TEMPERATURE REGULATION IN NEWLY HATCHED LAUGHING GULLS (*LARUS ATRICILLA*)

WILLIAM R. DAWSON,
Department of Zoology
The University of Michigan
Ann Arbor, Michigan 48104

JACK W. HUDSON,
Section of Ecology and Systematics
Division of Biological Sciences
Cornell University
Ithaca, New York 14850

AND

RICHARD W. HILL[1]
Department of Zoology
The University of Michigan
Ann Arbor, Michigan 48104

Field studies of young gulls (Barth 1951; Bartholomew and Dawson 1952, 1954; Behle and Goates 1957) have provided information on body temperatures of these animals and on thermally significant behavior of both the chicks and their parents. However, these studies have not permitted detailed comparisons of the various species investigated, due to a lack of standardized conditions. Moreover, they have not allowed precise examination of the quantitative aspects of the thermoregulatory process, for such examination requires procedures best undertaken in the laboratory. Some of these procedures have been utilized by Keskpaik and Davydov (1966) and Palokangas and Hissa (1971) for study of thermoregulation in chicks of the Black-headed Gull (*Larus ridibundus*), and by Drent (1967) for analysis of the functional aspects of incubation in embryos and hatchlings of the Herring Gull (*Larus argentatus*). We now report our laboratory findings on newly hatched chicks of the Laughing Gull (*Larus atricilla*). This species breeds along the Atlantic Coast of North America from Florida to as far north as Nova Scotia. Its breeding distribution also includes the Bahama Islands, The Greater and Lesser Antilles, the Gulf Coast of the United States, and points off Campeche and northern Yucatán, México, and northern Venezuela. Additional nesting colonies exist along the coasts of Sinaloa and Sonora, México, and on the Salton Sea in southeastern California.

MATERIAL AND METHODS

Twenty-six chicks were obtained from the breeding colony of Laughing Gulls on South Deer Island in West Bay, Galveston County, Texas, in the first half of July 1967. At that time of year, temperatures in the Galveston area average approximately 28° C, with the daily minima and maxima generally falling between 21° and 35° C. The recorded maximum for Galveston, Texas, is approximately 39° C. July rainfall at this locality averages about 4 inches.

Marked nests in the gull colony on South Deer Island were inspected daily to obtain chicks hatched within the preceding 24 hr. At this age, these birds were covered with a dense, fur-like down ranging in thickness from approximately 3 mm on the abdomen to 8 mm on the back. They called and engaged in such activities as stretching, preening, and begging for food, but their overall motor coordination was limited. They spent most of the time between feedings sitting quietly or sleeping. Unlike older chicks, they did not leave the vicinity of the nest and avail themselves of the shelter afforded by nearby vegetation. Hatchling Laughing Gulls are brooded extensively by their parents (Bent 1921).

Birds to be studied were transferred by boat and automobile to the nearby Marine Laboratory of Texas A&M University, where our laboratory measurements were performed. This transfer required about 45 min and was completed by 10:30 CST. The chicks weighed 28.4 ± 3.7 g (mean ± SD) on arrival in the laboratory. The physiological measurements reported here were made between 13:00 and 18:00. Thus the maximum interval between hatching and measurement would be approximately 32 hr. Most of the 26 birds used in the various parts of the investigation were studied within 24 hr after hatching. They were returned to their respective nests on South Deer Island at the end of the day's measurements.

Rectal temperatures (T_{re}) were determined at the end of 2-hr metabolic experiments, using a Schultheis thermometer designed for small animal work. Ambient temperature (T_a) within the metabolism chamber was held within 0.2° C of the particular level to be studied between 13.4 and 45.2° C, and measured with thermistors used in conjunction with a Telethermometer (Yellow Springs Instruments). Temperature control was achieved by placing the chamber in a cabinet fitted with a thermostat and cooling and heating elements.

Oxygen consumption ($\dot{V}_{O_2}$) and, in some cases, evaporative water loss ($\dot{m}_{we}$) were measured in an open circuit system similar to that described by Dawson and Fisher (1969). The darkened metabolism chamber containing the chick was fashioned from a 1-gal paint can. The floor of this chamber was covered to a

---

[1] Present address: Department of Biological Sciences, University of Delaware, Newark, Delaware.

The Condor 74:177–184, 1972

depth of 1 cm with paraffin oil over which the animal rested on a wire mesh platform. In each experiment, dry air that had passed through freshly regenerated silica gel and then through new indicating Drierite (anhydrous $CaSO_4$) was metered through the system at a constant rate, generally falling between 330 and 525 ml/min (not corrected to STP) at T_a's of 13.4–34.2° C. However, two of the tests conducted near 26° C employed flow rates of 232 and 815 ml/min, respectively. At T_a's over 35° C, flow rates were increased to between 998 and 1448 ml/min to prevent a buildup of water vapor within the metabolism chamber as the chicks resorted to evaporative cooling. Calculations based on the equation of Lasiewski et al. (1966) established that the higher flow rates held the vapor pressure of water below 12 mm Hg between 44.5 and 45.2° C, where the measurements of $\dot{m}_{we}$ were performed.

