INCUBATION TEMPERATURES AND THERMOREGULATION IN THE McCORMICK SKUA

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This report is concerned with body and incubation temperatures and some aspects of thermoregulation of the McCormick Skua (*Catharacta maccormicki*). This represents part of a study of the ecology and breeding behavior of the McCormick Skua made during the three austral summers of 1963/64, 1964/65, and 1965/66 at Cape Royds, Ross Island, Antarctica, latitude 77° 33′ S, longitude 166° 09′ E.

Birds of the family Laridae have been the subject of many thermoregulation studies but those of the Stercorariidae are essentially nonexistent. Valette (1906), Eklund (1945, 1959) and Eklund and Charlton (1958) have reported McCormick Skua body and incubation temperatures but no specific adaptations to the Antarctic environment were mentioned.

Cape Royds is a strip of ice-free land consisting of irregular lava flows and dotted with small lakes in numerous valleys. From November to March, Stevenson Screen temperatures ranged from –15.0°C to 5.0°C, rising above 0°C in late December and early January. On the areas around the lakes where the skuas were breeding, the temperature 10 cm above the ground rose little above 12.0°C, and throughout the summer this temperature was generally a few degrees higher than the screen temperature.

Blizzards lasting from a few to several days occurred each season and some breeding skuas were forced to desert their nests owing to the depth of some snow drifts.

MATERIALS AND METHODS

Measurements were taken from both unconfined birds (adults and chicks) in the field, and from birds in captivity under experimental conditions.

Temperatures were measured with copper-constantan thermocouples in conjunction with a Doran thermocouple potentiometer where the reference junction was at 0°C. All joints were soldered and insulated, and the selector switch was the double pole variety with individual connections on the groups of thermocouples. Temperatures could be recorded with an accuracy of ± 0.5°C.

Several active junctions were made, tested, and calibrated before use. One was placed in a hypodermic needle for insertion under the epidermis of the skin; another was placed in a thin lead metal plate 0.5 cm in diameter, for recording web temperatures. Core body temperatures were measured by inserting a thermocouple to a depth of 2.0 cm through the cloaca into the rectum, and a series of readings were taken to ensure that a constant temperature had been reached.

Egg temperatures were taken by drilling a small hole in the shell, and the thermocouple was placed between the shell and the outer membrane. The hole was sealed with wax and the wires were taped to the egg. Using this method the embryo was not disturbed and the chick eventually hatched. In some cases the wires were placed as near as possible to the center of the egg at the expense of the embryo.

Egg and nest temperatures could be measured up to 200 meters from the nest site using leads with weather-proof, heat-resistant, and insulated coverings. Readings could then be taken without disturbing the incubating bird.

To investigate adult body temperatures when the ambient temperature was higher than normally experienced at Cape Royds, a restraining apparatus was devised to hold the bird while it was being instrumented. The bird was placed on its back in the apparatus, with its head in a small cardboard tube, a strap over the breast, and straps holding the legs. Thermocouples were placed on the incubation patch, under the wing at the point of its articulation with the body, in the rectum, and on the webs of the toes. When the bird was relaxed and the ambient temperature had reached an equilibrium, temperatures were recorded every few minutes while the ambient temperature was raised or lowered. The pulse (heartbeat) was also recorded.

For these experiments, a high ambient temperature was obtained by placing the apparatus in the Base Hut which was heated with a kerosene heater; a low ambient temperature was obtained by placing the apparatus in a sheltered position outside the Hut and surrounding it with plastic bags of ice.

