

THE DEVELOPMENT OF ENDOTHERMY AND EXISTENCE ENERGY EXPENDITURE IN HERRING GULL CHICKS

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The development of thermoregulation has been studied in a large number of altricial species (summarized in Dunn 1975a), but only for a few semi-precocial species (Behle and Coates 1957, Dawson et al. 1972, Palokangas and Hissa 1971, summary of others in Dunn 1976a). Of these few, only Drent (1965) and Palokangas and Hissa (1971) had any information for semi-precocial chicks older than about one week, and no one has investigated energetic costs of thermoregulation in the wild.

The present study on young Herring Gulls (*Larus argentatus*) traced thermoregulatory development throughout the growth period, in the laboratory, but also included extrapolation of this development to the natural environment, through making an estimate of natural existence energy. This included the costs of resting metabolism (separating costs in and out of the thermoneutral zone), specific dynamic action (the calorogenic effect of feeding), and minimal activity. Although crude in methodology, this is the first time such an approximation has been made for a semi-precocial species, and the results can be compared directly to those from a more detailed investigation into energetics of nesting Double-crested Cormorants (*Phalacrocorax auritus*), carried out at the same location, in the same year and with the same methods.

METHODS

A portion of a large gull colony on Appledore Island, Isles of Shoals (43°N, 70°35'W), about 16 km from Portsmouth, N.H. was studied during the 1972 breeding season. Periodic observations of known-age young from a blind covered all hours of daylight, for young up to 35 days old. Observation times totaled 228 nest hrs, or 363 chick hrs. The amounts and termination ages of brooding were noted, as well as possible thermoregulatory behavior. Nest temperatures were measured via a Rustrak Model 2133/F137 continuous temperature recorder, whose probe tip was surrounded by a small bulb of wire screening to raise it off the nest floor and to prevent measurement of body surface temperature.

Weather data, including air temperature, cloud cover and wind speed, were gathered at 4-hr intervals by the U.S. Coast Guard at a station about 2 km from the colony. Occasional wind measures taken at the colony (methods of Stong 1971) were used to compare wind speeds at chick level to those at the Coast Guard station. Daily solar radiation totals came from U.S. Department of Commerce

records for Portland, Maine, approximately 80 km from the colony.

Oxygen consumption ($\dot{V}O_2$) of chicks was measured in the laboratory with a portable Beckman F3 Oxygen Analyzer, using an open flow system. Methods are described in detail for similar experiments done on Double-crested Cormorants (Dunn 1976b). Flow rates were constant throughout each experiment, but varied from about 230–2900 ml/min, depending on the size of the bird.

A Beckman DK2A spectrophotometer with a reflectance attachment was used in estimating absorption of solar energy by downy and feathered young. Thawed sections of skin from the backs of frozen specimens were scanned, and absorption calculated as 100 minus percent reflectance.

The method for estimating energy expended on existence and thermoregulation in nature is described in detail in Dunn (1976b), and will be only briefly summarized here. All calculations were for a hypothetical chick hatched 7 June, 1970 (a typical hatch date, and a year of close to 30-year average weather; U.S. Dept. Commerce climatological data).

Temperature was assumed to remain constant for 2 hrs to either side of each Coast Guard observation. Oxygen consumption of appropriately aged chicks in the laboratory, at the temperature indicated by the Coast Guard, was then assumed to be the same as would have been shown by wild chicks during each 4-hr period.

For such extrapolation to be accurate, laboratory conditions for convection, conduction, evaporation and radiation must all be the same as in nature. Experimental "wind" speeds were negligible, while average natural wind speed at chick level was 4–5 km/hr, causing my $\dot{V}O_2$ estimates to be low. Most chicks were usually sheltered from the wind, however, so this error may be small. Conductive and evaporative heat exchanges were arbitrarily assumed to be equivalent to those in nature. Radiation conditions probably approximated those under shaded natural conditions (Dunn 1976b). Also taken into account was a 25% reduction of $\dot{V}O_2$ at night (Aschoff and Pohl 1970). $\dot{V}O_2$ was then converted to energy expenditure using a heat equivalent of 4.75 kcal/l O_2 (Ricklefs 1974). Summation over each day gives an estimate for energy expended on metabolism under shaded and sheltered conditions.