$\dot{V}_{O_2}$ and, in the tests near 45° C, $\dot{m}_{we}$ were measured over the last 10–16 min of a 2-hr exposure of the chick to a given T_a. A Beckman paramagnetic oxygen analyzer (model G-2, range, 20–21% O_2), used with a Honeywell Class 15 strip chart recorder, determined the fractional concentrations of O_2 in dry, CO_2-free air entering and leaving the metabolism chamber. Ascarite served as the CO_2 absorbant. The appropriate equation of DePocas and Hart (1957) for upstream measurement of air flow was employed to calculate true $\dot{V}_{O_2}$. Total $\dot{m}_{we}$ was determined from the gain in weight of a Drierite train through which air leaving the metabolism chamber was diverted for the period of measurement. Corrections for the small amount of extraneous water vapor in the air flowing through the system were made with data obtained in blank runs at the flow rates to be employed in tests. Drierite trains were weighed with a Sartorius balance accurate to 0.3 mg.

Breathing rates were measured in a separate set of experiments. Two 40-ga constantan leads were bilaterally sutured onto the thorax of a chick. These leads were then connected to an impedance pneumograph used in conjunction with a recording oscillograph (E and M Instrument Co.). A thermistor designed for small animals was inserted into the rectum of the chick and fixed in place with an external silk suture. This bird was maintained in an open 1-gal paint can during measurements. An infrared lamp attached to a ring stand and connected to a variable transformer was positioned over this can. Temperature was controlled by adjusting the voltage supplied by the transformer to the lamp. Some radiant heat was probably absorbed by the bird. T_a was obtained from a thermistor suspended within the can and shielded from the heat source. Both this and the rectal thermistor were used with a second YSI Telethermometer. Although the arrangement for temperature control was crude, it did allow us to study breathing rate as a function of T_{re} and to estimate the T_a associated with a particular rate and T_{re}.

Twelve of the chicks brought into the laboratory were employed only in single metabolic experiments. The remaining 14 birds were used in either two such tests or in one metabolic experiment and one set of determinations of breathing rate. Precautions ensuring that the initial exposure to experimental conditions would not affect subsequent physiological performance included maintenance of these latter birds at T_a's of 26–29° C for an hour between periods of study and, in this interval, feeding them minced fish and water. The chicks were also fed at the end of the day, just prior to their return to South Deer Island.

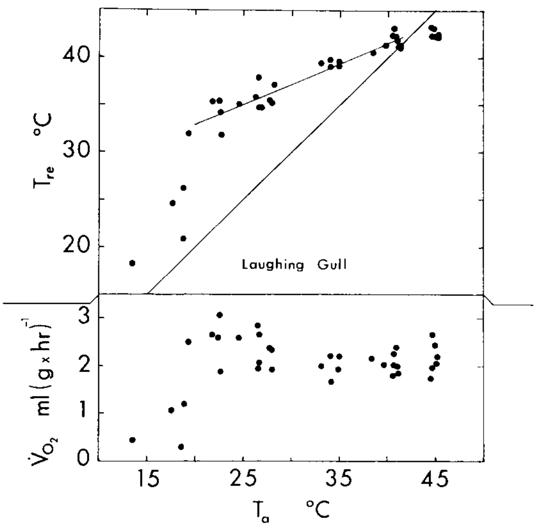

FIGURE 1. Rectal temperatures (T_{re}) and rates of oxygen consumption ($\dot{V}_{O_2}$ corrected to STPD) for 26 hatchling Laughing Gulls (*Larus atricilla*) at the end of 2-hr exposures to single ambient temperatures (T_a). The diagonal line in the upper graph marks equivalence between T_{re} and T_a.

RESULTS

T_{re} in hatchling Laughing Gulls at the completion of 2-hr experiments varied directly with T_a over the entire temperature range investigated (fig. 1). We have fitted a least squares straight line to the points for T_a's from 21.7° to 41.2° C ($T_{re} = 24.2 + 0.43\ T_a$, with temperature in degrees C; SE of slope ± 0.03). The chicks were approximately 12° C warmer than the environment at the end of 2-hr exposures to T_a's near 22° C. Below approximately 20° C, the thermoregulatory system of these animals evidently became overtaxed and T_{re} at the end of 2 hr generally lay below the levels predicted by extrapolation of the regression line (fig. 1) to cooler temperatures. However, even the chick tested at 13.4° C, the lowest T_a used in this study, showed a differential of 5° C between its body and the environment at the end of the experimental period. This bird suffered no apparent ill effects from being chilled to 18.4° C, calling weakly when removed from the metabolism chamber.