The McCormick Skua arrives in the McMurdo Sound area during mid October and leaves in mid March for the pack ice or further north (Spellerberg 1967). Although they experience 24 hours of daylight during the summer there is evidence of a circadian rhythm of activity (Hart 1964). Between 01:00 and 05:00 when the lowest atmospheric temperatures are recorded, all breeding pairs
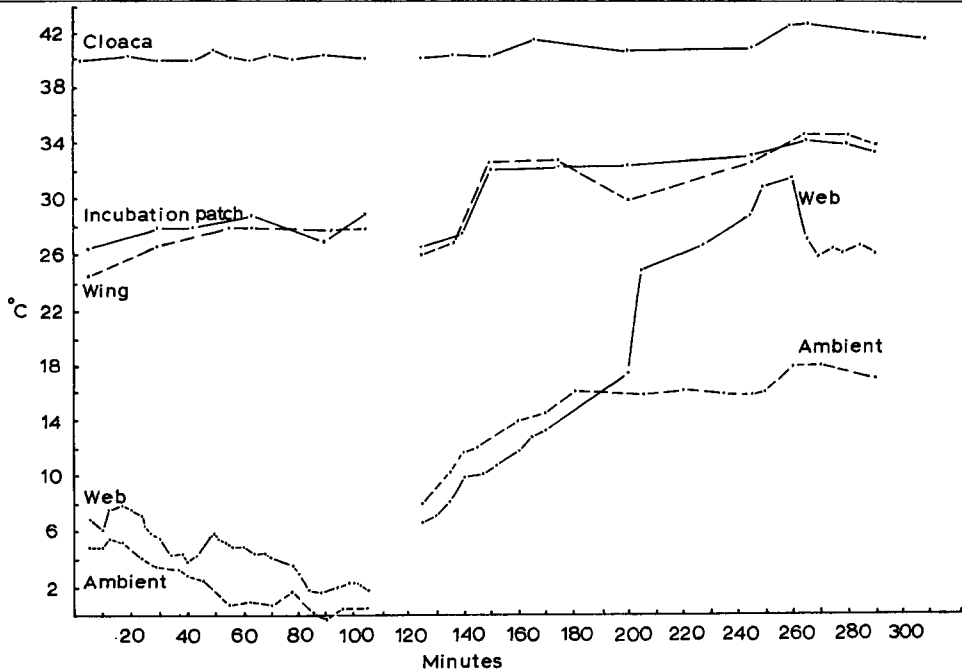
FIGURE 1. Body temperatures of a McCormick Skua in response to low then high ambient temperatures. Between 100 and 125 minutes the apparatus was shifted from a cold zone to a warm zone.

are roosting, incubating, or brooding, and little or no foraging takes place.

Scoops (nests) are scratched in the volcanic detritus and eggs are laid in late November followed by 29 days of incubation. Feeding of the chicks continues for six to eight weeks when adults and chicks leave the territories. Both parents have two incubation patches which are seasonal, and both participate in incubation, brooding, and feeding.

RESULTS

ADULT BODY TEMPERATURES

Core body temperatures of incubating female birds ranged from 40.0°C to 42.4°C with a mean of 41.4°C ($n = 23$). The temperature of a South Orkney example was 41.1°C. (Valette 1906), and Eklund (1959) found a mean value of 41.2°C for the same species.

Measurements taken from an adult male bird over a span of 24 hours showed a diurnal rhythm in core body temperature. At 21:00 it was 42.1°C and dropped to 41.0°C during 02:00–04:00. At midday there was a rise to 42.4°C. This gave a range of 41.0°C to 42.4°C over the 24-hour period.

Temperatures of the incubation patches of female incubating birds ranged from 38.4°C to 40.9°C, with a mean of 39.0°C ($n = 11$). This is 2.4°C lower than the core body temperature.

Dry web temperatures recorded in the field ranged from 3.3°C for a bird roosting on sea ice, to 12.3°C for a bird roosting on black rock. Other temperature recordings ranged between these, and it appears that the web temperature varies according to the immediate conditions of the bird's position.

An experiment was conducted on an adult male in which the webs were surrounded by ice, and sufficient light was passed from below so that the blood flow could be seen with a binocular microscope. Over a period of 45 minutes when the ambient temperature of the web was kept at 0.0°C, the web was between 1.5°C and 2.0°C, while the skin at the point where the feathers end on the ankle was at 38.0°C. That the tissues of the web can function at 2.0°C is an adaptation necessary when the bird is fishing. The temperature of the sea water off Cape Royds was −1.9°C (surface), and heat would be lost when fishing if the web was not kept at a low temperature, as the thermal conductivity of water is twenty times greater than that of air (Kahl 1963; Hart and Fisher 1964).

