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THE ROLE OF BEHAVIOR IN THE TEMPERATURE REGULATION OF THE MASKED BOOBY

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The Masked Booby (*Sula dactylatra*) is conspicuously altricial. Its chicks are completely dependent on the adults not only for food and protection from predators, but also for shelter from the extremes of the physical environment. The mutually supporting behavioral adjustments which the adults and young of this species make during the ontogeny of thermoregulatory ability of the chicks offer an unusually attractive opportunity for studying the interplay of behavioral adaptations and physiological capacities under natural conditions.

The Masked Booby is pantropical and from the meteorological point of view occupies one of the world's most equable climates. However, as is the case with many tropical sea birds, microclimatic conditions in its nesting rookeries are often extremely demanding, particularly for chicks, because of high surface temperatures, intense solar radiation, and the absence of fresh water.

No quantitative data are available on any aspect of the thermoregulatory performance of the Masked Booby although information is available on aspects of temperature regulation in one other booby, the pantropical species *Sula sula* (Howell and Bartholomew, 1962), and a gannet, *Sula* (*Morus*) *bassana* (Probine and Wodzicki, 1955).

METHODS

Temperatures were measured to the nearest 0.1° C with a portable, battery-powered, multichannel thermistor-thermometer. All the thermistor probes were calibrated with a Bureau of Standards thermometer. By using several sensing elements, virtually simultaneous measurements were made of black-bulb, air, substratum, and body temperatures. Deep-body (core) temperatures of both chicks and adults were obtained by inserting a steel-sheathed or vinyl-sheathed thermistor probe down the esophagus to, or into, the stomach. Surface temperatures were obtained with a "banjo-tip" thermistor. Air temperatures were measured with the sensor shielded from direct solar radiation but not from back radiation from the substratum, and held at a height equal to that occupied by the center of the body of the bird being studied. Masked Boobies, like many oceanic birds, are sufficiently indifferent to humans that they can readily be captured by hand on their nests. Temperatures of the adults were recorded within 15 or 20 seconds of the time the birds were grasped. Temperatures of pipped eggs were measured with a flexible, vinyl-sheathed probe slipped through the pip and placed as nearly as possible at the center of the egg.

Wind velocities were measured with a hand-held, Biram-type anemometer.

PHYSICAL ENVIRONMENT

All observations were made during February 1964, in a rookery containing about 350 pairs of Masked Boobies which were nesting along the rim of a completely barren sea cliff on the windward side of Punta Suarez on Isla Española (Hood Island) in the Galápagos Archipelago at 1° 22′ south latitude.

All the nests were within a few meters of the cliff edge, and nearly all were fully exposed to the southeast trade winds which blew vigorously throughout the period of study. The wind velocity to which the birds were exposed varied markedly depending on the location of their nests and the time of day. Wind velocities of 10 to 14 miles per hour were typical at a height of one meter above the nests, but the wind impinging on the actual nest sites was usually 6 to 8 miles per hour.

The air temperature measured in the wind at the cliff edge held steady between 27 and 29° C both day and night. In the rookery only a meter or so from the edge of the cliff in areas occupied by the nesting birds, at a height of 20 to 25 cm, air temperatures of 34 to 36° C and black-bulb temperatures from 48 to 54° C were common. Substratum temperatures in the full sun usually fell between 44 and 51° C. In the few small areas in the rookery that were shaded by rocks, the air and substratum temperatures were between 27 and 29° C, during both day and night.

NESTS

The nests of the Masked Boobies at Punta Suarez were completely unsheltered and consisted of shallow scrapes paved with small pebbles. Occasionally the nests also contained a fragment of driftwood or a half-dozen twigs. Because of their rudimentary nature, the nests afforded no shelter from the environment nor from predators for either chick or adult.

ADULTS

Adult Masked Boobies maintain impressively uniform body temperatures under a given set of conditions, and like most birds show a clear-cut difference between daytime and nighttime levels of body temperature (table 1). During the daytime the minimum body temperature recorded was almost half a degree higher than the maximum body temperature recorded at night. The difference between daytime and nighttime body temperatures cannot be assigned exclusively to the difference in level of activity between day and night because the birds in the rookery were alert at night as well as during the day. At least some of the observed elevation in temperature during the day was probably associated with the intense solar radiation which existed in the rookeries throughout the daylight hours, and which commonly produced black-bulb and substratum temperatures between 48 and 50° C.

