GROWTH AND DEVELOPMENT OF NESTLING BROWN PELICANS

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INTRODUCTION

Growth in birds has recently received considerable attention. Numerous one-year studies of various species exist, and their ecological implications relative to clutch size and growth rate have been thoroughly reviewed by Ricklefs (1968, 1972, 1974). Because of the wealth of weight data available, Ricklefs used weight as his standard for analysis. LeCroy and LeCroy (1974) present a detailed study of four years of growth in Common Terns (*Sterna hirundo*) and elucidate the complicated interactions of different growth parameters, especially in regarding weight and wing length as means for aging nestlings.

In the present study I analyze growth data of four nesting seasons for the Brown Pelican (*Pelecanus occidentalis*), attempting to elucidate the following points: (1) determine the age and growth parameters for this species; (2) examine weight, and other characters such as bill, wing, and tarsus lengths as a measure of growth in this species; (3) to determine if external measurements demonstrate the physical condition of the individual bird, and (4) to use these external measurements as an indication of the age of the nestlings, and thus be able to determine the seasonality of breeding by sampling once or twice during the season. This is important since access to breeding colonies is often difficult, either because of time constraints or the inaccessibility of the colony, and because disturbance of the colony causes undue mortality (Schreiber and Risebrough, 1972).

METHODS

I measured growth parameters of nestling Brown Pelicans in 1969, 1970, 1971, and 1972. The pelicans nest in discrete units on Tarpon Key, Pinellas County, Florida. I selected one of these units for my growth studies, and measured nestlings in the same area each year, marking a total of over 250 nests for individual study. After noting the presence of the first nest at the beginning of each year, I visited the colony unit at approximately weekly intervals, from early March through July. In all nests included in this analysis the hatching day for one chick in each nest was known precisely. The hatching day of the remaining chicks was known within one or two days. Another criterion for including a nest in this analysis was a minimum of five weekly sets of measurements for one or more nestlings. For most nestlings that fledged, I obtained seven to 11 weekly sets of measurements. Sample size for the later nestling period is smaller because of the difficulty in capturing large nestlings in the mangrove (*Avicennia germinans*) without undue disturbance.

Measurements were taken of the length of the exposed culmen, wing (unflattened manus and manus plus longest primary feather), and external tarsus using dial calipers or meter stick; nestlings were weighed on the most appropriate Pesola spring balance (100, 300, 1,000, or 5,000 g); and notes were recorded on plumages. Individual nestlings were initially marked with Magic Marker (Permanent Black) and then banded with Fish and Wildlife Service bands when large enough to retain them (at about 30 days of age).

For comparison to the nestlings, the mean ± one standard deviation and range for a sample of "healthy" adult plumaged pelicans of known sex are given in Figures 1-4.

Measurements of individual nestlings were used to compare growth by covariance analysis on an IBM 360/65 computer in order to assess the importance of clutch size, sequence in the brood, and individual and year-to-year variations (Table 1). Growth measurements for each bird on individual days between years were not compared. Differences do exist, but I believe they are not critical to my objectives. Rather, the total growth curve during the nestling stage is important, not the day-to-day variability.

Table 1.

Nestling Brown Pelicans analyzed for growth parameters on Tarpon Key, Pinellas County, Florida.

Clutch-Sequence-Year size in clutch	Total Nests	Number of chicks Fledged	Died	Age when found dead
1 - 1 - 1969		2	0	
2 - 1 - 1969		3	0	
2 - 2 - 1969		2	1	33 days
3 - 1 - 1969		6	0	
3 - 2 - 1969		5	1	30 days
3 - 3 - 1969		0	6	7, 16, 17, 19, 32, 33 days
	11			
1 - 1 - 1970		5	0	
2 - 1 - 1970		7	0	
2 - 2 - 1970		4	3	25, 27, Unknown, days
3 - 1 - 1970		3	0	
3 - 2 - 1970		0	3	22, 27, 33 days
3 - 3 - 1970		0	3	9, 12, 14 days
	15			
1 - 1 - 1971		7	0	
2 - 1 - 1971		4	0	
2 - 2 - 1971		3	1	26 days
3 - 1 - 1971		6	0	
3 - 2 - 1971		6	0	
3 - 3 - 1971		1	5	5, 9, 12, 18, 21 days
	17			
1 - 1 - 1972		5	0	
2 - 1 - 1972		7	0	
2 - 2 - 1972		4	3	11, 17, 31 days
3 - 1 - 1972		1	0	
3 - 2 - 1972		0	1	39 days
3 - 3 - 1972		0	1	11 days
	13			