In addition to the gradient of temperatures between the web and core body temperature there is a gradient between the skin and the surface of the plumage. This is evident during snow falls or blizzards when roosting adults have been found in small snow caves formed
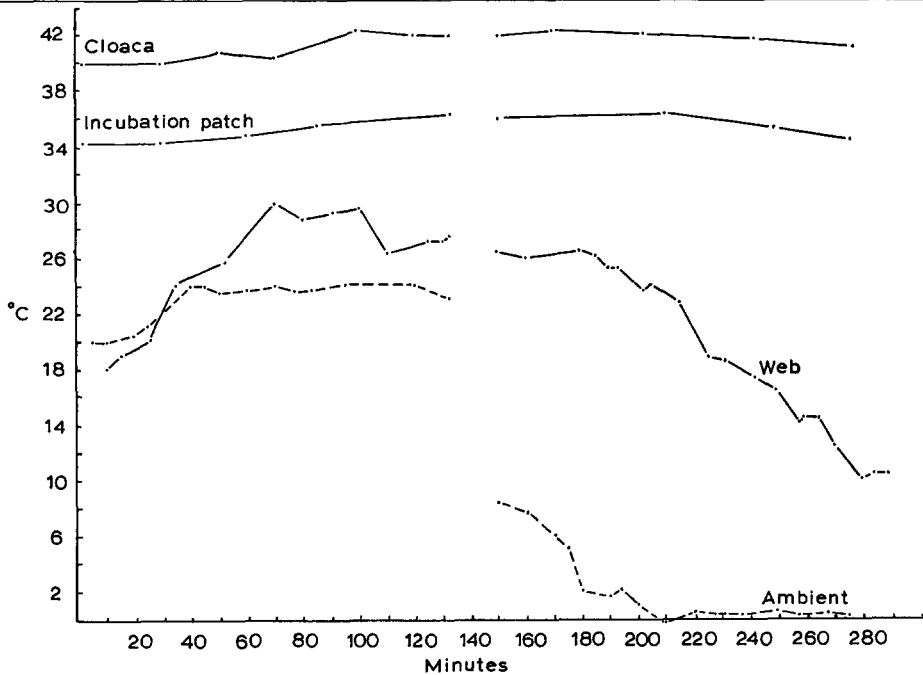
FIGURE 2. Body temperatures of a McCormick Skua in response to high then low ambient temperatures. Between 135 and 150 minutes the apparatus was shifted from a warm zone to a cold zone.

by the snow compacting and building up around the bird. The temperature gradient prevents snow from melting into the plumage and illustrates the effective insulation of the plumage.

While foraging at sea skuas will dive from the surface of the water and no damage occurs to the plumage, but after bathing in lakes, water may penetrate the plumage and adults have been found flightless because of ice forming in the primary feathers.

BLOOD SUGAR

Blood samples of the McCormick Skua were taken in order to measure the blood sugar concentration. Although the results are few they assist in a more detailed analysis of the mechanisms of thermoregulation. Blood sugar concentration in two breeding males of body weights 1079 g and 1136 g was 495 mg/100 ml and 230 mg/100 ml, respectively. In two non-breeding males of body weights 1048 g and 1164 g it was 340 mg/100 ml and 300 mg/100 ml, respectively. In two incubating females with body weights of 1306 g and 2020 g it was 265 mg/100 ml and 280 mg/100 ml, respectively.

REACTIONS OF ADULTS SUBJECTED TO HIGH AMBIENT TEMPERATURES

Although the Cape Royds environment is generally harsh and extremely variable, some

high temperatures have been recorded above snow-free areas in the breeding colonies. In the absence of wind the surface temperature sometimes reached 16.0°C to 21.0°C. In these conditions and particularly after flight the skua would frequently drink from the lakes and sometimes pant.

The results from two experiments in which adults were subjected to high ambient temperatures are given (figs. 1, 2). One bird (fig. 1) was a nonbreeding female with no incubation patches. The other (fig. 2) was a female that had laid a clutch of eggs five days before the experiment.