The Masked Booby's most conspicuous mechanism for heat dissipation is strong, sustained fluttering of the gular area. The Masked Boobies nesting at Punta Suarez employed gular flutter almost continually whenever the sun was shining (figs. 1, 2, 5), and it appears to be a highly important mechanism for heat dissipation in this species. The importance of gular flutter in the temperature regulation of boobies has previously been shown (Bartholomew and Howell, 1962), and its role in evaporative cooling, particularly in caprimulgids, has been examined in detail (Lasiewski and Bartholomew, 1966).

The thermoregulatory capacity of adult Masked Boobies is entirely adequate to meet the heat load imposed by the warm air, intense solar radiation, and the hot substratum on which they nest. Their attachment to nest, eggs, and young is marked; they remain at the nest site and do not seek out microclimatic conditions where the heat load can be avoided. The behavioral adjustments which facilitate thermoregulation in

TABLE 1
TEMPERATURES (°C) OF ADULT BREEDING MASKED BOOBIES IN RELATION TO ENVIRONMENTAL TEMPERATURES

Time	Body					Environment		
	Mean	Max.	Min.	SE	N	Black bulb	Air	Substrate
1350–1430	40.7	41.2	39.9	0.14	12	48–50	31.0–31.5	48.5–49.0
2000–2030	38.3	39.5	37.1	0.18	11	–	27.0	27.0

this species are primarily related to posture, ptilomotor activity, and orientation with regard to the sun.

When clouds covered the sun, both the brooding and the incubating adult boobies oriented themselves randomly with regard to compass direction and sun location. When the skies were clear and solar radiation was intense, the brooding and incubating birds, almost without exception, oriented themselves with their backs toward the sun, even when this orientation caused them to face downwind. By facing away from the sun they kept the gular area and feet in the shade of the head, neck, and body. Such an orientation should enhance the heat loss from these naked surfaces. In particular, it should facilitate the effectiveness of gular flutter, which is a highly important mechanism for heat dissipation, by shielding the heavily pigmented, naked, and vascular gular area from direct solar radiation. Because boobies have extremely short legs, the webbed feet, a potentially important site for heat dissipation, are apt to be shaded regardless of direction of orientation at least during the middle hours of the day.

In addition to keeping the gular area in the shade when they are exposed to a heavy heat load, adult Masked Boobies show two responses which should facilitate heat loss to the air from the feathered parts of the body. The more spectacular of these is a conspicuous local ptilomotor response. The birds elevate the scapulars so that they extend 4 or 5 cm above the normal contour of the back (fig. 1). This elevation of the scapulars should facilitate heat loss by allowing air to pass beneath the feathers and thus increase the local thermal conductance while still shading from the sun the integumentary area of heat exchange. The other response is a drooping of the wings (fig. 2), which allows circulation of air along the sides and flanks and also assists in shielding the feet from heat reradiated from nearby sources.

Although the adults are able to regulate their own body temperatures by supplementing the usual physiological mechanisms found in birds with adjustments in posture, orientation to the sun, local ptilomotor activity, and gular flutter, they face the additional problem of compensating for the thermoregulatory inadequacy of their chicks. Their solutions to this problem will be discussed after the temperatures of eggs and nestlings have been considered.

PIPPED EGGS AND CHICKS

On Isla Española the Masked Boobies usually had clutches of two eggs, but in most cases they were successful in rearing only one chick. The newly hatched chicks were naked and almost helpless. At no stage did they show the extensive development of superficial air sacs that is so obvious in the downy chicks of pelicans (Richardson, 1939; Bartholomew *et al.*, 1953).