In contrast to the limited control of T_{re} evident in hatchling Laughling Gulls at T_a's below 20° C, relatively effective capacities for thermoregulation were present in these birds at the upper end of the range of ambient temperatures used in this study. Indeed, the six chicks tested at 44.5–45.2° C had T_{re}'s averaging 2.3° C less than T_a at the end of the 2-hr test periods (fig. 1).

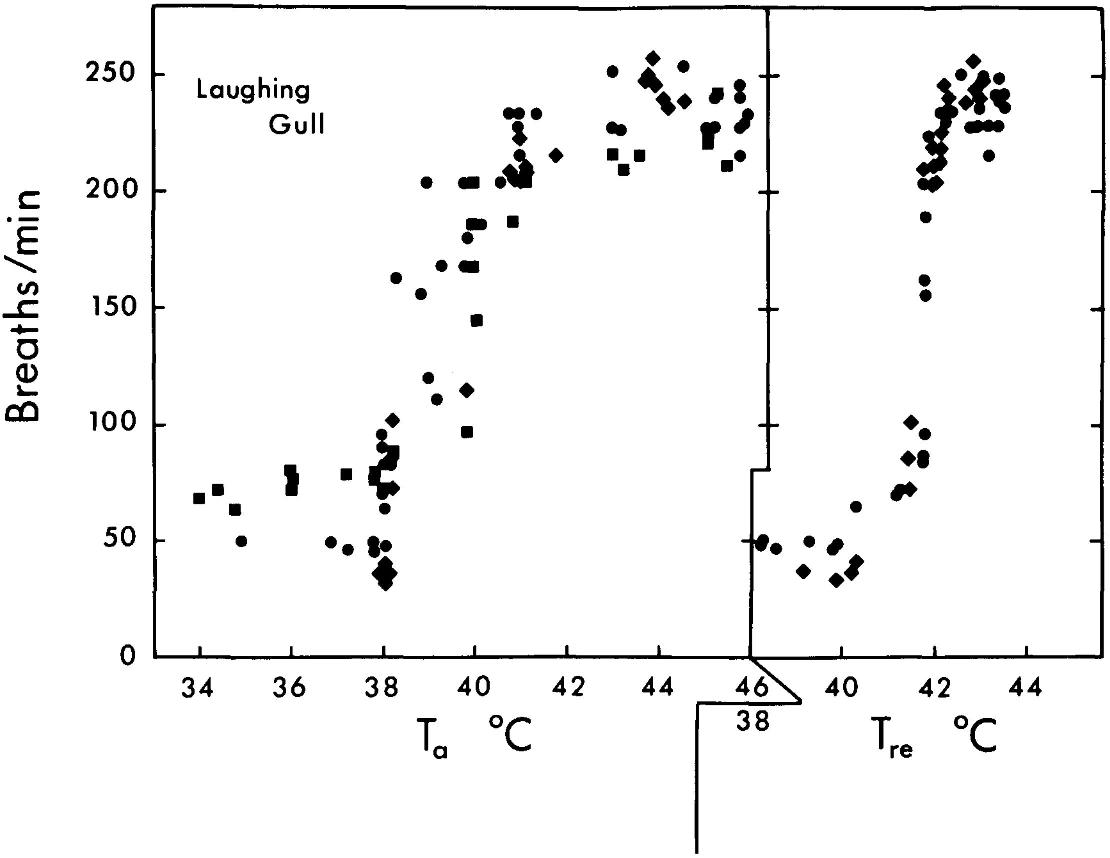

FIGURE 2. Breathing rates for three hatchling Laughing Gulls (*Larus atricilla*) in relation to ambient temperature (T_a) and rectal temperature (T_{re}) in the lefthand and righthand graphs, respectively. The three hatchlings are identified by circles, squares, and diamonds, respectively.

Values of $\dot{V}_{O_2}$ for hatchling Laughing Gulls in the final portions of 2-hr exposures to individual T_a's are presented in figure 1. A metabolism-temperature relation of the same general form as those characterizing adult homeotherms is apparent between approximately 20° and 45° C. In this range, $\dot{V}_{O_2}$ reaches a minimum at approximately 34° C. The mean for the five values obtained near this T_a is 1.99 ml O_2 $(g \cdot hr)^{-1}$. The $\dot{V}_{O_2}$'s of the hatchling gulls tended to increase with decreasing T_a between 30° and 20° C. However, the maximum values observed were only 1.5 times the mean of the values obtained near 34° C. As noted in the comments on T_{re}, our young Laughing Gulls tended to become markedly hypothermic during 2-hr exposures to T_a's below 20° C. $\dot{V}_{O_2}$'s associated with this hypothermia were two-thirds or less of the values observed in the vicinity of 34° C (fig. 1).

