GROWTH ENERGETICS OF THE WHITE IBIS

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Information on the energy used by birds from hatching through fledging is needed to estimate the amount of food that parent birds must obtain from the environment (Ricklefs 1974) and, thus, to assess the energetic role of a species in an ecosystem (Kendeigh 1974a). Because it is technically difficult to estimate accurately the total energy used for the growth and maintenance of wild nestlings, such studies have often been conducted completely or in part on captive birds. Determining the transferability to free-living birds of data obtained in the laboratory is a critical step in understanding the ecological implications of growth and development.

In this paper, I report on the growth and energetics of White Ibises (*Eudocimus albus*) and attempt to estimate the energy requirements of wild birds from those studied in captivity. My purpose is to provide a reasonable estimate of the total amount of energy used by growing nestlings. Several approaches to this problem have been tried previously. Ricklefs (1974) used basal metabolic rate, growth rate and energy density of tissues to measure energy requirements. This method has value in comparing growth in different species but produces only indirect estimates of total energy use and does not include energy required for thermoregulation or activity, both of which may be substantial under natural conditions.

Dunn (1975) attempted to measure caloric intake by estimating the meal size of wild nestlings and applying caloric value of average food and laboratory measures of digestive efficiency. This method, although marginally successful in cormorants, is difficult or impossible to use on many species, such as the White Ibis that are fed highly macerated, semi-liquid food directly from the parent's gullet in numerous small meals.

Kendeigh (1970) and his students have measured the energy required for growth and existence in the laboratory under conditions approximating those in nature and have used these data as estimates of the energy requirements of wild birds. This method has the advantage of directly measuring total food intake. It is useful for studying large birds and was previously used by Kahl (1962, 1966) and Shanholzer (1972) on wading birds. I have used it in this study as the basis of my estimates.

METHODS

Biomass growth was measured on five captive, young ibises taken from nests as pipped eggs. Concurrently, I measured growth of 33 wild nestlings in one coastal and one inland colony in southern Florida. All captive birds were from the first egg laid. Because the growth of second chicks was retarded, all wild birds were also the oldest nestling in each clutch. Data for all wild nestlings were combined because birds at the two colonies grew at similar rates.

Newly hatched birds were kept at 32°–35°C, similar to natural temperatures, in 15-cm diameter containers having screen bottoms. Each hour they were fed all they would consume of a ground mixture of two parts shelled shrimp (*Penaeus duorarum*) and one part sardine (*Harengula pensacolae*) by weight; I added 20 ml of water and 1 gm vitamin and mineral supplement per 100 g of food. Three larger container sizes were used successively through the first 2 weeks to avoid constriction of movement. On day 14, birds were placed in a wire-bottomed cage (0.3 m square) in a screened enclosure under ambient southern Florida temperature and humidity. This was done just after the time when brooding of wild nestlings is discontinued (day 10 to 12). When the birds were placed outdoors their diet was changed to shelled shrimp and anchovies (*Anchoa mitchilli*) in a 2:1 ratio. The composition of the diet was similar to that of wild ibises, which is about 53% crustaceans and 20% fish by weight (Kushlan and Kushlan 1975). At 3 weeks, the birds were moved outdoors to cages (0.5 × 0.5 × 1.1 m). Assimilated energy of older wild nestlings was determined on 8 birds of three ages. Ibises 23 days (3 birds), 30 days (2) and 40 days (3) old were taken from the nesting colony and subjected to experimentation, after two days acclimation to captivity.

I determined the energy required for aviary existence by subtracting the energy content of excreta (which included urinary and defecatory wastes) from the energy content of ingested food (Kendeigh 1970). Energy content of regurgitated bones and scales was also subtracted from intake. For birds without weight change, this procedure measured existence metabolism. The same procedure for growing birds measured metabolized energy, which includes energy for existence and energy for growth. All food consumed during the nestling period was weighed and converted to calories by multiplying its weight by its average caloric content, determined with a Parr adiabatic calorimeter. The caloric content of the previously frozen food given to captive nestlings was: shrimp, 0.91 kcal/g wet weight; shrimp-sardine-vitamin mixture, 0.76; and anchovies, 0.80. Its caloric content was similar to that of food samples collected in the wild, which varied from 0.75 to 1.3 kcal/g live weight. Excreta were collected throughout the nestling period. Since the caloric content of the excreta varied over the nestling

