

THE CONDOR

VOLUME 64

MAY-JUNE, 1962

NUMBER 3

BIOENERGETICS OF GROWTH IN NESTLING WOOD STORKS

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INTRODUCTION

The early days of an animal's life are frequently the most critical in its struggle for survival. The young altricial bird is particularly vulnerable during its developmental period in the nest because it is not only unable to escape predators but is also completely dependent upon parental care for food and protection from inclement weather. This phase of the life cycle is also one of heavy energy demands for the parents. Presumably high growth efficiency, coupled with the ability to ingest large quantities of food, allows the young altricial bird to leave the nest within the shortest possible time, thus reducing exposure to the aforementioned dangers. Although the morphological aspects of growth have been described in many species of birds, not enough quantitative data on the bioenergetics of the altricial growth pattern in large birds have been published to determine to what extent the food conversion is adaptive. The purpose of the present study is to relate growth to food consumption in the nestling Wood Stork (*Mycteria americana*), an altricial species, and to explore some aspects of the survival value of the altricial growth pattern. The present paper constitutes a phase of a continuing study of the breeding biology of the Wood Stork.

ACKNOWLEDGMENTS

I am grateful to Dr. Eugene P. Odum for guidance and advice throughout the study. A debt of gratitude is owed the members and officers of the National Audubon Society, under whose auspices the field work was conducted. I would also like to thank Robert P. Allen and Alexander Sprunt IV of the National Audubon Research Department for many helpful suggestions. Additional financial aid was received from the Frank M. Chapman Memorial Fund administered by the American Museum of Natural History; the Herbert L. Stoddard Research Prize of the University of Georgia; and a National Defense Education Act Fellowship at the University of Georgia. Invaluable assistance in caring for the captive nestlings was provided by Mr. and Mrs. Kirby Walter of Bartow, Florida, and A. Wentworth Erickson. Through the courtesy of the Florida Audubon Society and Armour and Company I was allowed to work at the Panther Point Sanctuary. My wife, Doris, assisted by typing the manuscript.

MATERIALS AND METHODS

During the spring and summer of 1960, four young storks were hand-raised for varying periods of time from hatching to normal fledging (about 60 to 65 days). The young were taken as pipped eggs from nests in the Panther Point stork colony near Bartow, Polk County, Florida. The eggs were hatched in a small incubator in which the nestlings were kept until they were seven or eight days old, after which they were transferred to an outdoor enclosure located a few miles from the colony.

The young were fed freshly caught small fish (*Gambusia*, *Mollenesia*, *Jordanella*,

Fundulus, *Chaenobryttus*, and *Lepomis*) until they were seven or eight days of age, at which time their appetite became so great that I was no longer able to catch enough food for them. From this age on, they were fed gizzard shad (*Dorosoma cepedianum*) which could be purchased frozen from a local fish market. Feedings were as frequent as eight times per day when the young were from 4 to 8 days old and were as few as two or three times per day just before fledging; at each feeding, the young were given as much food as they would eat. Records were kept of the daily food consumption (in grams, live weight) of each bird and of its growth in terms of body weight and lengths of culmen, tarsus, middle toe, and longest primary wing feathers. Growth measurements were made daily during the first four weeks and less frequently thereafter as the birds became increasingly difficult to handle. Since it was not always possible to weigh the birds at the same hour each day, diurnal variations (Baldwin and Kendeigh, 1938) may have influenced the day-to-day changes in body weight; however, the overall pattern of weight increase was unaffected by these diurnal fluctuations.

Since no determination of the caloric content of the feces was made, no definite statement can be made regarding the assimilation efficiency (the ratio of caloric intake to metabolized energy) of the young. The amounts of feces were always quite low in comparison to food intake. These were estimated to be less than 5 to 10 per cent by weight and indicated that only a small fraction of ingested food was lost in the feces. It is assumed that the assimilation efficiency remained constant during development because the type of food eaten was the same and, therefore, ecological growth efficiency, or the ratio of intake to growth, can be calculated. The terminology of Odum (1959) is followed with regard to efficiencies.