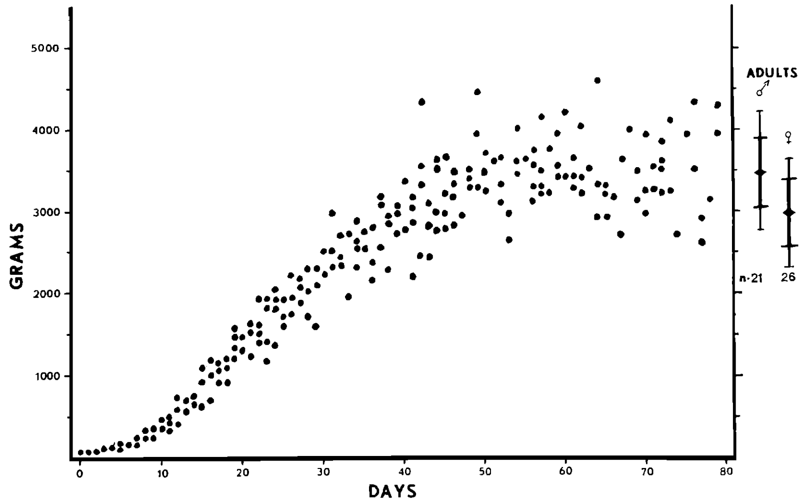

FIGURE 1. Changes in weight with age of nestling Brown Pelicans. Each point represents the mean weight for that day in each of four years, 1969–1972.

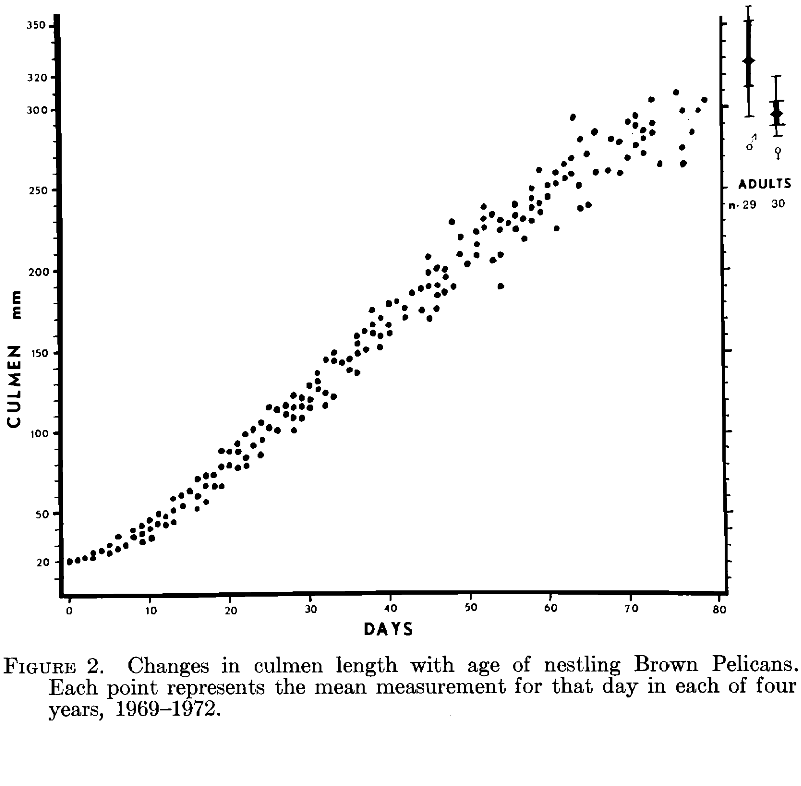

FIGURE 2. Changes in culmen length with age of nestling Brown Pelicans. Each point represents the mean measurement for that day in each of four years, 1969–1972.

