

DEVELOPMENT OF ENDOTHERMY AND EXISTENCE ENERGY EXPENDITURE OF NESTLING DOUBLE-CRESTED CORMORANTS

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The pattern of gradual development of thermoregulatory abilities by nestling altricial birds has now been documented for over 20 species (Dunn 1975c). However, very little is known of the relationship of these patterns to the natural environment. Knowledge of this relationship is important, for natural conditions act as selective forces in the evolution and adaptation of metabolic development. In addition, very little is known of total metabolic costs of free-living nestlings. These costs affect food requirements, which in turn influence the number of young raised by an altricial parent for a given degree of effort. Consequently, the energetics of nestlings have considerable importance in demographic studies (Dunn 1973, Ricklefs 1974).

This paper reports on the development of thermoregulation and the energy requirements of natural existence in nestling Double-crested Cormorants (*Phalacrocorax auritus*). Existence energy includes basal metabolism, the cost of thermoregulation, and specific dynamic action (the calorogenic effect of feeding), thus covering all metabolic costs exclusive of activity.

Calculation of existence energy entailed extrapolation of oxygen consumption of nestlings in the laboratory to natural conditions, with corrections where the laboratory did not duplicate nature. A more direct method would have been to monitor caloric intake, growth and excretion in the field and to calculate existence energy by subtracting growth and excretory energy from caloric intake (Royama 1966, Westerterp 1973). However, this proved impractical for cormorants. In the one case where the results of the indirect method I employed have been compared to those from direct measures of free-living existence energy based on the use of doubly-labelled water, correspondence was very close (Mullen and Chew 1973). Such correspondence between the two methods required that activity costs be discounted, and this condition is met in studies of relatively inactive altricial nestlings.

METHODS

SOURCES OF DATA

This study was carried out during the 1971 and 1972 breeding seasons, using young from a colony

of about 250 pairs of cormorants on Duck Island, Isles of Shoals, New Hampshire (43°00'N, 70°35'W). Observations of brooding, activity and possible thermoregulatory behavior were made from a blind. Young of known age were watched throughout the day (for 278 nest hours or 445 nestling hours).

A Yellow Springs Instrument Co. telethermometer (model 44TD) and a Rustrack potentiometric recorder (model 2133/F137) were used to measure temperatures in the nest during brooding. The tips of the thermistor probes were covered with wire screening to raise them off the nest floors and prevent measurement of body surface temperature. Measurements were brief, as adult birds soon pulled probes loose and built them into their nests.

Weather data for 4-hr intervals were obtained from the U.S. Coast Guard at the White Island Station, about 3 km from the study island. I occasionally measured wind speed at the colony (using methods of Stong 1971) to compare wind speeds at chick level to those at the Coast Guard station. Daily solar radiation totals were obtained from U.S. Weather Bureau records (U.S. Dept. Commerce 1970) for Portland, Maine, about 80 km north of the colony.

A Beckman F3 paramagnetic oxygen analyzer was used in an open circuit system to monitor oxygen consumption ($\dot{V}O_2$) of nestlings. Methods were similar to those described elsewhere (Dawson and Evans 1957, 1960), except that no insulation was provided, and nestlings were always measured singly. Flow rates were maintained at a constant level through each experiment and varied from 500–4000 cm³/min, depending on the size of the bird. One-gallon paint cans and larger opaque plexiglass boxes with lids which sealed when clamped shut were used as metabolic chambers. These were placed in a darkened constant temperature cabinet, in which temperatures were kept constant to within 1°C by a Yellow Springs Instrument Co. temperature control (model 63RC).

Nestlings removed from the colony in the morning were weighed before and after measurement of $\dot{V}O_2$, and fed a portion of fish after the first weighing. They were generally put into the metabolic apparatus within 2 hr of removal from the colony. At least 2 hr of equilibration in the chamber were allowed before readings were taken. Body temperatures (T_b) before and immediately after each experiment were taken with a thermistor probe inserted approximately 1.5 cm into the cloaca.

Reflectance of plumage by downy and feathered young was measured with a newly-calibrated Beckman DK2A spectroreflectometer with a reflectance attachment. Thawed sections of skin from the backs of frozen specimens were scanned, and absorbance of radiant energy (500–2500 nm) was calculated as 100 minus percent reflection. The thawed skin and feathers did not appear to the eye to be different in color from those in live young.

