# TEMPERATURE REGULATION IN THE RED-TAILED TROPIC BIRD AND THE RED-FOOTED BOOBY

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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. Our previous publications (Howell and Bartholomew, 1961*a*, 1961*b*) have dealt with Laysan and Black-footed albatrosses (*Diomedea immutabilis* and *D. nigripes*), Bonin Island Petrels (*Pterodroma hypoleuca*), and Wedge-tailed and Christmas Island shearwaters (*Puffinus pacificus* and *P. nativitatis*). Bailey (1956) gives a useful account of the natural history of these and other species found on Midway.

In the course of visits to Midway Island in June and July, 1959 and 1960, we were able to obtain data on thermoregulation in the Red-tailed Tropic Bird (*Phaëthon rubricauda*) and the Red-footed Booby (*Sula sula*). Aside from the work of Probine and Wodzicki (1955) on the Gannet (*Sula bassana*) and that of Bartholomew, Dawson, and O'Neill (1953) and Bartholomew and Dawson (1954) on pelicans (*Pelecanus*), we know of no quantitative studies on thermoregulation in pelecaniform birds.

## ENVIRONMENTAL CONDITIONS

Data from the navy meteorological station on Midway Island show that the macroclimate is remarkably equable. In January and February, the mean low is 15°C. and the mean high is 21°C. (extremes, 12.0° and 24.5°C.). In June and July, the mean low is 21.0°C. and the mean high is 28.5°C. (extremes, 18.5° and 31.0°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 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, 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 or vinyl-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 foot webbing. 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.

Tropic birds could be seized when on land or at their nests without difficulty, and boobies could often be caught by hand at their nests. Temperatures were recorded within 15 or 20 seconds after grasping the birds, and it is highly improbable that any significant elevation of temperature due to struggle or excitement would occur in this brief interval.

## ACKNOWLEDGMENTS

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## RED-TAILED TROPIC BIRD

The Red-tailed Tropic Bird breeds on various islands in the tropical parts of the Indian and Pacific oceans; the subspecies *rothschildi* is found in the Hawaiian chain. On Midway Island the time of greatest abundance and breeding activity of this species occurs in spring and summer, and in June and July tropic birds may be found on eggs or with young of all ages up to well-grown juveniles. The nest is a shallow scrape in the sand in partial or complete shade, and the clutch is invariably a single egg. Both parents participate in incubation and care of the young. There is no incubation patch in this species, and the sexes are indistinguishable externally.

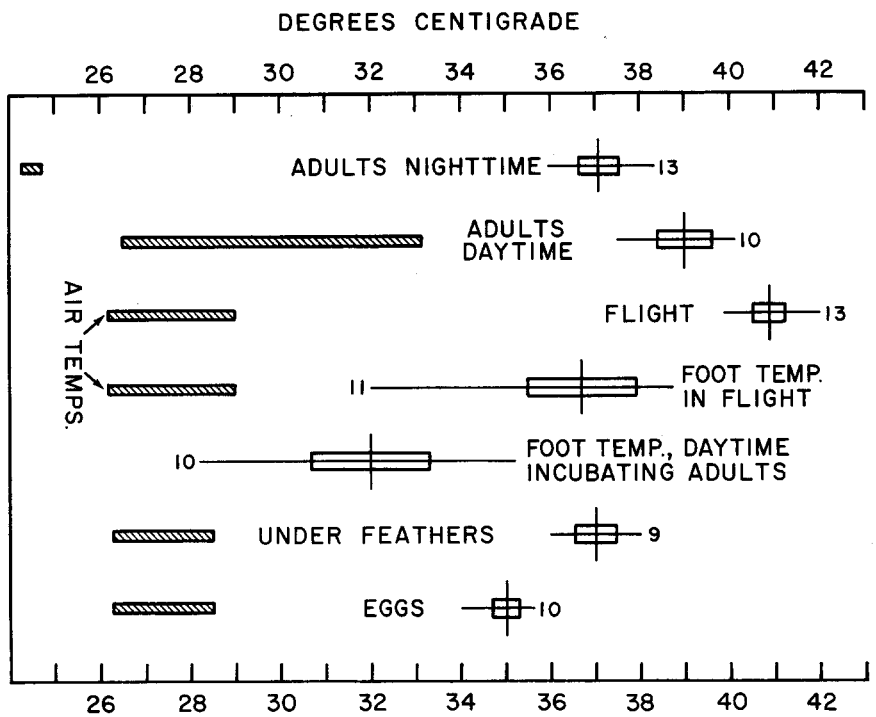


Fig. 1. Summary of temperature data for the Red-tailed Tropic Bird (*Phaëthon rubricauda*). Horizontal lines indicate the ranges; vertical lines indicate the means (M); rectangles indicate the interval $M + 2\sigma_M$ to $M - 2\sigma_M$; the numbers show the sample size.

