

METABOLISM AND THERMOREGULATION IN HATCHLING RING-BILLED GULLS

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The extensive efforts to analyze the size dependence of various parameters of thermoregulation in birds (King and Farmer 1961, Lasiewski and Dawson 1967, Lasiewski et al. 1967, Herreid and Kessel 1967, Crawford and Lasiewski 1968, Aschoff and Pohl 1970) have been useful in defining certain physiological characteristics of these animals. However, the analyses have tended to obscure the fact that variation beyond that associated with general allometric relations can occur in these parameters within particular taxa. For example, House Sparrows (*Passer domesticus*) show geographic variation in heat resistance, thermal conductance, and metabolic responses to cold (Hudson and Kimzey 1966, Blem 1973, 1974, Kendeigh and Blem 1974). Horned Larks (*Eremophila alpestris*) in deserts surpass their counterparts from more mesic situations in thermoregulation in hot environments (Trost 1972). Basal metabolic rate of certain pigeons is inversely correlated with the degree of aridity of their respective environments (Dawson and Bennett 1973). Variation in thermoregulatory parameters is also evident among young of closely related species, judging by the results of Koskimies and Lahti (1964). These authors demonstrated that hatchling ducks of species breeding exclusively at arctic and subarctic latitudes tended to have better control of body temperature at cool ambient temperatures than those of species with wider and more southerly distributions. We feel that variation of this type within taxa may well reflect functionally significant adjustments. To evaluate the physiological role of these adjustments more precisely, we have studied the metabolism and thermoregulatory capacities of hatchling gulls in the genus *Larus*. This group is a particularly useful one for considerations of physiological variation, for it is represented by more than 30 species over a latitudinal span extending from the arctic to the sub-antarctic. Our initial study in this series (Dawson et al. 1972) concerned the Laughing Gull (*Larus atricilla*). We now report results obtained on the Ring-billed

Gull (*Larus delawarensis*). This species nests predominantly on lakes at midlatitude in northern United States and southern Canada. It also breeds in maritime situations in Quebec and Newfoundland (A.O.U. Check-list 1957).

MATERIALS AND METHODS

Chicks were obtained from the breeding colony of Ring-billed Gulls located at Rogers City, Presque Isle County, Michigan (latitude 45° 23' N), in the first half of June, 1971. This colony is located on a man-made peninsula serving as a breakwall for the dock area of the Calcite Plant of U. S. Steel Corp. This peninsula projects ENE into Lake Huron, as shown in the map presented by Southern (1969). The topography of the area surrounding the colony varies from year to year with the deposition and removal of storage piles of limestone. In 1971, the colony was located on the southern portion of the landward half of the peninsula, with most of the nests placed in a flat area where annual plants such as common burdock (*Arctium minus*) provided scattered cover. Some nests were located on the approximately 15-ft high southern facing of the peninsula, among large granite boulders placed there to protect against wave action. A few nests of Herring Gulls (*Larus argentatus*) were present on the outskirts of the Ring-billed Gull colony, which numbered approximately 2500 breeding adults in 1971.

We inspected marked nests daily to obtain chicks hatched within the preceding 24 hr. The individuals selected on a given morning were transferred by car to The University of Michigan Biological Station, near Pellston, Michigan, for laboratory study. The transfer required approximately an hour and was completed by 11:00 EST. Most of the physiological measurements recorded here were made between 13:00 and 17:30. However, some measurements pertaining to shivering and to determination of nocturnal levels of basal metabolism were performed between 20:00 and 23:00. The birds were fed canned fish at the end of the afternoon and the next morning, prior to their being returned to the colony.

FIELD OBSERVATIONS

Measurements of some factors affecting heat exchange between gull chicks and the environment were made on three days in June, 1971. Body (T_b) and ambient temperatures (T_a) were determined with thermistor probes (Yellow Springs Instruments, no. 402) used in conjunction with a YSI Telethermometer. The measurements of T_a were made at a height of 1 m in the shade. Temperatures of the sky and of the ground and down surfaces were estimated using a Barnes PRT-10L infrared thermometer. A Belfort pyroheliometer recorded the intensity of solar radi-

ation during the observation periods. Wind speeds at various heights were determined with a Hastings wind speed meter.

LABORATORY OBSERVATIONS

We weighed chicks to the nearest 0.1 g and measured their body lengths (bill tip to pygostyle) and the thickness of their down on arrival in the laboratory. They were reweighed upon completion of metabolic tests. We placed the birds to be used in these tests in metabolism chambers in a constant temperature cabinet set between 9.2° and 45.6°C ($\pm 0.2^\circ\text{C}$). These chambers rested on a refrigerator shelf over a stainless steel partition that shielded them from the heating elements in the cabinet. Ambient temperatures within the chambers were monitored with thermocouples connected to a suitably calibrated Honeywell 16 multipoint recorder. Rates of oxygen consumption ($\dot{V}\text{O}_2$) and evaporative water loss (\dot{m}_{w_e}) reported here refer to values observed over the last 10 min of 2-hr exposures of chicks to particular Ta's. Body temperatures were determined rectally using a thermistor probe (YSI no. 402) connected to a YSI Telethermometer. The measurements of Tb in metabolic tests were made just before the chicks, which had been at Ta's of 24°–27°C, were placed in the metabolism chambers (see below), and at the end of the 2-hr exposures to a particular Ta. Determination of $\dot{V}\text{O}_2$ (all volumes refer to STPD) followed the procedure described by Dawson et al. (1972), except that the inner surfaces of the metabolism chambers were painted flat black (see Porter 1969) and that a model F-3 rather than G-2 Beckman oxygen analyzer was used. A flow rate of 365 ml of air/min was employed in tests conducted below 37°C. At higher Ta's, flow was increased sufficiently to maintain chamber humidity equivalent to 10–12 mm Hg vapor pressure (see below). The flow rates utilized ranged up to 1610 ml/min. These maintained the FO_2 and FCO_2 in the metabolism chambers above 20% and below 1%, respectively.

Rates of evaporative water loss by the chicks were also measured with the procedure described by Dawson et al. (1972). However, chamber humidities were monitored during the 2-hr tests, using a sensor for an electronic hygrometer (Hygrodynamics model 15-3001) in the outflow line from each metabolism chamber. This provided the basis for the adjustments of air flow described in connection with the measurement of $\dot{V}\text{O}_2$.

