

ON THE VARIABILITY IN ENERGY ALLOCATION OF NESTLING BIRDS

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ABSTRACT.—An energy budget is presented for free-living nestling Double-crested Cormorants (*Phalacrocorax auritus*), an altricial species, and is compared to those from four other studies performed under natural conditions, for another altricial species, two semi-precocial, and a precocial species. Total energy intake, standardized for body size, appears variable, and there are several important differences among the budgets, including differences between budgets for the same developmental mode. Although limited in extent, these data and other evidence support the hypothesis that nestling energy budgets are molded by natural selection, correlate to adult reproductive strategy, and can reflect adaptation to selective pressures on a species. *Received 9 April 1979, accepted 27 August 1979.*

ENERGY allocation has recently been emphasized as an important, and measurable, component of reproductive strategy in animals, reflecting their adaptation to different environments (King 1973, Ricklefs 1974). The amount of energy going into different aspects of reproduction (courtship, egg-laying, raising chicks, and so on) should indicate the overall pattern most likely to produce the maximum genetic contribution to future generations relative to the contributions of genetic competitors, assuming that reproductive strategy has evolved through natural selection.

Most studies of adult energy budgets give a simple figure for energy going into reproduction or into various components of parental reproductive outlay (eggs, incubation, etc., for example, El-Wailly 1966, Brisbin 1969, King 1973, Ricklefs 1974, Kendeigh 1976). It is my contention in this paper that additional insights into the evolution of adult reproductive strategies can be gained by examining energy budgets of the young.

In many ways, adult and nestling energy budgets act as a unit. The adult must expend energy on the young, not only in laying eggs, but also in feeding, brooding, and protecting. Nestling birds show varying patterns of development, however, and each will require a different pattern of energy allocation on the part of the adult. Precocial chicks require of their parents a large energetic commitment to eggs, while post-hatching energy goes largely into protection. At the opposite extreme, altricial chicks require extensive energy input from their parents in the form of feeding and brooding. The energy allocation of the young to growth, thermoregulation, and so on, therefore, affects the time and energy the parents must put into offspring on a daily as well as long-term basis. Thus, it becomes important to know what costs and benefits are involved in having chicks of different developmental patterns and what constraints such patterns put on the parents in allocating their resources to other activities.

If a given developmental mode calls for a particular pattern of energy outlay by the parent (a certain proportion for growth, for thermoregulation, and so on), then nestling energy budgets cannot be modified in response to the environment, and the adult birds can only optimize energy allocation by varying clutch size or other aspects

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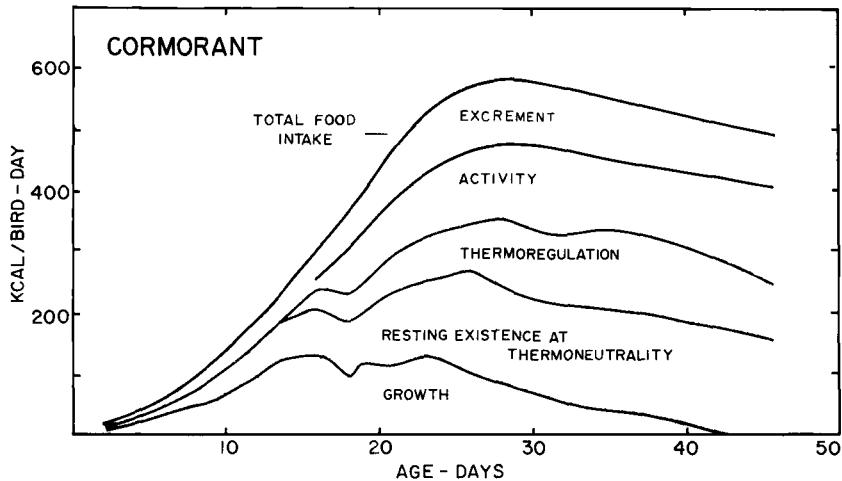


Fig. 1. Energy budget of nestling Double-crested Cormorants. The lines are cumulative, such that the vertical scale is directly applicable only to growth and total energetic intake.

of reproduction. However, if nestling energy budgets are modifiable within a developmental mode, implying variation within species that has been acted upon by selection to produce differences between species, then the evolution of reproductive strategies can involve subtle modifications of nestling energy allocation, and energy budgets of young should be closely adapted to the prevailing ecological and demographic environment. Study of nestling energy budgets in the latter case should lead to interesting insights into the selective pressures facing different species.