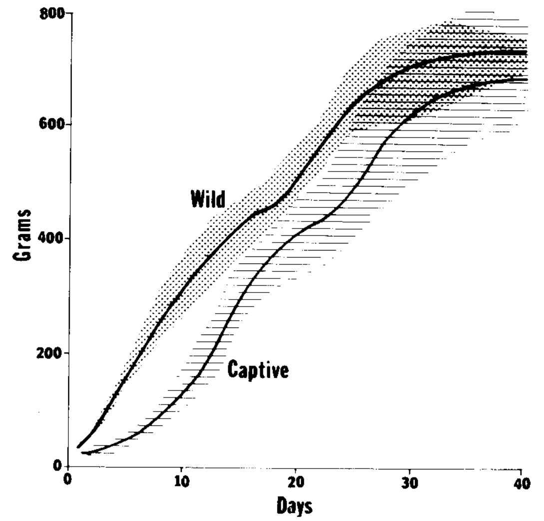

FIGURE 1. Comparison of growth of captive and wild White Ibises to day 40. Shaded zones are the range; solid curves are averages. Growth curve of wild nestlings fits the equation dw/dt = –.200 W(lnW), asymptote 750 g; growth curve of captives fits the equation dw/dt = .185 W(l-W), asymptote 700 g; adults size 1036 g ♂♂, 764 g ♀♀ (Kushlan 1977).

period, calorimetry was performed on all material by combining samples for three-day intervals for each nestling.

RESULTS

I examined in detail the growth and energy use of captive nestlings and then made comparisons to wild birds. The growth of White Ibises in captivity can be roughly fitted to a Gompertz-type of growth curve following Ricklefs' (1967) method (fig. 1). Growth

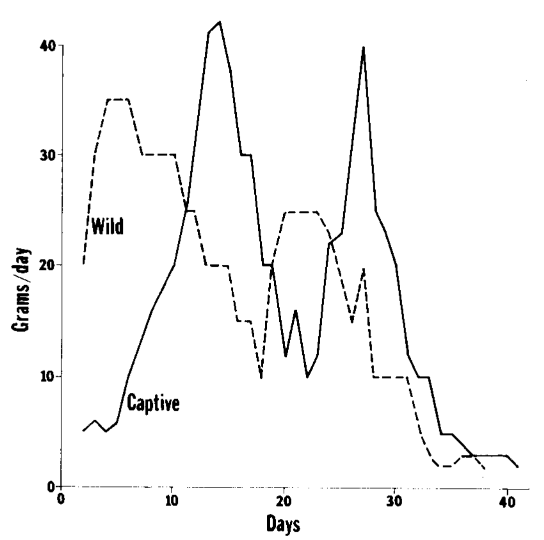

FIGURE 2. Daily growth rate of captive and wild White Ibises.

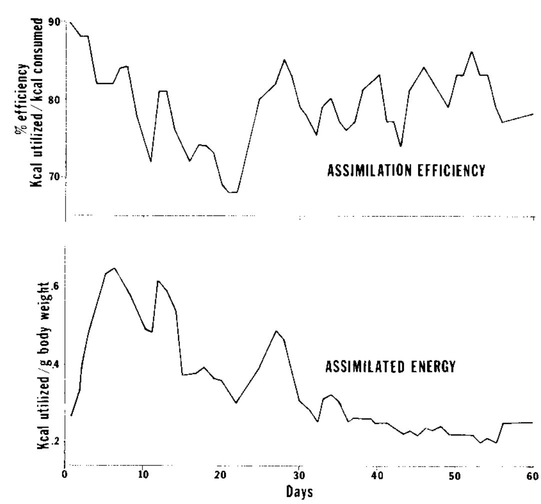

FIGURE 3. Changes in assimilation efficiency and energy assimilated (per g body weight) of nestling White Ibises. Both curves graphed as moving 3-day averages.