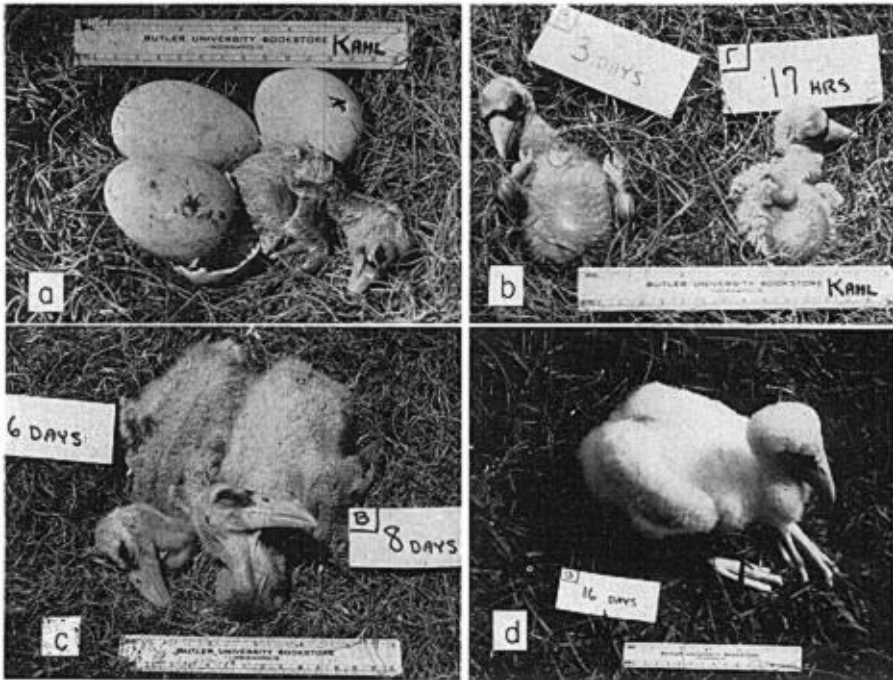


Fig. 1. Nestling Wood Storks (*Mycteria americana*): a, hatching; b, three days old and 17 hours old; c, six days old and eight days old; d, 16 days old. Ruler shown in a, b, c, and d is 15 cm. long.

Measurements of the four selected body parts were made with vernier calipers (when under 120 mm.) and dividers (when over 120 mm.) as follows: (1) the tarsal measurement included the tarsometatarsus and its condyles; (2) the culmen measurement represented the chord of the exposed culmen; (3) the middle toe (left foot) was flattened and measured without the nail; and (4) the longest primary wing feather was measured as the chord of the shaft from the tip to the insertion in the skin. All of the young studied here had 11 primaries, and the longest primary was the ninth (third from outermost). However, H. G. Deignan (*in litt.*) examined the primaries of specimens of *Mycteria* in the United States National Museum and found that "while the great majority have but eleven, at least one adult and one nestling have twelve." Because of this seeming variation in number of primaries, and because the primaries are numbered from the wrist out, the designation of "longest primary" cannot be assigned to any specific feather in all individuals. Deignan also noted that "all non-molting adults . . . have the third from the distal end of the wing longest," thus "third from the outermost" is probably the best designation for the longest primary.

The four young storks were studied for the following periods: Young A, from hatching to 10 days of age; Young B, from hatching to 41 days of age; Young C, from hatching to 65 days of age; and Young D, from 42 to 69 days of age. In the example of Young A, which was returned to its original nest in good health at 10 days of age, only measurements of tarsus, culmen, and middle toe were taken; no data on body weight,

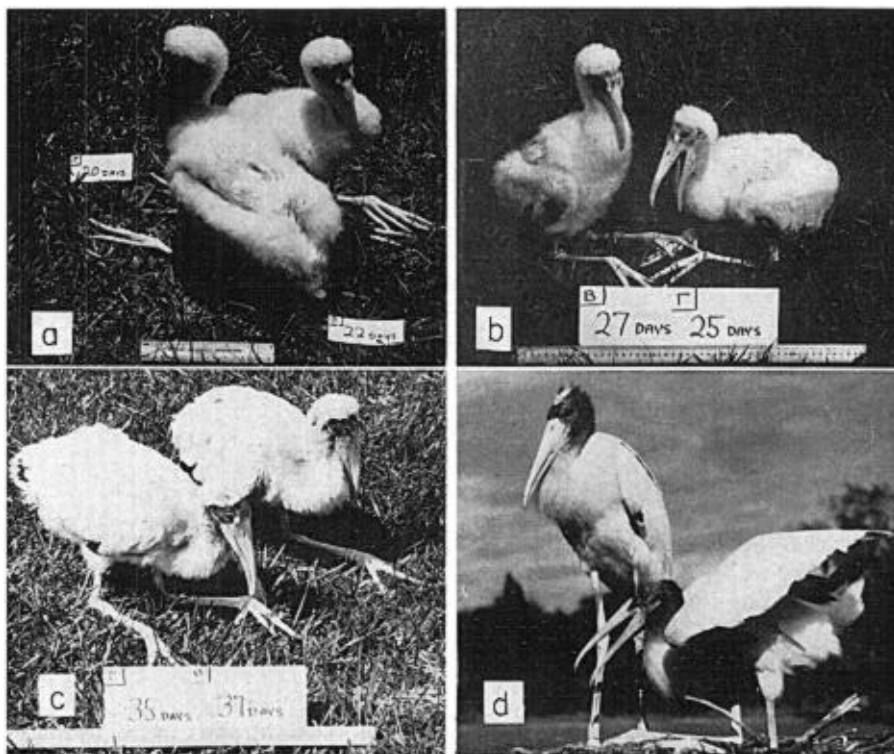


Fig. 2. Nestling Wood Storks: a, 22 days old (front) and 20 days old (rear); b, 27 and 25 days old; c, 35 and 37 days old; d, 67 days old (left) and 63 days old (right). Ruler in "a" is 15 cm. long; ruler in "b" and "c" is 50 cm. long.

food consumption, or longest primary growth were obtained. Except in the example of Young B (a male), which died as a result of a handling accident at 41 days of age, it was not possible to determine the sex of the young birds. Adult Wood Storks have a slight sexual dimorphism in size, males being larger than females. The four linear measurements (culmen, tarsus, middle toe, and longest primary) were also taken from Young D in its natural nest at 33 days of age.