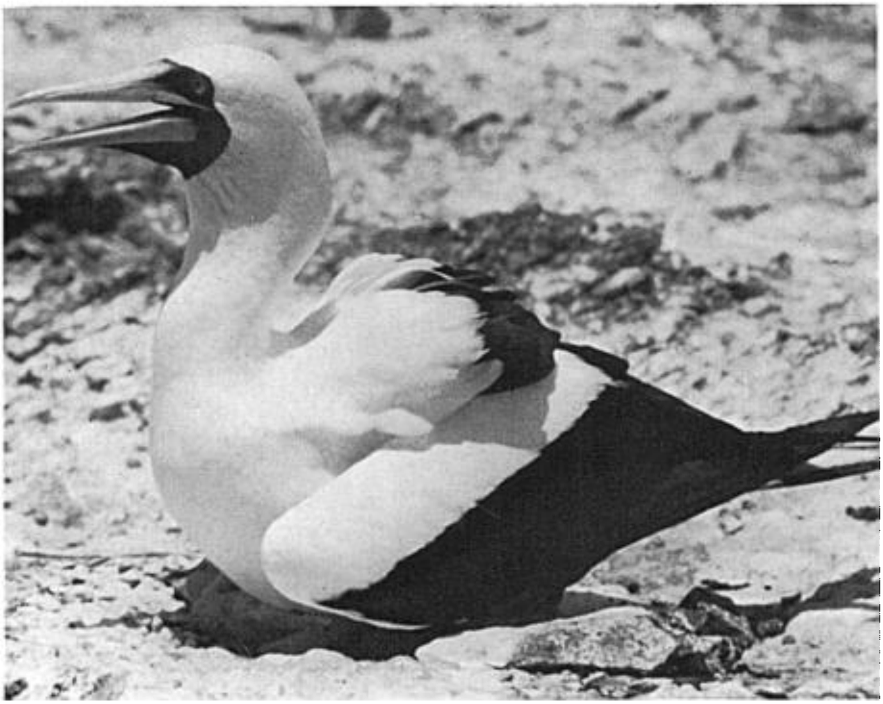

Figure 1. Masked Booby on its nest in full sun in mid-afternoon, showing elevated scapulars, drooping wings, orientation with back to sun, and open-mouthed gular flutter. Note that gular pouch and feet are in shade.

During the period of my visit pipped eggs and young of all sizes were present in the rookery. The ontogeny of thermoregulatory ability in the species was reconstructed by removing pipped eggs and young of various sizes from the nests and exposing them to the two principal thermal environments which existed in the rookery—the relative coolness of open shade and the intense heat of direct sunlight. The data on body temperatures and behavior during these periods of exposure serve as an index to the development of thermoregulation in the chicks.

Cooling. Since air temperatures in the shade during the day were virtually identical with air temperatures at night, a record of the changes in core body temperatures of young animals when removed from the brooding or incubating adult and placed in the open shade allows an ecologically realistic appraisal of their homeothermic capacity under conditions as cool as they would normally encounter in dry weather.

The temperatures of the pipped eggs and chicks when they were removed from beneath the adults on the nest were all between 38.0 and 40.3° C (figs. 3 and 4). This uniformity of temperature was, of course, not a result of a uniform thermoregulatory capacity on the part of the chicks, but of the attentiveness of the adults. Freshly hatched but dry chicks showed almost no capacity to maintain their body temperatures above ambient temperature. When plotted semilogarithmically, the decline in body temperature of the smaller chicks can be approximately fitted by a straight line. The rate of diminution of body temperature decreased regularly as body weight increased, and downy chicks weighing 400 g or more showed no decline in body temperature when

Figure 2. Adult Masked Booby shading a 400-g downy chick in the characteristic drooped-wing posture.

they were removed from their parents and put in the shade (fig. 3). It was conspicuous that chicks still inside pipped eggs cooled less rapidly than did dry, newly hatched chicks of the same or greater weight. This difference is presumably a function of the insulation furnished by the shell and embryonic membranes and the minimal surface for heat exchange afforded by the egg as compared with the hatchling chick.

Even though air temperatures remained between 27 and 29° C during the cooling experiments, the larger chicks shivered conspicuously. The newly hatched, naked chicks did not shiver visibly, but by the time the chicks weighed about 200 g and were approximately half covered with down, very faint, intermittent shivering could be seen. When their weight had reached 375 to 380 g and their downy covering was complete except for the axillas, strong and sustained shivering was always apparent when the unbrooded chicks were placed in the shade.