To estimate the effect of direct solar radiation on metabolism, I applied a rather complicated correction. The only data for the amount of metabolic reduction due to full exposure to radiation are for cowbirds (*Molothrus ater*, Lustick 1969). Herring Gulls exposed to the same amounts of radiation as these cowbirds were arbitrarily assumed to have the same reduction in metabolism as the cowbirds. If the radiation was less than in the cowbird experiments, the gulls were assumed to reduce their metabolism in direct proportion to the reduction of incident radiation. For a more detailed discussion of the validity and weaknesses of this estimation procedure, see Dunn (1976b).

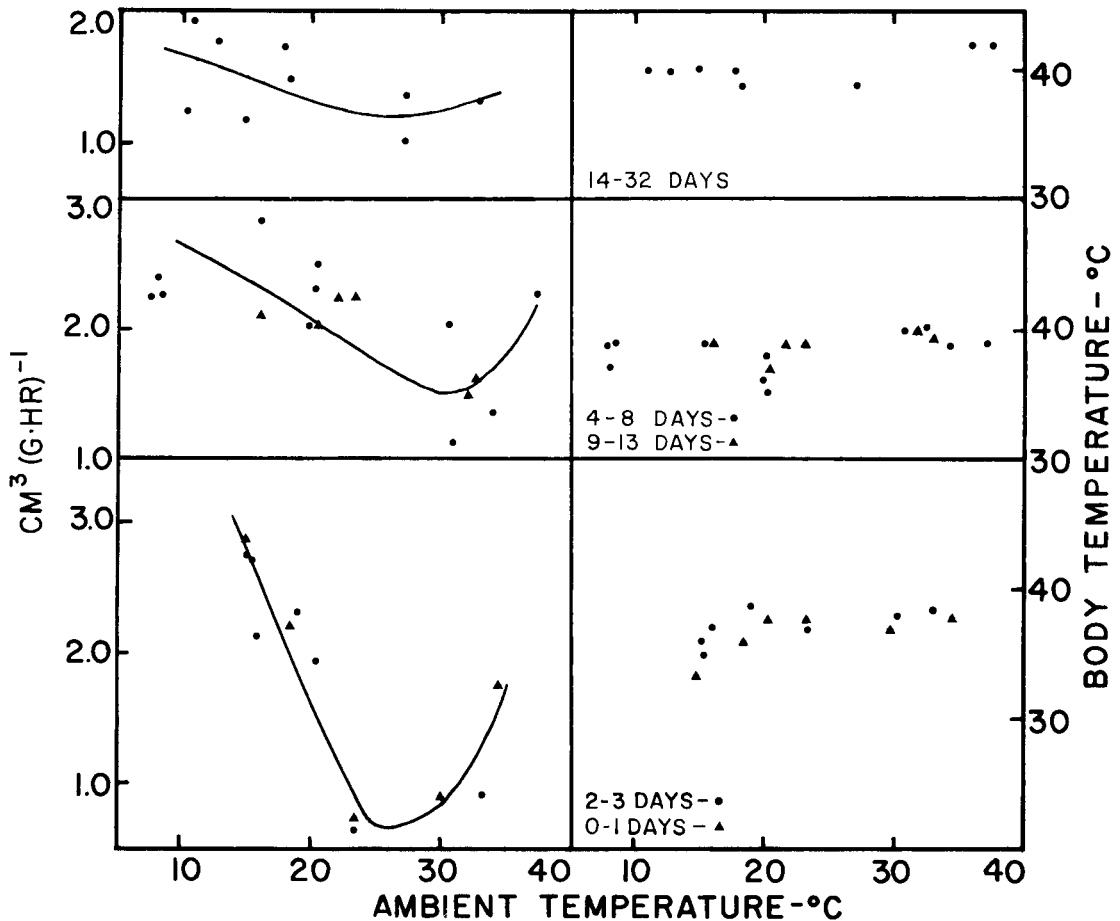


FIGURE 1. Body temperature and oxygen consumption of Herring Gull chicks after 2 hrs exposure to a constant ambient temperature. Ages at right refer also to corresponding portions of graph on left. $\dot{V}O_2$ curves were drawn through the points by eye, and used in all calculations of existence energy expenditure.