Integrated electromyographic activity (EMG) was determined for a fixed volume of leg muscle (see Hudson et al. 1974); this provided an estimate of the capacities of hatchling Ring-billed Gulls for shivering. This entailed the use of an electronic integrator (Narco Biosystems Inc., model GPA-10). In these measurements of EMG's, the chicks rested on paper towels in an open 1-gal can. This can was maintained in a drying oven fitted with a YSI Thermistemp unit to provide precise temperature control at Ta's between 20° and 35°C. Estimates of capacities for muscular thermogenesis were supplemented by determination of the weight and myoglobin content of pectoral and leg muscles. These muscles were dissected from 8 chicks sacrificed for the purpose, and weighed immediately. The samples for five of these animals were homogenized in 0.04 M phosphate buffer (pH 6.6) and assayed immediately for myoglobin using the spectrophotometric procedure of McPherson and Tokunaga (1967).

Breathing rates of chicks at moderate and high Ta's were determined with an impedance pneumo-

graph connected to a Physiograph (Narco Biosystems, Inc.) (see Dawson et al. 1972). A connection from this pneumograph to an a.c. preamplifier in a second channel of the Physiograph allowed simultaneous registration of breathing movements and electrocardiograms.

In the 2-hr metabolic tests conducted at cool Ta's (below 20°C), the gull chicks tended to become hypothermic. The rewarming of certain of these birds when returned to Ta's of 23°–25°C was followed and behavioral observations recorded. Body temperatures in the rewarming period were measured esophageally using a thermistor (YSI no. 402) and YSI Telethermometer.

RESULTS

FIELD OBSERVATIONS

Climatic records for the Rogers City, Michigan, area indicate that air temperatures are relatively mild during June, averaging 17.7°C, with the average maximum and minimum being 25.2°C and 10.1°C, respectively. Over the period of our study, the recorded temperature extremes were 30.0° and -0.06°C. Rain occurred on five days, ranging in amount from 3.8 to 15 mm.

Our microclimatological observations made during three days in mid-June obviously cannot provide a comprehensive description of the physical conditions affecting our nestlings, but they do illustrate some of the thermal problems confronting these birds and their parents. Knowledge of these problems facilitates interpretation of the behavioral and physiological observations presented in this report. The intensity of solar radiation reached 1.3 cal (cm²·min)⁻¹ during the middle of sunny days in mid-June. On such days, the temperature of the north sky approximated -6°C, while that of cloud surfaces ranged between 2° and 8°C. Surface temperatures of the unshaded ground in the colony varied between 22° and 37°C, with most of the values falling below 30°C. Time of day, and extent of cloud cover strongly influenced these ground temperatures. They were probably also affected by wind. However, only gentle breezes with maximum speeds below 4.5 m/sec (10 mph) occurred during our observations. Our measurements with the Hastings wind speed meter did provide indications of the well known logarithmic attenuation of wind speed with decreasing height above the surface. In one set of observations, a speed of 2.3 m/sec (5 mph) was recorded 1 m above the surface. Wind speed dropped to 1.3–0.9 m/sec at 30 cm and to 0.2 m/sec in the low vegetation surrounding many of the nests. Shade temperatures at ground level out of the wind varied between

TABLE 1. Development of heat stress in unbrooded Ring-billed Gull hatchlings in full sun on a day in mid-June with ambient and soil surface temperatures of 17° and 27°C, respectively, 20% cloud cover, wind speed < 2.2 m/sec (5 mi/hr), and incident radiant energy > 1.0 cal·cm⁻²·min⁻¹.

Time unshaded (min)	Temp. dorsal down surface (°C)	Body temp. (°C)		Remarks
		Chick 1	Chick 2	
0.5	40	40	41	Chick 2 begins to pant
5	46	—	—	Both chicks panting and attempting to move to shade
7	—	40.8	41.9	Both chicks panting
10	48-49 ^a	41.8	42.8	vigorously

^a This provides a reasonable index of combined air and radiant temperatures, but it exceeds the average temperature to which the chicks were exposed, since their ventral surfaces were shaded and exposed to the relatively cool air and substrate.

12.5° and 18.4°C over the course of our microclimatic observations.

Body temperatures of recently brooded hatchlings were measured in conjunction with the microclimatic measurements. With ambient and soil surface temperatures at 16°-18°C and 24°-30°C, respectively, Tb's of 14 chicks averaged 40.1°C (range, 39.0°-40.6°C) immediately after the cessation of brooding. Further observations on these birds established that they could encounter heat or cold stress when briefly unprotected by a parent. At the ambient and sky temperatures (less than 18° and 0°C, respectively) affecting the gull colony, the hatchlings began vigorous shivering almost immediately after the cessation of brooding if the sun was covered by cumulus clouds. However, signs of heat stress appeared almost as rapidly in these chicks if they were exposed to direct sunlight at these ambient and sky temperatures.

Even adult gulls appeared to incur significant heat loads while standing in full sun at cool ambient temperatures. Such individuals panted frequently, especially while brooding or shading their chicks. Low frequency pumping movements of the gular area often accompanied this panting.

While hatchling Ring-billed Gulls obviously can encounter both heat and cold stress in the course of a single day when unattended, their thermal problems normally tend to be minimized by the attentive behavior of their parents, which appear to share in caring for them. We were impressed with the intensive brooding the chicks received over the first two days after hatching. The attentiveness of the adults is illustrated by our experience with

one adult Ring-billed Gull that we drove from its nest. It hovered over us, periodically defecating or diving on us, approaching close enough in the latter case to strike our backs with its wings. This bird returned to shade its young chicks immediately after we left the vicinity of its nest. While unshaded, these chicks quickly became hyperthermic (table 1), Tb rising nearly 2°C in 10 min, despite the relatively cool Ta (17°C). Similar results were noted on other occasions where chicks were left unshaded before our arrival at the nest. The highest temperatures noted on the dorsum of these unshaded birds approximated 50°C. Hatchlings could move a few cm to reach the shadow of a parent, if this adult were standing by the nest. Slightly older chicks (ca. 2 days) were observed in some instances to move out of the sun into the vegetation surrounding the nest. While these movements might have been primarily related to concealment, they certainly would reduce the radiant heat loads to which the young gulls were subjected. The reliance of chicks on their parents for thermal protection declines steadily after the second day. Individuals approximately a week old huddled with their siblings, care by the parents during the daytime being largely confined to feeding. Older chicks are even more independent, leaving the nest, wandering about the colony, and, in some instances, moving out onto the water. Feeding constitutes their main tie with their parents after the first week following hatching.

LABORATORY OBSERVATIONS

Body weight and developmental state of hatchlings. The hatchling Ring-billed Gulls used in our study weighed 34.6 ± 4.0 g (mean and standard deviation) on arrival in the laboratory. Body length averaged 13.8 cm. The young were covered with a luxuriant down that was approximately 11 mm thick on both the back and abdomen. As the down dried and the young became more active in the hours following hatching, the feather sheaths disintegrated and the down then became fluffier.

