROSS

The Black-footed Albatross (*Diomedea nigripes*) breeds on many Pacific islands between 10° and 30°N latitude and ranges over most of the Pacific Ocean in the Northern Hemisphere and into the Bering Sea. This species arrives on Midway in mid-October, about two weeks earlier than the Laysan Albatross. The breeding cycle closely parallels that of the latter species but is about two weeks in advance. Our observations on *D. nigripes* cover the same stages as mentioned for the Laysan Albatross.

The Black-footed Albatross nests commonly on both Sand and Eastern islands but is much less abundant than the Laysan Albatross. *Diomedea nigripes* tends to nest on open, wind-swept sand as well as among the bushes and trees, but it seems to avoid human habitation more than does *immutabilis*. Both forms, however, are often found nesting side by side in a randomly distributed manner. The nest of *nigripes* is generally lower and shallower than that of *immutabilis* and often consists only of a depression in the sand (fig. 6). Incubation of the single egg and the brooding behavior are essentially the same as in *immutabilis*.

We recorded body, incubation patch, and foot temperatures of brooding adults during the day and body temperatures at night. We also recorded temperatures of advanced eggs, pipped eggs, chicks of various ages, and large juveniles. The results are summarized in figures 7 and 8; noteworthy points are as follows:

1. Daytime body temperatures of brooding adults (mean 38.1°C.) under overcast skies average 1°C. higher than nocturnal body temperatures and the difference is statistically significant.

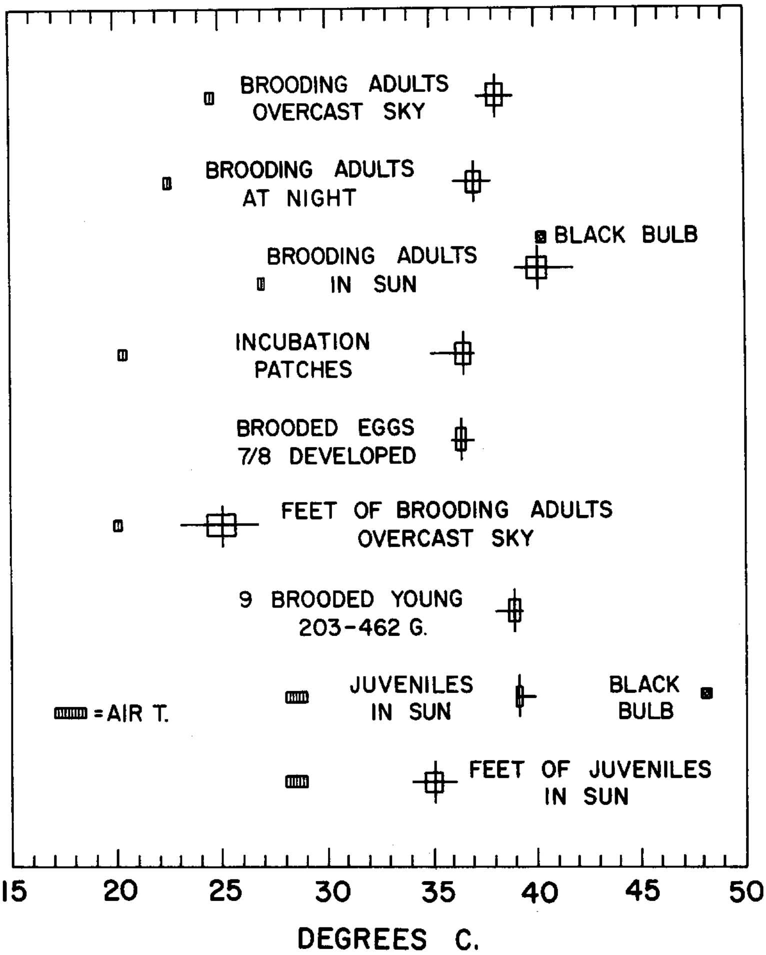

Fig. 7. Summary of temperature data for the Black-footed Albatross. For explanation of symbols see figure 2. Sample size is 10 with one exception as noted.