The energy budgets presented here consist of quantifications of the following formula: kcal food intake = kcal growth + kcal resting metabolism + kcal waste + kcal activity. The aims of this paper are to present the energy budget for nestling Double-crested Cormorants (*Phalacrocorax auritus*), to compare it to those few budgets available for other species, and to discuss the results in light of the considerations outlined above.

METHODS

Detailed methods used in determining energy in food intake, growth, and metabolism are described in Dunn (1975a, b, 1976a). Generally, the approach was as follows. Cormorants were studied at the Isles of Shoals, 16 km off the coast of New Hampshire. Food intake was estimated from observation of meal size and feeding rate of free-living nestlings and from caloric analysis of collected food samples (Dunn 1975a). Growth of known-age young was followed in the wild, and energy content was obtained from bomb calorimetry of individuals of different ages. Energy in waste was determined from calorimetry of excrement collected from temporary captives provided with natural food (Dunn 1975b). I estimated metabolism by measuring $\dot{V}O_2$ of known-age young and extrapolating results to temperatures measured in the field, while attempting to correct for the effects of specific dynamic action, solar radiation, wind, and behavior (Dunn 1976a). To estimate activity costs, all other costs were subtracted from total metabolizable energy.

Other energy budgets discussed in this paper also were based on the estimation of energy use of free-living chicks and were obtained with similar methods.

RESULTS AND DISCUSSION

The energy budget constructed for nestling Double-crested Cormorants is shown in Fig. 1 and budgets for other species in Fig. 2. The cormorant is an altricial