The least squares regression line relating $\dot{V}_{O_2}$ of young Laughing Gulls to T_a above 34° C has a slope that does not differ significantly from zero ($P > 0.05$). Our inability to demonstrate any direct thermal dependence in the metabolism of hatchlings at high T_a's is noteworthy in view of the vigorous evaporative cooling that they initiate in the heat. Such cooling involves a conspicuous rise in breathing rate (fig. 2). This occurs at T_a's between 37° and 41° C; breathing rates below and above this interval falling between 58–85 cycles/min and 215–260 cycles/min, respectively. The transition is even more abrupt if this respiratory function is considered in relation to T_{re} (fig. 2).

The six values of $\dot{m}_{we}$ obtained for hatchling Laughing Gulls at 44.5–45.2° C (T_a) averaged 26.6 mg H_2O $(g \cdot hr)^{-1}$ (range, 19.9–33.6 $mg \cdot g^{-1} \cdot hr^{-1}$). This mean value is about 10 times that obtained for one chick of this species at 26.6° C, 2.5 mg $(g \cdot hr)^{-1}$, and 6 times the rate anticipated at 25° C for a 28-g adult bird, on the basis of the equation relating $\dot{m}_{we}$ to body weight in nonpasserines (Crawford and Lasiewski 1968).

DISCUSSION

The acquisition of information on metabolism and body temperature of newly hatched Laughing Gulls under controlled conditions permits a more detailed analysis of the thermoregulatory abilities of these birds than has generally been possible in field studies of colonially nesting seabirds. However, we want to emphasize that this analysis is meant to supplement, not supplant, field studies. We hope that it will ultimately facilitate interpretation of the full thermal significance of various aspects of the behavior of parents and young.

BODY TEMPERATURE AND METABOLISM

The T_{re}'s obtained for hatchling Laughing Gulls at the end of the 2-hr metabolic experiments conducted at T_a's between 20° and 40° C generally fall below levels noted for adult gulls (see Neumann et al. 1968). This difference probably disappears in the initial weeks after hatching, for Palokangas and Hissa (1971) noted a rise in body temperature from 39.3° to 40.8° C between 0 and 20–27 days after hatching in young Black-headed Gulls tested at thermoneutrality. The hypothermia observed in Laughing Gull chicks in experiments carried out between 13.4° and 20° C is conspicuous, but it would not appear to constitute much of a hazard for birds hatched in the South Deer Island gull colony, even if they were less tolerant of reduced body temperatures than they appear to be. Temperatures on this island are usually mild to warm when the eggs of Laughing Gulls hatch. This and the protection the chicks receive from brooding by their parents, from huddling with their siblings, and from the insulation of the nest probably allow a greater independence of T_{re} from T_a than was evident in our laboratory tests. This view is supported by results of field studies on young gulls of other species (Barth 1951; Bartholomew and Dawson 1952, 1954; Behle and Goates 1957).

Newly hatched Laughing Gulls resemble Black-headed Gulls of similar age in undergoing a decline of body temperature with decreasing T_a in laboratory tests. However, the extent of this decline at T_a's between 35° and 15° C is less than in our birds, if the performance of the young Black-headed Gulls after their first feeding (the condition most comparable to that of our chicks) is considered. It should be noted that chicks of this latter species were exposed to test temperatures for 1-hr periods, rather than the 2-hr periods used in our study. Therefore it is unclear whether the apparent disparity in thermoregulatory capacities between chicks of the two kinds of gulls reflects differences in experimental conditions or physiology.

Hatchling Laughing Gulls compare favorably with adult birds of several species in their ability to maintain T_{re} below T_a in tests at approximately 45° C (see Lasiewski et al. 1966). It will be of interest to analyze the quantitative aspects of the heat defense for hatchlings in other species of gulls and terns. Field observations of such animals (e.g., Barth 1951; Howell 1959; Howell and Bartholomew 1962; Drent 1967) indicate the presence of capacities for augmenting evaporation. However, these do not appear to eliminate an extensive dependence of very young gulls and terns on their parents for shade from the sun (e.g., Barth 1951; Howell and Bartholomew 1962).

We have taken the $\dot{V}_{O_2}$'s of the hatchling Laughing Gulls at 34° C (T_a) to represent standard metabolic rate (SMR). The average value, 1.99 ml O_2 $(g \cdot hr)^{-1}$, corresponds to 110% of the SMR predicted from the relevant equation of Lasiewski and Dawson (1967), for an adult nonpasserine weighing 28 g (the approximate weight of the gull chicks). Comparable metabolic values for hatchling gulls of other species [Herring Gull (Drent 1967), Glaucous-winged Gull, *Larus glaucescens* (Drent 1967); Black-headed Gull (Keskpaik and Davydov 1966)] comprise 72% to 94% of the respective levels of SMR predicted from the Lasiewski-Dawson equation for adult nonpasserines of corresponding weight. Both nocturnal and diurnal values are available for young Herring Gulls (Drent 1967). The fact that the latter exceed the former by approximately 20% suggests the existence of a circadian oscillation in metabolism of young gulls, which parallels the situation in many adult birds (see Aschoff and Pohl 1970).