2. Brooding adults exposed to full sun have body temperatures (mean 40.1°C.) averaging 2°C. higher than those of birds not under heat stress.

3. Although the samples of adult body temperatures under given conditions are impressively uniform, the overall range of deep body temperatures covers 5.5°C.—from 36.2°C. (night) to 41.7°C. (sun).

4. Incubation patch temperatures (mean 36.6°C.) are virtually identical with the temperatures of advanced brooded eggs (mean 36.4°C.).

5. The feet do not contribute to the heat of incubation.

6. Temperatures of brooded, recently hatched young (mean 38.8°C.) are significantly higher than temperatures of the incubation patch or body temperatures of unstressed, brooding adults.

7. The body temperatures of large juveniles (mean 39.2°C.) exposed to intense solar radiation are much higher than the body temperatures of unstressed brooding adults. They are not as high, however, as those of brooding adults exposed to heat stress even though the heat stress was less for the adults than for the juveniles.

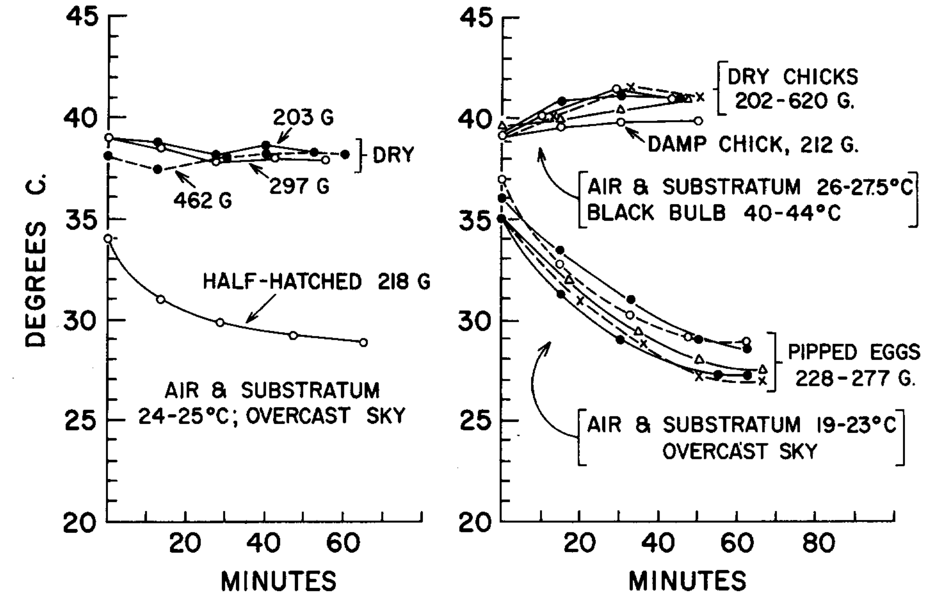

Fig. 8. Temperatures of unbrooded pipped eggs and unbrooded chicks of the Black-footed Albatross under various conditions.

8. Large juveniles under heat stress with feet raised in the air had foot temperatures (mean 35.1°C.) that were always higher than air temperatures (28°–29°C.). Presumably the role of the feet in heat exchange is the same as that discussed with regard to the Laysan Albatross. Panting rates and the use of evaporative cooling by *nigripes* also appear to be the same as in *immutabilis*.

Temperatures of pipped eggs taken from nests and exposed to moderately cool ambient temperatures showed a steady decline to a point about 6° to 8°C. above that of the environment and leveled off thereafter (fig. 8). Damp, newly hatched chicks of both *nigripes* and *immutabilis* under similar conditions showed essentially the same pattern. However, dry hatchlings at the same ambient temperature as damp ones showed a very slight initial decline and then stabilized their body temperature at about 38°C. (fig. 8). The mean for adults under similar circumstances is approximately the same.