Data on temperature of the environment, the internal temperature of brooded eggs, and temperatures of the relevant parts of the body under different conditions are summarized in figure 1. Noteworthy features are as follows:

*Daily temperature cycles.*—The mean daytime body temperature (39.0°C.) of incubating birds on shaded nests is significantly higher than the mean nocturnal tem-

perature (37.1°C.) of incubating birds. This accords with the generally diurnal habits of this species. As there is little difference between air temperature at shaded nests in the daytime and the nocturnal air temperature, the higher figure for body temperature in the daytime must be related to activity. Of the 13 birds seized on nests at night between 9:00 p.m. and 12:00 midnight, five were asleep. All five had body temperatures (36.0° to 36.6°C.) that were lower than those of the other eight birds (37.0° to 38.3°C.) that were awake.

Fig. 2. Two-day-old chick of the Red-tailed Tropic Bird.

*Flight temperatures.*—This term refers to deep body temperatures of birds captured within 10 seconds of alighting after sustained flight. Tropic birds returning to their nests hover above the site and then crash-land into the vegetation (usually a *Scaevola* thicket) or the sand. They are extremely awkward on land and move by a series of lunges rather than by walking. We were therefore able to seize the birds just after they reached a bush or the ground, or even in the last moments of hovering. Body temperatures taken in such circumstances are, in all probability, no different from those in sustained flight. The lowest temperature of a flying bird was approximately equal to the highest recorded temperature of an incubating bird in the daytime. The mean flight temperature (40.9°C.) was almost 2°C. higher than the mean for these incubating birds. Tropic birds in flight during the midday hours are often seen to have bills agape, apparently panting in response to heat stress. Foot temperatures of flying birds were always lower than body temperature in flight and always higher than the air temperatures (26.2° to 29.0°C.). It is apparent that heat may be dissipated from the feet to the surrounding air. The foot

temperatures of flying birds (mean 36.7°C.) are markedly elevated above those of resting, incubating birds (mean 32.0°C.), showing that body heat is transferred (presumably by vasodilatation) during flight to the feet; the latter thus provide an avenue of heat loss that must aid in preventing excessive heat loading during flight.

*Incubation temperatures.*—There is no incubation patch in tropic birds, and the feathering on the abdomen is dense and compact. Nevertheless, the mean internal temperature of incubated eggs is 35.0°C. The sample included eggs without visible embryos