RESULTS

Figure 1 shows the results of body temperature and $\dot{V}O_2$ measurements, after 2 hrs exposure of chicks to various ambient temperatures. By one day after hatching, Herring Gull chicks can maintain homeothermic body temperatures (T_b) at ambient temperatures (T_a) above 20°C. At T_a below 20°C, chicks under 32 hrs old have poor powers of thermoregulation, as has also been shown for Laughing Gulls (*Larus atricilla*; Dawson et al. 1972). Similarly, Barth (in Farner and Serrenty 1959) noted that Mew Gulls (*L. canus*), Lesser Black-backed Gulls (*L. fuscus*), Greater Black-backed Gulls (*L. marinus*) and Herring Gulls show moderate temperature control by the end of day 0. After 3 days, control is said to be complete except under extreme conditions. Black-legged Kittiwakes (*Rissa tridactyla*), on the other hand, have a slower development of homeothermy, as do Common and Roseate

terns (*Sterna hirundo* and *S. dougallii*; LeCroy and Collins 1972). The range of thermoregulatory abilities in larids is similar to that in alcids (Dunn 1976a), less than in precocial ducklings and better than in precocial gallinaceous chicks (Koskimies and Lahti 1964).

Even though T_b of Herring Gull chicks can be effectively controlled after 3 or 4 days, the pattern of $\dot{V}O_2$ continues to change as the chicks grow, with decreasing metabolic effort being required at low T_a . This fits the pattern shown for growing chicks of all developmental modes (Ricklefs 1974).

In the colony observed, chicks were brooded almost continuously for about a half day, and frequently thereafter until three days after hatching (temperature under the adult about 33°C). I rarely saw brooding during the day after the chicks were 4 days old. At night, brooding was continued longer, and was seen just after 2000 or just before 0800 EDT in chicks as old as 10 days. Weaver