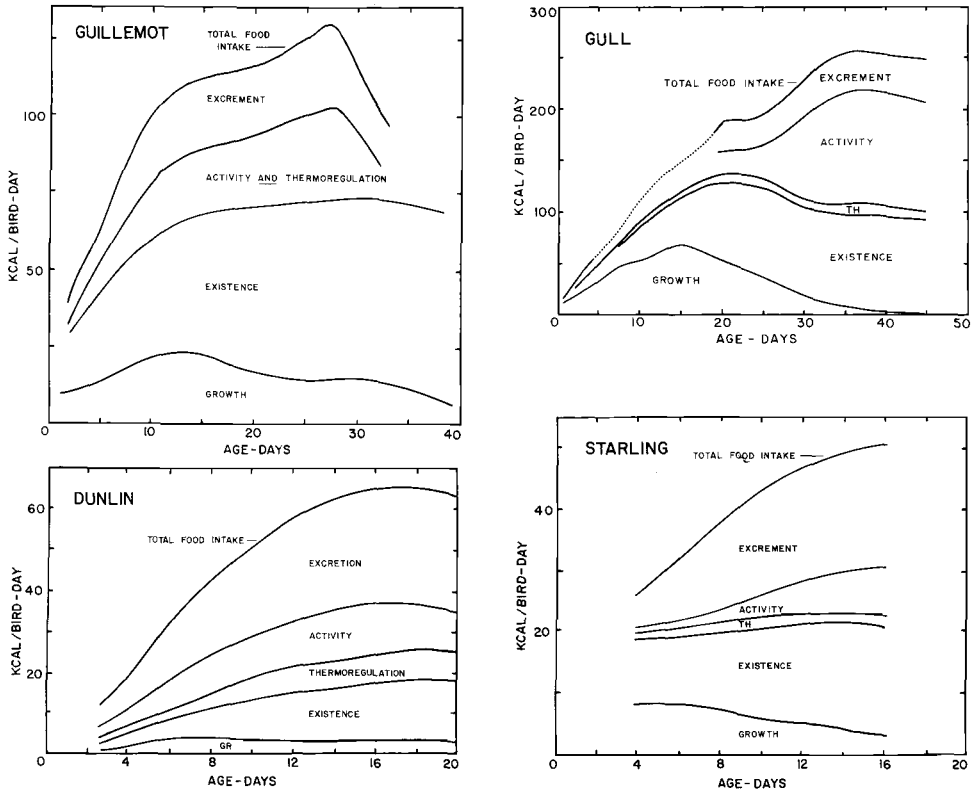


Fig. 2. Energy budgets for other nestlings, from the literature. See text for sources. Lines are cumulative, as in Fig. 1. Abbreviations: GR = growth energy, TH = thermoregulation energy. Dotted line in Herring Gull budget represents an educated guess where data were not available.

species, as is the Starling (*Sturnus vulgaris*, data from Westerterp 1973). The Herring Gull (*Larus argentatus*) and Pigeon Guillemot (*Cepphus columba*) are semi-precocial (data from Dunn 1976b and Dunn and Brisbin MS, and from Koelink 1972, respectively), while the Dunlin (*Calidris alpina*) is precocial (from Norton's 1970 estimate for wild young based on data from captives).

It is difficult to compare energy budgets directly, because larger birds have lower per gram metabolic costs than do small ones (Hart and Berger 1972), as well as different total energy requirements. Instead, comparisons should be made on the amount of energy given over to various functions relative to that used for some basic metabolic process that would be standard for all species. Basal metabolic rate (BMR) is such a standard cost. It relates directly to the birds' abilities to mobilize energy into further expenditures, such as existence in thermoneutrality and locomotion, that have energetic costs that are approximately constant multiples of BMR regardless of body size (Kendeigh 1970, Hart and Berger 1972, Schmidt-Nielson 1972). Although BMR was not measured in the studies cited here, existence costs in thermoneutrality were. On the assumption that nestlings spend the same proportion of energy on thermoneutral existence over basal metabolic costs at each stage of development as would adults the same size (BMR plus 30%, Kendeigh 1970), all values were converted to percent BMR (Fig. 3). The underlying assumption is justified for

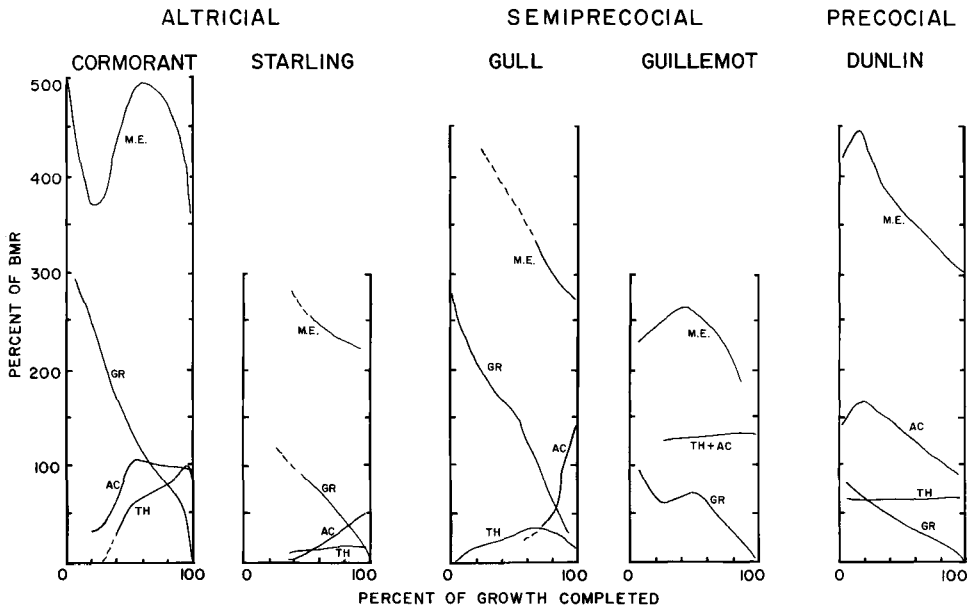


Fig. 3. Energy allocation of various birds during development, expressed as percentage of basal metabolic rate (see text). Abbreviations: M.E. = metabolizable energy, GR = growth energy, TH = thermoregulatory energy, AC = activity energy.

cormorants at least (Dunn 1973). Although very small nestlings (under 50g) have lower existence costs than would adults of the same size (Drent 1965, Kendeigh et al. 1977), there is some evidence that BMR still bears the same proportional relationship to existence costs as it does in adults (Dunn unpubl. data).