Responses to moderate and cool ambient temperatures. The relation of oxygen consumption to Ta at the completion of 2-hr tests is illustrated in figure 1. The VO₂'s of the hatchlings, each of which was used in only a single test, rose from 1.6 ml (g·hr)⁻¹ near 35°C to approximately 3.3 ml (g·hr)⁻¹ at 20°C. The equation for the least squares regression line fitted to 25 metabolic values

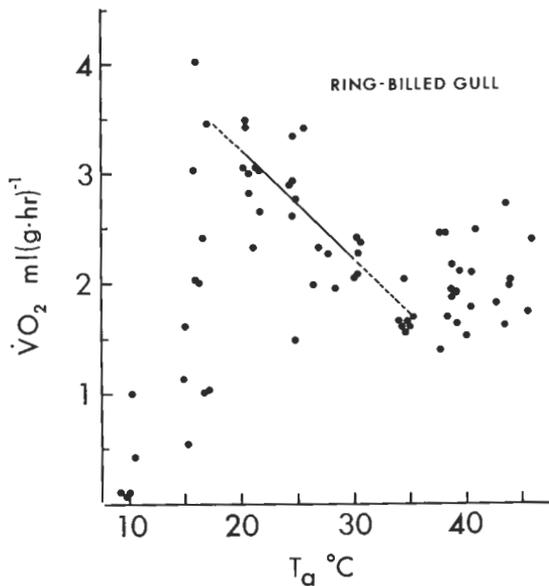


FIGURE 1. Relation of rates of oxygen consumption ($\dot{V}O_2$ corrected to STPD) by 66 hatchling Ring-billed Gulls to ambient temperature (T_a). The rates illustrated occurred at the end of 2-hr exposures to single T_a 's. The lowest $\dot{V}O_2$'s at approximately 20° and 25°C were not utilized in fitting the least squares regression line shown, as they pertain to individuals with body temperatures below 34°C.

for T_a 's between 20° and 31°C is $\dot{V}O_2 = 5.18 - 0.10 T_a$, where $\dot{V}O_2$ and T_a are in $\text{ml (g}\cdot\text{hr)}^{-1}$ and degrees Celsius, respectively. These 25 values pertain to chicks with T_b 's above 34°C at the end of 2-hr tests. Abilities of the hatchlings to sustain high metabolic rates at T_a 's of 14.8°–17.2°C varied considerably with the $\dot{V}O_2$'s at the end of tests ranging from 0.5 to 4.0 $\text{ml (g}\cdot\text{hr)}^{-1}$. These values are not significantly correlated with T_a . However, they are strongly correlated with T_b ($r = 0.98$; $P < 0.01$), as might be anticipated. A significant correlation also exists between T_b and body mass ($r = 0.73$; $P < 0.01$). Larger chicks tend to surpass smaller ones in resisting the chilling effects of T_a 's of 14.8°–17.2°C in 2-hr tests. Whether this reflects the greater maturity or larger size of the former cannot be determined from the available data. Greater uniformity of performance occurred in tests conducted near 10°C, where deep hypothermia routinely developed over the 2-hr tests. None of the $\dot{V}O_2$'s observed in the vicinity of this T_a exceeded 1.1 $\text{ml O}_2 \text{ (g}\cdot\text{hr)}^{-1}$.

The T_b 's measured at the end of the metabolism tests are plotted against T_a in figure 2. With two exceptions, the chicks demonstrated relatively effective thermoregulation between 20° and 35°C. (Performance of birds tested at T_a 's exceeding 35°C is discussed in a sub-

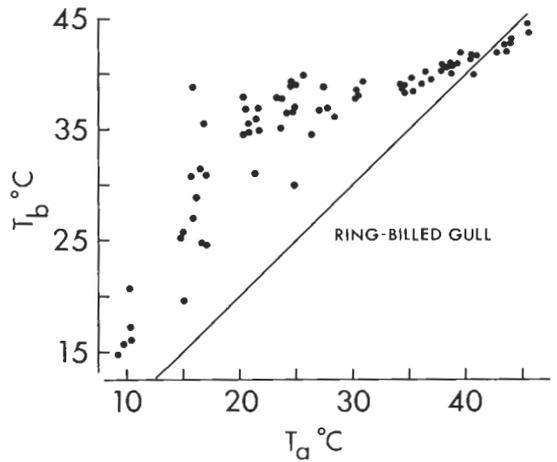


FIGURE 2. Relation of body temperature (T_b) of 74 hatchling Ring-billed Gulls to ambient temperature (T_a). The diagonal line marks equivalence between T_b and T_a . All measurements were made at the end of 2-hr exposures to single T_a 's.

sequent section.) As noted in the metabolic comments, hypothermia became prevalent as T_a declined below 17°C. This appears to result from an overtaxing of the regulatory capacities of the chicks, for $\dot{V}O_2$'s of the individuals that subsequently became hypothermic rose in the early part of the 2-hr tests. The mean level attained (mean for five individuals, 3.21 $\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) approximated that indicated by the regression line in figure 1 as the summit metabolism of homeothermic individuals. After 20–45 min, metabolism began to fall toward the rates recorded at the end of the tests. Despite the fact that some of these chicks cooled to as low as 15°C in tests conducted near 10°C, all recovered from hypothermia without apparent ill effect after return to warmer surroundings (23°–25°C).

Recovery from hypothermia. Hatchling Ring-billed Gulls chilled to 16°C or below exhibited no spontaneous movement; the limbs were rigid and the pectoral or leg musculature did not visibly shiver. Occasionally, barely audible cries were uttered. As T_b increased after the chicks were transferred to warmer surroundings, some poorly coordinated movements began. Spasmodic bouts of leg kicking with a frequency of 2–3/min commenced at 17.5°C. Shivering became visible in the legs at 20°C and coincided with the first loud calls. The chicks began to utter plaintive calls continuously at 21°C. When placed on their backs, the chicks first attempted to right themselves at 22°C. Their eyes were open at this temperature, but the chicks did not respond to visual stimuli until