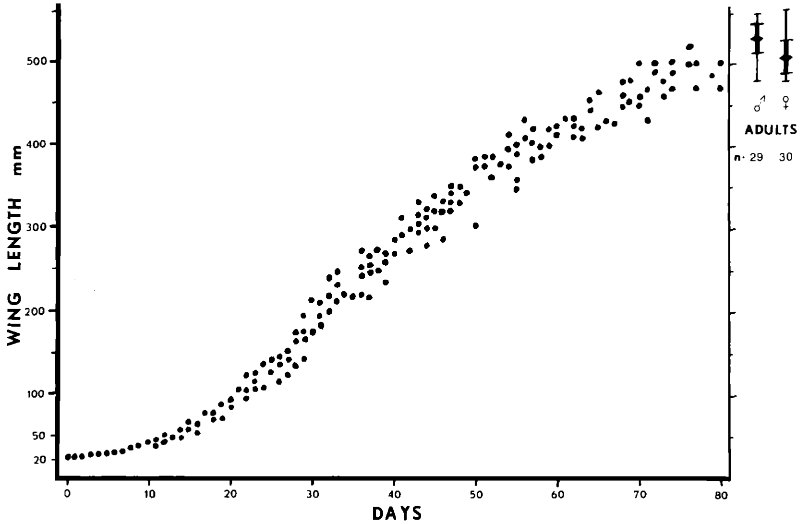

FIGURE 3. Changes in wing length with age of nestling Brown Pelicans. Each point represents the mean measurement for that day in each of four years, 1969–1972.

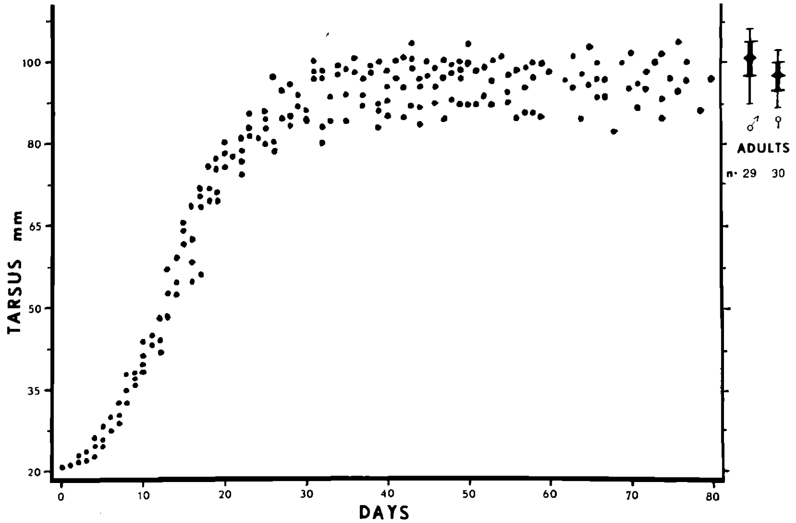

FIGURE 4. Changes in tarsal length with age of nestling Brown Pelicans. Each point represents the mean measurement for that day in each of four years, 1969–1972.

In 1970, I raised one nestling and in 1971 two nestling Brown Pelicans. The 1970 bird was approximately two weeks old when found on the ground below a nest. Probably it had been out of the nest for less than a day. This bird was kept in a wire cage approximately 4 × 4 × 4 feet, in an air conditioned building at approximately 72° F, under an irregular light/dark regime. I measured and weighed the nestling daily (usually during mid-morning hours) and then fed it thawed frozen fish once daily. The nestling fed readily by taking individual fish as they were offered. Daily intake was recorded when it would not accept another fish. Food intake was converted to percent of the daily initial weight. The two nestlings raised in 1971 were approximately 30-34 and 38-42 days old when found on the ground in the colony. Neither of these birds was fed for 13 days, but then they were kept on the same regime as the 1970 nestling.

RESULTS

Plumage development. Plumage criteria provide a relatively straightforward classification of nestlings into weekly age-classes (Table 2). Using external appearance alone most nestlings can be aged within about 10 days. Generally, naked pink young are less than 3-5 days old. They are purple between 4-9 days. Down first appears fluffy white on the rump at 10-12 days. Nestlings up to three weeks old are always closely brooded by one or both parents. The scapular feathers appear through the thick white down at about 30 days of age. A bird with a gray-brown head and back is approximately 45 days old. By 60 days the marginal coverts are all visible and most down is gone by 70 days. Nestlings have down only on the inside of the legs and wings at an older age and the backs, heads, and necks are brown-gray during their 10-11th weeks. The belly remains white throughout the nestling stage.