Although in an unfamiliar form, Fig. 3 has the merit of allowing direct comparison of relative energy intake and shows the changes in energy allocation throughout growth. Although the data are too few for extensive comparison, a few tentative conclusions can be drawn. There does not seem to be an obvious relationship between overall metabolizable energy intake and developmental mode. Energy going to growth is nearly as low in one altricial species and one semi-precocial species as in the precocial Dunlin, and activity and thermoregulatory costs are as different between the two altricial species as they are between any other pair of species. Thus, the hypothesis that energy budgets differ within a given developmental mode seems reasonable.

Growth energy is compared in more detail in Fig. 4. The four species fed by adults allocate relatively more energy to growth than does the precocial Dunlin (although guillemot growth energy is very low), and allocation is roughly correlated to overall growth rates (Fig. 5). The Starling allocates less energy to tissue than might be expected from its more rapid than average growth rate; this may result from the lower accumulation of fat in the Starling (Westerterp 1973) than in young cormorants (Dunn 1975b) and Herring Gulls (Dunn and Brisbin MS).

A comparison of energy expenditure by nestlings on thermoregulation and activity after brooding has ended is given in Table 1. Thermoregulatory costs are apparently not correlated to developmental mode and probably depend more on differences in climate, thermoregulatory adaptations, and size (e.g. Dunn 1976c). Even the pattern

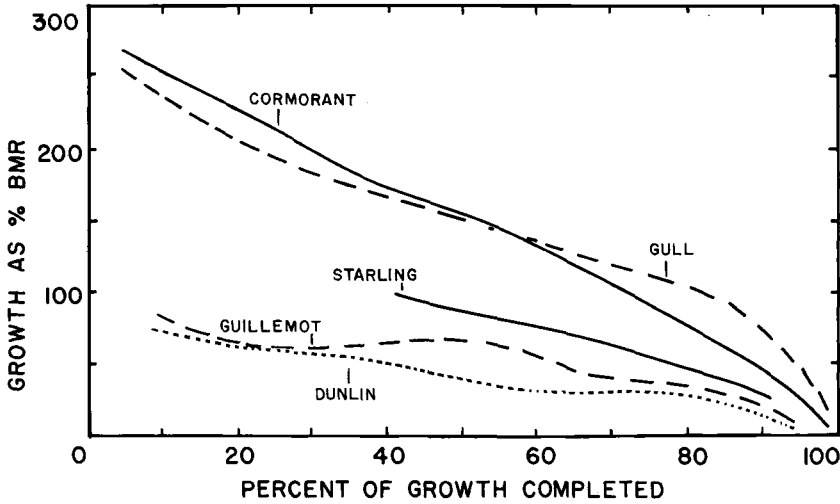


Fig. 4. Comparison of energy allocated to growth by various birds, expressed as percentage of BMR. Solid lines are for altricial species, dashed lines for semi-precocial species, and the dotted line for the precocial Dunlin.

of allocation with time does not appear fixed by developmental mode. Both the altricial Starling and precocial Dunlin have more or less constant thermoregulatory costs, while cormorants show a steady increase (Fig. 3).

Energy allocated to activity was estimated as that portion of metabolizable energy left over when other costs had been accounted for, so the accuracy of this measure depends on the accuracy of all the others. A comparison of relative expenditures on activity after brooding has ceased (Table 1) should therefore be considered with caution. Activity costs of the altricial cormorant do not appear much lower than those of precocial Dunlin chicks, although the latter might be expected to have higher activity levels, as they must feed themselves.