The rise of $\dot{V}_{O_2}$'s of the hatchling Laughing Gulls with decreasing T_a between 30° and 20° C probably involved shivering, for Keskpaik and Davydov's (1966) electromyographic observations on young Black-headed Gulls indicate the participation of the leg muscles and, later on the first day after hatching, the pectoral muscles in this activity. Some recent studies of chicks of the domestic fowl (see Freeman 1967, 1970; Wekstein and Zolman 1968, 1969) suggest that a form of nonshivering thermogenesis may exist in these young birds. Whether or not such a mechanism is involved in the chemical thermoregulation of young gulls remains to be determined. Palokangas and Hissa (1971) found that injections of catecholamines and thyroxin failed to stimulate the metabolism of chicks of the Black-headed Gull. However, administration of corticosterone produced a 15% rise in their oxygen consumption within 20 min. Whatever the sources of augmented heat production in hatchling Laughing Gulls, the thermogenic capacities of these birds are very limited in comparison with those of various adult birds, which can respond to cold by maintaining metabolic rates three to five times their respective SMR's for many hours (Scholander et al. 1950; Dawson and Hudson 1970). Thermogenic capacities of hatchling Black-headed Gulls also appear limited, maximal metabolic rates exceeding ones at 35° C by factors of 1.6 and 2.2 in dry chicks before and after the first feeding, respectively (Keskpaik and Davydov 1966).

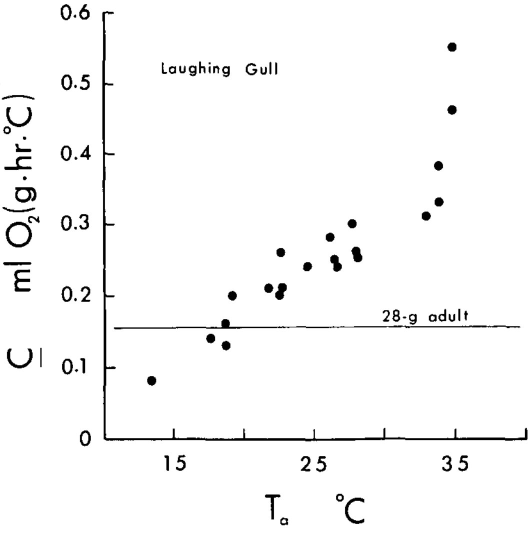

FIGURE 3. Thermal conductance (*C*) of 14 hatchling Laughing Gulls (*Larus atricilla*) in relation to ambient temperature (T_a). The horizontal line in the graph indicates the minimal value of *C* anticipated for an adult bird of similar weight (28 g), on the basis of the equation of Lasiewski et al. (1967). (See text for method of calculation of the values of *C* for the hatchlings.)

THERMAL CONDUCTANCE

With simultaneous values for $\dot{V}_{O_2}$, T_{re}, and T_a, the ability of hatchling Laughing Gulls to adjust whole-body conductance, i.e., thermal conductance between the body core and the environment, can be estimated. This estimate is based on the following equation: $C = \dot{V}_{O_2} \cdot (T_{re} - T_a)^{-1}$, where *C* is conductance and T_{re} and T_a are measured in degrees C. This equation differs from more rigorous ones (see King and Farner 1964; Coulombe 1970), but it is adequate for our purposes. The reciprocal of the conductance obtained from the equation presented here has been used as an index of overall insulation in small birds and mammals (e.g., West 1962; Musser and Shoemaker 1965; West and Hart 1966). Between 13.4° and 35° C, the range of T_a to which we have confined the analysis, the thermal conductance of our hatchling gulls varied directly with T_a (fig. 3). This occurred despite the birds' initiating some chemical thermoregulation between 30° and 20° C and becoming markedly hypothermic below 20° C. Such a pattern contrasts with the typical situation in adult birds, in which conductance reaches a minimum at a T_a coincident with or slightly below the T_a at which chemical thermoregulation is initiated (e.g., West 1962; Coulombe 1970). The continued decline in the conductance of the young Laughing Gulls with decreasing T_a is sufficient over the range studied so that the lowest values obtained actually fall below the minimal level anticipated for adult birds weighing 28 g (Lasiewski et al. 1967). We believe that this situation primarily reflects the physiological consequences of the marked hypothermia developing in the hatchlings at moderate to cool T_a's (fig. 1). The drop of T_{re} should be accompanied by decreases in breathing and other bodily movements, in peripheral circulation, and in evaporative water loss, all of which should curtail thermolysis under the conditions with which we are concerned.

Even if the probable effects of hypothermia on conductance are ignored, the indicated level of insulation in hatchling Laughing Gulls is still in the same range as that found in adult birds weighing approximately 28 g (see Lasiewski et al. 1967). It thus appears that the limited extent and manner of use of the capacities for thermogenesis are most directly responsible for such inadequacies of thermoregulatory performance as are apparent in these chicks at the cooler T_a's investigated.