Not only did the vigor of shivering increase with size, but the larger the chick the higher the body temperature at which shivering first appeared. The naked chicks showed no visible shivering at any of the body temperatures observed. Chicks sparsely

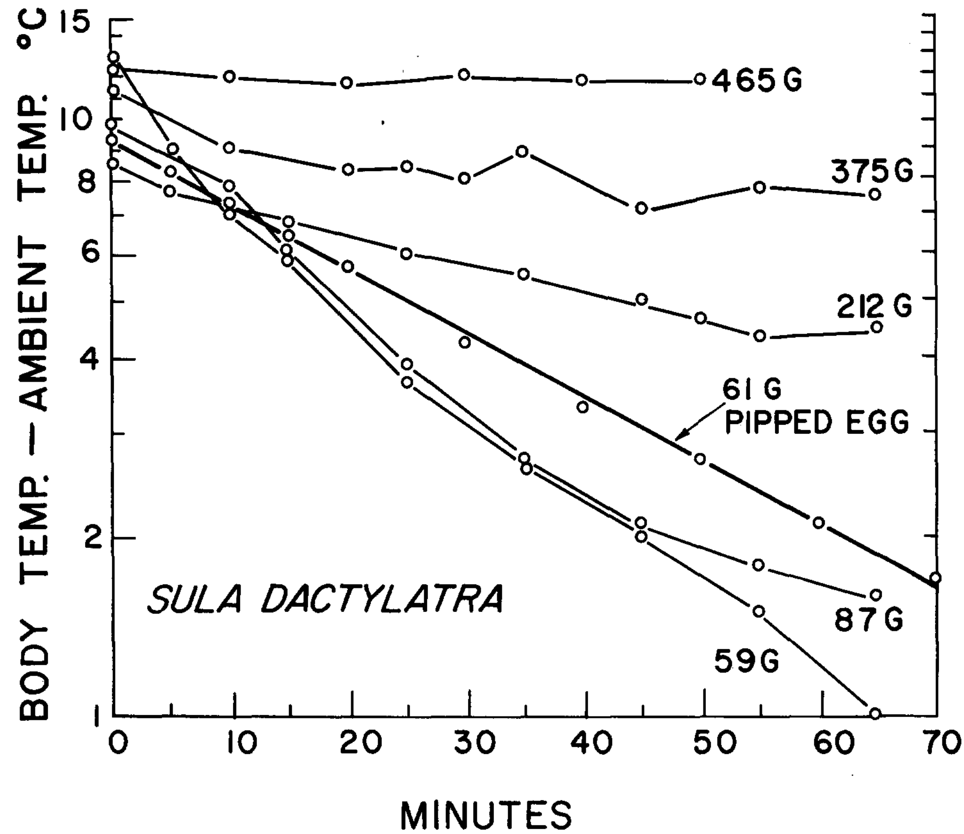

Figure 3. Cooling rates of chicks of the Masked Booby placed in the open shade and sheltered from the breeze. Ambient temperatures in all cases were between 27° C and 29° C. Numerals show weights in grams.

covered with down and weighing about 200 g began to show visible shivering when their body temperature declined to 36 to 37° C. The chicks which weighed between 375 and 500 g and were well-covered with down shivered powerfully even when their body temperatures were as high as 38.5° C, which is in the lower range of body temperatures that they experienced while being brooded.

Heating. The effect of solar radiation, hot substratum, and elevated air temperatures on the body temperatures of nestlings was investigated by removing chicks of various ages from beneath the brooding adults and placing them within a meter or two of the nest in an area that was exposed to the sun and sheltered from the wind, and then measuring their body temperatures at regular intervals and recording their behavior.

As in the cooling experiments the thermoregulatory capacity of the chicks increased directly with increasing weight (fig. 4). Hatchlings weighing less than 100 g heated so rapidly that they would have died within 20 minutes or less had they not been removed to the shade or returned to their parents as soon as their body temperatures exceeded 44° C. Sparsely downy chicks weighing between 200 and 250 g were unable to stabilize their body temperatures, but the rates of increase in their temperatures