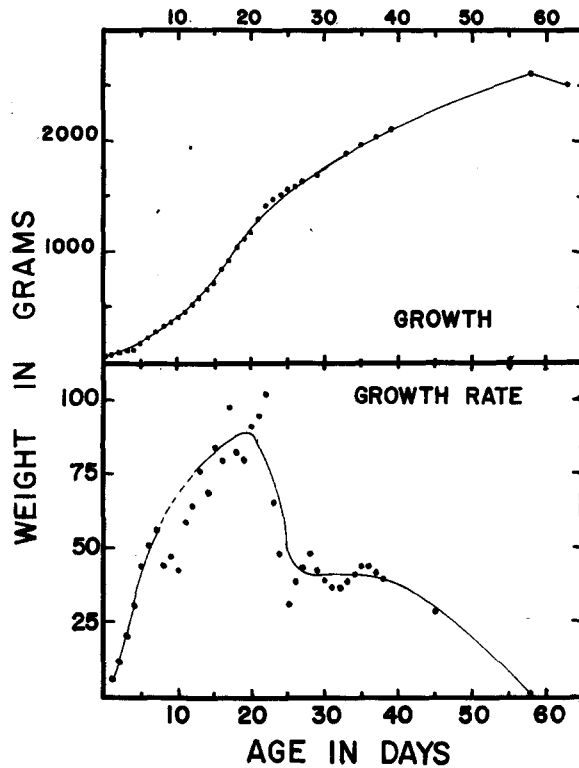


Fig. 3. Mean growth in body weight (upper) and mean growth increments per day (lower) in three nestling Wood Storks. See text for explanation of dotted portion of lower curve. Lower curve plotted as moving averages of five.

The general development and increase in size of the captive young paralleled that of wild young which were being observed concurrently under natural conditions in the nesting colony. It is believed that the information obtained from the hand-raised young was representative of natural development as it occurred in the Panther Point colony during the 1960 season.

RESULTS

Growth.—The gross morphological changes from hatching to fledging are shown in figures 1 and 2. The young were covered with a sparse gray down (protoptiles) at hatching which was replaced after about ten days with a very dense, woolly, white second down (mesoptiles). By the end of the third or fourth week, the nestlings were over half

as large as the adults and had well developed coordination; they were able to stand for long periods and frequently exercised their wings. The plumage, which had remained predominantly white except for the developing black remiges and retrices, turned smoky gray on the head and neck during the sixth and seventh weeks. By the eighth week the young could fly, and, when ready to leave the nest during the ninth week, resembled the adult in size; only the feathered head and yellow bill marked them as immatures.

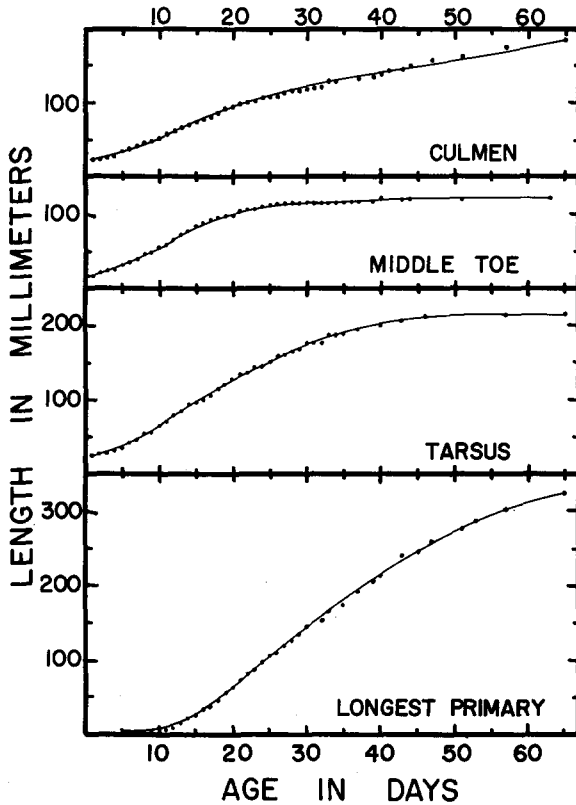


Fig. 4. Mean increases with age of linear anatomical dimensions in four nestling Wood Storks.

Mean growth in body weight and growth rate (grams added/day) are shown in figure 3. The increases of linear anatomical dimensions with age are shown in figure 4.

The average weight at hatching was 62 grams. From hatching to about six or seven days of age, the amount of body weight added each day increased rapidly; growth was exponential between the third and sixth days. Between eight and eleven days of age the young became ill, and growth was somewhat retarded. After that body weight increments again increased until approximately the twenty-third day when the rate of growth began to decrease sharply (fig. 3). Therefore, the time between 11 and 23 days was the period of most rapid growth as measured by gross gain in body weight. However, instantaneous relative growth calculated from the formula given by Brody (1945:508), which shows growth at a given time in relation to body size at that time, reached a peak of about 28 per cent between the third and sixth days and then declined steadily (fig. 6).