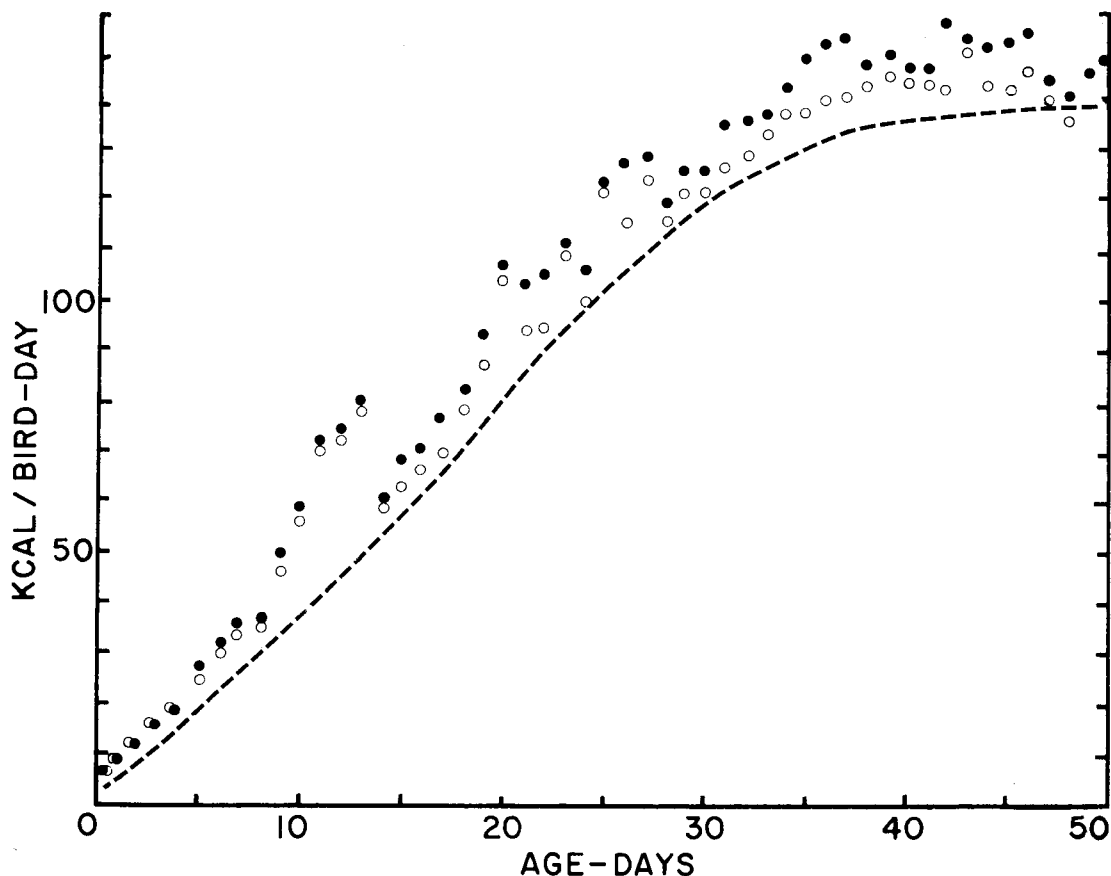


FIGURE 2. Estimated existence energy expenditure of Herring Gull chicks under average natural conditions. Dotted line represents thermoneutral existence costs, and includes the metabolic costs of growth, specific dynamic action, and minimal activity. Solid circles show total costs (including thermoregulation) under shaded conditions, while open circles represent costs in sunny conditions (see text for methods).

(1970), in a study of Herring Gulls at a colony in the same region, indicated the following percentages of brooding time in a day according to chicks' age: Age 0, 87-98%; age 1, 55-82%; age 2, 40-90%; age 3, 30-40%; age 4, 22-36%; age 6, 6-45%. One parent was seen trying to cover 11- and 12-day-olds in a heavy rain, but the oldest effectively-covered chick was 8 days old. Tinbergen (1960) occasionally saw chicks as old as 3 weeks being covered in heavy rain. The timing of cessation of brooding, then, seems to depend on the weather, and probably also on the number of chicks to be covered.

Chicks which are not brooded spend much of their time in the shelter of nearby rocks or vegetation, allowing them to stay out of both wind and sun. Thus, chicks living under natural conditions can avoid expending large amounts of energy on thermoregulation by choosing milder microhabitats within their parent's territory.

Figure 2 shows the estimated energy ex-

penditure of a hypothetical Herring Gull chick hatched on a typical date in a year of average weather conditions (fig. 3). In calculating the estimated effect of absorption of solar radiation I assumed that a chick would seek the sun when it could benefit from it energetically, and to seek shade otherwise. This is not always possible under natural conditions (e.g. the entire territory may be shaded), so the estimate represents an optimum. As noted previously, the estimates in figure 2 assume negligible wind. I stress again that the estimation of existence energy is indirect, and based on numerous assumptions, some of them rather tenuous (Dunn 1976b). Figure 2 should be considered only as a first approximation of metabolic costs in the natural environment.

Under shady conditions, a Herring Gull chick expends an average of about 12% of its total metabolic costs on thermoregulation, the rest being used in other existence expenditures (thermoneutral metabolism, the