parameters derived from the allometric curve showed that captive ibises required 23 days to grow from 10 to 90% of their final size. Fledglings achieved 79% of the adult size before growth leveled off. The single captive who was followed required 630 days to reach adult weight. The observed values are only approximately fitted by the allometric curve because weight increase was not uniform (fig. 1). A plot of daily growth rate (fig. 2) shows that ibises exhibited bimodal peaks of growth separated by a period of slowed growth. In captive White Ibises, assimilation efficiency (kcal used/kcal consumed) varied between 68 and 92% (fig. 3), with high efficiencies being attained during the first several days. Caloric content of feces averaged 2.48 kcal/g dry weight (CV = 9%, SD = 0.22, range 1.89–2.95, n = 66). Weight-specific energy use (fig. 3) was highest during the first 14 days and peaked again in the fourth week before leveling out. The second peak of energy use (fig. 3) corresponded to the last peak of growth (fig. 2). Energy use as a function of body weight (fig. 4) corresponded to the altricial pattern (Ricklefs 1974), but also showed an early plateau that suggests a precocial developmental pattern. Daily energy use (fig. 5a) peaked during the fourth week reaching a maximum of 240 kcal/day on day 27. Cumulative energy assimilation of captive birds (fig. 5b) rose smoothly through the nesting period, reaching 5360 kcal on day 40.

The advisability of extrapolating the data obtained on captive birds to wild nestlings can be evaluated by comparing growth curves

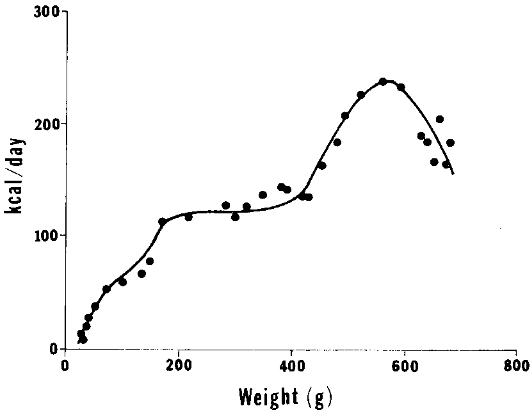

FIGURE 4. Energy use as a function of body weight for White Ibises.

of wild nestlings to captive ones. Biomass growth of wild White Ibises differed from that of captive birds in several respects (fig. 1). Wild birds grew faster initially, achieving 10% of their final weight on day 3 as contrasted with day 7 for captive birds. In increasing from 10 to 90% of final weight, captive birds grew faster than wild birds. As a result, both groups reached 90% of their final weight on day 30. However, wild birds reached the fledging stage of development at a higher weight (750 g vs 700 g) than did captive birds. The weight attained by wild birds was 85% of adult weight. Wild and captive nestlings also showed differences in the timing of rapid and slowed growth phases (fig. 2). The rapid growth phase of captive birds was delayed by about 7 days but they achieved higher growth rates during the peak of rapid growth.

Because of the differences in biomass growth and final size, energy utilization must have differed in the two groups and direct application of the energy use of captive birds to the wild population would underestimate the requirements of wild birds. An estimate for wild birds can be calculated using the following rationale. The energy use (assimilated energy) of nestlings consists of the energy used in maintenance and that used for growth and development. The maintenance energy of nestlings is nearly equivalent to existence metabolism, defined as the energy required for existence without weight change (as measured in a small container where movement is possible and food and water are freely available). These conditions approximate those prevailing during the nestling pe-