The patterns of linear growth of the middle toe and tarsus were roughly similar to that of body weight. Middle toe growth reached its highest rate (ca. 5.3 mm./day) in the period between four and sixteen days of age, and by the thirtieth day of life, the middle toe had almost reached its full length. Tarsal growth was most rapid in the period between six and 29 days of age (ca. 5.5 mm./day) and continued until approximately the fortieth or forty-fifth day. Development of the longest primary wing feather started

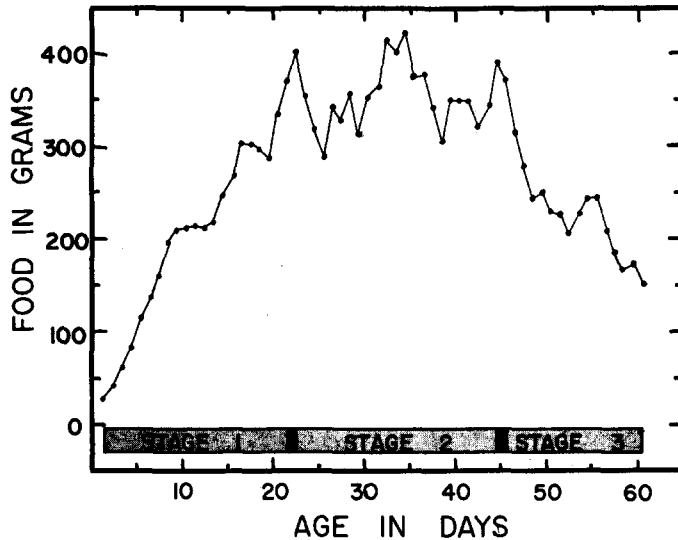


Fig. 5. Mean daily food consumption (live weight) of three nestling Wood Storks. Points plotted as moving averages of three. Horizontal bar graph indicates duration of the three feeding stages (see text).

later than the other measured body parts. It first broke through the skin at six days of age, reached a maximal rate of growth (ca. 7 mm./day) between 15 and 50 days and was still growing at a diminished rate at the time of normal fledging at about 60 to 65 days. Although measurements of other feathers were not taken, the growth of all the flight feathers seemed to parallel that of the longest primary (cf. figs. 1, 2). The culmen increased at a rather uniform rate (ca. 2.5 mm./day) from hatching until after fledging. At the time the young were ready to leave the nest, their bills were noticeably shorter and less decurved at the tip than the bills of most adults. The culmens of the captive young averaged about 50 mm. shorter at fledging age than the bills of two adult storks collected in southern Florida in 1959. Obviously the bills continue to grow for some time after the young leave the nest. It is not definitely known when the juvenile assumes the appearance of an adult, but it is probably not until its second or third year.

Food consumption.—In nature the young Wood Stork is fed by regurgitation. The meal is deposited on the floor of the nest by the parents. Both sexes feed the young. Hundreds of feedings were watched at the nesting colony, and no instance was observed of a parent placing food directly into the mouth of the young, although occasionally a hungry nestling caught the food before it hit the floor of the nest. The diet consists mainly of fish, which vary in length from 20 to 250 mm., depending on the feeding areas frequented by the parents and the swallowing capabilities of the young birds. In general, the average size of the prey eaten increases with the size of the young.

Food-grabbing motions, directed at the nest floor, were shown by the young immediately after hatching, but they were largely uncoordinated and usually unsuccessful until about the second day of life. By then the young were able to see and pick up food from the floor of the nest quite efficiently.

The pattern of food consumption is shown in figure 5. The amount of food consumed daily by the nestlings was subject to fluctuations of some magnitude; a possible cause of these variations will be discussed later in this paper. For purposes of graphing, these

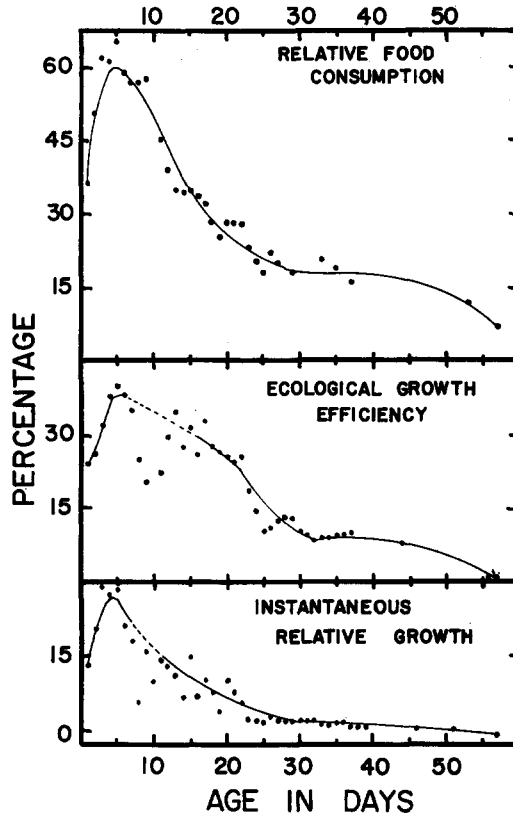


Fig. 6. Relative food consumption, ecological growth efficiency, and instantaneous relative growth in three nestling Wood Storks. See text for explanation. Curves plotted as moving averages of five.