TABLE 1. Sample calculation of existence energy expenditure of a nestling Double-crested Cormorant.^a

	"Shaded" Conditions					
	0400	0800	1200	1600	2000	2400
Time period (4 hrs; 2 to each side of the hour indicated)						
Air temperature (°C, from 1970 weather data)	11.1	18.3	20.2	16.6	15.6	13.7
$\dot{V}O_2$ (cm ³ g ⁻¹ hr ⁻¹ , from fig. 3)	1.90	1.35	1.13	1.47	1.55	1.72
$\dot{V}O_2$ corrected for nocturnal reduction of 25%	1.42	1.35	1.13	1.47	1.55	1.29
kcal/(bird·time period) ^b	47.84	45.48	38.07	49.52	52.21	43.46
kcal/(bird·day) = sum of above = 276.77 kcal						
	"Sunny" Conditions					
Estimated % of radiation to fall in each time period ^c	10.5	21.6	27.6	21.6	10.5	8.2
Radiation in each time period (2.121 cal cm ⁻² min ⁻¹ for day 30 of hypothetical nestling period)	0.220	0.458	0.585	0.458	0.220	0.174
Per cent reduction in $\dot{V}O_2$ resulting from absorption of radiation ^d	6.4	13.2	16.9	13.2	6.4	5.0
$\dot{V}O_2$ corrected for absorption of radiation	1.33	1.17	0.94	1.26	1.45	1.23
kcal/(bird·time period) ^b	44.80	39.41	31.67	42.45	48.85	41.44
kcal/(bird·day) = sum of above = 248.61						

^a Calculation for expenditure on day 30 by a hypothetical nestling hatched 22 May 1970. Weight is 1773 g (from average growth curve, Dunn 1975b).

^b kcal/(bird·time period) = (cm³O₂/g·hr) (0.001 l/cc) (4 hr) (weight of bird in g) (4.75 kcal/l O₂).

^c The U.S. Weather Bureau recorded downward radiation, which consists on a clear day of about 49% atmospheric thermal radiation (Gates 1970). This is spread evenly throughout the day, such that 8.2% of the measured total falls in each time period. The remaining 51% is direct solar and skylight. This was distributed throughout the day (according to Gates 1970) such that the following percentages of the measured total radiation fell into each time period: 0400, 2.3%; 0800, 13.4%; 1200, 19.4%; 1600, 13.4%; 2000, 2.3%; 2400, 0%.

^d Calculated as (radiation for time period) (0.26)/0.9 cal cm⁻²min⁻¹. See text. If the ambient temperature was below cormorant thermoneutrality (less than 25°C), metabolism was reduced by the calculated percentage; at ambient temperatures above 30°C, metabolism was increased; and in thermoneutrality, no correction was made.

CALCULATIONS

To estimate average existence energy expenditure for a typical nestling, I calculated the costs for a hypothetical cormorant hatched on 22 May 1970 (a typical hatch date and a year of average weather conditions, as compared to 30-yr averages). Table 1 shows a sample calculation. Each day of the hypothetical nestling period was divided into six 4-hr periods (2 hr to each side of the time when weather observations were taken at the Coast Guard station). For each period, $\dot{V}O_2$ (from fig. 3) of an appropriate aged nestling at the temperature indicated by the Coast Guard was converted to kcal, using a conversion factor of 4.75 kcal/l O₂ (Ricklefs 1974). I assumed that ambient temperatures (T_a), and therefore energetic expenditures, remained constant for 4-hr periods. Oxygen consumption declines at night (Dawson and Hudson 1970), so calculated oxygen consumption between 2200 and 0600 hours was reduced by 25% (Aschoff and Pohl 1970). Estimated expenditures were then summed over each day.

Body heat is lost through conduction, convection, evaporation and radiation, and can be gained only by increases either in metabolism or in the amount of heat gained by heat transfer from the environment (Porter and Gates 1969). Unless the experimental conditions of heat gain and loss are similar to natural

conditions, extrapolation of laboratory measured existence energy to nature is not justified.

Rates of heat exchange depend on air temperature, humidity, posture, wind speed, body surface temperature and thermal radiation. Natural air temperatures were duplicated, and humidity and postures of the birds were assumed to be similar to those on the colony. Average wind speed at chick level on the island averaged only 4–5 km/hr, but even a light breeze increases convective heat loss and, therefore, metabolic levels (Porter and Gates 1969). Air speeds through the experimental chambers were negligible, and this makes my estimates of energy expenditure conservative.