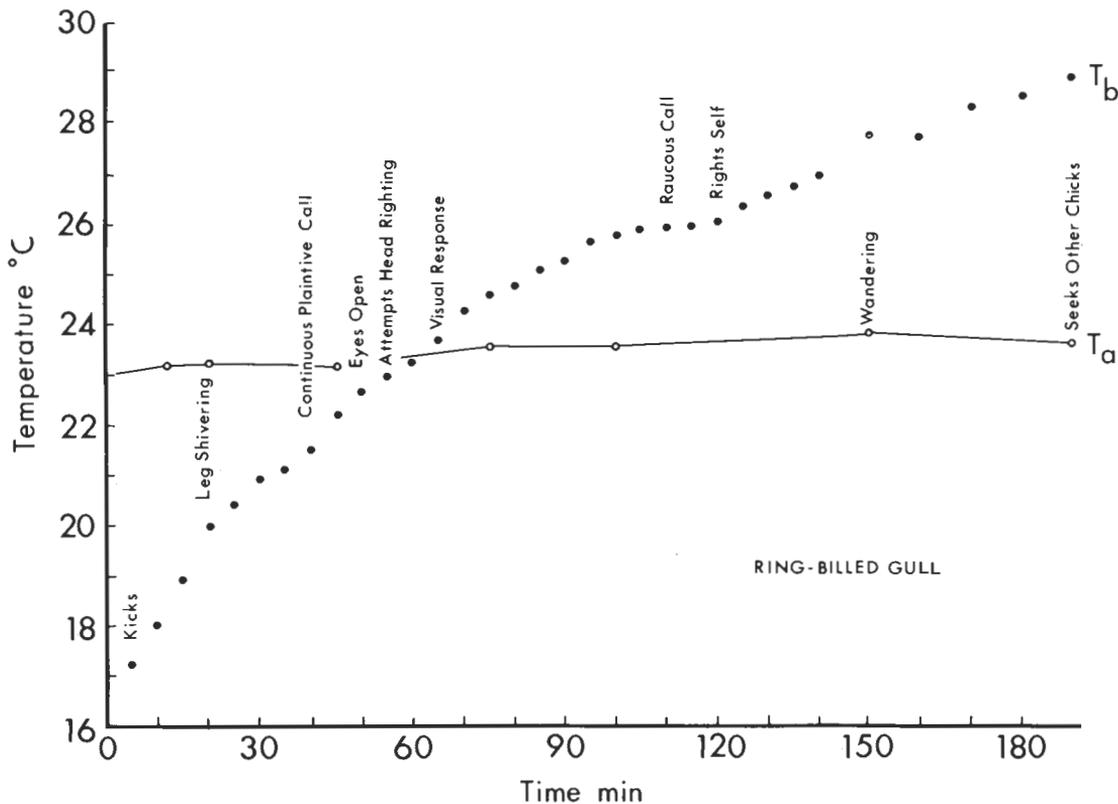


FIGURE 3. Behavioral correlates of rewarming in a hatchling Ring-billed Gull that became hypothermic during a 2-hr test at 10°C. The rewarming (body temperature = T_b) began when the chick was transferred to a warmer ambient temperature (T_a).

they warmed to 24°C. They could right themselves at 26°C, at which temperature pectoral shivering became visible. More raucous calls commenced at this T_b . The chicks began wandering around at 28°–29°C. These events are summarized for a single chick in figure 3.

Myoglobin and muscle mass. Weight of the pectoral musculature of hatchling Ring-billed Gulls averaged 0.34 g, or 1.1% of the body weight of the chicks sampled. Comparable figures for the leg musculature are 1.63 g and 5.1%. The nearly fivefold difference in the masses of these muscle groups suggests that the legs are more important than the pectoral region in the thermogenesis of the hatchlings. Average myoglobin contents of the leg and the pectoral musculature were 2.02 and 2.35 mg/g of tissue, respectively. The muscles lacked the robust red color characteristic of the skeletal muscle of adult gulls, which presumably reflects high concentrations of myoglobin and cytochromes. The levels of myoglobin found in the young Ring-billed Gulls match those of white skeletal muscle from cats (McPherson and Tokunaga 1967), but are lower than those reported for skeletal muscle from most mammals studied (Lawrie

1953). Quantitative information on myoglobin contents of avian muscle is so limited at this time as to preclude meaningful comparisons of the data for hatchling Ring-billed Gulls with those for other birds (however, see George and Berger 1966, for a qualitative description of avian muscle composition).

Electromyographic activity. The values obtained for integrated EMG's from legs of 14 hatchling Ring-billed Gulls maintained at various T_a 's are summarized in figure 4. The complex relation between these values and temperature probably is not directly comparable to that apparent for the metabolism-temperature relation (fig. 1), owing to differences in experimental design. However, this former relation does indicate the relative vigor of the shivering response evident in the leg with exposure of chicks to moderate and cool T_a 's. The range of the integrated values observed in these birds at T_a 's near 19°C before substantial decrease in T_b extends from 500 to 1610 $\mu\text{V}\cdot\text{sec}/\text{min}$, whereas that for 32°–34°C (where VO_2 is at the minimal level for euthermic birds) runs from 30 to 690 $\mu\text{V}\cdot\text{sec}/\text{min}$. Considerable variation in electromyographic activity is evident among birds tested

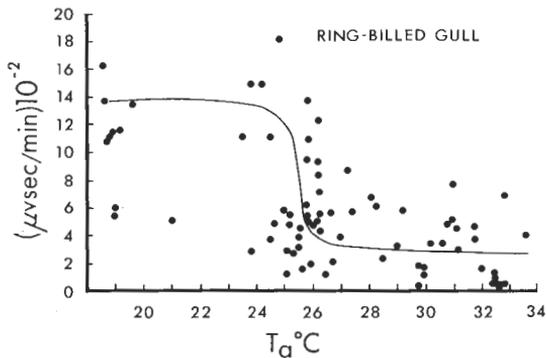


FIGURE 4. Relation of integrated electrical activity (in $\mu\text{V}\cdot\text{sec}/\text{min}$) from skeletal muscle of 14 hatchling Ring-billed Gulls to ambient temperature (T_a). Electromyograms were obtained from a fixed volume of leg muscle and integrated electronically. Multiply numbers on the ordinate by 100 to obtain actual $\mu\text{V}\cdot\text{sec}/\text{min}$.

at similar temperatures. The meaning of this in relation to thermogenesis is unclear. Perhaps some of the variation reflects differences in electrode placement.

While we were unable to interpret fully the thermal dependence of EMG activity in hatchling Ring-billed Gulls, it is clear that such activity is not linearly related to temperature. A major shift between low and high levels of electrical activity occurs near 26°C (T_a). Below this temperature, integrated muscle potentials remain essentially stable in chicks maintaining high T_b 's. This appears to contrast with results of EMG recordings obtained from pectoral muscles of adult Common Pigeons (*Columba livia*) (Steen and Enger 1957) and Common Redpolls (*Acanthis flammea*) (West 1965), in which peak-to-peak voltages increase progressively with declining T_a in the zone of chemical thermoregulation. Perhaps the thermal dependence of EMG activity in hatchling gulls reflects the differing thermal sensitivities of the various muscle masses noted in chicks recovering from hypothermia (fig. 3). In such a case, recording from a single muscle mass might well provide a distorted picture of the relation of total muscular thermogenesis to T_a . It is also possible that the electromyographic picture for the hatchling Ring-billed Gulls is complicated by the presence of non-shivering thermogenesis (see Discussion).