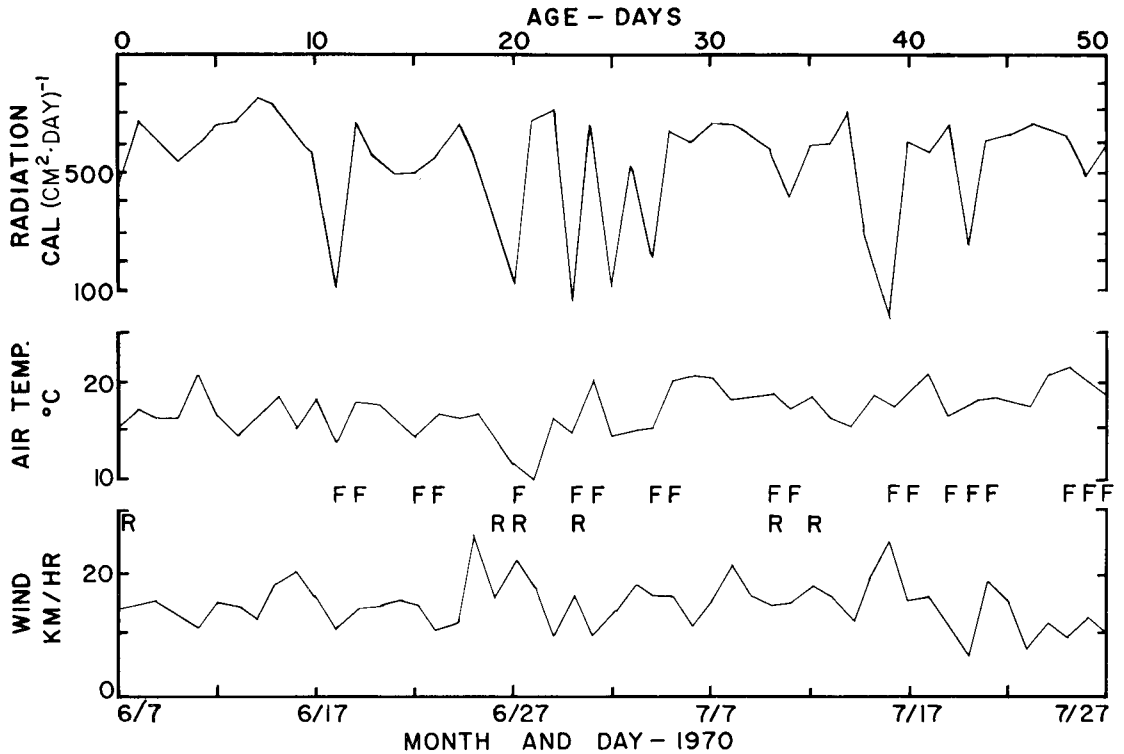


FIGURE 3. Weather during the growth period of a Herring Gull chick hatched June 7, 1970 (an average hatch date and a year of typical weather at the colony studied). The metabolic costs in figure 2 were calculated for the conditions faced by this chick. F = fog, R = rain.

“work” of growth, and specific dynamic action). Under sunny conditions, it uses 7% on thermoregulation; a savings of about 5%.

DISCUSSION

A study similar to this one for altricial Double-crested Cormorant chicks (Dunn 1976b), for the same location, year and weather conditions, showed that after the age at which parental brooding ceases, an average of 38% of daily total metabolic expenditure is used for thermoregulation in sunny conditions over a period of about seven weeks. This is in sharp contrast to the 7% estimate for Herring Gull chicks, over a similar period (6.5 weeks). There is little reason to think that the non-thermoregulatory costs of the two species are markedly different: basal metabolic costs take up about the same proportion of thermoneutral existence energy costs regardless of size or developmental type (Kendeigh 1970); Herring Gulls grow about as rapidly for their size as cormorants (Ricklefs 1968), thereby equalizing the metabolic cost of growth; specific dynamic action is likely to be comparable, as the two species eat similar foods (Dunn 1975b, Hunt 1972). Thus, I conclude that thermoregulatory costs

are proportionally much lower in young Herring Gulls than in young cormorants.

The most important factor in this difference is probably that of insulation provided by plumage. The increase in gull metabolic rate between moderate and low T_a 's is far smaller than in cormorants (fig. 1 and Dunn 1976b), indicating lower conductance and better insulation in the gulls. Cormorant plumage is better at absorbing solar radiation (fig. 4), but this evidently does not compensate for poor insulative properties in the climate where studied.

Although my methods in this study are crude approximations at best, the magnitude of the difference between thermoregulatory costs in the two species is probably real, given that any biases should be in the same direction for each. If anything, the gap should be wider still, because cormorant chicks in the wild are exposed to more wind than Herring Gull chicks.