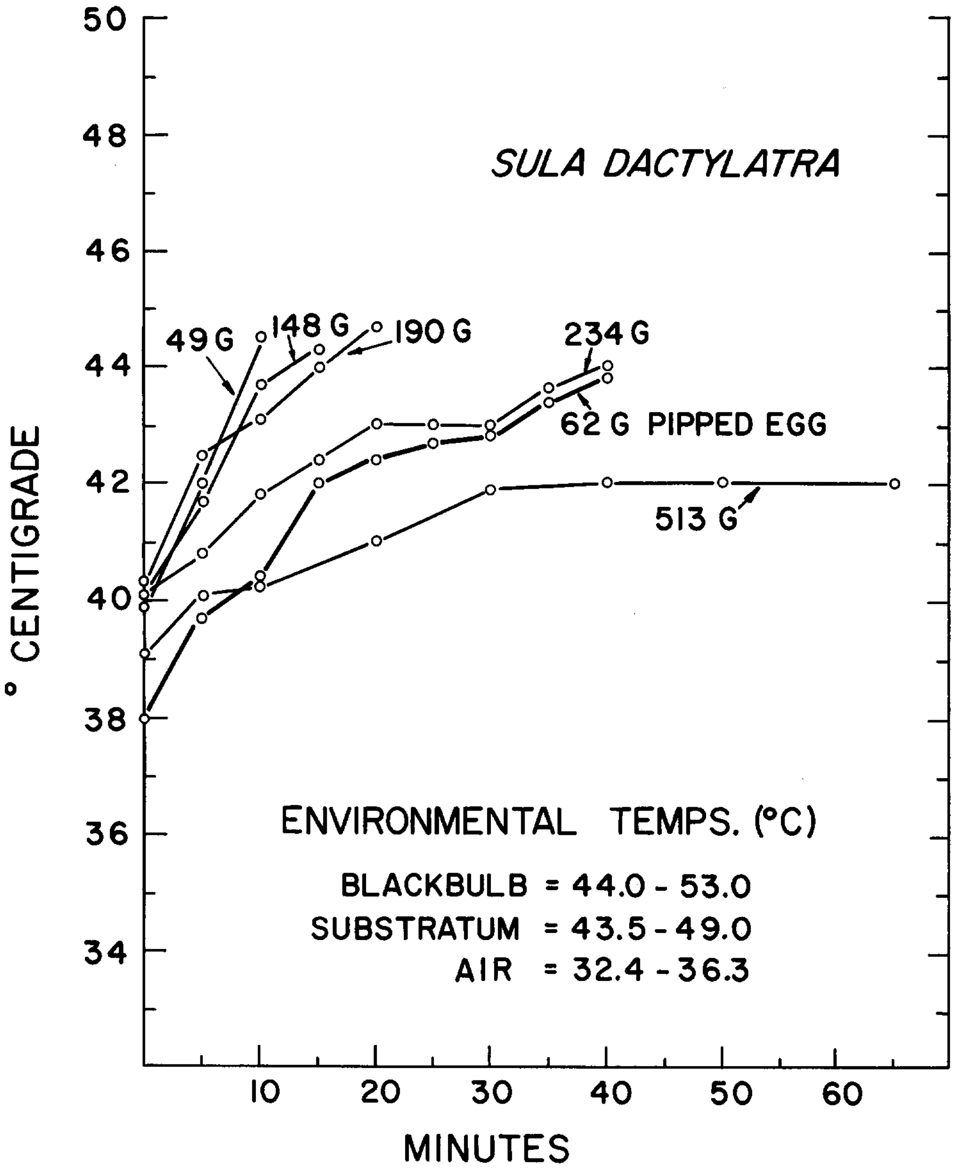

Figure 4. Heating rates of chicks of the Masked Booby placed in the full sun. Wind velocities between 4 and 7 miles per hour.

were much slower than that of the small naked chicks. The temperature of large downy young weighing between 400 and 500 g rose when they were exposed to direct sunlight, but they were able to stabilize their body temperature at about 42° C, which is somewhat higher than the highest record for any of the adults measured under similar environmental conditions (table 1).

The effects of the insulation supplied by the egg shell and fetal membranes, and the minimal surface for heat exchange afforded by the pipped egg, were even more conspicuous in the heating than in the cooling experiments. Chicks inside pipped eggs heated much more slowly than the hatchlings. The heating rate of pipped eggs was about the same as that of chicks weighing 5 or 6 times as much as hatchlings (fig. 4).

The most obvious behavioral response of the chicks to heat stress is vigorous fluttering of the naked and vascular but unpigmented gular area. Gular flutter, unlike the shivering, is present immediately after hatching. Chicks still damp from the egg showed a strong intermittent gular flutter when exposed to heat stress. The naked and partly naked young began gular flutter so rapidly when exposed to direct sunlight that the activation of this cooling mechanism preceded any detectable elevation in deep body temperature. In all cases gular fluttering was begun at relatively low body temperatures. In the eight instances where the body temperature at the time of onset of gular flutter was determined, the mean ($\pm$ SE) was $40.4 \pm 0.45°$ C.