Comparisons of diurnal and nocturnal levels of standard metabolism. We have taken the values of VO_2 obtained at $34.3^\circ\text{--}35.3^\circ\text{C}$ (where T_b approximates 39°C) as representing the basal metabolic rate (BMR) of hatchling Ring-billed Gulls. The BMR of adult birds may differ by approximately 20% be-

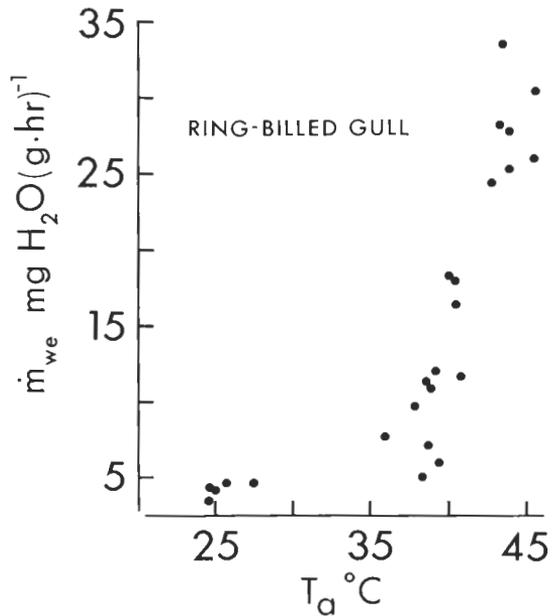


FIGURE 5. Relation of rates of evaporative water loss (\dot{m}_{we}) of 24 hatchling Ring-billed Gulls to ambient temperature (T_a). All rates were determined during the last 10 minutes of 2-hr tests conducted at single T_a 's. Absolute humidities in these tests were maintained at 10–12 mm Hg (aqueous vapor pressure).

tween the active and inactive phases of their daily cycle (Aschoff and Pohl 1970). Since the BMR of the hatchlings is important to our analyses, we measured it both at night (21:00–23:30 hours) and during the day. The values for 7 chicks tested during the day and 9 measured at night average 1.69 ± 0.16 (S.D.) and 1.57 ± 0.15 $\text{ml O}_2(\text{g}\cdot\text{hr})^{-1}$, respectively. The difference between the two means is not significant ($P > 0.05$). In the subsequent discussion, we shall utilize the mean of the combined sets of values, 1.62 $\text{ml O}_2(\text{g}\cdot\text{hr})^{-1}$, as the BMR for hatchling Ring-billed Gulls.

Responses to high ambient temperatures. Hatchling Ring-billed Gulls greatly increase their evaporative output of water at high T_a 's, with values of \dot{m}_{we} rising approximately five-fold between 37.8° and 45.6°C (fig. 5). The rates at the highest T_a 's may represent slight overestimates, since the chicks' salt glands became active during the 2-hr tests. In some cases a few droplets of the fluid produced fell on the walls of the metabolism chamber, rather than into the mineral oil over which the birds rested.

The augmentation of \dot{m}_{we} at high T_a 's is associated with a well developed panting response involving at least a trebling of breathing rate from the minimal levels observed at $34^\circ\text{--}35^\circ\text{C}$ (average of minima for 7 birds, 46.6 breaths/min). Our pneumographic rec-

ords indicate considerable variation among chicks in the maximal rates attained. Most lay between 220 and 260 breaths/min. However, the maximal rates for two of the birds were 145 and 168 breaths/min, respectively, and that of a third was 310 breaths/min. All the chicks tested showed a well defined increase in breathing rate with body temperature at T_b 's exceeding $40^\circ \pm 0.5^\circ\text{C}$. However, one chick that was subjected to heating a second time showed a reduced threshold of 38.5°C (T_b) for this increase. Whether comparable lability exists in the neural centers governing thermal polypnea remains to be determined. The maximal breathing rates observed in five of the eight Ring-billed Gull chicks studied are similar to those noted previously for three Laughing Gulls at a comparable age (Dawson et al. 1972).

Despite the increased breathing rates developing in Ring-billed Gulls at higher T_a 's, the correlation coefficient for $\dot{V}O_2$ and T_a between 37.8° and 45.6°C is not significant ($P > 0.1$). A significant correlation was also lacking over a similar temperature range in the Laughing Gull (Dawson et al. 1972). Presumably, these results reflect the relatively effortless character of the breathing movements contributing to increased evaporation.

Body temperature of hatchling Ring-billed Gulls rises with T_a between 35° and 45.6°C (fig. 2). Nevertheless, the chicks still remained cooler than their surroundings during 2-hr tests conducted above 41°C . The T_b 's of the two individuals tested near 45.5°C were 43.8° and 44.6°C , respectively.

Measurements of heart rates of euthermic chicks were obtained in the process of determining breathing rates at moderate to high T_a 's. The extreme values obtained for eight birds ranged from a minimum of 300 beats/min at 34° – 35°C to a maximum of 528 beats/min at 44.1°C , the highest T_a at which electrocardiographic observations were made. The mean value for the minimal heart rates of the four birds studied at 34° – 35°C (which essentially coincides with the temperature interval in which the values for BMR were obtained) was 337 beats/min. Muscle potentials associated with shivering obscured electrocardiograms at lower T_a 's and thus precluded determination of heart rates in the zone of chemical thermoregulation.

DISCUSSION

FIELD OBSERVATIONS

Despite the temperate latitude of the colony from which our experimental subjects were

drawn and the thermal buffering afforded by Lake Huron, these gulls may be exposed daily to heat as well as cold stress. Ambient temperatures during the periods of our observations were at levels at which hypothermia occurred in 2-hr metabolism tests in the laboratory. Moreover, conditions on sunny days in the Rogers City colony induced significant heat stress in unshaded chicks. Unprotected individuals soon began to shiver when the sun was shaded by clouds. On the other hand, they quickly began to pant in the direct sunlight. Insolation appears to be a potential hazard for gull chicks in colonies even farther north than the one in which we worked; Barth (1951) suggested that exposure to direct sunlight results in increased mortality among very young chicks of *Larus argentatus*, *L. marinus*, and *L. fuscus* in colonies along the coast of southern Norway. Despite cool air and sky temperatures and direct and indirect effects of solar radiation, the T_b 's of hatchling Ring-billed Gulls appear to remain near 40°C . This results from the supplementation of the thermoregulatory capacities of these birds with attentiveness by the parents, which provides either warmth or shade depending on the circumstances. While our field observations did not happen to coincide with periods of inclement weather, little doubt can exist concerning the importance of parental behavior in protecting the young from the chilling effects of rain and high winds, which are not uncommon in the Rogers City area in late spring. The general contribution of parental attentiveness to stabilizing the temperatures of their young should be kept in mind in the interpretation of the laboratory results discussed in the ensuing sections of this report.

Given the importance of parental behavior to thermostasis in hatchling Ring-billed Gulls, it is reasonable to question the functional significance of the thermoregulatory capacities of these young. Presumably, these capacities are of particular importance in situations involving disruption of the parental attentive pattern, e.g., the entrance of predators into the colony or agonistic behavior among adults. Such circumstances would render important the hatchlings' capacities for defense against heat and cold.