The radiational environment of the chamber was assumed to simulate natural shade, in which all reflected sunlight, skylight and thermal re-radiation from the ground were absorbed by the bird. Those sources account for about 77% of total radiation on a horizontally suspended flat plate (Gates 1970). Direct light and atmospheric thermal radiation make up the remainder, and the correction next described was calculated to estimate the effect of these on metabolism (see table 1 for sample calculation).

Daily atmospheric radiation totals at Portland, Maine, were divided into six parts, corresponding to the 4-hr periods of temperature recordings. Par-

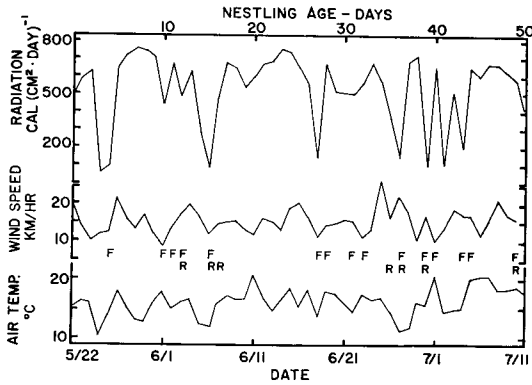


FIGURE 1. Average daily weather conditions at Isles of Shoals, New Hampshire during the 1970 breeding season. Radiation figures are from U.S. Department of Commerce records for Portland, Maine. Wind speed and air temperatures are shown as daily averages of six measurements, taken at four-hour intervals, by the U.S. Coast Guard. Letters refer to days in which fog (F) or rain (R) were recorded at at least one of the six observation times.

tioning was unequal, and radiation was distributed according to the pattern illustrated by Gates (1970). Consequently, most of the energy was assigned to the middle of the day (table 1). Nearly one-third of the days had at least some fog (fig. 1), but I assumed that the pattern of distribution of radiation was not affected.

Lustick (1969), using a radiation source of $0.9 \text{ cal}(\text{cm}^2 \cdot \text{min}^{-1})$, found a 26% reduction in $\dot{V}\text{O}_2$ of irradiated as compared with non-irradiated Brown-headed Cowbirds (*Molothrus ater*) in a variety of T_a 's. The radiation calculated for the Isles of Shoals during each 4-hr period was divided by $0.9 \text{ cal}(\text{cm}^2 \cdot \text{min}^{-1})$ to give the proportion of radiation received by cormorants as compared to the experimental cowbirds. This figure was then multiplied by 0.26 (the proportional reduction in cowbird $\dot{V}\text{O}_2$ when irradiated), as I assumed that metabolic savings would be directly proportional to the amount of radiation received. The resulting figure is the percentage by which oxygen consumption was reduced for each 4-hr period, and corrected metabolism was then summed for each day.

The above calculation assumes that: (1) the radiation source used by Lustick had a similar spectral distribution to natural sunlight; (2) cormorants and cowbirds absorb the same amount of radiant energy; and (3) cormorants reduce their metabolic rate to the same degree as cowbirds when exposed to the same amount of radiation. Lustick's radiation source gave off light from 400–1400 nm, which is the range of natural sunlight containing the most energy (Gates 1966). Figure 2 indicates that cormorants absorb more energy than cowbirds in that range, but as most incident radiation is of wavelengths shorter than 900 nm (Gates 1966), the difference is probably not critical. I can accept the third assumption only arbitrarily, as there are no other data available on degree of metabolic reduction during exposure to radiation.

The estimate for existence energy includes an expenditure on specific dynamic action (SDA) during all time periods. A high protein diet, as eaten

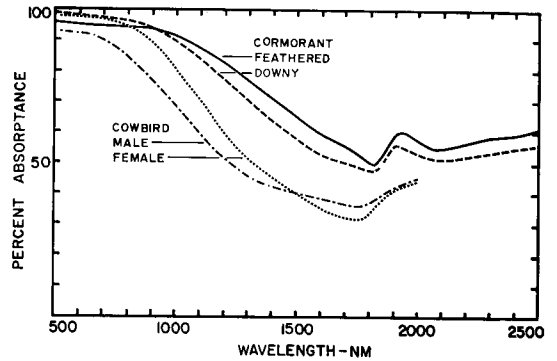


FIGURE 2. Absorbance of skins of nestling Double-crested Cormorants and adult Brown-headed Cowbirds. Data for cowbirds from Lustick (1969).

by cormorants, can result in SDA elevating standard metabolism as much as 45% (Ricklefs 1974). As the nestlings do not eat between 2300 and 0600 EST (Dunn 1975a), existence metabolism may be slightly overestimated. A probable underestimation has already been mentioned in regard to wind speeds. Calculations were also made for thermoneutral existence energy expenditure, in which thermoneutrality was taken as 30°C .