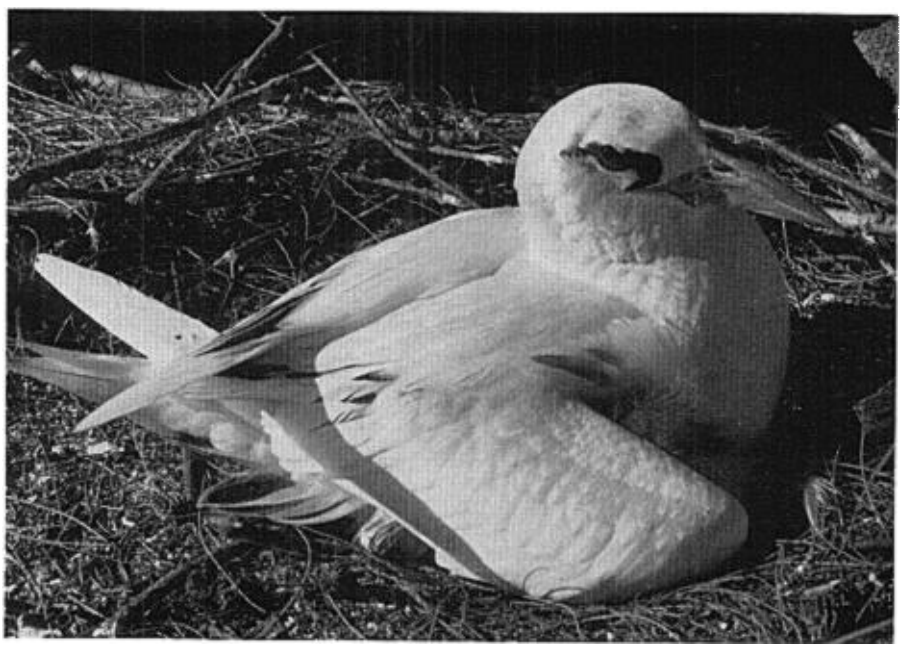

Fig. 3. Red-tailed Tropic Bird brooding its chick under one wing.

to those with embryos about $\frac{5}{6}$ developed. There was no correlation between temperature and degree of development. This mean incubation temperature is slightly higher than the mean (34.3°C.) for fresh eggs of the Wedge-tailed Shearwater (Howell and Bartholomew, 1961*b*) and slightly lower than the means (36.0° and 36.4°C.) for advanced eggs of the Laysan and Black-footed albatrosses (Howell and Bartholomew, 1961*a*). These three procellariiform species have well-developed incubation patches in both sexes. It is obvious that transfer of heat from the parent tropic bird to the egg must take place either through the feet or from the ventral surface of the body, even though it is fully feathered. The mean foot temperature of incubating birds was only 32.0°C. and the highest foot temperature was 35.2°C. These temperatures are too low to allow the feet to contribute to the heat of incubation, although the feet may help to diminish heat loss. The feet of tropic birds are totipalmate but quite small and cannot effectively cover the egg; the birds seldom place their feet on the egg as some other pelecaniforms do.

The egg is firmly tucked against the abdominal feathers during incubation although it is not actually in contact with the skin. A "banjo-tip" thermister was placed under the abdominal feathers but not against the skin, and the mean temperature recorded was

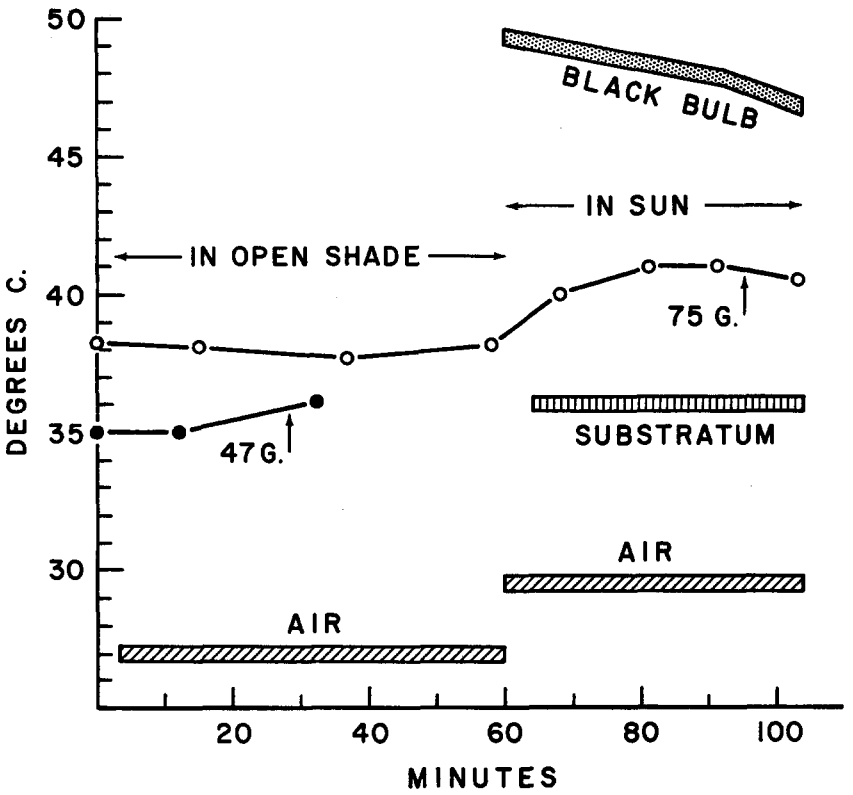


Fig. 4. Body temperatures of chicks of Red-tailed Tropic Birds in shade and sun.