LABORATORY OBSERVATIONS

Thermal conductance. Simultaneous measurements of $\dot{V}O_2$, T_b , T_a and in certain instances, \dot{m}_{we} for hatchling Ring-billed Gulls that remained warmer than 30°C at the end of 2-hr metabolic tests permit estimation of thermal

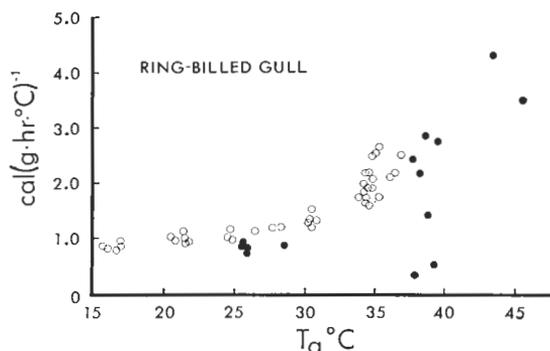


FIGURE 6. Relation of thermal conductance ($\text{cal}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}\cdot^{\circ}\text{C}^{-1}$) to ambient temperature (T_a) in hatchling Ring-billed Gulls (based on data in figs. 1, 2, and, in some cases, 5). Shaded circles indicate values corrected for evaporative heat loss (these values referred to as θ in text). Unshaded circles are uncorrected for such heat loss and refer to C (see text). All the values presented refer to instances in which the differential between body temperature (T_b) and T_a exceed 1.5°C . Even so, this did not eliminate the scatter evident between 35° and 40°C , where the temperature differential tends to be relatively small in all cases (see fig. 2). Values of 4.8 cal/ml O_2 and $0.58\text{ cal/mg H}_2\text{O}$ were used to convert data on metabolism and water loss to calories.

conductance (heat transfer coefficients) with the following equations:

$$C = P(T_b - T_a)^{-1} \text{ or } \theta = (P - E)(T_b - T_a)^{-1},$$

where C and θ (King and Farner 1964) represent conductance values in $\text{cal}(\text{g}\cdot\text{hr}\cdot^{\circ}\text{C})^{-1}$ uncorrected and corrected for evaporative heat loss, respectively; P is heat production in $\text{cal}(\text{g}\cdot\text{hr})^{-1}$, E is evaporative cooling in $\text{cal}(\text{g}\cdot\text{hr})^{-1}$, and T_b and T_a are in degrees Celsius. The values of C and θ are plotted against T_a in figure 6. The minimal figures of C (ca. $0.85\text{ cal}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}\cdot^{\circ}\text{C}^{-1}$) represent about 40% of those noted at 34° – 35°C , where the metabolism of euthermic chicks reaches its minimum level. Stated in another way, the hatchlings increase their insulation by a factor of approximately 2.5 with a decline in T_a from 34° – 35°C to approximately 20°C . The values of θ continue rising over the band of temperatures (37.8° – 45.6°C) in which the chicks have activated their heat defenses. At 25°C , C exceeds θ (which is corrected for evaporative heat loss) by approximately 20%.

The values of θ for these hatchlings (mean $0.87\text{ cal}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}\cdot^{\circ}\text{C}^{-1}$) can be converted to surface specific terms using Meeh's formula. The values obtained, which average $0.28\text{ cal}(\text{cm}^2\cdot\text{hr}\cdot^{\circ}\text{C})^{-1}$, fall at the upper limit of the data on this function computed for adult birds of comparable size (Drent and Stonehouse 1971). The minimal values of C for our chicks

(0.78 – $0.95\text{ cal}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}\cdot^{\circ}\text{C}^{-1}$) exceed the figure of $0.67\text{ cal}(\text{g}\cdot\text{hr}\cdot^{\circ}\text{C})^{-1}$ predicted for a 34.6-g adult bird with an equation based on that of Lasiewski et al. (1967) relating thermal conductance to body weight. This discrepancy does not seem to result from substantial differences in rates of evaporative water loss between the hatchlings and adult birds of comparable size; values of m_{we} at 25°C observed for the former and estimated for the latter using the equation of Crawford and Lasiewski (1968) are 4.2 and $3.7\text{ mg H}_2\text{O}(\text{g}\cdot\text{hr})^{-1}$, respectively. The difference between these two values in caloric terms is negligible when compared with the calories associated with heat production in these birds. Evidently, the down covering of the gull chicks affords less effective insulation than the plumage of adult birds of comparable size.

One of our objectives was to compare thermoregulatory parameters among hatchling gulls from different environments. Minimal values of C for hatchling Ring-billed and Laughing gulls (Dawson et al. 1972) can be compared, having been studied with similar procedures. The minimal values of C for chicks of these species at T_b 's greater than 30°C are 0.78 – 0.95 and $0.96\text{ cal}(\text{g}\cdot\text{hr}\cdot^{\circ}\text{C})^{-1}$, respectively. Precise comparison requires elimination of the effect of the size differential between hatchlings of the two species. Mass-specific thermal conductance of adult birds varies as the -0.51 power of body mass (Lasiewski et al. 1967, Herreid and Kessel 1967) so this effect should be eliminated by expressing the values of C in $\text{cal}(\text{g}^{0.49}\cdot\text{hr}\cdot^{\circ}\text{C})^{-1}$. The values for the Ring-billed and Laughing gull chicks then become 4.72 – 5.75 and $5.25\text{ cal}(\text{g}^{0.49}\cdot\text{hr}\cdot^{\circ}\text{C})^{-1}$ respectively. The similarity of the values for these chicks is surprising, since the young Ring-billed Gulls evidently possess a thicker coating of down than that reported for the Laughing Gulls (Dawson et al. 1972).

Metabolic level. Koskimies (1962), Koskimies and Lahti (1964), and Drent (1967) considered levels of metabolism of various precocial and semi-precocial hatchlings in relation to BMR's anticipated for adult birds of corresponding size. Their studies were directed toward determination of the extent to which limitations of thermoregulatory capacity evident in these chicks might be associated with low metabolic levels. The allometric equation (Brody and Procter 1932) employed by the authors mentioned above to calculate BMR's for adults has been superseded first by those of Lasiewski and Dawson (1967), which recognized the difference in meta-

TABLE 2. Basal metabolic rates (BMR) of hatchlings as percentages of values predicted for adult birds of comparable size.