Behavior of the chicks. Aside from the thermoregulatory activities of shivering and gular fluttering, the responses of the chicks when removed from the nest and exposed either to the full heat of the sun or to the relative coldness of the open shade are similar. The displaced chick typically maintained a steady series of low, quiet clucks at a rate of about one per second. This steady clucking vocalization was commonly produced by chicks still within the pipped egg, and it was also often uttered by chicks weighing as much as 375 g. However, it was not regularly used by chicks weighing more than about 400 g, at which weight they were able to thermoregulate without assistance from the parents and were almost too large to be brooded beneath the adults.

Nestling boobies have only limited locomotor ability. They crawl rather than walk, and use both wings and feet for leverage. Until their weight exceeds 200 g they often assist their crawling by hooking the beak on irregularities in the rocks and dirt and flexing the neck. They show a strong tendency to crawl beneath any object they touch. This has obvious survival value in that it tends to shelter them from the sun and the wind; it also assists the brooding reactions of the adults. As soon as the young can locomote effectively, of course, they actively seek out shade. For the first few days, however, they are extremely limited in mobility; even with continuous effort they move only a meter to a meter and a half per minute.

When subjected to thermal stress by exposure to the sun or by being placed in the open shade, both the partly downy and the fully downy chicks preen the synsacral region regularly but ineffectively. This response does not appear to serve a thermoregulatory function and may be analogous to the displacement preening so often reported in birds of other orders.

INTERACTIONS OF ADULTS AND CHICKS

From the data presented above, it is apparent that unbrooded chicks of the Masked Booby can neither stay warm in shade nor avoid overheating in the sun until their weight exceeds about 300 g. It is obvious, therefore, that the maintenance of body temperature in the chicks of this species, after as well as before hatching, depends in large measure on the behavioral interactions between the chicks and the adults.

At night or on an overcast day the adult can solve the chick's problem of heat loss simply by brooding it. On sunny days the thermoregulatory problem is more complex. The chicks must be shaded from the sun to prevent them from becoming overheated, but at the same time they must be partly brooded so that they do not cool. Since boobies do not have brood patches, the egg or chick cannot be in contact with the skin on the venter of the adult. Therefore the adults cannot use temperature receptors in the skin of the belly for sensing the temperature of chick or egg being brooded or being incubated. In the absence of a brood patch, the most likely site for sensing the temperature of chick or egg is the feet; there is some circumstantial evidence in support of this suggestion. The large totipalmate feet of boobies are regularly involved in brooding and in incubating. The Masked Booby, when incubating, usually covers the egg with the webbing between the first and second toes of each foot as does the Red-footed Booby, *Sula sula* (Howell and Bartholomew, 1962). Small chicks normally are brooded on top of the feet, as occasionally are eggs, particularly if the adult is trying to cover both a chick and an egg simultaneously. Newly hatched chicks characteristically lie prostrate on top of the parent's feet, which are often overlapped so as to make a large, flat platform on which the chick can sprawl without even touching the nest platform. The larger young crouch on top of the feet of the adults and are inclosed in the space between the feet and venter of the parent. Despite the absence of a brood patch, the smaller young are so closely brooded on top of the feet of the adult as to be invisible.

The adults make no effort to retrieve either young or eggs which have been displaced from the nest. When a chick is removed from beneath a brooding adult and placed on the ground nearby, it crawls back beneath the parent and onto the top of the parent's feet. The adult merely stands up and shifts about slightly while letting the chick crawl underneath it. The adult settles down on the chick once the latter has located itself on the top of the parent's feet. Under very hot conditions the adults stand up so that 1 or 2 cm separate their bellies from the young chick or egg. Under such conditions the wings of the adult are characteristically drooped, completely shading the young or the egg but still allowing space for air circulation.

Even young that are too large to be brooded are regularly shaded by the adults. The adult stands quietly at the nest site with its back to the sun, and the chick orients itself, usually facing the adult, in such a manner that it is in the shade of the parent. Quite often an adult and a large chick will thus stand facing each other so that the chick is shaded not only by the adult's body, but by its head and neck as well (fig. 5).