37.0°C.; this temperature is adequate for maintaining egg temperatures in the range observed.

An egg that contained a large embryo was prepared for continuous temperature recording by inserting a flexible thermister probe through one end of the egg so that the sensitive tip lay just under the shell at the point closest to the incubating bird. During one and one-half hours of continuous incubation by the parent, the thermister registered temperatures between 36.0° and 36.5°C. The superficial position of the thermister probably accounts for these slightly higher figures as compared with those for other incubated eggs.

The weights of 12 eggs of tropic birds ranged from 51 to 65 gm., with a mean of 61.8 gm. These included eggs with no visible embryos to those with embryos about $\frac{5}{6}$ developed; there was no clear correlation between egg weight and degree of development.

*Nestlings.*—The chicks are covered with fine, long down at the time of hatching, and the down is retained until gradually replaced by juvenal contour feathers; thus, the young birds are well insulated at all stages of growth. The length in centimeters of the down on parts of the body of a two-day-old chick (fig. 2) was as follows: head, 2.5; dorsum, 2; wings, 1.5; venter, 0.7 to 0.8. In the 7- to 10-day-old chick the down measurements in centimeters were as follows: head, 4; dorsum, 3; venter, 1.

For the first three or four days after hatching the chick is brooded under the body of the parent, but from then on it is brooded under one wing (fig. 3). This unusual habit,

which is doubtless well known and characteristic of all tropic birds, seems to have escaped mention in most of the standard references and even in monographic studies of species of *Phaëthon*. Plath (1914) remarks briefly on this type of brooding in *P. lepturus*.

The chicks are brooded by one or the other parent at almost all times. Even newly hatched chicks, however, are able to maintain body temperature very effectively when unbrooded in shade (fig. 4). Chicks of all ages show an elevation of body temperature when taken from the nest and exposed to the heat of direct sunlight, but they are able to prevent their temperature from rising above 42°C. by vigorous panting (figs. 4 and 5). Four young chicks weighing between 77 and 128 gm. were taken from under the wings of the parents and placed in the open in direct sunlight. The panting began immediately after the chicks were placed in the sun, before any detectable elevation in body temperature occurred. Body temperatures increased and then stabilized at a level between 41° and 42.5°C. The bills of the birds were then fastened shut with masking tape, preventing panting, and cloacal temperatures were recorded after 12 to 16 minutes. In each case there was a sharp rise in body temperature, and in three of the four birds it reached approximately 45°C.—equal to the lower range of black bulb temperatures at the time and undoubtedly close to the lethal level. The bills were then untaped. Vigorous panting was resumed, and within a few minutes the body temperatures declined to a safe level. The smallest bird (77 gm.) had to be put in the shade, however, before its body temperature declined. All birds were returned to their nests and observed on subsequent days to be in good condition.

Tropic birds lack a conspicuous unfeathered gular pouch and do not show the "gular