Species	Body mass ^c (g)	BMR (ml O ₂ ·g ⁻¹ ·hr ⁻¹)	BMR as percentage of adult value ^a			Reference
			L-D	A-P _α	A-P _ρ	
Ducks						
<i>Anas crecca</i>	16.8	1.71	81	(71)	(90)	Koskimies and Lahti (1964)
<i>Anas penelope</i>	26.4	1.59	85	(75)	(95)	
<i>Anas platyrhynchos</i>	28.8	1.18	65	(57)	(72)	
<i>Aythya ferina</i>	40.1	1.33	81	(70)	(88)	
<i>Aythya fuligula</i>	34.1	1.33	77	(67)	(85)	
<i>Bucephala clangula</i>	32.4	1.58	90	(79)	(99)	
<i>Melanitta fusca</i>	54.7	1.33	88	(76)	(96)	
<i>Mergus merganser</i>	46.2	1.24	78	(68)	(86)	
<i>Mergus serrator</i>	44.2	1.23	76	(67)	(84)	
<i>Somateria molissima</i>	61.4	1.25	85	(74)	(93)	
Gallinaceous birds						
<i>Gallus gallus</i>	33	1.15	(66)	(58)	72	Koskimies (1962)
<i>Lophortyx californica</i>	7	0.96	(36)	(32)	40	
<i>Phasianus colchicus</i>	17	0.90	(43)	(38)	48	
Gulls						
<i>Larus argentatus</i>						
(day)	57.4	1.38	(92)	80	(101)	Drent (1967)
(night)	59.1	1.06	(71)	(62)	78	
<i>Larus atricilla</i>	28.4	1.99	(109)	96	(121)	Dawson et al. (1972)
<i>Larus delawarensis</i>	34.6	1.62 ^b	(94)	82	103	
<i>Larus glaucescens</i>	60.3	1.22	(82)	(72)	90	Drent (1967)
<i>Larus ridibundus</i>	26.8	2.27	123	(108)	(135)	Palokangas and Hissa (1971)
Alcids						
<i>Cephus columba</i>	37.5	1.48	(88)	(77)	97	Drent (1967)

^a Values for adults predicted from the Lasiewski-Dawson (L-D) equation for non-passerine birds (Lasiewski and Dawson 1967) and from the Aschoff and Pohl equations for non-passerines in the active (α) and resting (ρ) portions of their daily cycle (Aschoff and Pohl 1970). The most pertinent percentage for each species, depending on whether the birds were measured during the day (A-P_α) at night (A-P_ρ), or at an unspecified time (L-D), is not enclosed in parentheses.

^b The basal metabolic rate of hatchling Ring-billed Gulls did not differ significantly between day and night. The value presented is the mean of both diurnal and nocturnal BMR's.

bolic levels between passerine and non-passerine birds, and then by those of Aschoff and Pohl (1970), which differentiated between the metabolic levels associated with the active and quiescent phases of the daily cycles of these animals. It now seems appropriate to consider the BMR of the Ring-billed Gull chicks, utilizing these newer equations for definition of adult metabolic levels. As indicated in table 2, the "basal" rate for our hatchlings is quite close to the value predicted for an adult non-passerine of comparable size. The heart and breathing rates of these birds at Ta's near 35°C are also close to values anticipated for adult birds of comparable size from the equations developed by Calder (1968): 337 beats/min observed vs 338 beats/min predicted and 47 breaths/min observed vs 49 breaths/min predicted.

Observed and predicted values of basal metabolism for a number of other precocial and semi-precocial birds are included in table 2. The BMR's of other hatchling gulls are generally close to the most appropriate values

predicted for adults. This is also the case in hatchling Pigeon Guillemots (*Cephus columba*). The BMR's of various ducklings represent 65-90% of values predicted for adults with the most relevant equation. The rates for hatchlings of gallinaceous birds represent an even smaller proportion, ranging from 40-72% of predicted values. Thus, conspicuous interordinal differences appear to exist in relative levels of BMR. We are uncertain about the importance of these differences to the cold defense of the young birds. The gallinaceous chicks seem most limited in their capacities for maintaining high Tb's at cool Ta's (Koskimies 1962). However, the ducklings, which are intermediate in level of BMR are more cold-hardy than gull chicks (Koskimies and Lahti 1964).

Thermogenic capacities. The abilities of hatchling gulls to remain homeothermic at cool and moderate Ta's is intimately linked with their abilities to increase the rate of heat production. As noted previously, hatchling Ring-billed Gulls could increase VO₂ from

the basal level of $1.6 \text{ ml (g}\cdot\text{hr)}^{-1}$ to $3.3 \text{ ml (g}\cdot\text{hr)}^{-1}$, values that differ by a factor of 2.1. This performance resembles that of hatchling Black-headed Gulls (*Larus ridibundus*) after their first feeding (Keskpaik and Davydov 1966). Both of these species surpass hatchling Laughing Gulls in this respect. This latter species could only increase VO_2 by a factor of 1.5 (Dawson et al. 1972). The thermogenic capacities of various hatchling ducks greatly exceed those of gulls, the former being able to increase VO_2 in the cold to at least 2.4 to 5.2 times standard levels (Koskimies and Lahti 1964). The superiority of the ducklings over the gull chicks is further indicated by the fact that hatchling Mallards (*Anas platyrhynchos*) and Lesser Scaups (*Aythya affinis*), which are similar in size to the hatchling gulls on which information is available, can attain peak VO_2 's of 6.1 and $7.0 \text{ ml (g}\cdot\text{hr)}^{-1}$, respectively (Untergasser and Hayward 1972). None of the hatchling gulls has been found to reach rates higher than $4.0 \text{ ml O}_2(\text{g}\cdot\text{hr)}^{-1}$ (Keskpaik and Davydov 1966, Palokangas and Hissa 1971, Dawson et al. 1972, this study). It would be of considerable interest to determine the functional basis of this difference in thermogenic capacity. Such a determination would be facilitated by procurement of information of the type we have presented for the Ring-billed Gull chicks on myoglobin concentrations, muscle mass, and EMG activity. We suspect that the relatively limited capacities of these gull chicks for augmenting heat production are linked with the small mass of their muscles on the day of hatching and with the fact that aerobic metabolic capacities of these muscles are not highly developed, judging by the low myoglobin concentrations observed.