DISCUSSION

The Masked Boobies which nest on Isla Española face a formidable set of problems despite the fact that environmental temperatures probably never fall low enough to damage either the chicks or the developing embryos (see Baerends, 1959:357). The newly hatched chicks have virtually no thermoregulatory capacity, and if left unbrooded and exposed to the sun their body temperature rises to lethal levels in 15 or 20 minutes. The adults' choice of nest site does nothing to compensate for the chicks' lack of thermoregulatory ability. The nests are on the ground in barren rocky areas, exposed to direct solar radiation and to the large quantities of heat reradiated from adjacent rocks and dry soil. The nest consists of a platform of pebbles and affords no shelter. Moreover its location on the ground often places it in areas of reduced air movement, and consequently air temperatures at the nest are often conspicuously elevated.

If the Masked Booby built a substantial nest several meters above the ground, exposed to the relatively cool trade winds, as does the Red-footed Booby (Howell and Bartholomew, 1962), the problem of the chick's overheating would largely be eliminated. However, because of its ground-nesting habits and the nature of the nest and nest site, the adult Masked Booby must by its own behavior protect its young from

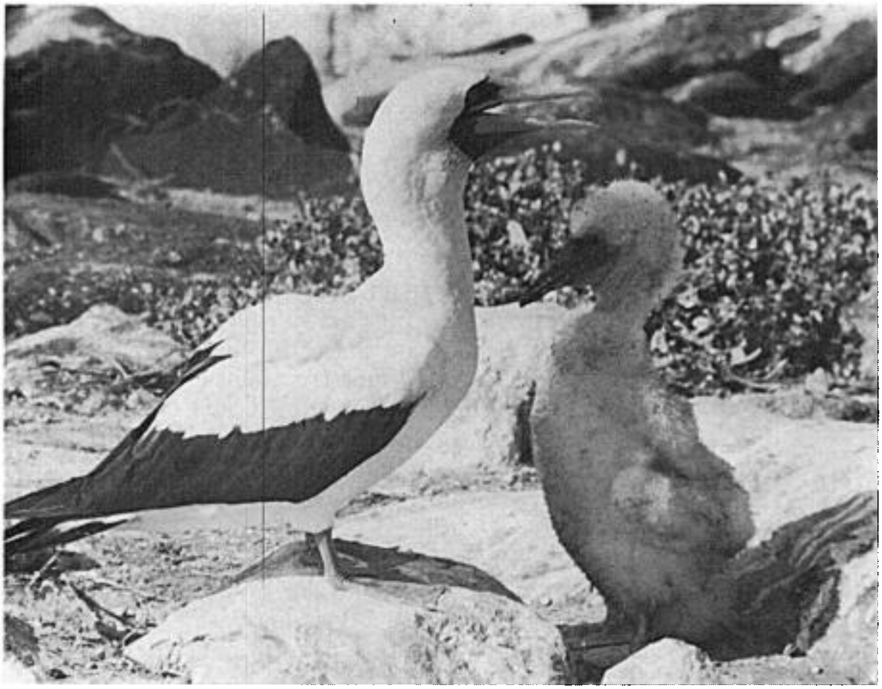

Figure 5. Adult Masked Booby shading a large chick.

death from overheating for many hours daily. The intensity of solar radiation is such that the adults must be continuously in attendance on the chicks from hatching until they have increased approximately 10-fold in weight. Even after the chicks are fully covered with down and too large to be brooded, the adults still shade them from the sun.

This performance by the adults obviously demands that they have adequate capacity to avoid overheating during the nesting period. Although it is not yet possible to assess quantitatively the relative contributions of the several mechanisms that avert overheating, a qualitative exposition of the ways in which behavior and morphology support physiological thermoregulatory capacity is possible. The rate of heat gain from radiation is minimized by the dense plumage and by the birds' habit of orienting with back to the sun so that the naked and vascular feet and gular area receive no direct solar radiation. The deep body temperature of the adult booby during the day averages about 41° C, which is several degrees higher than the usual air temperature. Thus, if they can expose their skin to the air while shielding it from the sun, they can lose heat to the air by convection. Convective heat loss from the skin in feathered areas is facilitated by elevating the scapular feathers and by drooping the wings and holding them away from the body (figs. 1 and 2). Convective heat loss from the naked parts of the body is facilitated by keeping the very large feet and extensive gular area in the shade of the feathered parts of the body. It may be significant that the legs of boobies are so short that the feet are readily kept shaded by the body.