Age at fledging. I determined the exact day of fledging (departure from the nest) for the following nestlings:

	1969	1970	1971	1972
mean age at fledging	76	76	77	74
sample size	9	8	12	7

The earliest fledging occurred at 71 days (in 1971) and I know of several nestlings that remained in the nest for between 83 (in 1971) and 88 days (in 1972). Age at fledging did not relate to brood size.

Daily growth means. I believe that annual, mean measurements for each day (Figs. 1-4) illustrate the "normal" growth of Brown Pelicans and allow a ready comparison between years. I must stress that *means* obviously do not indicate the range of variation between individuals. However, most individuals that fledge grow within the bounds that the daily means closely estimate. Individual variation will be discussed below.

At hatching, weight varies between 45 and 80 g. Increase in weight occurs rapidly, and asymptotic weight is reached by approximately 50 days (Fig. 1). Comparison of weights of nestlings with adults indicates that some nestlings prior to fledging are

TABLE 2.

Summary of plumage and other characteristics of Brown Pelican nestlings. A (-) between numbers indicates a range in size. A (/) between numbers for feather length indicates the length of the sheath/length of unfurled feather.

Day	Descriptions
1	Naked, pink; lie prone in the nest, unable to hold head upright; eyes open but nictitating membrane does not respond in characteristic manner; neossoptiles present along posterior margin of the manus; closely brooded; egg tooth present; call extensively.
2-4	Purplish pink; nictitating membrane seems to function; chick tends to push itself backwards in nest, frequently crawling off edge of nest if left unattended.
5-6	Purple; egg tooth present but reduced in size; nestling covered with guano.
8-10	Egg tooth gone; can hold head upright and move in coordinated manner.
11-12	Neossoptiles still present on wing; down appears on rump as tufts less than 1 mm long.
13-14	Toenails black; down on back and rump 2-3 mm, head and neck naked.
16-17	Head begins to show down less than 1 mm long; body down is 5-6 mm; neck naked; chick covered with considerable guano.
19-20	Down present in primary region about 5 mm, no feathers or sheaths show.
21-23	Primary sheaths 4 mm, tipped with white puffy down up to 15 mm; head completely covered with light tan down, neck essentially naked but 1 mm down appears; rest of body down is 10-20 mm long.
24-25	Primary sheaths 5-8 mm; greater primary coverts 8/4 mm; manus naked of down, neck down 1 mm; secondaries 5/5 mm; scapulars may be visible as stubs. Bill greenish gray; feet white-cream. Spend considerable time sitting or standing upright rather than lying prone as up to about this time.
27-29	Primaries 15-18/7-10; greater primary coverts 10-14/12-20 mm; secondaries 9-12/20-24 mm; all primaries and secondaries have down on tips about 15 mm long; marginal coverts show white down; scapular feathers visible about 20 mm long; no stubs of rectrices visible.
30-32	Scapulars about 25 mm long and bird shows brown on back for first time. Primaries 15/25, longest primary is no. 6; greater primary coverts 15/25; secondaries 12-15/25; rectrices show as stub. Head is gray. About one-fifth of the marginals are brown.
35-37	Longest primary 20/35; greater primary coverts 12/30; secondaries 12/30; scapulars 25-35; outer 2-3 rectrices 5 mm long; down all over body is about 25 mm.
40-42	Primary no. 6 is 25/95, no. 1 is 25/70; greater primary coverts are 5/80; secondaries 20/70, all approximately the same length; 4 of the alula feathers present, longest 10/45; outer rectrix 22 mm, inner two are 28 mm, ones in between are 18 mm.
45-47	Primary no. 6 is 30/120; greater primary coverts 100 mm; longest secondary is 20/80 mm, most of them same length. Between ½ and 3/4ths of the marginal coverts are brown; all rectrices are 30-35 mm long with down on tips about 15 mm; circle of feathers present around the uropygial gland is visible through down, anterior ones

	are about 45 mm long; scapular feathers about 90 mm; back appears all gray-brown.
49-51	Primary no. 6 is 40/100 mm; greater primary coverts 75 mm; secondaries 20/90 mm; tertiaries 25 mm; rectrices 60 mm; scapulars 75 mm.
55-58	Primaries 25/125; greater primary coverts 75 mm; secondaries 10/120 mm; rectrices 90-100 mm. Marginals are about 7/8ths visible.
62-65	Primaries 25/180 mm; rectrices 115 mm; scapulars 100 mm; marginals fully cover the wings, no down on wing. Neck is about 1/3rd gray, rest downy. Down remains only on rump, mid-back, lower neck, belly, and in the axilla.
69-71	Most down gone, remaining only on flanks and under wings. Tail is 140-150 mm. Unable to fly, but move around well in mangrove.
72-75	Primaries 280 mm; rectrices 150-170 mm. Down only under legs and wings. Belly is white, rest of body is brown. Some are able to fly but most remain at or around nest for a few more days.