HEAT DEFENSE

The four- to fivefold increase of breathing rate noted in hatchling Laughing Gulls during exposure to high T_a's (fig. 2) is the most conspicuous manifestation of their heat defense. The pattern of thermal dependence involving a transition of breathing rate from a relatively low to a relatively high level over a narrow band of temperature has been noted in several other birds: e.g., the Ostrich, *Struthio camelus* (Crawford and Schmidt-Nielsen 1967); Rock Dove, *Columba livia* (Calder and Schmidt-

Nielsen 1967); Roadrunner, *Geococcyx californianus* (Calder and Schmidt-Nielsen 1967); Brown Pelican, *Pelecanus occidentalis* (Bartholomew et al. 1968); Barn Owl, *Tyto alba* (Bartholomew et al. 1968); and Burrowing Owl, *Speotyto cunicularia* (Coulombe 1970).

Our failure to detect a rise in $\dot{V}_{O_2}$ at high T_a's (fig. 1) suggests that the panting of hatchling Laughing Gulls must be very economical from a metabolic standpoint. Low energy requirements for augmenting respiratory evaporation have hitherto been noted principally in caprimulgiform birds (Bartholomew et al. 1962; Lasiewski and Dawson 1964; Dawson and Fisher 1969; Lasiewski 1969; Lasiewski et al. 1970), most of which employ gular fluttering as a primary feature of their heat defense. We did not detect gular fluttering in our chicks. However, Calder and Schmidt-Nielsen (1968) list gulls (presumably adults) among birds that employ this mechanism in response to heat loads. Drent (1967) also believes that adult Herring Gulls utilize gular fluttering as well as panting in heat defense.

The marked augmentation of evaporative water loss by hatchling Laughing Gulls in combination with a low energetic cost for panting allowed them to dissipate an average of 131% (range of six values, 108–168%) of their heat production at T_a's near 45° C. This ability to dissipate heat more rapidly than it was produced permitted these birds to maintain T_{re} 2.3° C below T_a at these high temperatures (fig. 1), as noted previously. The luxuriant down characterizing chicks of the Laughing Gull undoubtedly enhanced this performance by restricting heat flow from the environment. Calculations involving $\dot{V}_{O_2}$, $\dot{m}_{we}$, T_{re}, and T_a at 44.5–45.2° C place the average heat gain from the environment at 1.4 cal $(g \cdot hr\ ^\circ C)^{-1}$. This indicates a conductance in the same range as that noted for the chicks at T_a's near 34° C (fig. 3; detailed comparisons do not appear meaningful, since the equation used to estimate conductance at 44.5–45.2° C includes a term for evaporative heat dissipation whereas that used at lower T_a's does not).

In the maritime situation where our Laughing Gulls were hatched, it is unlikely that T_a ever reaches the highest level employed in our experiments. The capacities of these chicks for augmenting evaporative cooling therefore are probably more significant under natural conditions in allowing them to cope for short periods with the combination of radiant heat loads and warm T_a's that could develop with any daytime absences of the parents, than with high T_a's per se. The extent of the reliance of the chicks on evaporative cooling probably declines slightly within the first few days after hatching, as their locomotor abilities improve to the point where such shelter as is available can be reached and utilized in the manner described for young Western Gulls, *Larus occidentalis* (Bartholomew and Dawson 1954).

VARIATION IN THERMOREGULATORY CAPACITIES OF YOUNG PRECOCIAL BIRDS

Considerably more variation in thermoregulatory capacities exists among birds at hatching than is implied by the convention of classifying species alternatively as "precocial" or "altricial." This is considered in detail by King and Farner (1961). The variation must partially reflect interordinal differences in developmental patterns. Thus, among nominally precocial birds, newly hatched ducklings can regulate body temperature more effectively in the cold than either gallinaceous birds or gulls of comparable age (Koskimies 1962; Koskimies and Lahti 1964). However, some variation in thermoregulatory capacities in the cold also exist among hatchlings within the same order. In one case this appears correlated with differences in distribution of the species considered; hatchlings of ducks breeding at higher latitudes having better control of body temperature at cool T_a's than those of ducks breeding at somewhat lower latitudes (Koskimies and Lahti 1964). Variation of this type is of considerable interest, for it occurs at what appears to be a particularly vulnerable stage in the life of birds.

Some differences in thermoregulatory capacities seem to exist among young gulls. Thus the young of certain species appear to resist cooling more effectively than those of others (Rol'nik 1948; Koskimies and Lahti 1964). In certain instances this may reflect differences in body size among the birds considered. In other cases the actual factors responsible are unknown. It would be interesting to determine whether or not any of the variation in thermoregulatory capacities that may exist in hatchling gulls under standardized conditions is correlated with the breeding distributions of the species considered. The genus *Larus* alone is represented by species whose breeding ranges collectively embrace a span of latitude extending from the Arctic to the sub-Antarctic (Peters 1934).