Conductive heat loss to the substratum should be possible as long as the bird shades the substratum with its body so that the temperature of the substratum remains near that of the air. In this circumstance the substratum should afford a convenient sink into which heat from the body could be lost by conduction from the feet as is the case in the Laysan and Black-footed albatrosses, *Diomedea immutabilis* and *D. nigripes* (Howell and Bartholomew, 1961). Masked Boobies also use evaporative cooling by means of the sustained gular flutter, which is such a conspicuous aspect of their behavior. Like many other members of the Pelecaniformes (Schmidt-Nielsen, 1960), Masked Boobies have a nasal gland for the excretion of salt, and presumably they can obtain adequate quantities of water for evaporative cooling from their food and from the sea. It seems probable that the Masked Booby's habit of keeping the gular area shaded allows convective heat loss from the outer surface of the gular area as well as evaporative cooling from its inner surface.

Because air temperatures (in the absence of rain) do not fall below about 27° C during the breeding season of the Masked Booby on Isla Española, chicks are probably rarely or never damaged by chilling. But because of the intensity of solar radiation for many hours each day they are only minutes from death through overheating. It is of interest, therefore, that the naked hatchlings show no visible shivering when they are cooled. But as soon as they are exposed to direct solar radiation and before their deep body temperature has begun to rise above the level maintained when being brooded, they initiate vigorous gular flutter. I interpret this to indicate that gular flutter can be evoked by peripheral receptors. From the functional point of view such a situation would have the advantage of allowing a chick to activate its mechanism for cooling prior to any significant rise in body temperature whenever it was in a situation where heat stress was imminent.

Nonshivering thermogenesis has been reported for a number of kinds of mammals, but has not been demonstrated in birds (Hart, 1962; West, 1965). The metabolic heat which birds use in the regulation of body temperature appears to be derived exclusively from muscular activity—movements associated with feeding and locomotion, increased muscle tone, and shivering. Large downy chicks shiver visibly even when air temperature is as high as 30° C. There is a close correspondence between extent of downy covering of the chicks of the Masked Booby and the onset and vigor of their shivering. This correspondence has obvious utility. Shivering prior to the development of down would be nonfunctional, since the heat generated would be lost relatively rapidly. However, once down is present, the resultant decrease in thermal conductance should allow retention of the heat released by shivering and hence should enhance thermoregulatory capacity under cool conditions.

SUMMARY

The development of the capacity for regulation of body temperature in the Masked Booby was studied on Isla Española in the Galápagos Archipelago during February 1964. In a macroclimatic sense the thermal environment on Isla Española is remarkably equable, but intensely hot microclimatic conditions exist locally in the rookery of the Masked Booby.

Body temperatures of adults averaged 40.7° C during midday and 38.3° C after dark. At least part of the daytime elevation in temperature was associated with intense solar radiation during the day. The temperature regulation of the adults under conditions of heat stress involves a number of behavioral adjustments. Among these are (1) orienting with back to the sun regardless of wind direction, which shades the naked gular area and feet and allows them to act as sites of convective and conductive heat loss, (2) elevation of the scapulars and drooping of the wings, which fa-

cilitates convective heat loss from the feathered parts of the body, and (3) sustained gular flutter, which contributes to evaporative cooling.

Brooded chicks and incubated pipped eggs had temperatures between 38° and 40° C. When placed in the open shade (air and substratum temperatures between 27° and 29° C), hatchlings cooled rapidly. The rate of diminution in body temperature is inversely related to body weight. By the time the chicks weigh about 400 g and are covered by down, they can maintain a high and uniform body temperature. The amount of visible shivering in chicks increases directly with size.

Ability to regulate body temperature when placed in the full sun increases directly with body size. The body temperature of hatchlings rises to near lethal limits within 20 minutes or less. Downy chicks weighing 400 g, however, are able to stabilize their body temperatures near 42°, and they use the same behavioral patterns as the adults except that they seek shade. Chicks of all sizes employ gular flutter, and the fluttering response is initiated even before body temperature starts to rise when the chick is exposed to direct solar radiation.

Pipped eggs heat more slowly and cool more slowly than do newly hatched chicks, presumably because of the insulation afforded by the egg shell and by the fetal membranes.

Young chicks are dependent on brooding by the adults for protection against the lethal heat conditions which exist for them throughout the rookery. The adults stand over the smaller chicks and pipped eggs and keep them from overheating. When the chicks are too big to be brooded, the adults stand at the nest site and the large chicks remain in the shade of the adults.

The adults may sense the temperature of the eggs and chick with their feet, which are in contact with the eggs during incubation and on which the smaller chicks lie during brooding.

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