heavier than adults. As expected, there is considerable variation in weights on any given day and weight variation is the greatest of all measurements recorded, both as a colony mean and between individuals.

The culmen (Fig. 2) varies between 20 and 22 mm at hatching and growth is rapid and essentially a straight line from day 4-5 to fledging. Comparison of culmen length of nestlings with adults indicates that on the west coast of Florida, probably only some females achieve full bill length prior to fledging whereas the bills of most males continue to grow after they leave the nest. Some variation exists in average culmen length, especially between 40 and 80 days but prior to that time, daily measurements vary little.

The manus (Fig. 3) varies between 19 and 22 mm at hatching and little growth occurs during the first week. Growth increases notably during the second and subsequent weeks. Most nestlings have not reached full wing length prior to fledging. Some variation exists in wing length, especially late in the nestling period, probably related to the sex of the individuals. On a year-to-year comparison, mean wing length was the least variable parameter measured.

The tarsus (Fig. 4) varies between 20 and 22 mm at hatching and within 2-3 days it has begun to grow rapidly so that within 24 to 30 days the tarsus has reached full adult length. During growth the tarsus shows little variability but the size of legs does vary considerably once full length is achieved. Measurements of an individual vary little beyond 35 days but tend to decrease 2-3 mm during the last 2 or 3 weeks in the nest. While I did not measure the diameter of nestling legs, the leg is definitely thicker and rounder than in adults. Possibly this is due to fluid or fat accumulation around the tarsus. This condition is lost late in the nestling stage. I consider the roundness of the tarsus as an excellent indicator of the general health of an individual bird: those with round legs are healthier than those with flat or angular legs.

Statistical analysis. Covariance analysis of the mean growth curves of weight, culmen, wing, and tarsus indicate that no statistical differences existed between years for each parameter. Additionally, comparing individuals by brood size and position within the brood indicates no statistical differences in growth *between young that fledge.*

Growth of individuals. Figure 5 shows the changes in weight for the individuals in four broods of different brood size and two different years to illustrate weight changes of individual birds during the nestling stage. Six of these individuals fledged successfully (the first hatchling of 3 in 1969, first and second hatchlings of 3 in 1971, and both hatchlings of 2 in 1971) and gained weight in a similar manner. In all these birds maximum weight was achieved between 45 and 60 days of age and then as much as 600 g (16% of maximum) was lost prior to fledging. Three nestlings (second and third of 3 in 1969 and third of 3 in 1971) died within about a month after hatching. It is obvious that they stopped gaining weight during the week or so prior to death. The heaviest of the surviving nestlings was the first to hatch in a 3-chick brood and its two siblings died at 27 and 34 days of age. The chick from a 1-chick brood included here as an example gained weight at a level between the nestlings in larger broods. Based on the above data I believe that the growth of a given nestling is dependent on how often and how much the parents provide food and the chick's own genetically determined size.

Within brood survival. The above information along with interpretation of the number and sequence of the chicks that died or fledged contained in Table 1 clearly indicates that fledging success is greatest in the first chick to hatch in a multi-egg clutch or the single chick in a nest: None died (3-chick nests: 10 first hatchlings fledged, none died; 2-chick nests: 21 first hatchlings fledged, none died; 1-chick nests: 19 first hatchlings fledged, none died). However, in multi-chick nests, chances of survival of second and third hatchlings are reduced: (3-chick nests: 11 second hatchlings fledged and 5 died; 2-chick nests: 13 second hatchlings fledged and 8 died; and only 1 of 16 third hatchlings in 3-chick nests survived). Additionally, there is yearly variation in survival of second and third hatchlings: compare 1971 (a "good" year when only 1 of 8 hatchlings in 2-chick nests and 5 of 18 hatchlings in 3-chick nests died) with 1970 (a particularly "bad" year when 3 of 14 hatchlings in 2-chick nests and 6 of 9 hatchlings in 3-chick nests died). However, in chicks that fledge there are no statistical differences in the growth parameters measured here.