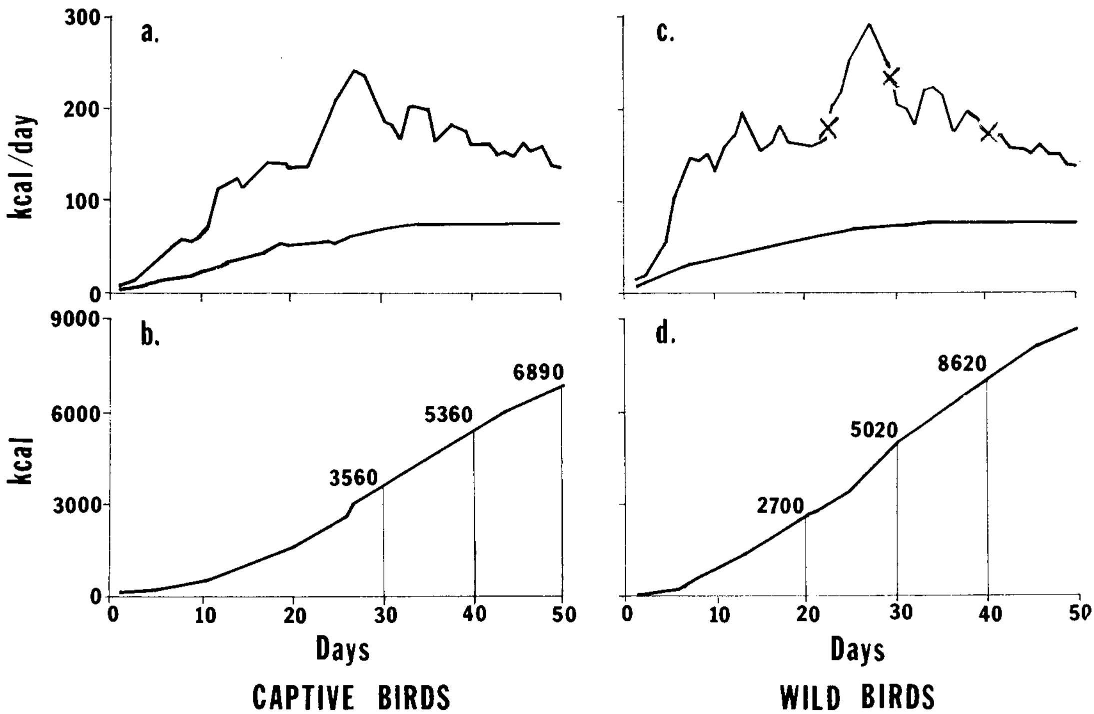

FIGURE 5. Energy use of captive and wild nestling White Ibises. Daily energy use shown by curves *a* and *c*, and cumulative use by curves *b* and *d*. Assimilated energy was calculated as energy consumed minus energy excreted. Existence metabolism was calculated by log EM = -0.2673 + 0.7545 log W (Kendeigh 1970). Assimilated energy of wild birds was estimated as described in the text. Independently derived values for existence metabolism of wild nestlings are shown (X) for comparison with the energy curve estimated for wild birds.

riod of wild birds. Existence metabolism depends on body weight and can be estimated at 30°C for nonpasserines by the equation log EM = -0.2673 + 0.7545 log W (Kendeigh 1970), where W is weight in grams. Daily weight-specific energy for growth of captive nestlings (kcal/g) can be calculated by subtracting existence metabolism calculated by the above equation from the assimilated energy measured in the laboratory and dividing by weight of the captive for each day. If the growth of body parts were approximately dependent on age but independent of weight, the growth energy of wild birds could be estimated by multiplying the weight-specific growth energy of captives (kal/g) by the body weight of wild birds (grams) on the same day of life. The total assimilated energy of wild birds can then be obtained by adding the existence metabolism computed by Kendeigh's equation to the computed growth energy. The results of these calculations are shown in figure 5c.

I conducted a set of experiments to test the computation by determining maintenance energy of nestlings from the wild at three stages of development. These birds showed average assimilation energy values very close to those computed (fig. 5c).

The cumulative energy assimilation of wild White Ibises was estimated to be 8620 kcal from hatching to fledging on day 40 (fig. 5d) as contrasts with 6890 kcal required over 50 days for captive birds to achieve their final body weight. Thus the total energy use of wild birds to achieve final weight was 1.25 that of the captive birds.

DISCUSSION

LABORATORY DATA AND WILD POPULATIONS

Previous studies of ciconiiform species have used data obtained from captive birds to estimate directly the energy requirements of the wild birds. Whether such an approach is justified depends on the similarity of the developmental processes in the two groups. However, Kahl (1962, 1966) did not make a study of growth of wild birds throughout the nesting period. Siegfried (1972), Junior (1972) and Shanholzer (1972) made some comparisons and concluded that there were no meaningful differences between the rates of increase of weight of captive and wild ciconiiform nestlings. Direct application of the energy used by captives was unacceptable in the White Ibis because of the different growth patterns that emerged when captive and wild nestlings growth were compared. In the White Ibis, captive nestlings grew slower initially, had delayed peaks of high growth rate, and reached a smaller final size than did wild nestlings. These results suggest that care should be exercised in using energy data obtained on captive birds if comparable concurrent data on wild birds are not obtained. They also emphasize the need for a method to extrapolate data to the wild populations.

I used existence metabolism or metabolized energy to estimate the energy requirements of wild birds. This measure contains all components of energy use in wild birds, differing only in the amount allotted for activity and thermoregulation, when the thermal environment differs between laboratory and the nest (Kendeigh 1974b). I approximated these components as closely as possible by supplying heat and humidity to nestlings before attainment of homeothermy, enlarging cages to accommodate increasing activity with increasing size and, after two weeks, maintaining the birds under ambient conditions comparable to the nesting colony. Despite my attempt to closely approximate natural conditions in measuring metabolized energy, heat loss and activity were probably different than in the wild, and White Ibises grew at different rates in captivity than in the wild. Growth differences would be expected to occur when thermal conditions differ between laboratory and field (Ricklefs 1974). Making concurrent measurements of growth of captive and wild nestlings provides a way to determine the extent of growth differences and allows for reasonable extrapolations.