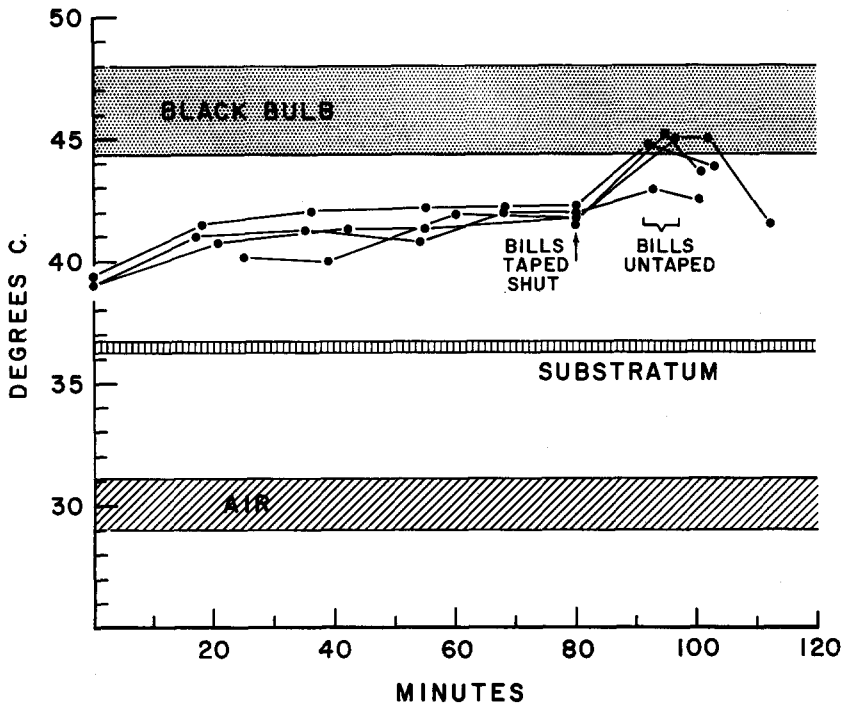


Fig. 5. Body temperatures of chicks of Red-tailed Tropic Birds exposed to full sun with panting permitted, then prevented, then permitted again.

flutter" of other pelecaniforms, and panting by adults and young appears to be like that in most other birds.

## RED-FOOTED BOOBY

The Red-footed Booby has a pan-tropical distribution and breeds on islands where conditions permit building of its stick nest in trees or shrubs. The subspecies *rubripes* is found on Midway Island, and all the birds there are of the white phase. There is a protracted nesting period on Midway, but the peak of breeding is reached in spring and

Fig. 6. Red-footed Booby (*Sula sula*) at nest in *Scaevola*.

early summer. During June and July, 1959 and 1960, we observed all stages of the breeding cycle, from fresh eggs in the nests to fully fledged young on the wing. On Midway the nest is built in *Scaevola* bushes, and the clutch consists of a single egg (fig. 6). Both parents participate in incubation and the care of the young. There is no incubation patch, and the sexes are indistinguishable externally.

Data on temperature of the environment, the internal temperature of brooded eggs, and temperatures of relevant parts of the body of adults and young under different conditions are summarized in figure 7.

*Daily temperature cycle.*—The boobies are noisy and active during the day, and the birds whose temperatures we recorded at night were also fully awake and alert. All adults were seized at nests which contained an egg or a nestling. The nests are almost always exposed to full sun during the day, and gular flutter was noted in the parents and juveniles during most of the daylight hours. The mean daytime body temperature of adults (40.3°C.) is significantly higher than the mean nighttime body temperature (38.0°C.). This difference presumably reflects the effects of activity and insolation, for air temperatures at night averaged only about 1.5°C. lower than those during the day.

*Incubation temperatures.*—The mean internal temperature of incubated eggs was 36.0°C. Of 11 eggs measured, two were addled, two were fresh with no visible embryos, and seven had embryos varying from ¼ to ⅞ developed. There was no correlation between internal temperature and degree of development within the egg.

Incubating boobies cover the egg with the webbing between the first and second toes of each foot. This webbing is present only in the pelecaniform birds, and as an incubation patch is lacking in this group it has often been assumed that the heat for incubation is provided by the feet. We obtained data on the foot temperatures of nine