Growth as a percent of asymptote. To examine aspects of growth not illustrated in the actual growth curves I analyzed the measurements of all nestlings that fledged as an accumulated increase in weight and linear measurements as represented as a percentage of the asymptote achieved prior to fledging. Weight is about 2% of asymptote at hatching, more than doubles during the 1st, 2nd,

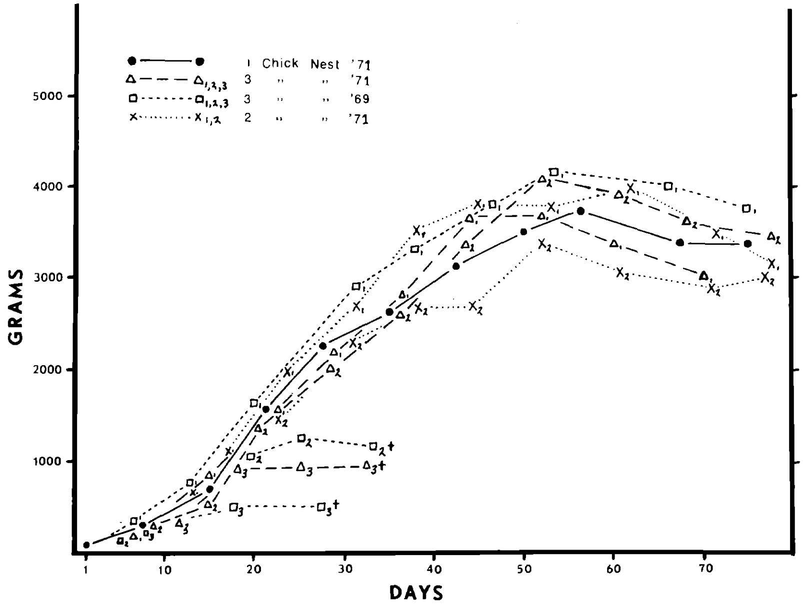

FIGURE 5. Changes in weight of individual nestlings in four nests of the Brown Pelican.

and 3rd weeks, and full weight is achieved at 8 weeks (Fig. 6). The tarsus is 21% of asymptote at hatching and achieves full length at 5 weeks. The culmen is approximately 7% of asymptote at hatching and the wing is approximately 4% at hatching. Increase in culmen length is essentially a straight line from the first week to fledging. The wing grows more slowly during the first 2-3 weeks but the wing and culmen parallel very closely during the 6-10th weeks and both closely approach full growth at fledging (Fig. 6).

Growth as actual gain or loss. Weight gain is 120 g the first week; 380-450 g during the 2nd, 4th, and 8th weeks; between 600 and 830 g during the 3rd, 5th, and 6th weeks; between 100-120 during the 7th and 10th weeks; and actual weight decreases during the 9th and 11th weeks (Fig. 7). The pattern of a decrease in g gained after the 5th week parallels the decrease in actual weight after reaching asymptote. This is especially noticeable in the weight loss during the 9th and 11th weeks. The increase in weight gained during the 8th and 10th weeks probably has parallels in the food consumption patterns of captives discussed below. The decline in weight gained during the 4th week seems unusual but perhaps is related to the growth spurt of the feathers during this time and the maximum growth of the legs. As these extremities undergo their maximum change in length the nestlings' energy allocation is channeled into leg and feather growth rather than into increasing weight. The tarsus increases 8 mm the 1st week, 15 mm the 2nd,