In figure 1 the web temperature became stable at 2–4°C, 90 minutes after the start of the experiment when the ambient temperature was below 5.0°C. The web and the skin of the breast where the incubation patch is normally found rose about 4.0°C during 100 minutes, while the pulse remained between 104 and 108 beats per minute. At 110 minutes the apparatus was taken inside the Base Hut and recording resumed at 125 minutes. The ambient temperature was raised from 8.0°C to 16.0°C over a period of 70 minutes. During this period the web temperature rose rapidly, and at 200 minutes the bird began to pant while the pulse was 156 beats per minute. At 200 minutes the bird's feet were released from the straps for six minutes and
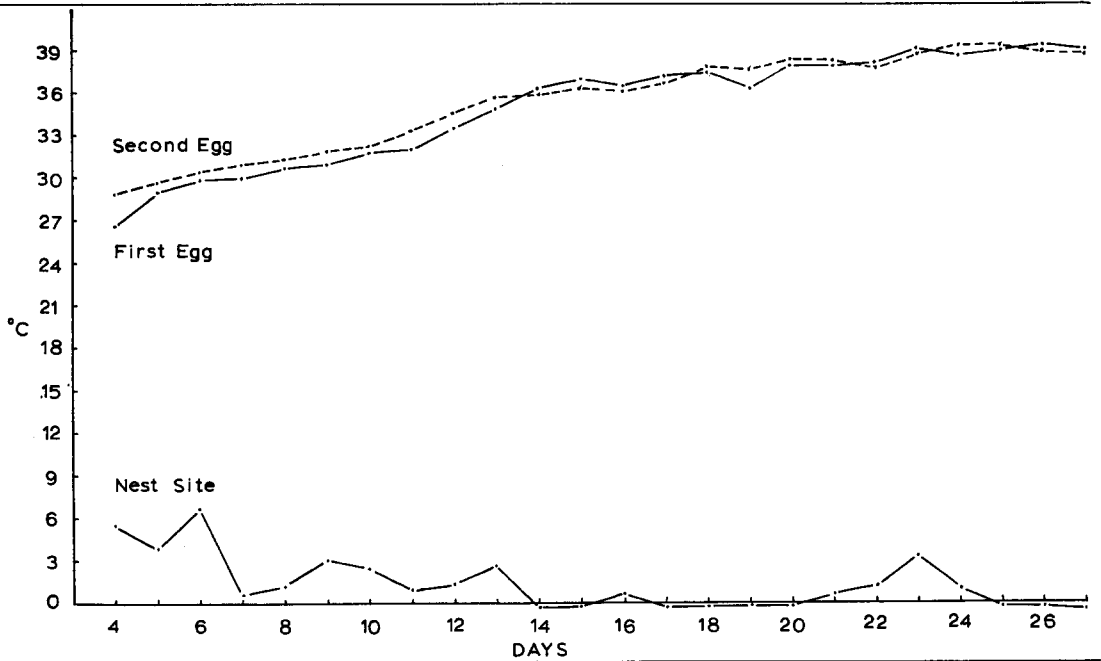
FIGURE 3. Temperatures taken daily at midday for the two eggs (98 and 96 g) of the McCormick Skua; from the fourth day of incubation to the twenty-seventh with thermocouples in the egg's air chamber. Nest-site temperatures are shaded air temperatures 4 cm above the ground beside the nest.

immediately the web temperature rose to 31.0°C. At the same time the rectal temperature rose three degrees and the pulse reached 176 beats per minute. From 260 minutes onward the bird panted vigorously and the web temperature became stable at 26.0°C. At this point the experiment was terminated as the bird's breathing had become erratic.

In the second experiment (fig. 2) the ambient temperature was raised to 23.0°C while the web temperature reached 30.0°C. At this point the bird was panting and the pulse had increased from 108 to 164 beats per minute. At 100 minutes there was a rise in the rectal temperature and a sudden drop in the web temperature, and at the same time the breathing became erratic. At 135 minutes the apparatus was taken outside where a low ambient temperature was recorded. The web temperature dropped slowly then became stable at 10.5°C at 280 minutes. At 212 minutes the bird was taken out of the apparatus and allowed to flap its wings while being held by the legs; this produced only a slight drop in the web temperatures and incubation patch temperatures. This was probably a direct result of the sudden activity of the bird. Similar results have been found for other bird species (Farner 1956; Farner and Serventy 1959).

INCUBATION TEMPERATURES

The mean temperature of the center of eggs fourteen days after laying was 36.4°C (n = 18). This is five degrees lower than the average core body temperature. Eklund (1959) gave a mean value of 35.8°C measured with an electronic temperature telemeter placed inside the egg and replacing the embryo.