Whether young gulls or, indeed, any birds, rely to any extent on non-shivering thermogenesis has not been resolved. Pharmacologic evidence for such a process has been obtained in the Skua (*Catharacta skua*). Injecting propranolol, a beta-adrenergic blocking agent, impairs thermoregulation in 1- and 3-day-old Skua chicks, an effect that is reduced if the beta-activating amine, isoproterenol, is administered (Murrish and Guard 1973). Non-shivering thermogenesis, if it exists in gulls, appears neither to be mediated by catecholamines nor to involve brown fat (Palokangas and Hissa 1971). Shivering apparently constitutes the primary mode of thermogenesis by gull chicks in the cold. The leg musculature of hatchlings appears particularly important in this, owing to its relatively large mass. We were impressed by the fact that

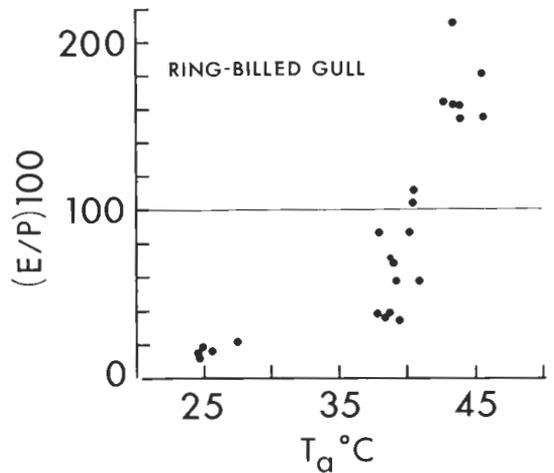


FIGURE 7. Ratios of evaporative cooling (E) to heat production (P) at various ambient temperatures (T_a) in hatchling Ring-billed Gulls (based on data from figs. 1 and 5). Values of 4.8 cal/ml O_2 and $0.58 \text{ cal/mg H}_2\text{O}$ were used to convert data on metabolism and water loss to calories.

it was the first site of visible shivering in chicks recovering from hypothermia (fig. 3), with activity commencing at a T_b of 20°C . Shivering in the pectoral musculature commenced only after rewarming was well underway and T_b had reached 26°C . The threshold for the reinitiation of leg shivering, 20°C , appears to set the lower bound of T_a for arousal of hatchlings in environments where radiant heating is not a significant factor. Ambient temperatures above 20°C were not recorded at the Rogers City colony during any of our observation periods. Recovery of chicks from hypothermia there apparently would require parental assistance or solar radiation.

Evaporative cooling. The availability of simultaneous values for VO_2 (fig. 1) and \dot{m}_{we} (fig. 4) allows determination of the effectiveness of the capacities of hatchling Ring-billed Gulls for evaporative cooling. Ratios of evaporative cooling to heat production at various T_a 's are shown in figure 7. They rise from approximately 15% at 25°C to more than 150% at T_a 's of 42° – 45.6°C . As would be anticipated with ratios in excess of 100%, the hatchlings can remain cooler than their surroundings at high T_a 's, when intense radiant heating is not a problem. In nature this cooling capacity is probably more important in allowing the chicks to cope with solar radiation than with high air temperatures, judging from weather records for the Rogers City area and our field observations in the colony. We were impressed by the

rapidity with which these young gulls commenced panting when exposed to direct solar radiation, even though the Rogers City colony has a cool to moderate climate in late spring by most standard indices.

Rates of \dot{m}_{we} by hatchling Ring-billed Gulls at Ta's of 42.7°–45.6°C average 28.0 mg (g·hr)⁻¹. This is close to the mean of 26.6 mg (g·hr)⁻¹ noted for hatchling Laughing Gulls near 45°C (Dawson et al. 1972). The ratio of calories evaporated to calories produced at 44.5°C ± 1°C averaged higher in the Ring-billed than in the Laughing gulls (168% vs 131% with the number of birds tested being five for each species), but the difference is not statistically significant ($P > 0.2$).

The relatively vigorous heat defense evident in hatchling gulls is reminiscent of that demonstrated in a variety of altricial and precocial chicks (Dawson and Hudson 1970). Evidently, priority is given to the development of heat defenses in the ontogeny of avian thermoregulation. Perhaps this is not too surprising, given the tolerance of markedly reduced body temperatures by most young birds and the narrowness of the thermal band separating temperatures of brooded young and the upper lethal levels characterizing birds (Dawson and Hudson 1970).

Comparisons of thermoregulatory characteristics of hatchling gulls. We began our study to further comparisons of thermoregulatory parameters in hatchlings of gulls breeding in different climates. Our data indicate that these young birds possess vigorous powers of heat defense that could be important for species breeding at mid and high latitudes. Solar radiation can stress chicks even in areas characterized by cool temperatures during the breeding season. Comparisons of data for hatchling Ring-billed and Laughing gulls indicate similarity in thermal conductance values when allowance is made for differences in body size. Hatchling gulls all have basal rates of metabolism approaching or exceeding values anticipated for adult birds of comparable size. Thus their thermoregulatory capacities appear unhampered by low metabolic level. However, their abilities for chemical thermoregulation are limited by an inability to raise their heat production substantially above standard levels. As noted previously, hatchling Black-headed Gulls (Keskaik and Davydov 1966) and Ring-billed Gulls can attain peak metabolic rates slightly more than double their BMR's. On the other hand, hatchling Laughing Gulls can increase their metabolic rate only 1.5 times. This lesser capacity for thermogenesis is of

interest because the breeding distribution of this species, while extending as far north as Nova Scotia, mainly includes maritime localities characterized by warm to hot climates during the nesting season, e.g., the Gulf Coast of the United States, the Greater and Lesser Antilles, and the Salton Sea in southeastern California. It will be interesting to examine further the variation in thermogenic capacity among hatchling gulls, drawing on species breeding in cool, variable, and hot climates.

SUMMARY

Thermoregulatory capacities of young Ring-billed Gulls (*Larus delawarensis*) were studied within the first 24 hr after hatching. These birds controlled body temperatures (T_b) effectively over 2-hr tests conducted at single ambient temperatures (T_a) between 20° and 45.6°C. Increasing heat production constitutes an important element in this control between 20° and approximately 34°C. Metabolic rates of hatchlings at the lower temperature were approximately double those at the higher, where minimal rates for euthermic birds occurred. Electromyographic observations indicated that shivering contributes importantly to increasing heat production. The chicks also possess some capacities for controlling insulation. They additionally displayed a well-developed panting response at high T_a's, which contributed to effective evaporative cooling. Below 20°C, T_b varied directly with T_a at the end of 2-hr tests, but the birds remained at least 5°C warmer than their surroundings even when exposed to 10°C. The chicks tolerated hypothermia. Field observations indicated that hatchling Ring-billed Gulls in the absence of their parents can be exposed to either heat or cold stress on June days, depending on whether they are in the sun or shade.

Comparisons of the thermoregulatory capacities of hatchling Ring-billed Gulls with those of hatchlings of other species are presented. Among gulls, some interspecific variation seems to exist in thermogenic capacities of the chicks.

ACKNOWLEDGMENTS

This study was facilitated by use of laboratory space at The University of Michigan Biological Station provided by Frederick K. Sparrow, Director at the time. We are grateful to the United States Steel Corp. for permission to work in the Rogers City gull colony, which is located within the boundaries of the Calcite Plant. Our research was supported in part by grants from the National Science Foundation (GB-25022 to W.R.D. and GB-6269 to J.W.H.) and from the U.S. Public Health Service (GM-15889 to J.W.H. from the National Institute of General Medicine).

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