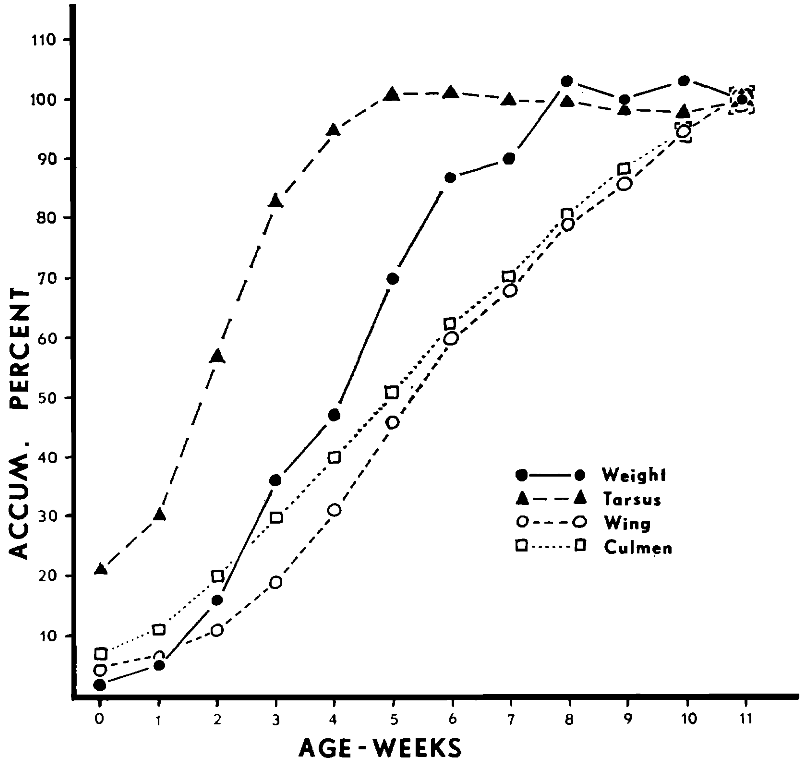

FIGURE 6. Accumulated increase in weight and linear measurements of nestling Brown Pelicans, represented as a percentage of asymptote achieved prior to fledging. Asymptote calculated as the combined adult male and female mean measurements.

and 26 mm the 3rd week; growth slows during the 4th and 5th weeks after which growth stops when full length is achieved during the 6th week (Fig. 7).

As expected from the growth curve of the culmen it increases between 15 and 30 mm per week after the 1st week with the greatest increase occurring during the 4th, 5th, and 6th weeks (Fig. 7). A decrease occurs concommitantly with a weight decrease during the 7th week. Growth decreases slightly during the 9th-11th weeks. The slower increase during the 3rd week is opposite to growth in weight, tarsus length, and wing length, because they continue to increase during this period. Perhaps the decrease in bill length increment is somehow related to the maximum growth of the tarsus during this period.

The wing exhibits increasing growth of 8, 24, 42, 59, 72, and 71 mm during each of the first 6 weeks after which time growth decreases to fledging. It is interesting that the irregular pattern of decrease-increase in mm growth of the wing so closely parallels the pattern of weight decrease-increase in g of weight gained during the last 5 weeks of the growth period.

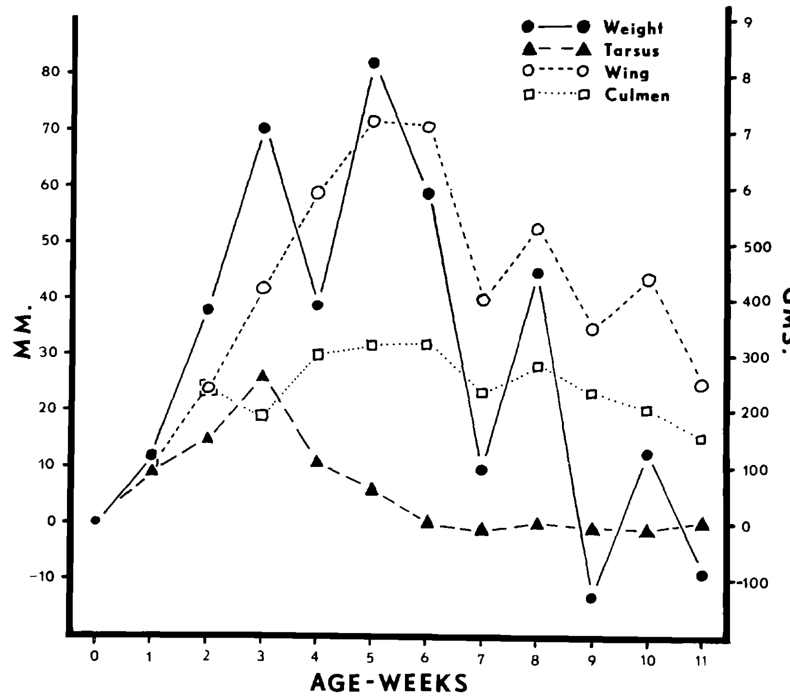

FIGURE 7. Weekly changes in weights and linear measurements of nestling Brown Pelicans.