When dry chicks of various ages (weights 202 to 620 gm.) were exposed to moderate heat stress, the pattern of response was surprisingly uniform (fig. 8). There was a slight initial rise in body temperature and then a leveling off; all stabilized at 41°C. This is within the range of adult temperatures under similar heat stress but is significantly higher than that of large juveniles under more severe conditions. The downy chicks began to pant soon after being exposed to the hot sun, but the feet-in-air posture used by the large juveniles was not employed.

A single damp hatchling was exposed to the same heat stress as the other young ones just discussed. Its initial body temperature was about the same as the others and the shape of its temperature curve is similar, but the body temperature remained slightly lower than that of the dry chicks and stabilized at about 40°C. instead of 41°C. Presumably this difference was the result of cooling by evaporation of moisture from the wet down and skin. It is of interest that the same factor that makes for poor regulation under cool conditions is helpful in preventing overheating under moderate heat stress.

The interpretation of the role of down in temperature regulation in the chick of the

Laysan Albatross is further supported by the data on the species discussed here. Under cool conditions, damp hatchlings do not show any improvement in temperature regulation over those still in the pipped-egg stage. Dry hatchlings, although insignificantly "older" and in some cases weighing less than the damp ones with which they are compared, show a vast improvement in regulatory capacity and under moderate environmental conditions maintain body temperatures close to those of adults.

Large juveniles that are hatched in entirely exposed nests on open sand face severe heat stress in the summer. During the hotter parts of the day, many or most of them retreat into dense *Scaveola* thickets where they are shaded from the intense sun. Some, however, are too far from such shelter and must depend entirely on their physiological capacity for heat loss in order to regulate body temperature.

DISCUSSION

On Midway Island these two congeneric species show slight differences in the timing of reproduction and in nest site preference, but there is much overlap in both of these aspects of their breeding activity. These albatrosses are similar in the physiological characteristics that we were able to study, and we could detect no evidence of significant differences in adaptations influencing temperature regulation under natural conditions. During January and February, the time of hatching and of the early nestling stages of these species on Midway Island, the climate is generally equable and mild. Occasionally there may be flooding rains or sandstorms caused by high winds, but apart from these exceptional and irregular conditions the early nestling period does not coïncide with any severe environmental stress. Whether or not the dry, newly hatched chicks could regulate body temperature under conditions of greater stress as adequately as larger and older chicks do is uncertain. The ability to regulate body temperature well under rigorous conditions is almost never required of very young nestlings because of the moderate climate and the behavior of the parents. The eggs and the young chicks are normally closely brooded at all times, and only the adult birds meet the stress of the macroclimate. The effective environment of the egg or hatchling is actually a dry, shaded chamber kept at about 36°C. Even moderately heavy and sustained rains do not penetrate into the concavity of the nest although the sand surrounding the brooding adult may be thoroughly soaked. The strong attachment of the parents to their nest, as exemplified by the continuous brooding for days or weeks and by the reluctance to give place to the mate except after a prolonged change-over ceremony, insures that the egg or hatchling is well protected during its most critical period.

After the young birds become too large to be brooded, they are sufficiently well insulated and physiologically adequate to withstand all but exceptional environmental stress. With the advent of intense solar radiation in summer, the juveniles are able to lose enough heat through panting and by way of the foot webbing to maintain body temperature within quite narrow limits. The rapid panting of young birds in the sun undoubtedly results in considerable water loss. The food (mostly squid) provided by the parents has a high water content but it is virtually isotonic with the sea. The water in the body fluid of the squid, although highly saline, is physiologically available since the excess salt is excreted by the nasal gland (Frings and Frings, 1959). We often noted fluid dripping from the bills of juveniles. Thus, although the nonflying young birds never drink, they are provided by their diet and salt-excretion mechanism with enough water for both metabolic reactions and evaporative cooling.