SUMMARY

The thermoregulatory capacities of young Laughing Gulls (*Larus atricilla*) were studied

within the first 32 hr after hatching. These birds had moderately effective temperature control, rectal temperature declining 0.43° C for each 1° C lowering of ambient temperature, on the basis of 2-hr tests conducted at constant temperatures between 21.7° and 41.2° C. The decline in rectal temperature was much more conspicuous in similar tests carried out below 20° C. The chicks were quite effective in their thermoregulation at high ambient temperatures, remaining an average of 2.3° C cooler than their surroundings during 2-hr exposures to 44.5–45.2° C. Oxygen consumption varied with ambient temperature between 22° and 45° C in a manner reminiscent of that observed in adult birds. However, the maximum rates observed at cooler T_a's were only about 1.5 times the ones noted near 34° C, the ambient temperature near which the minimal rates for homeothermic individuals occurred. These minimal rates slightly exceeded the level anticipated for an adult nonpasserine bird of the same weight as the chicks (28 g). Minimal values for thermal conductance in these chicks matched or fell below that predicted for a 28-g adult bird. Oxygen consumption decreased conspicuously as the young gulls became markedly hypothermic in the course of 2-hr exposures to ambient temperatures below 20° C.

Hatchling Laughing Gulls greatly increased breathing rate when exposed to high ambient temperatures, changing from 58–85 cycles/min below 37° C to 215–260 cycles/min above 41° C. This increase was achieved without any significant rise in the rate of oxygen consumption. Hatchling Laughing Gulls displayed effective evaporative cooling near 45° C, dissipating 131% of their heat production by this means.

ACKNOWLEDGMENTS

This investigation could not have been undertaken without the laboratory facilities made available to us at The Marine Laboratory of Texas A&M University by Sammy M. Ray, Director. We also wish to acknowledge the generous assistance we received in our field work from Harold W. Harry of that laboratory. Our research was supported in part by grants from the National Science Foundation (GB-1455 to W. R. D., and GB-6269 to J. W. H.) and from the U.S. Public Health Service (NIH Grant 11368 to J. W. H.).

LITERATURE CITED

Aschoff, J., and H. Pohl. 1970. Rhythmic variations in energy metabolism. Fed. Proc. 29:1541–1552.

Barth, E. K. 1951. Kroppstemperatur hos måkeunger. Nytt. Mag. Naturvidenskapene 88:213–245.

Bartholomew, G. A., and W. R. Dawson. 1952. Body temperatures in nestling Western Gulls. Condor 54:58–60.

Bartholomew, G. A., and W. R. Dawson. 1954. Temperature regulation in young pelicans, herons, and gulls. Ecology 35:466–472.

Bartholomew, G. A., J. W. Hudson, and T. R. Howell. 1962. Body temperature, oxygen consumption, evaporative water loss, and heart rate in the Poor-will. Condor 64:117–125.

Bartholomew, G. A., R. C. Lasiewski, and E. C. Crawford, Jr. 1968. Patterns of panting and gular flutter in cormorants, pelicans, owls, and doves. Condor 70:31–34.

Behle, W. H., and W. A. Goates. 1957. Breeding biology of the California Gull. Condor 59:235–246.

Bent, A. C. 1921. Life histories of North American gulls and terns. U.S. Nat. Mus. Bull. 113.

Brody, S., and R. C. Proctor. 1932. Growth and development, with special reference to domestic animals. XXIII. Relation between basal metabolism and mature body weight in different species of mammals and birds. Missouri Univ. Agr. Exp. Sta. Res. Bull. No. 166:89–101.

Calder, W. A., and K. Schmidt-Nielsen. 1967. Temperature regulation and evaporation in the pigeon and the Roadrunner. Amer. J. Physiol. 213:883–889.

Calder, W. A., and K. Schmidt-Nielsen. 1968. Panting and blood carbon dioxide in birds. Amer. J. Physiol. 215:477–482.

Coulombe, H. N. 1970. Physiological and physical aspects of temperature regulation in the Burrowing Owl, *Speotyto cunicularia*. Comp. Biochem. Physiol. 35:307–337.

Crawford, E. C., Jr., and R. C. Lasiewski. 1968. Oxygen consumption and respiratory evaporation of the Emu and Rhea. Condor 70:333–339.

Crawford, E. C., Jr., and K. Schmidt-Nielsen. 1967. Temperature regulation and evaporative cooling in the Ostrich. Amer. J. Physiol. 212:347–353.

Dawson, W. R., and C. D. Fisher. 1969. Responses to temperature by the Spotted Nightjar (*Eurostopodus guttatus*). Condor 71:49–53.

Dawson, W. R., and J. W. Hudson. 1970. Birds. p. 223–310. *In* G. C. Whittow [ed.] Comparative physiology of thermoregulation. Vol. I. Academic Press, New York.

DePocas, F., and J. S. Hart. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag, closed circuit apparatus J. Appl. Physiol. 10:388–392.