fluctuations were smoothed by plotting the points as moving averages of three of the mean daily food consumption. The general pattern of food intake may be divided into three stages (fig. 5) as follows: (1) hatching to 22 days—linear increase in daily food intake; (2) 23 to 45 days—plateau of maximal food intake (ca. 350 gms./nestling/day); and (3) 46 days to fledging—linear decrease in daily food intake. On the basis of the averages obtained, we may estimate that a young Wood Stork consumed about 16,500 grams (nearly 40 pounds) of food during the nestling period of approximately 60 to 65 days, when it is completely dependent upon parental feeding. Of this total, over 50 per cent is eaten during the middle third of the nestling period, between the ages of 23 and 45 days.

Relation between food consumed and growth.—Early in their life, the young storks consumed a much larger quantity of food in proportion to their size than they did later (fig. 6). The three- to five-day-old young ate over 60 per cent of their own weight in food. Thereafter, the amount eaten in relation to body weight steadily declined. As is shown in figure 6, ecological growth efficiency and instantaneous relative growth also reached their peaks during the same period as relative food intake reached its peak. Over 35 per cent (live weight) of ingested food was converted to biomass between the third and seventh day. Since the caloric values per gram (live weight) of birds and fish are similar, the ratios in figure 6 probably also represent actual efficiency of conversion of ingested calories to "production of calories."

The points below the dotted portions of the smoothed curves in figures 3 and 6, during the period of eight to eleven days, resulted from an illness which affected the birds being studied at that time. After several days of hand-feeding and administration of vitamin supplements, they returned to normal.

By the thirtieth day, the food intake in relation to body size, the ecological growth efficiency, and the absolute and relative growth rates had declined sharply. The ecological growth efficiency and the growth rates continued to decline, until in the 50- to 60-day-old bird, practically all food was used for energy requirements and maintenance, and very little was channeled into the production of additional body material.

DISCUSSION

The rapid increase and then decrease in growth rate results in the typical sigmoid growth curve (fig. 3). Brody (1945) has shown that a growth pattern of this type can be divided into two theoretical phases: the self-accelerating phase, which occurs early in the growth pattern and is characterized by an increasing rate of growth, and the self-inhibiting phase, during which the rate of growth progressively decreases. In the nestling stork (fig. 3), the rate of increase climbs rapidly (growth is exponential between the third and sixth days) until approximately the seventh day (self-accelerating phase), slows between the eighth and twenty-third day, and then drops (self-inhibiting phase).

It is an accepted physiological fact (cf. Bertalanffy, 1957) that the relative metabolic rate (that is, respiration/gram tissue) of an organism varies inversely with the body size. Thus it would be expected that, while the total metabolic rate (respiration/bird) would be lower, the relative metabolic rate would be higher in a smaller than in a larger (older) nestling. Using the values of growth and food consumption measured in the present study, it is possible to calculate the respiration rates of the nestlings at different ages on the assumption that the food consumed which was not incorporated into growth was used for respiration. It should be emphasized that these calculations, shown in table 1, are based on an estimated assimilation efficiency of 90 per cent. In view of the statement by King and Farner (1961:271) that assimilation efficiencies in birds vary between 70 and 90 per cent (depending on species of bird, type of food, and environmental conditions) and the fact that in the nestling storks the volume of fecal and urinary loss was quite small compared to the volume of food intake, this seems a reasonable estimate. The validity of the calculated respiration rates depends upon the accuracy of this estimate. Estimated caloric values of stork biomass and stork food are shown in table 3 and discussed on page 179.

Table 1 shows, as expected from the statement above, that total body respiration increased as body weight increased, whereas the relative respiration (per kilogram of tissue and per kilocalorie of tissue) decreased as body weight increased. By the ninth

TABLE 1
WEEKLY RATES OF TOTAL BODY AND RELATIVE RESPIRATION IN NESTLING WOOD STORKS,
CALCULATED FROM MEASURED VALUES OF GROWTH AND FOOD CONSUMPTION
AND ASSUMING A 90 PER CENT ASSIMILATION EFFICIENCY