It is now known that the adult birds drink sea water and indeed require salt to maintain good health (Frings and Frings, *op. cit.*). There are often puddles of fresh water present on Midway Island immediately after rains, but we never saw any albatrosses attempt to drink from such sources. However, adult birds sitting on nests will nibble and snap at falling raindrops when a shower passes over. It is a remarkable sight when hundreds of incubating birds almost simultaneously begin catching raindrops as a squall reaches the island. We interpret this as a response to a long period of deprivation of food and water associated with long-continued brooding.

The mechanism of heat loss through the feet, although advantageous to juveniles on land and to adults in flight, could bring about excessive cooling when the feet are immersed in the sea. Even in the tropics the temperature of sea water is much lower than that of the bird, and the cooling power of water is 20 to 50 times that of air at the same temperature (Scholander, 1955). Excessive heat loss by way of the feet is doubtless minimized by vasomotor control. It is not known if albatrosses have tarsal arteriovenous *retes* which could provide a counter-current heat exchange system (Scholander, *op. cit.*) for heat retention when the birds rest on the open sea.

The nesting areas of albatrosses, like those of many other pelagic birds, are largely restricted to islands that are free of native terrestrial predators. Such islands, however, are usually predator-free because of their remote location and/or ecological conditions under which most terrestrial vertebrates could not become permanently established. Severe conditions that help to insure an absence of predators nevertheless pose serious problems for the birds that must tolerate the environmental stress if they are to nest successfully.

The large size of albatrosses and their specialized mode of flight are associated with a prolonged period of growth and development, and the duration of incubation and parental care spans three seasons of the year. This circumstance poses great potential difficulties for the birds. Either (1) they must avoid nesting in areas with extremes of seasonal climate, or (2) they must be adequately adapted at all stages of development to the stresses of such an environment, or (3) they must strike a balance between these two ways of meeting the problem. The two species of albatross discussed here demonstrate such a balance. They breed in a region where severe low temperatures do not occur. The timing of the reproductive cycle is such that the chicks hatch in a period of mild temperature, and by the time the extremes of summer heat are reached the young birds are well grown and the adults no longer need to brood. During this period of climatic stress, the physiological and behavioral mechanisms for heat loss enable adults and juveniles to regulate adequately their body temperature. A recognition and analysis of these mechanisms is therefore essential in the interpretation of the ecology and distribution of the species.

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SUMMARY

Temperatures of eggs, chicks, juveniles, and adults of Laysan (*Diomedea immutabilis*) and Black-footed (*Diomedea nigripes*) albatrosses were measured under a variety of environmental conditions on Midway Island.

Daytime body temperatures of brooding adults (means: *immutabilis*, 37.5°C.; *nigripes*, 38.1°C.) average about 1°C. higher than nocturnal body temperatures.

Incubation patch temperatures (means: *immutabilis*, 36.7°C.; *nigripes*, 36.6°C.) are significantly lower than body temperatures and are essentially the same as the temperatures of advanced brooded eggs.

The temperatures (means: *immutabilis*, 38.8°C.; *nigripes*, 38.9°C.) of brooded, recently hatched young are significantly higher than either incubation patch temperatures or body temperatures of brooding adults.

The body temperatures of juveniles and adults are elevated by exposure to intense solar heat. Under such conditions the birds pant vigorously, and the juveniles often sit balanced on their heels with their feet off the ground. This posture permits heat loss from the vascularized foot webbing to the air.

Temperatures of pipped eggs and damp, newly hatched chicks exposed to an ambient temperature between 21° and 23°C. decline to about 6°C. above that of the environment. Dry, newly hatched chicks at the same ambient temperature maintain a body temperature of about 38°C. The greater capacity for body temperature regulation in the latter group is attributed to more effective insulation.

The climate of Midway Island is generally mild and the birds are never exposed to severe cold stress. The timing of the breeding cycle is such that the young birds are well grown before the onset of summer heat. Physiological and behavioral adaptations to heat stress and their relation to the ecology of the two species are discussed.

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