Drent, R. H. 1967. Functional aspects of incubation in the Herring Gull (*Larus argentatus* Pont.). E. J. Brill, Leiden.

Freeman, B. M. 1967. Some effects of cold on the metabolism of the fowl during the perinatal period. Comp. Biochem. Physiol. 20:179–193.

Freeman, B. M. 1970. Thermoregulatory mechanisms of the neonate fowl. Comp. Biochem. Physiol. 33:219–230.

Howell, T. R. 1959. A field study of temperature regulation in young Least Terns and Common Nighthawks. Wilson Bull. 71:19–32.

Howell, T. R., and G. A. Bartholomew. 1962. Temperature regulation in the Sooty Tern *Sterna fuscata*. Ibis 104:98–105.

KESKPAIK, J., AND A. DAVYDOV. 1966. Factors determining the cold-hardiness of the *Larus ridibundus* L. on the first day after hatching. Toimetised Eesti NSV Teaduste Akadeemia XV, Biol. Seeria Nr. 4:485–491 [in Russian with English summary].

KING, J. R., AND D. S. FARNER. 1961. Energy metabolism, thermoregulation and body temperature, p. 215–288. *In* A. J. Marshall [ed.] Biology and comparative physiology of birds. Vol. II. Academic Press, New York.

KING, J. R., AND D. S. FARNER. 1964. Terrestrial animals in humid heat: birds, p. 603–624. *In* D. B. Dill [ed.] Handbook of physiology, Section 4: Adaptation to the environment. American Physiological Society, Washington, D.C.

KOSKIMIES, J. 1962. Ontogeny of thermoregulation and energy metabolism in some gallinaceous birds. Ric. Zool. Appl. Caccia Suppl. 4:149–160.

KOSKIMIES, J., AND L. LAHTI. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. Auk 81:281–307.

LASIEWSKI, R. C. 1969. Physiological responses to heat stress in the Poorwill. Amer. J. Physiol. 217: 1504–1509.

LASIEWSKI, R. C., A. L. ACOSTA, AND M. H. BERNSTEIN. 1966. Evaporative water loss in birds—I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. Comp. Biochem. Physiol. 19: 445–457.

LASIEWSKI, R. C., AND W. R. DAWSON. 1964. Physiological responses to temperature in the Common Nighthawk. Condor 66:477–490.

LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A reexamination of the relation between standard metabolic rate and body weight in birds. Condor 69:13–23.

LASIEWSKI, R. C., W. R. DAWSON, AND G. A. BARTHOLOMEW. 1970. Temperature regulation in the Little Papuan Frogmouth, *Podargus ocellatus*. Condor 72:332–338.

LASIEWSKI, R. C., W. W. WEATHERS, AND M. H. BERNSTEIN. 1967. Physiological responses of the Giant Hummingbird, *Patagona gigas*. Comp. Biochem. Physiol. 23:797–813.

MUSSER, G. G., AND V. H. SHOEMAKER. 1965. Oxygen consumption and body temperature in relation to ambient temperature in the deer mice, *Peromyscus thomasi* and *P. megalops*. Occas. Pap. Mus. Zool. Univ. Mich. 643:1–15.

NEUMANN, R. L., J. W. HUDSON, AND R. J. HOCK. 1968. Body temperatures, birds. Table 59, Part II, p. 334–343. *In* P. L. Altman and D. S. Dittmer [eds.] Metabolism. Fed. Amer. Soc. Exp. Biol., Bethesda, Md.

PALOKANGAS, R., AND R. HISSA. 1971. Thermoregulation in young black-headed gull (*Larus ridibundus* L.). Comp. Biochem Physiol. 38A:743–750.

PETERS, J. L. 1934. Check-list of birds of the world, Vol. II. Harvard Univ. Press, Cambridge.

ROL'NIK, V. V. 1948. Development of thermoregulation by certain northern birds. Zool. Zhur. 27:535–546 [in Russian; English translation by Translation Division, Foreign Technology Division, Wright-Patterson Air Force Base, Ohio, FTD-TT-64-783/1 + 2].

SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, AND L. IRVING. 1950. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull. 99:237–258.

WEKSTEIN, D. R., AND J. F. ZOLMAN. 1968. Sympathetic control of homeothermy in the young chick. Amer. J. Physiol. 214:908–912.

WEKSTEIN, D. R., AND J. F. ZOLMAN. 1969. Ontogeny of heat production in chicks. Fed. Proc. 28:1023–1028.

WEST, G. C. 1962. Responses and adaptations of wild birds to environmental temperaure, p. 291–333. *In* J. P. Hannon and E. Viereck [eds.] Comparative physiology of temperature regulation. Arctic Aeromedical Laboratory, Fort Wainwright, Alaska.

WEST, G. C., AND J. S. HART. 1966. Metabolic responses of Evening Grosbeaks to constant and to fluctuating temperatures. Physiol. Zool. 39: 171–184.

Accepted for publication 1 August 1971.