During the 29 days of incubation there was a rise in the egg temperature from about 28.0°C to about 39.0°C (fig. 3). As there is no correlation of egg temperatures with nest temperatures, the increase in egg temperature may be due to a progressive increase of brood patch temperature during incubation, or to thermogenesis of the developing embryo (Romijn and Lokhorst 1956; Drent 1965), or to a combination of both.

On the fourteenth day of incubation, hourly observations were taken over a 24-hour period. The maximum temperature recorded was 37.1°C, and the minimum was 32.4°C (fig. 4). During the 24 hours the wind did not rise above 11 mph, and there was little cloud cover. A daily rhythm in the amount of heat applied to eggs has been observed in many birds (Kendeigh 1963).

During incubation the eggs are completely surrounded by the brood patch, the plumage, and the web. This effectively insulates the egg
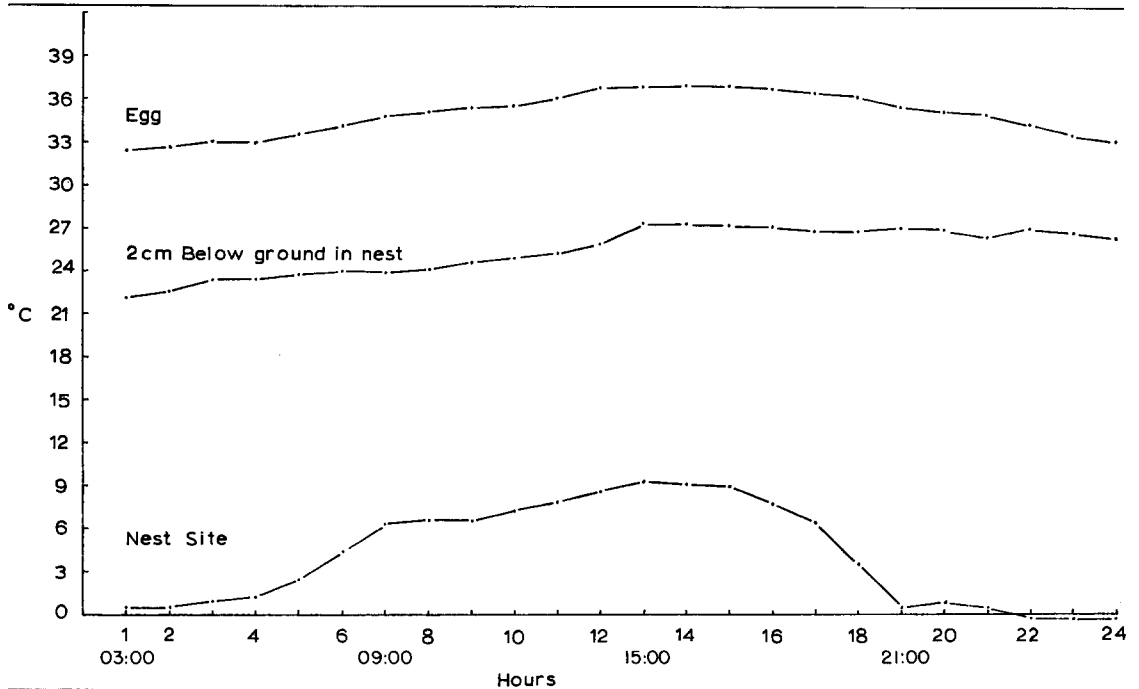
FIGURE 4. Hourly temperatures of a McCormick Skua egg (98 g) on the fourteenth day of incubation using a thermocouple in the egg's air chamber. Nest-site temperature is the shaded temperature 4 cm above the ground beside the nest.

against loss of heat. There is, however, a slight gradient of internal temperatures from the lower side of the egg to the upper side. Results from thermocouple readings showed a variation of 30.0°C to 35.0°C ($n = 8$) on the lower side, and 38.0°C to 40.0°C ($n = 8$) on the upper side during the period of 10 to 18 days after laying.

To investigate the possible cooling effect of the environment and to find out how quickly the adult can promote normal incubation temperatures, adults were forced to leave their nests for a short period of time. Temperatures taken from the egg's air chamber every few minutes when the adult was settling (Beer 1961) on the eggs showed that it took approximately 25 minutes to raise the egg temperature from 0.0°C to 32.0°C (fig. 5). In this case the egg had cooled during a period of fourteen minutes. At the point in figure 5 where the temperature drops slightly (by 2.5°C) the bird shifted and adjusted its feet until they were under the egg (settling movement).