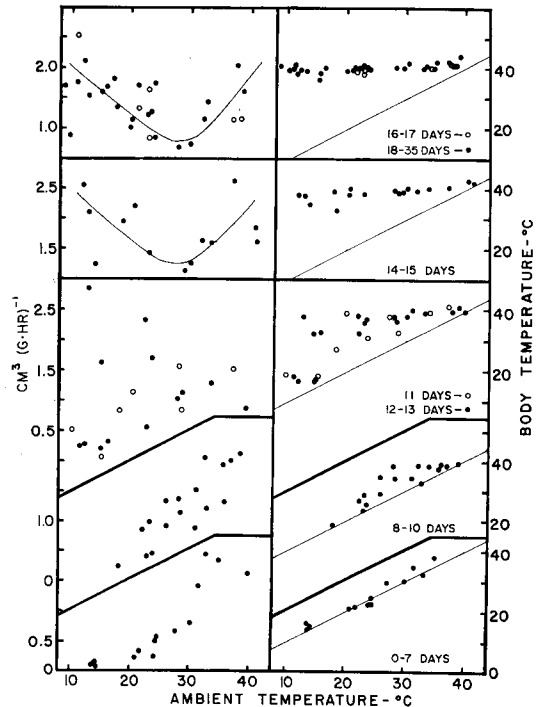


FIGURE 3. Oxygen consumption and body temperature of nestling Double-crested Cormorants at different ambient temperatures. The ages at the right refer also to the corresponding oxygen consumption data on the left. Thin diagonal lines on the right represent equivalence of T_b to T_a . Thin concave curves on the upper left were drawn by eye and represent the average value of $\dot{V}\text{O}_2$ at a given T_a (calculations used values from these curves).

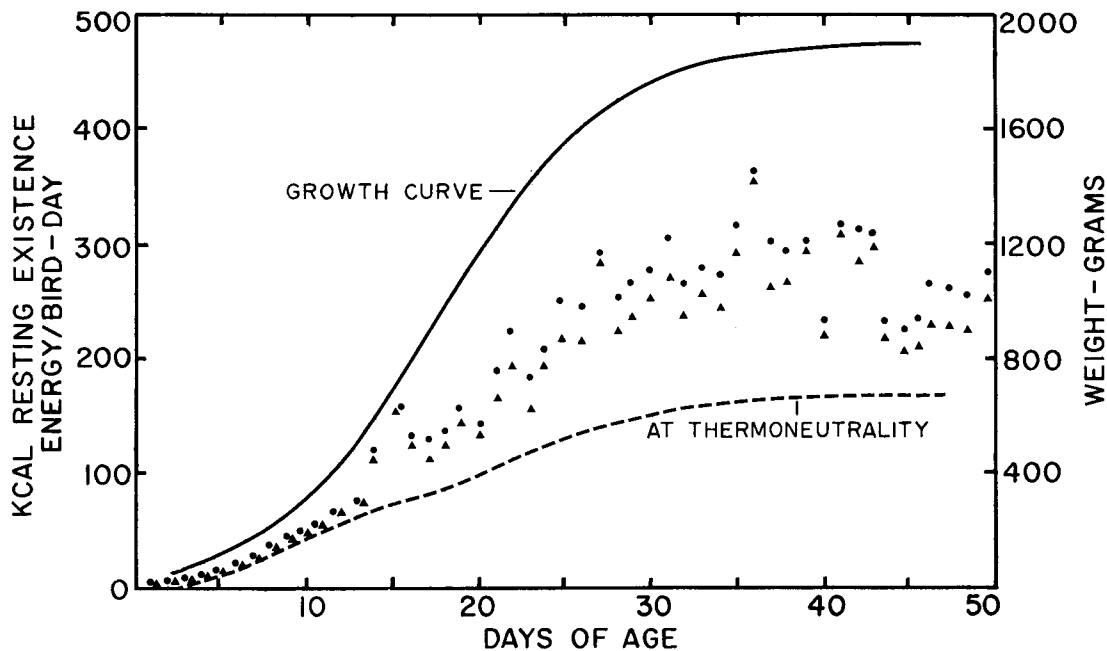


FIGURE 4. Calculated resting existence energy expenditures of nestling Double-crested Cormorants. The growth curve of young is included for reference. Existence requirements at thermoneutral temperatures are shown by the dashed line. Circles indicate existence expenditures at normal ambient temperatures, while triangles show existence expenditure corrected for the effects of absorption of solar radiation. See table 1 for method of calculation.