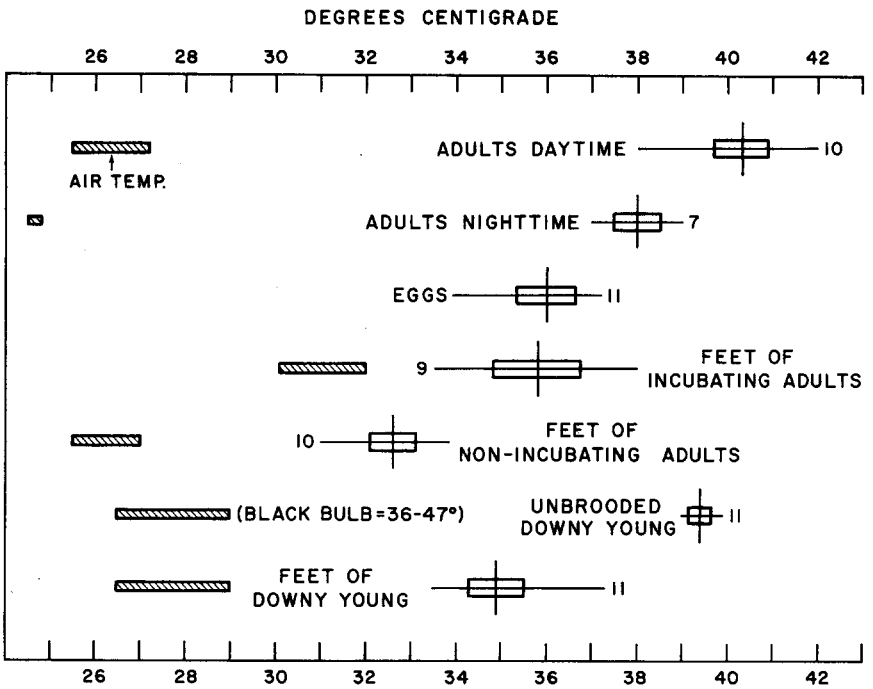


Fig. 7. Summary of temperature data for the Red-footed Booby. See figure 1 for explanation of symbols.

incubating birds; five of these birds were on eggs and four were brooding naked, newly hatched chicks. The mean foot temperature was 35.8°C., which is slightly but not significantly lower than the mean internal egg temperature. We interpret these data as suggesting that the feet do not provide the main source of heat for incubation. It seems more likely that, as in the tropic bird, the principal source of heat is the ventral body surface and that the feet are warmed along with the egg. The feet perhaps function more importantly in holding the egg in place and as a site of tactile reception contributing to the incubation response.

The mean foot temperature (32.6°C.) of 10 adult birds on the nest with large, unbrooded nestlings was significantly lower than that of incubating birds. The nonincubating adults stood in the nest much of the time, and their feet were exposed to a constant breeze.

The weights of 16 eggs of boobies ranged from 47 to 60 gm., with a mean of 53.3 gm. These included eggs from those with no visible embryos to those with embryos about

⅞ developed; there was no clear correlation between weights of eggs and degree of development. The egg of the booby is relatively small compared to that of the tropic bird or the Wedge-tailed Shearwater (mean wt. 19 shearwater eggs: 59.5 gm.), both of which are smaller birds than the booby.

*Nestlings.*—Young birds of all ages, even naked, newly hatched chicks, show gular flutter almost immediately whenever exposed to solar heat. The mean body tempera-