During incubation relief, the egg temperature drops a few degrees. The maximum recorded drop was 8.0°C ($n = 11$), and the minimum recorded drop was 2.5°C ($n = 11$). The eggs were left for a minimum of time while one bird left the eggs and was replaced

by its mate. Eggs were sometimes left exposed for as long as 23 minutes on calm days, while the male fed the female; and although no temperatures were recorded, it seems possible that the temperature of the ground is sometimes sufficiently high to keep the eggs alive.

BODY TEMPERATURES OF CHICKS

To investigate the thermoregulatory ability of McCormick Skua hatchlings, chicks of known weights were instrumented for rectal temperatures (fig. 6). The time was noted as soon as the adult left the nest. During the investigation there was a wind of 3–4 mph, overcast sky, and ground-surface temperature of –3.0°C. The results indicate that the chicks can maintain essentially adult temperatures in an environment of 0.0°C from about 50 hours after hatching. The chicks aged 12, 22, and 46 hours died soon after the termination of the investigation.

Observations of chick behavior have shown that chicks up to 6–7 days old require some protection (brooding) by the parent, especially during unfavorable weather (wind with snow). If not sheltered by the parent they will shiver, and where there are two chicks they will huddle (Cendron 1953; Prévost
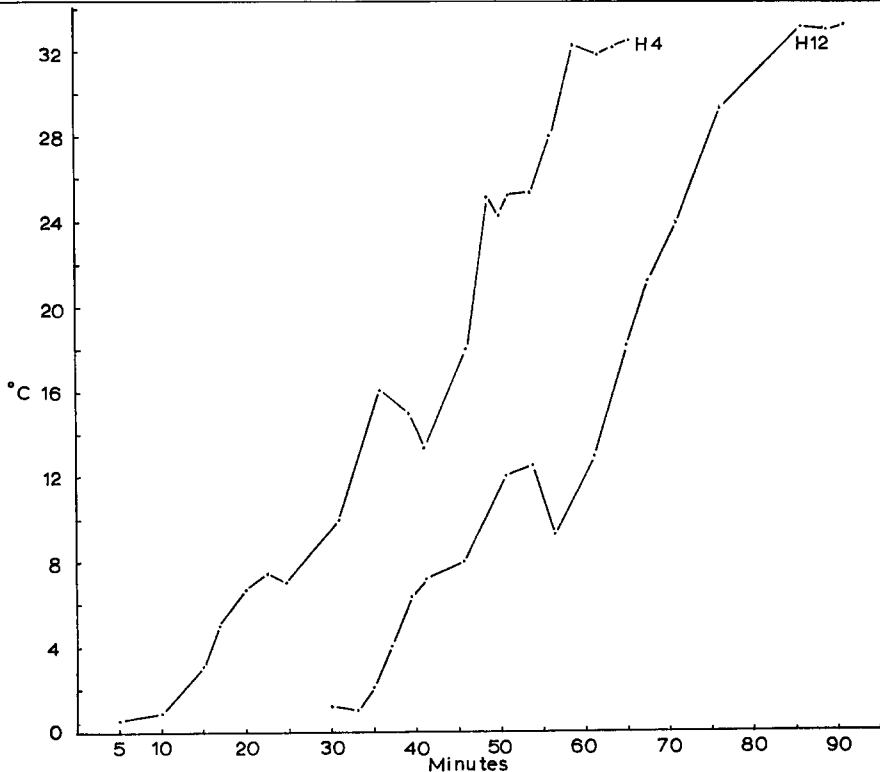
FIGURE 5. Two records of McCormick Skua egg temperatures, while the adult was settling on the eggs, using thermocouples in the egg's air chamber. In both cases the atmospheric temperature was between -2.0°C and -4.5°C. H4 = two-day-old egg (101 g). H12 = four-day-old egg (98 g). Both eggs hatched later.

1963) although they are normally aggressive towards each other.

Chicks 10 days of age and older appear to maintain adequate body temperatures, and they have been seen swimming on the lakes when the water temperature was between 0.0°C and 4.0°C. After 40 minutes in the water they appeared to suffer no damage to their webs.