RESULTS

DEVELOPMENT OF ENDOTHERMY

Figure 3 shows $\dot{V}O_2$ and T_b 's of nestling cormorants after 2-hr exposures to various T_a 's. Hatchlings are unable to maintain T_b above ambient, but 8–10 day old nestlings in moderate T_a 's can keep T_b at nearly adult levels (39–40°C; Neumann et al. 1968). By 2 weeks of age, young can maintain T_b above 35° under all thermal conditions normally encountered during the breeding season. The age at which thermoregulation becomes effective is similar to that for nestlings of other large altricial birds, but comes at a much earlier stage of growth than in smaller species (Dunn 1975c).

The pattern of $\dot{V}O_2$ also changes with age. While being brooded (at about 33°C), nestlings of all ages consume about 1.0 to 1.5 $\text{cm}^3 (\text{g}\cdot\text{hr})^{-1}$. Below this temperature, $\dot{V}O_2$ of the youngest birds decreases. As the nestlings get older, $\dot{V}O_2$ begins to increase with declining temperature, and a thermoneutral zone becomes apparent, extending from about 25° to 30°C. These changes in metabolic pattern parallel the changes in abilities to maintain a constant body temperature, and are typical of those described for other altricial species (Ginglinger and Kayser 1929, Kendeigh 1939, Dawson and Evans 1957,

1960, Breitenbach and Baskett 1967). The metabolism-temperature relation characterizing adults first develops at 2 weeks of age, but $\dot{V}O_2$ at that time is about 0.5 $\text{cm}^3 (\text{g}\cdot\text{hr})^{-1}$ higher at every T_a than for nestlings aged three weeks or older. Thus, $\dot{V}O_2$ at moderate T_a 's initially increases, then declines throughout the remainder of the growth period—a pattern typical for numerous other species studied, both altricial and precocial (Diehl and Myrcha 1973, Ricklefs 1974).

EXISTENCE ENERGY

Figure 4 shows the estimates of resting existence energy expenditure per day calculated for “shady” conditions (extrapolated directly from laboratory data) and corrected for absorption of solar radiation (“sunny” conditions). Also shown are expenditure in the thermoneutral zone and the growth curve of the young. Expenditure during the period of parental brooding (the first 14 days) should be interpreted carefully, as the method of indirect measurement exposed the nestling to greater heat loss than a wild, brooded nestling would face. Of the total amount of energy expended on resting metabolism after brooding ceases, about 38% represents thermoregulation (using the figures for “sunny” conditions). The reduction in total energy

expenditure between shaded and sunny conditions is about 9%, and the reduction in the costs of thermoregulation alone is about 28%. Figure 4 is based on numerous assumptions, some quite tenuous, and must be considered only as a first attempt to approximate true metabolic expenditures in the wild.

DISCUSSION

Nestling cormorants are brooded continuously for the first 12 days after hatching, except for occasional breaks of 10–20 min. Thereafter, diurnal brooding declines rapidly, the rate probably depending on weather conditions and the number of nestlings to be protected. Although single chicks may be partially brooded until 19 days of age, most diurnal coverage ends at about 13–14 days. I observed nocturnal brooding for only a few days longer, and Mendall (1936) reported that brooding in the third week is confined to particularly cold nights. The age at which brooding ceases (14–15 days) coincides closely with the appearance of effective endothermy (fig. 3).

The timing of feather growth is related to the exposure of the young. Hatchlings are completely naked, but after about a week, dense short down starts to appear. By 2 weeks, when a chick is first exposed to the elements, the whole body is covered with a thick black coat. Wing feathers and rectrices begin to lengthen at about this time (Dunn 1975b), but body contour feathers do not develop until later, appearing first on the back. The last areas to lose down are the upper legs, which are easily covered by crouching, and the head.