Altricial birds are characterized by rapid growth and also show delayed completion of homeothermy. Dawson and Evans (1957 and 1960) suggested that altriciality was an important step in the evolution of small eggs and birds, resulting in a system in which rapid and efficient growth is possible. Several authors since seem to have interpreted this to mean that the reduction in the energy that would otherwise be used in thermoregulation leads directly to an increase in allocation of energy to growth (e.g. Westerterp 1973). This suggestion implies that each species has a fixed energy income and must obtain energy for one process by detracting from another.

Examination of Fig. 3 indicates that this is not so. First, a comparison of total metabolizable energy between the two altricial and the two semi-precocial species suggests that total budgets are flexible. Second, the semi-precocial Herring Gull (which thermoregulates soon after hatching, Dunn 1976b) grows as rapidly as other birds its size (Fig. 5). The energy required for growth appears to be provided by taking in larger quantities of food when costs of growth are high, rather than by reducing energy going to thermoregulation. Third, the hole-nesting Starling, which has very low thermoregulatory costs, apparently does not allocate extra energy to growth; instead, it simply takes in less total energy. Thus, although it is true that most altricial birds show rapid growth during the period in which they are brooded, this rapid growth is not directly dependent on saving energy from thermoregulation.

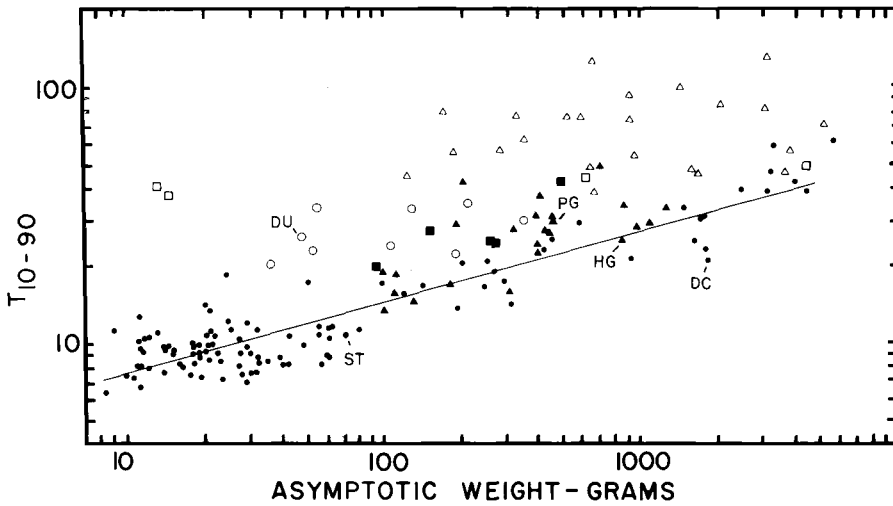


Fig. 5. Growth rates of birds according to asymptotic weight. T_{10-90} represents the number of days between attainment of 10 and 90% of asymptotic weight (Ricklefs 1968). Symbols are as follows: solid circles = altricial species, solid triangles = semi-precocial species, open circles = precocial shorebirds, open triangles = precocial ducks, rails and gallinaceous birds. DU = Dunlin, ST = Starling, HG = Herring Gull, DC = Double-crested Cormorant, PG = Pigeon Guillemot. Data from Ricklefs (1968 and 1973), Dunn (1973), and Sealy (1973).

There is no reason to suppose that natural selection always leads to energetic efficiency, and the Herring Gull chick's rapid growth during periods of high thermoregulatory cost is an example (see also data for Common Tern, *Sterna hirundo*, Ricklefs and White MS). Energetic "extravagance" can be sound, and selected for, when a particular ecological situation requires it (Norton 1973; O'Connor 1975, 1978a).

TABLE 1. Thermoregulatory and activity costs of several birds during development, expressed as the average percentage of daily BMR, after the age at which brooding ceases (see text).

Species	Average °C of measure	Thermo-regulatory costs	Activity costs	Activity plus thermo-regulatory costs
<i>Altricial species</i>				
Double-crested Cormorant	15-25	80	100	180
Starling	12 ^a	15	40	55
<i>Semi-precocial species</i>				
Herring Gull	15-25	20	105	125
Pigeon Guillemot	unspecified			135
<i>Precocial species</i>				
Dunlin (captive)	35	0	65	65
(wild) ^b	5	65	130	195

^a Temperatures outside the nest-box system that was being studied. Effective temperature for the nestlings inside probably averaged higher (Dunn 1976c).