My method for estimating the energy requirements of growth of wild birds was based on several assumptions. Use of Kendeigh's (1970) equation for birds less than 300 g involves extrapolation beyond the data used in generating the equation. Wild ibises weighed less than 300 g during the first 10 days of life and captives were under this weight for the first 15 days. Kendeigh's equation was derived from adult birds, not nestlings. It is not known whether the equation gives good estimates for nestlings after the attainment of homeothermy. Prior to acquiring homeothermy, existence metabolism of nestlings depends on the success of ectothermic maintenance of body temperatures, and Kendeigh's equation would not be expected to hold. An additional assumption is that growth of body parts depends on age rather than weight. This may be generally true in birds provided starvation is not a factor (Ricklefs 1968). Among wild nestling ibises, feather development of siblings was generally similar although weights differed considerably. This suggests that development did proceed independent of weight, as McVaugh (1973) noted in herons.

Given these assumptions, the resulting estimate of energy consumption has unknown cumulative errors. The important consideration, however, is the effect of the error factor in estimating the total energy used during growth. The possible failure of energy use to follow standard relations before nestlings attain homeothermy may have little effect on total energy consumption, because only 11% of the total energy is used in the first quarter of the nestling period (fig. 5). As shown by the data from older wild nestlings, the estimates were close to the actual energy use in the late and most energy-demanding stages of growth. Thus, assuming that existence metabolism of nestlings follows the standard weight relations curve for adult birds may not make a significant difference in estimating the total energy used during growth. However, because basal metabolic rate of growing birds is known to exceed that of adult birds of similar weight (Ricklefs 1974, Kuenzel and Kuenzel unpubl. ms.), the assumption that existence metabolism follows standard regressions probably would introduce serious error in precise comparative studies of growth. Nonetheless, the method in this study may have some value in determining total energy used during growth. It may be especially useful when more data become available on the maintenance requirements of nestlings. Particularly if the relation between nestling size and metabolized energy were determined, it could be used in place of Kendeigh's equation.

GROWTH OF WHITE IBISES

Wild White Ibises grow at the rate predicted for birds of their size (Ricklefs 1973). The curve of biomass growth of White Ibis does not, however, smoothly increase but shows a distinct slowing of growth in the middle of nesting (fig. 1). For wild birds, the two peak periods of growth occur during the first and third weeks (fig. 2). The adaptive significance of the initial peak may be that it reflects rapid weight gain to the point where nestlings can be left alone during the day while both parents forage. The period when weight gain slows may correspond to a period involving differential growth of body parts and the onset of the use of energy for endogenous maintenance of body temperature. The late peak is a rapid increase toward fledging size and corresponds to the highest peak of total energy use (fig. 5c). The long period required for one captive to achieve adult size is not an artifact of captivity since wild second-year White Ibises have a significantly lower weight than adults (Kushlan 1977).

The difference in growth rates shown in figure 2 is caused by the initially slowed growth of captives and by their higher rates during the two peaks of growth. If the growth of captive birds was similar to that in the wild under stressful conditions, the comparison suggests that when unfavorable conditions affect early growth in the wild, ibises are able to achieve higher rates later in development in order to "make up for lost time." Such compensation in growth rate would be highly adaptive for a bird that must locate and obtain ephemeral food supplies many kilometers from the nest site. This would be particularly important for second chicks in a clutch that experience an initially slowed growth rate and low probability of survival. Loss of the first chick or increased food supply during nesting might permit survival of a second chick because of its ability subsequently to increase growth rate.

SUMMARY

Energy required for growth and development of White Ibises was studied in captives by measuring daily metabolized energy through the nestling period. Captives used 5360 kcal, but their biomass growth differed from that of wild birds. By using the standard relation between existence metabolism and body weight, and assuming that energy requirements per gram biomass were age-dependent, I estimated that the energy used by wild nestlings during growth was 8620 kcal. The results suggest that the applicability of laboratory data to wild populations should be verified by concurrent study of wild birds. The method used in this study of estimating the energy requirements of wild birds depends on several assumptions which require further examination; however, they may not seriously affect the estimated total energy use. Differences between growth of wild and captive birds show that biomass growth is slowed under unfavorable conditions, but also can accelerate to compensate for periods of slow growth.

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