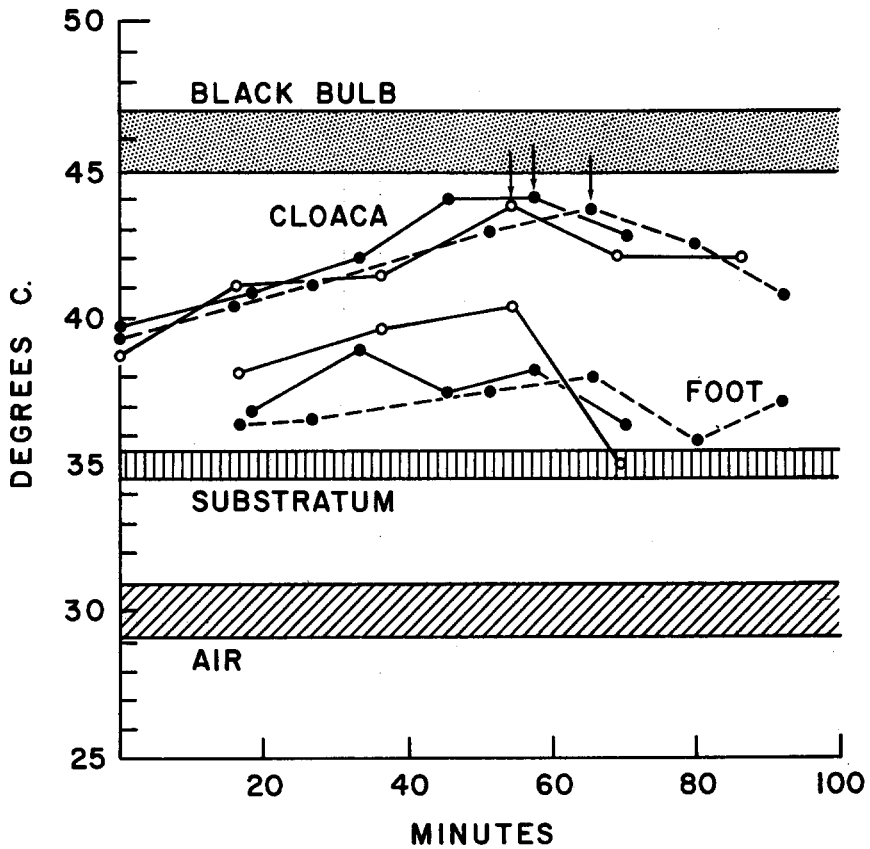


Fig. 8. Effects of prevention of gular flutter in three downy young of Red-footed Boobies placed on ground in full sun. Bills were taped shut immediately after initial temperature reading at 0 minutes and untaped as indicated by vertical arrows.

ture of 11 large, unbrooded, downy young 16 to 17 inches long in nests in full sun was 39.4°C. All showed conspicuous gular flutter, and their foot temperatures were 4°C. or more above the air temperatures. Some heat would therefore be lost from the feet to the air, and this plus the evaporative cooling effected by gular flutter enables the downy young to maintain a body temperature averaging somewhat lower than that of active adults. The importance of both gular flutter and the webbed feet in lowering of body temperature is shown in figure 8. Three large downy nestlings were removed from their nests and placed in full sun on the ground. They had been in full sun in the nests, and the initial body temperatures shown in figure 8 represent the result of several hours of exposure to insolation. The bills were then fastened shut with masking tape, allowing for slight gaping to permit breathing as these birds appear to lack external nostrils

(fig. 9). Cloacal and foot temperatures were taken at regular intervals. In each case, body and foot temperatures rose steadily at about the same rate; when body temperatures reached about 44°C., the birds showed extreme distress and the bills were unsealed. Rapid gular flutter commenced at once, and within a few minutes body and foot temperatures declined markedly. Foot temperatures actually went below the initial level, indicating a reduction of blood flow to the feet.

Fig. 9. Young Red-footed Booby with bill taped shut to prevent gular flutter. Note the large totipalmate feet.

## DISCUSSION

Although the Red-tailed Tropic Bird and the Red-footed Booby are both pelagic pelecaniform birds, they differ widely in many of their adaptations. Tropic birds are unique in having all but lost the capacity for effective terrestrial locomotion without having extreme specialization for swimming (as in loons and grebes) or facility in arboreal perching (as in the Fregatidae). Skeletons of *Phaëthon* show a remarkable reduction in the size of the synsacrum and hind limb bones that is comparable to the reduction of the pectoral girdle and fore limb elements of the Flightless Cormorant (*Nannopterum harrisi*). Tropic birds are strong and graceful flyers once they are airborne, but takeoffs and landings are extremely labored and the birds lack the high degree of reduction of the body weight or great specialization of wing morphology that is usually found in primarily aerial species. The tropic birds appear to represent an adaptive complex that is well suited for life over wind-swept oceans and remote islands, but they would be totally incapable of survival in any other type of environment. In

the environment they occupy, however, the tropic birds are conspicuously successful. They nest in enormous numbers on Midway, often beside busy streets, airplane hangars, or residences, but mortality appears to be extremely low. We almost never came across an abandoned egg or dead nestling of this species. This is in striking contrast, for example, to the albatrosses or the Sooty Terns (*Sterna fuscata*) on Midway, in which species considerable failure of eggs to hatch or young to survive is evident.

The tropic birds' requirements for a nest site seem to be only a sandy substratum, in which a slight scrape can be made, and partial or complete shade. Of thousands of tropic birds' nests observed, we saw extremely few that were largely or completely in open sun for even part of the day. Among these few we noted the only nesting failures that seemed attributable to climatic conditions. The solar heat appeared to be too great for the adult birds, and they left the nest during the hotter periods; the eggs exposed to the sun became overheated and were eventually abandoned by the parents.

The tropic birds often have nests located many yards inside dense *Scaevola* thickets. To reach such a nest, a bird arriving from the air must either crash-land into the bush and slither and struggle down through the tangled branches, or it must land at or near the thicket edge and lurch along under and among the branches to its destination. A bird leaving its nest can take only the latter route, and it often emerges from the shrubbery panting and apparently fatigued. As there is no shortage of space for nesting and as there seems to be no predation on these birds on Midway, we must assume that shade governs the choice of such sites.