It has long been known that there are differences in insulation, which will affect thermoregulatory costs, but these two studies are among the first attempts to demonstrate the potential range of thermoregulatory costs in growing chicks in the wild. The only comparable study, on Starlings (*Sturnus vul-*

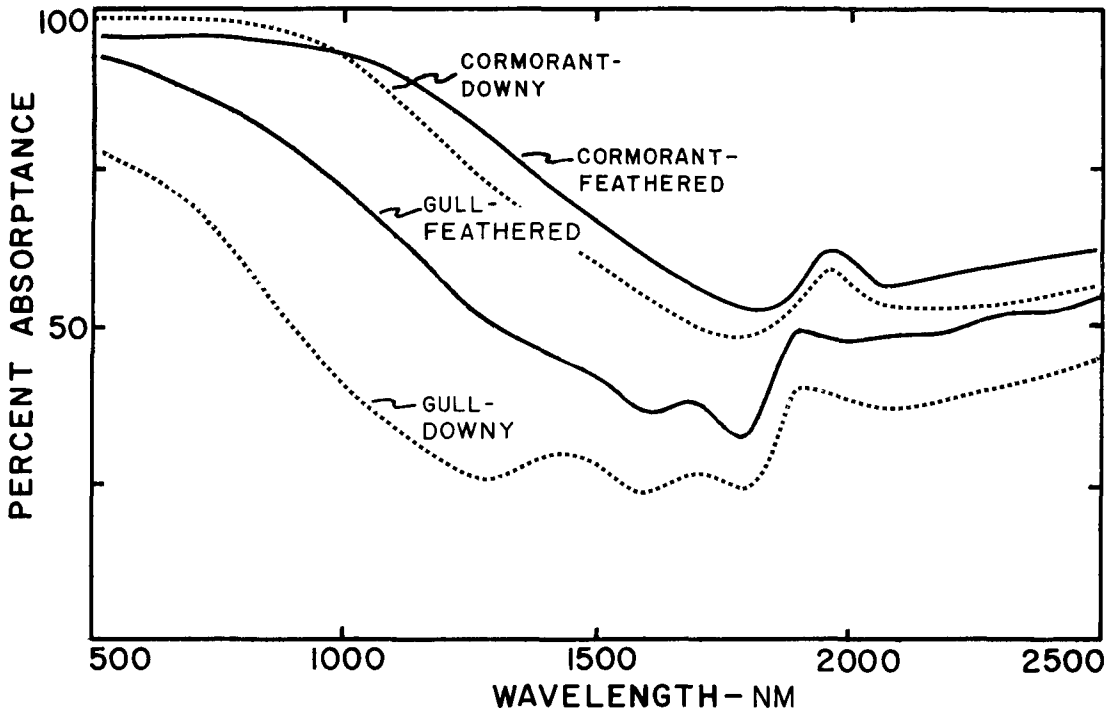


FIGURE 4. Absorbance of thermal radiation by downy and feathered Herring Gull and Double-crested Cormorant chicks.

garis), showed thermoregulatory costs of free-living young, with siblings, in nest-boxes, to be about 10% of thermoneutral metabolic costs (Westerterp 1973).

More sophisticated, quantitative data on free-living existence costs would be of great interest, both for their own sake, and for use in ecological studies aimed at examining the interaction between energetic constraints and parental reproductive strategies. For example, if the Herring Gull chicks in this study had had thermoregulatory costs as high as did cormorant chicks, they would have required an additional 670 g of food during the growth period (based on 85% digestive efficiency, Dunn, unpubl.; and 1.19 kcal/g for average gull foods, Hunt 1972). This would amount to about 40–50g/day over the last three weeks of the nestling period, or on the order of a 25% increase in daily food consumption by the chick (I. L. Brisbin, unpubl. data). Not enough is known of Herring Gull energetics at present to say whether this would prove a significant increase from the parents' point of view.

Increased thermoregulatory costs may have a retarding effect on growth rates, and energetic studies of chicks of one species in very different temperature regimes might prove of use in analyzing variation of reproductive strategy across a species' range.

SUMMARY

Herring Gull chicks maintain homeothermic body temperatures in moderate ambient temperatures by 24 hrs after hatching, and in all but extreme temperatures after three days.

A crude estimate of total metabolic costs of non-active chicks in the natural environment shows that a much smaller proportion (7%) is expended on thermoregulation than in Double-crested Cormorant chicks (38%). The magnitude of this difference suggests that chick energetics might be important in the study of parental reproductive strategies.

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