On calm days the chicks would lie prone on the ground with wings and tarsi outstretched. Obviously the chicks were suffering from heat stress (Howell and Bartholomew 1961), although they were not seen to pant.

DISCUSSION

From the present information it appears that the McCormick Skua does not have any attributes not possessed also by similar sized gulls in adaptations to coastal antarctic summer conditions. Despite the continuous daylight of the summer there is a 24-hour cycle of activity and rest (roosting) which is accompanied by a core body temperature cycle, and during the period of rest the lowest atmospheric temperatures are recorded. Thus

during the normal midnight hours the adult is resting and metabolic activity is at its lowest, an adaptation that has been found in many birds (Hoffman 1959; Kareila 1961). The high incubation-patch temperatures (2.4 degrees lower than the rectal temperature) is not unusual and is partly due to the increased blood supply in this region (Bailey 1952). The gradation of temperatures in the leg and between the body and the surface of the plumage has been reported also in gulls. Irving and Krog (1956) have shown that in the leg of *Larus glaucescens* there is, in addition to reduced blood flow at low ambient temperatures, some kind of vascular heat exchange in the tarsus so that blood flowing into the unfeathered portions of the leg has a low temperature, so reducing heat loss.

Panting by adults in the field was observed on a few occasions, but under experimental conditions with a high ambient temperature panting was frequent and vigorous. As the low temperatures in this region of Antarctica result in low absolute humidities, loss of heat by way of the pulmonary surfaces or respiratory passages may not be economical for the Skua in terms of water loss (Lasiewski et al.
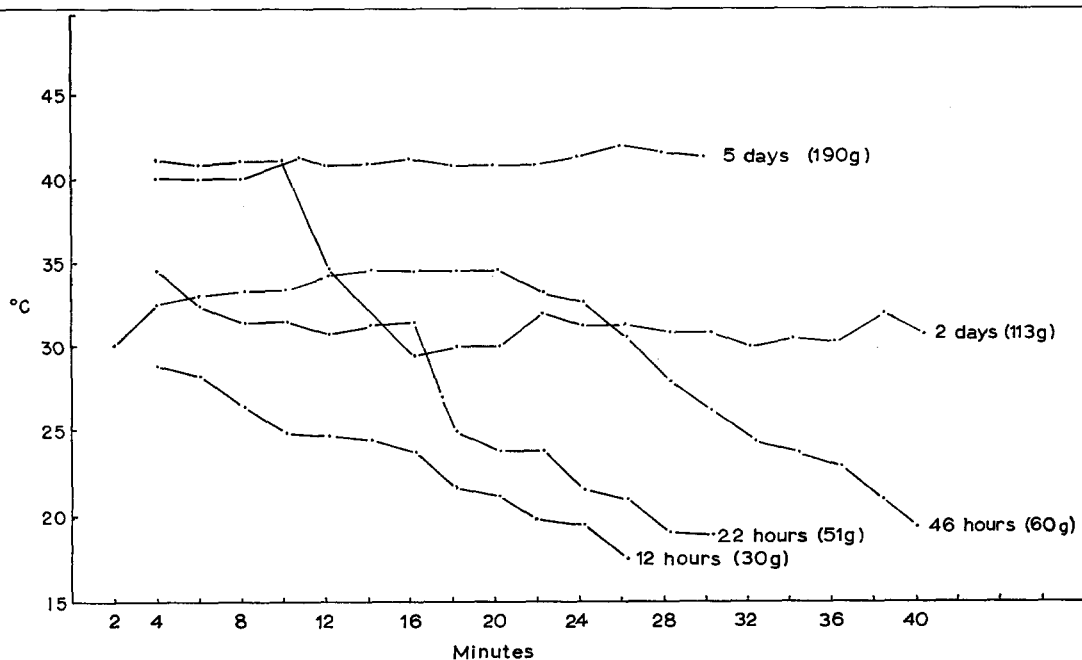
FIGURE 6.   Rectal temperatures of five McCormick Skua chicks up to five days old, taken with thermocouples. The ambient temperature in all cases was between 1.0°C and –4.0°C. The time is taken as soon as the adult leaves the chick.