It is unusual for birds which are hatched naked to develop a complete coat of down before growing contour feathers. Growth of down provides insulation by the end of parental brooding, when the young are only a quarter mature size (Dunn 1975b and fig. 4), and may reduce high heat loss from well-vascularized developing feathers (Morton and Carey 1971, Ricklefs 1974). This does not explain, however, why cormorants do not hatch with a down covering.

Figure 4 was calculated for a year of average weather conditions, and in normal years periods of greater energy expenditure would occur due to poor weather. Modification of existence energy could also be made through behavioral responses to heat and cold. The variety of postures noted in nestlings, from supine to upright, and exposure to the elements of varying surface areas of different degrees of feather cover, probably are very

important in minor modification of metabolism.

Behavioral responses to heat stress by cormorants included short periods of gular flutter, known to be effective in dissipating heat (Lasiewski and Snyder 1969). In addition, nestlings less than a week old would sometimes move into the shade of the parent. Heat stress in this colony was probably minimal, however, as air temperatures were nearly always below thermoneutrality, and there was usually a light breeze (fig. 1). None of the specialized cooling behaviors noted for other cormorant species in hotter climates was seen here (e.g., regurgitation of water onto chicks by the parent, Yamamoto 1967; excretion onto the legs, Jefford and Urban 1972). Behavioral responses to cold probably included huddling of nestlings on cold nights, although this was rarely seen in the daytime, and no other responses to cold were noted outside of postural changes.

The effect of behavioral thermoregulation on resting existence energy expenditure as shown in fig. 4 is probably very small, as climate at the colony was quite moderate. Behavior should have far more significant effects where environmental extremes are greater, and in species which can move in and out of shelter (e.g., Bartholomew et al. 1953, Bartholomew and Dawson 1954).

Dawson and Evans (1957) noted that some growing altricial birds have thermoneutral metabolic expenditures lower than would be expected of adults the same size, while others (pigeons) have higher expenditures. Such a comparison for cormorants indicates that nestlings have resting metabolic expenditures at thermoneutrality very similar to those expected of adults the same size, at most stages of growth.

Altricial nestlings hatch with a high water content; caloric density, which should represent the amount of actively metabolizing tissue, increases gradually throughout growth (Dunn 1975b, Ricklefs 1974). One might therefore expect metabolic levels of nestlings to be lower than those of adults the same size, merely because of their lower proportion of metabolizing tissue. Thus, the correspondence of adult and nestling thermoneutral existence expenditure in cormorants suggests that nestlings spend more energy per unit of metabolizing tissue than adults, and the extra energy is probably going into the "work" of growth (Ricklefs 1974). Basic levels of metabolism are known to increase in adults, as well, during periods of molt, egg-laying, etc. (Payne 1972, Ricklefs 1974). It should not

be expected that nestling existence energy expenditure of all altricial species should have the same relationship to adult costs as it does for cormorants, because patterns of growth differ widely.

The brooding patterns of adult cormorants and feather growth of the young are closely synchronized with the physiological development of endothermy in the young. After brooding has ended, metabolic energy expenditure of completely exposed cormorant young is probably directly related to the weather. The situation may be very different for other species of altricial birds, in which larger broods and substantial nests provide insulation even after brooding has ended. Westerterp (1973) indicated that Starling (*Sturnus vulgaris*) chicks use only about 10% of total metabolic energy on thermoregulation, as compared to 38% in cormorants. House Wren (*Troglodytes aedon*) nestlings thermoregulate earlier in the wild with increasing brood size (Dunn 1976), and Mertens (1969) has shown that individual thermoregulatory costs in young Great Tits (*Parus major*) are reduced as brood size increases. Because the effects of the natural environment on energy expenditure of the young are so great, and may influence brood size (e.g., Royama 1969, Dunn 1976), they deserve much more study.

SUMMARY

Double-crested Cormorant nestlings can effectively maintain homeothermy in the natural environment at about 14–15 days after hatching, when 25% of growth is completed. Parental brooding ceases at about the same time. Feather development seems closely correlated with the extent to which the young are exposed at different ages.

Existence energy expenditure of resting birds was estimated, and about 38% represents the cost of thermoregulation. Nestlings are completely exposed to the elements after brooding ceases, and there appears to be little behavioral thermoregulation. Nestling cormorants expend more energy per unit of metabolizing tissue than do adults, with the extra cost probably directed to the work of growth. The costs of thermoregulation in cormorants are substantially higher than for Starlings raised in a nest-box, and other examples are cited suggesting a substantial effect of insulation in reducing existence energy expenditure in wild nestlings.

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