The tropic bird chick is well developed at hatching and, unlike other pelecaniform hatchlings, it is covered with a dense coat of down. Indeed, it appears capable of tolerating environmental conditions that are considerably more rigorous than it is likely to encounter on Midway. As the nest site is almost always in the shade, the young bird will rarely be confronted with any severe thermal stress even if unattended. Although it is able to maintain a constant body temperature independent of prevailing ambient temperatures, the chick is closely brooded by the parents most of the time.

The lack of the well-developed gular pouch and the gular flutter that is characteristic of other pelecaniforms may keep the effectiveness of evaporative cooling in the tropic birds below the level achieved by the other members of this order. The shade-nesting habit of the tropic birds, as opposed to the full-sun nesting of the other marine pelecaniforms, is perhaps related to the lack of the capacity for gular flutter.

The Red-footed Booby on Midway Island presents quite a different picture. The population is small compared to that of the tropic bird, and nesting is limited to small areas of *Scaevola* bushes on a sparsely populated portion of Midway. The boobies are accomplished flyers, and although we never saw them on the ground, they alight and take off expertly from trees and shrubs. The stick nests are almost always exposed to full sun. The egg is rather small relative to the size of the adult, and the chick is naked at hatching. Hatchlings and young chicks are constantly brooded by the parents, and chicks too large to be brooded are well covered with down. Although solar radiation on the nest site is intense, there is usually a brisk breeze that helps to keep down the air temperature in all but sheltered locations. Evaporative cooling by means of gular flutter is undoubtedly the most important avenue of heat loss in boobies of all ages, but heat loss from the large webbed feet is also significant. As the birds perch on exposed branches or on the loosely-made stick nest, there is usually some air movement across the feet. The water lost by evaporative cooling through gular flutter can only be replaced by saline fluids in the diet or by sea water. Presumably the excess salt is excreted by the nasal gland, as it is in many other marine birds (Schmidt-Nielsen, 1960).

## SUMMARY

Temperatures of eggs, chicks, juveniles, and adults of two pelecaniform species, the Red-tailed Tropic Bird and the Red-footed Booby, were measured under a variety of environmental conditions on Midway Island.

Nesting tropic birds show a clear-cut diurnal body temperature cycle (means: daytime, 39.0°C.; nighttime, 37.1°C.). Body temperature is significantly higher during flight (mean: 40.9°C.). There is no incubation patch, but the under-feather temperature of the abdomen (mean: 37.0°C.) is adequate to keep the mean internal temperature of the egg at 35.0°C. The temperature of the webbed feet of incubating birds (mean: 32.0°C.) is too low to allow them to contribute to the heat of incubation, but they appear to serve as an avenue of heat loss in flying birds.

Tropic bird chicks are covered with down at hatching and are able to maintain body temperature effectively in sun or shade although they are closely brooded most of the time. The birds pant but do not show gular flutter when exposed to solar heat. Small nestlings placed in full sun commence panting before there is any detectable elevation of body temperature.

Nesting boobies are active both day and night, but they also show a clear-cut diurnal body temperature cycle (means: daytime, 40.3°C.; nighttime, 38.0°C.). There is no incubation patch, but the mean internal temperature of incubated eggs is 36.0°C. The bird incubates with the webbed feet placed on top of the egg, and the mean foot temperature of incubating birds was 35.8°C. This suggests that the feet do not provide the main source of heat for incubation, but the feet seem to provide an avenue of heat loss for flying or nonincubating birds.

Booby nestlings are naked at hatching and are closely brooded. Older chicks and juveniles are covered with down and are exposed to full sun most of the time; they show conspicuous gular flutter whenever exposed to solar heat and maintain a body temperature slightly below that of active adults. Even naked hatchlings show gular flutter almost immediately when placed in full sun, before there is any detectable elevation of body temperature.

The importance of evaporative cooling by panting (tropic bird) or gular flutter (booby) was shown by taping shut the bills of nestlings of both species placed in full sun. There was a rapid rise in body temperature, approaching the lethal level. When the bills were untaped, panting and gular flutter resumed and body temperatures declined to safe levels.

The relation of thermoregulation to the breeding habits of the two species is discussed.


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