Week	Food intake kcal.	Food assimilation kcal.	Growth added kcal.	Assimilation		Respiration	
				—production kcal./bird/week	kcal./bird/day	kcal./kgm./day	kcal./kcal./day
1	1023	921	392	529	75.6	425	.242
2	2521	2269	721	1548	221.1	424	.242
3	3648	3283	1073	2210	315.7	306	.175
4	3853	3468	646	2822	403.1	261	.149
5	4526	4073	486	3587	512.4	278	.159
6	3762	3386	404	2982	426.0	202	.115
7	3716	3344	343	3001	428.7	187	.107
8	2716	2444	343	2101	300.1	121	.069
9	1412	1271	-140	1410	201.4	79	.045

week, when growth had virtually stopped, the relative respiration had dropped to 79 kcal./kgm./day. This is in close agreement with the metabolism values obtained by Benedict and Fox (1927) for adults of similar species of wild birds and probably closely approximates the existence metabolism, that is, the energy used in normal maintenance of the body, of the adult Wood Stork. Benedict and Fox found metabolic rates of 50 kcal./kgm./day for a Jabiru Stork (*Jabiru mycteria*) which weighed 5.47 kilograms and 73 kcal./kgm./day for Great Blue Herons (*Ardea herodias*) which weighed an average of 1.82 kilograms. It should be taken into consideration that the figures given by Benedict and Fox represent values for birds confined in respiratory chambers and, therefore, are probably slightly lower than the normal existence metabolism of these birds. It might be argued that the nestling storks during their ninth week did not fly and, therefore, did not use as much energy as would be used by normal adults. While this is true, they did engage in frequent lusty foot-races with the investigator in attempts to escape, and this probably helped to raise their average daily energy consumption to near that of free-flying storks.

As body mass and total respiration increased in relation to energy intake, the portion left for bodybuilding became progressively less and the ecological growth efficiency and relative growth rate (fig. 6) dropped. Although relative food consumption (fig. 6) dropped after five days of age, absolute food consumption (fig. 5) continued to increase at a sufficient rate to keep the absolute growth rate (fig. 3) increasing until the twenty-third day. The rapid decline in the rate of weight increase shown in figure 3 corresponds precisely with the leveling off of food intake shown in figure 5 (beginning of Stage 2). The middle plateau of maximum food consumption of about 350 gms./nestling/day, when the nestlings were from 23 to 45 days old, apparently represents the upper limit of food that can be ingested by the young birds. This limit may have evolved to equal the maximum amount that the parents can normally provide.

The considerable day-to-day fluctuations in food consumption mentioned earlier seemed to be the result of an unlimited food supply in captivity. In the presence of superabundant food, the birds showed a tendency to overeat for one or two days, succeeded by a seemingly compensatory loss of appetite on the following day or two. A detailed discussion of the regulative mechanisms of appetite may be found in Hollander (1955). Occasionally the eating cycles of two birds became synchronized, and the amplitude of the average fluctuation was increased. The ability to overeat is probably advantageous

in nature in that it allows the birds to take fullest advantage of a temporarily abundant food supply and then survive intervening periods of food scarcity.

As previously mentioned, the nestlings were affected by an illness between the eighth and eleventh days; at the time, the nature of that illness was a mystery. A fact uncovered since then in the literature may offer a tentative explanation. Until about three days before the illness developed, the young had been fed freshly caught fish of a type similar to those normally fed to young Wood Storks by their parents. Then their diet was changed to gizzard shad exclusively. It happens that this species of fish contains "considerable amounts" of thiaminase (Miller, 1960), and this enzyme in fish has been shown to cause a thiamine (vitamin B₁) deficiency in some animals (Melnick, Hochberg, and Oser, 1945). The symptoms present in the young storks, for example, loss of appetite, weakness, and loss of coordination, resembled the thiamine deficiency syndrome of Chastek paralysis (Stare, 1942). Although I was at the time ignorant of the thiaminase content of shad, I suspected some type of dietary deficiency and administered vitamin supplements (*Geritex*, Tex Drug Co., Philadelphia, and *ABDEC*, Parke-Davis) which contained thiamine, among other ingredients. The birds promptly recovered and remained apparently healthy thereafter; the vitamin supplement was given at least twice weekly throughout the rest of the study period. Green, Carlson, and Evans (1942) report that Chastek paralysis in foxes was cured with thiamine administration.

A number of fish species have been tested for the presence of thiaminase (Deutsch and Hasler, 1943), and it is interesting to note that none of the six Centrarchidae examined showed the enzyme; this family of fish, including such genera as *Lepomis* and *Chaenobryttus*, makes up a large part of the normal diet of the Wood Stork. Clearly further experiments are necessary to reveal whether the illness described here was truly Chastek paralysis. Such a study would have interesting ramifications in the investigation of food preferences of storks and other fish-eating birds. In this connection it should be noted that Trautman (1940:110) reported gizzard shad to be an important food at certain times for fish-eating birds at Buckeye Lake, Ohio. This, of course, does not rule out the possibility that those birds were utilizing another source of thiamine and thus were not adversely affected by the thiaminase in the shad.

It is possible that the development of the large feathers of the body, as shown by the longest primary (fig. 4), contributes to the decrease in the growth rates of other body parts; that is to say, the feather follicles "compete" with the other body parts for a share of the incoming energy. The growth curves show that the rates of increase of body weight, middle toe, tarsus, and to a slight extent culmen, decrease shortly after the longest primary begins its fastest rate of increase on about the fifteenth day. Portmann (1945), Sumner (1933), and Weller (1957) have also suggested that the development of flight feathers in young birds may cause a reduction in the growth of other body parts.