1966). It is possible that replacement of water is physiologically difficult, and both adults and chicks appear to be dependent on fresh water to replace water used in metabolic processes and evaporative cooling. The breeding colonies in southern McMurdo Sound are all near fresh-water lakes, ponds, or melt streams, and frequently, particularly after feeding, chicks and adults have been seen drinking or eating snow from the drifts.

The importance of the legs in thermoregulation of birds has been shown previously (Howell and Bartholomew 1961, 1962). The McCormick Skua reduces its web temperature in cold surroundings while the rectal temperature remains stable; but in high ambient temperatures the web temperature is also high, suggesting that heat is emitted from this region and also suggesting the presence of some heat exchange mechanism in the webs (Scholander 1955).

By cooling the webs in cold surroundings and by using the webs as vascularized radiators in hot surroundings the McCormick Skua may be able to increase the range of its thermoneutral zone, an important adaptation for this southern latitude where temperaures are frequently below 0.0°C, even though ground (rock) temperatures may sometimes be relatively high.

During incubation each tarsus is placed

under an egg and it is probable that the webs contribute to the heat of incubation, at least through the insulation that they provide.

The environmental temperatures at Cape Royds during the summer encourage almost continuous incubation, and other than man there is no stimulus which might force the bird to leave its eggs. The strong attachment of the parents to their nest, as exemplified by the continuous brooding and by the reluctance to give place to a mate except after a prolonged brooding period, ensures that the egg is well protected. During blizzards the adults continue incubating while the snow builds up around them except for a small breathing hole, a condition found also in penguins (Arnaud et al. 1964).

The average rate of cooling for eggs in the nest in the absence of the adult was found to be 2.3°C/minute and the average rate of rise in egg temperature was 1.3°C/minute. Here the rate of heating the egg is slower than its rate of cooling, the time required for heating the egg being 1.7 times longer than the time required for an equivalent amount of cooling. When the bird is incubating, the temperature on top of the eggs is the same as the incubation-patch temperature; but when exposed the eggs are subjected to an ambient temperature of –3.0°C and cool more quickly by radiation and convection (Kendeigh 1963).

During late December and early January, the time of hatching, the climate at Cape Royds is at its best. This is advantageous for the chicks for it does not seem possible that the wet, newly-hatched chicks could regulate their body temperature during adverse weather conditions as adequately as older chicks. Although the hatchlings are precocial and may leave the nest at 12–24 hours after hatching (Reid 1966), during the first five days the rectal temperature of the chick is at least 5°C lower than that of the adult, and up to two days they could not maintain a constant body temperature in ambient temperatures of –3.0°C. It would appear that there is an improvement in thermoregulation and an increase in body temperature during the first few days after hatching. A sure criterion of efficient thermoregulation is provided by the termination of continuous breeding by the adults, providing weather conditions remain calm. At Cape Royds continuous brooding was found at eight nests until the chicks were three days old (ground surface temperature of 1.2°C–4.5°C).

Development of good thermoregulation by the end of the first day and near-adult temperatures by three days has been reported for many gulls (Barth 1951; Bartholomew and Dawson 1952, 1954).

After the chicks become too large to be brooded (at 14 days and 405 g) they are sufficiently insulated to withstand high winds, blown snow, and low temperatures. This was illustrated after blizzards when chicks were found alive and apparently well in snow caves formed by the compacting snow.

SUMMARY

Body and incubation temperatures and thermoregulation of the McCormick Skua were studied at Cape Royds, Antarctica, in three austral summers.

The mean rectal temperature of the adult skua at midday was 41.4°C, 1.4°C higher than that taken at 03:00. The incubation patch temperature was 39.0°C, which was 2.4°C lower than the rectal temperature.

The web temperature varied with the ambient temperature. The vascularized web permitted heat loss at high ambient temperatures and heat conservation at low ambient temperatures.

The effective insulation provided by the plumage permits the adult to continue brooding during periods when snow may completely cover the bird.

The temperature of the egg on the four-

teenth day of incubation was 36.4°C. This varied during the day and rose slightly through the period of incubation.

Chicks up to the age of about fifty hours could not maintain a constant body temperature in an ambient temperature of –3.0°C. Brooding by the adult protects the hatchlings for the first few days after hatching.

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