^b Norton's (1970) estimates for wild chicks from data on captives. For cost of thermoregulation, no allowance was made for behavioral thermoregulation, including brooding, or for metabolic reductions due to absorption of solar radiation or nighttime lowering of metabolic rate. Cost of thermoregulation may therefore be overestimated.

The data for captive vs. wild Dunlin (Table 1) illustrate the desirability for energy budget studies to consider the climatic and food conditions of free-living birds. Because thermoregulation has a definite energetic cost and different foods have vastly different nutritional and energy value (Dunn 1973), artificial food and thermal conditions will make energy budgets useless in examining adaptations to the environment. A number of nestling energetic studies had to be excluded from this paper for that reason, and several others were omitted because the variables measured were not comparable to those presented here (e.g. Kahl 1962, Myrcha et al. 1972, Diehl and Myrcha 1973, Blem 1975, Cain 1976). I am skeptical of conclusions based on energy budgets constructed from growth and metabolic costs alone (Ricklefs 1974, Ricklefs and White MS), as the resulting pattern of overall energy intake can be incorrect (see for example the consequences for the Herring Gull and Starling budgets in Fig. 2 if waste and activity were omitted). Many of these studies, however, are suitable for comparison of particular components of energy allocation, and Kendeigh et al. (1977) have noted differences within and between developmental modes using this approach.

CONCLUSIONS

The results of this limited comparison of nestling energy budgets suggest definite differences within developmental modes, but the data are too few for correlation of these differences to environments. More recent and extensive work by O'Connor (1978a and b) on altricial development provides further evidence from sophisticated analyses of growth parameters that energy allocation of young is varied within a developmental mode, as well as that nestling energy budgets are finely tuned to the overall selective regime of a species. Case (1978) also concluded that growth rates are adapted to certain aspects of a species' environment.

Looking at the problem from the opposite viewpoint, there are many arguments that can be brought to bear against the notion that nestling energy allocation is, in most respects, fixed (for example, against the hypotheses that young are provided with as much food as is available, Lack 1966 and 1968; or that they grow as fast as is physically possible, Ricklefs 1969). These arguments are too involved to present here but have been laid out elsewhere (Dunn 1973: 85-100). My conclusions from available evidence are that the only limits on developmental energy allocation that are essentially beyond the control of selection are: 1) growth cannot be faster than a certain (unknown) maximum, 2) at least some energy must be spent on metabolism and waste, and 3) in a few species, food supply or time available to feed offspring may sometimes directly limit energy input to young. In addition, there are restrictions on energy allocation that have been arrived at through selection but are perhaps no longer modifiable (e.g. adaptations for specializing on certain food types). And last, there are sets of environmental conditions that may tend to favor certain patterns of development, such that the variability found in nature is reduced below that theoretically possible.

The restrictions on variability in energy allocation that cannot be modified seem minor, and the hypothesis that nestling energy budgets are responsive to selective pressures seems a sound one. Because the selective regime for every species is likely to be unique, it should be incorrect to make generalizations about single factors controlling nestling energy allocation. About all that can be said is that development is one multifaceted adaptation among all the others that make up a bird's life history

and are selected according to the combination leading to optimal lifetime reproductive success, given the ecological and evolutionary background from which that species arose. Such a statement is somewhat unsatisfying in its generality but is an important observation. Many authors have sought single causes for control of reproductive adaptations without considering feedback to and from other adaptations.

More informative at this time than further theorizing would be a larger number of detailed studies on the selective pressures and developmental responses of individual species. Because energy budgets of free-living young are difficult to obtain, they should not be considered the only method of examining adaptation of nestling development, and the kind of approach used by O'Connor (1978a and b) may ultimately prove more fruitful. On the other hand, energy budgets of nestlings will continue to be studied for other reasons, and, whenever possible, methods should be used that will make the results applicable to studies of selective responses in developmental patterns as well.

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