As Portmann (1945, 1950, 1955) has shown, altricial birds are hatched with poorly developed organs of locomotion and sense but with highly developed organs related to metabolism, for example, alimentary tract, lung, liver, and kidney. This type of development is apparent in the Wood Stork during its first week (fig. 1). Consequently the young altricial bird can ingest and metabolize enormous quantities of food in relation to its size and grow rapidly during early life when growth efficiency is the highest. On the other hand, precocial birds, which leave the nest soon after hatching, have more "balanced" organs and may be expected to show a slower growth rate and take a longer time to attain adult size.

Table 2 shows a direct comparison of instantaneous relative growth rates of the Sandhill Crane (*Grus canadensis*), a precocial species (data from Walkinshaw, 1949:

TABLE 2
COMPARISON OF INSTANTANEOUS RELATIVE GROWTH RATES IN AN ALTRICIAL (WOOD STORK)
AND A PRECOCCIAL SPECIES (SANDHILL CRANE)

Period (days)	Average Instantaneous Growth Rates			
	Wood Stork (altricial)		Sandhill Crane (precocial)	
	Per cent	Grams	Per cent	Grams
Hatching	(62) ¹	(133)
0-6	21.9	(232)	4.8	(177)
6-12	14.2	(544)	7.3	(275)
12-15	10.6	(748)	7.0	(342)
15-20	9.0	(1176)	4.8	(435)
20-26	4.9	(1581)	8.0	(704)
26-28	3.0	(1680)	4.1	(764)
28-35	2.2	(1958)	7.2	(1262)

¹ Actual weight at end of each period is shown in parentheses.

107), and the altricial Wood Stork, both of which attain approximately the same adult size. For the first three weeks, the altricial stork grows much faster than the precocial crane. At 20 days of age, the stork has reached almost half (1176 gms.) of fledging size, while the crane has attained about 12 per cent (435 gms.) of its full growth, in spite of the fact that the crane weighed over twice (133 gms.) as much as the stork (62 gms.) at hatching. Thus in the first 20 days of life, the stork undergoes an 18-fold weight increase and the crane only a 2.3-fold weight increase. After the third week, the crane continues to grow at about the same moderate rate, and it is still growing at 175 days (Walkinshaw, *op. cit.*). The relative growth of the stork decreases after three weeks to a rate less than that of the crane, and by the ninth week, weight increase in the stork has virtually stopped. Dawson and Evans (1957, 1960) and Banks (1959) have shown that smaller altricial species have even higher instantaneous relative growth rates and that these species reach adult size very rapidly.

It has been suggested that biological systems may sometimes sacrifice maximum efficiency for maximum output (Odum and Pinkerton, 1955). It therefore might be expected that altricial species are less efficient than precocial species in food conversion during their rapid growth. In this connection, it is interesting to compare the ecological growth efficiencies (using calories produced/calories ingested) in the altricial stork and the precocial chicken (*Gallus*). Chicken efficiencies were figured using the data of Reed and Skoglund (1959) on food consumption and growth. In converting these data into a form comparable to the stork data, the following assumptions were made (see table 3): (1)

TABLE 3
ASSUMED WATER CONTENT AND CALORIC VALUES USED IN CALCULATING RESPIRATION
AND EFFICIENCIES

	Per cent of water content	Kcal./gm. (dry wt.)	Kcal./gm. (live wt.)
WOOD STORK			
Biomass	65	5	1.75
Food (= gizzard shad)	70	5.5	1.65
CHICKEN			
Biomass	65	5	1.75
Food (= broiler food)			
Mash form (1st 2 weeks)	10	4.5	4.05
Pellet form (after 2nd week)	5	4.5	4.275

TABLE 4
COMPARISON OF ECOLOGICAL GROWTH EFFICIENCIES AND INSTANTANEOUS RELATIVE GROWTH RATES IN ALTRICIAL (WOOD STORK) AND PRECOCIAL SPECIES (CHICKEN)¹

Period (weeks)	Growth efficiency (calories production/ calories intake)		Average instantaneous relative growth rate (per cent)	
	Wood Stork	Chicken	Wood Stork	Chicken
1	0.38	0.34	19.8	12.8
2	0.29	0.26	12.7	9.6
3	0.29	0.23	9.0	8.0
4	0.17	0.23	3.5	6.7
5	0.11	0.21	2.2	5.3

¹ See text for treatment of data.

chicken and stork biomass are equal in caloric value per gram, that is, water content and tissue composition are the same; (2) high energy broiler food, which has a high corn and soy bean content (Titus, 1955), has a caloric value of about 4.5 kcal./gm. dry weight, according to a mimeographed table printed by F. B. Golley in 1959; broiler feed in mash form, fed for the first two weeks, contains about 10 per cent water, and the pellet form, used after the second week, contains about 5 per cent water; (3) stork food (shad) contains about 70 per cent water and has a caloric value of about 5.5 kcal./gm. dry weight; about 15 per cent of live weight of shad is protein and 12 per cent is fat (Miller, 1960); (4) a chicken averages 34 grams at hatching (Witschi, 1956:318). The ecological growth efficiencies for the stork and chicken calculated using these assumptions are shown in table 4. It is surprising to note that the chicken was slightly less efficient than the stork in its conversion of food to biomass during the first three weeks of life, being 34, 26, and 23 per cent efficient during the first, second, and third weeks, respectively, whereas the stork was 38, 29, and 29 per cent efficient during the same periods. Moreover, the stork was growing at a much faster relative rate (20, 13, and 9 per cent) than the chicken (13, 10, and 8 per cent) during that time.

What at first appears to be a contradiction of the principle discussed by Odum and Pinkerton is due, I believe, to the effects of at least two complicating factors. First, the stork in eating a relatively larger amount and growing faster, reduces the maintenance costs during growth below those of the chicken by compressing the process of growth in time. Second, while the young chicken is quite active during its growing period, the stork nestling spends most of its time between meals sleeping and thereby reduces its energy demands. These factors act to produce a higher efficiency in the altricial species.

The rapid early growth pattern exhibited by altricial birds adapts them to survive in several ways. In the Wood Stork, as in many other altricial species, the nestling period is one of high mortality from various causes, such as predation, adverse weather, failure of food supply, death or desertion of parents. Therefore, any mechanism tending to shorten this period of helplessness and vulnerability will have survival value and be selected during the evolution of the group.

In nature, the young storks are seldom if ever left alone by their parents while less than approximately three weeks old. Up to that time one parent remains at the nest while the other forages. Apparently such behavior provides protection not only against inclement weather, but against other storks as well, which were frequently observed attacking and attempting to take over occupied nests. By the end of the third week, both parents begin gathering food at the same time. The young are then large enough (fig. 2a) to stay alone and to effectively defend the nest against intruders. This shift in parental

behavior coincides with the beginning of greatest food consumption by the young (fig. 5) and also with a striking change in behavior on the part of the young. They change from docile creatures, with no outward sign of fear or aggression, to quite fierce attackers when confronted with strange or frightening objects, either animate or inanimate. In captivity they attacked vigorously with their sharp-edged bills and, on one occasion, drew blood from the hand of an innocent human bystander. A similar change in temperament was noticed in wild young which were handled during banding operations. Those less than about three weeks old were very tame and crouched low in the nest when approached, whereas those that were older attacked viciously and sometimes attempted to leave the nest. Comparable behavior changes have been described for the young of the White Stork (*Ciconia ciconia*) by Schüz (1943). These shifts in behavior of parents and young, which free both parents to search for food, undoubtedly add to the chances of survival of the young by insuring a more plentiful food supply. As Schüz (1942) and Owen (1960) have shown for other ciconiiform species, food supply is often a critical factor in nestling survival.

SUMMARY

Growth in relation to food consumption was studied in four nestling Wood Storks raised under semi-natural conditions in captivity during the 60- to 65-day nestling period. Growth of the middle toe and tarsus roughly paralleled that of body weight; the middle toe had attained its full length by about the thirtieth day and the tarsus by about the fortieth or forty-fifth day. The culmen grew at a rather uniform rate throughout the nest life. Growth of the longest primary, which started later than the other measured body parts, reached its highest rate about the time that body weight, middle toe, and tarsal growth slowed, suggesting that plumage growth may compete with other body parts for a share of the ingested energy.

Food consumption was measured daily and may be divided into three stages: (1) hatching to 22 days (linear increase); (2) 23 to 45 days (plateau of maximum food consumption; ca. 350 gms./nestling/day); (3) 46 days to fledging (linear decrease). Behavioral changes by both the parents and the young observed in nature appeared to be correlated with these stages in food consumption. From the averages obtained in this study, it is calculated that the young Wood Stork consumes approximately 16.5 kg. (live weight) of food during the nestling period; over 50 per cent of this total is eaten during the middle third of the nest life.

Relative growth reached an early peak at three to six days of age that coincided with high relative food consumption. Absolute growth reached a later peak at 15 to 23 days of age that coincided with high absolute and medium relative food consumption. After the peaks in relative and absolute growth, a progressively greater portion of the energy intake was channeled into respiration, resulting in a decreasing ecological growth efficiency.

A comparison of relative growth between the altricial Wood Stork and the precocial Sandhill Crane shows that the former grows at a much faster rate and reaches full size sooner. A comparison of relative growth and ecological growth efficiency between the stork and the precocial chicken shows that the stork grows at a faster rate during the first three weeks and is slightly more efficient in food conversion than the chicken.

An illness, apparently caused by a vitamin B₁ deficiency induced by the thiaminase contained in their food, gizzard shad, lowered both the growth rate and growth efficiency when the young were eight to eleven days old. The birds recovered after being given vitamin supplements which contained thiamine.

It is suggested that the altricial mode of growth is adaptive in that it results in the shortest possible exposure to mortality during the nestling stage of development. Rapid early growth during the period of high relative food intake, coupled with high growth efficiency, results in the young storks being large enough to defend the nest by the end of the third week of age and allows both parents to forage during the period of greatest food consumption by the young, thus insuring a more plentiful food supply.

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