Growth rate. Weight increases at a tremendous rate (Fig. 8) in the 1st, 2nd, and 3rd weeks, but then drops distinctly in the 4th week and thereafter, probably as the feathers begin developing. The increased rate during the 5th week probably reflects a recovery from the initial feather growth. A negative rate occurs in weight in the 9th week, and a very low rate of increase in the 7th, 10th, and 11th weeks, as asymptotic weight is reached and maintained. The tarsus exhibits maximum growth rate during the first 3 weeks, this slows during the 4th and 5th weeks, and then a negative or very near zero rate is maintained during the 6th through 11th weeks (Fig. 8). The wing grows slightly slower than the tarsus during the 1st week but the wing exhibits a maximum growth rate during the 2nd and 3rd weeks, this slows gradually and steadily from the 3rd to the 7th weeks, and then slower from the 7th to the 11th weeks but growth does continue to fledging, just as it does in the culmen. The culmen exhibits a high growth rate during the first week and reaches its maximum rate of increase during the 2nd week; rate slows markedly during the 3rd week, remains essentially the same during the 4th week, and decreases to fledging. During the 7th through 11th weeks the rates of the culmen and wing are remarkably similar and while the rate of growth of the

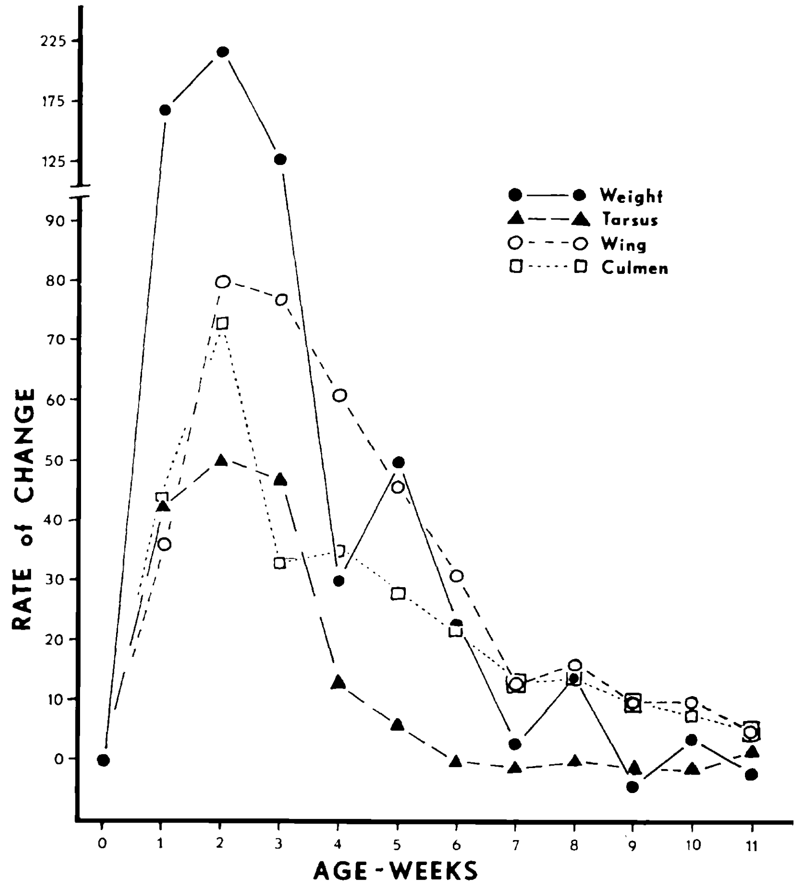

FIGURE 8. Weekly growth rate of nestling Brown Pelicans, calculated as the average week's increase divided by the average measurement in the preceding week times 100.

culmen is slower than that of the wing during the 3rd through 6th weeks, they change in close parallel during that time.

These different methods of analyzing the growth parameters of Brown Pelican nestlings present a varied picture. Obviously, the growth of a nestling depends primarily on the amount of food made available by the parents, and, as in many other studies, measurements of weight are the most variable of the parameters measured. Asymptotic weight is achieved in the Brown Pelican at approximately 50 days of age, or at about 60% of the time in the nest (Figs. 1 and 6). However, the maximum rate of weight change is achieved in the first 3 weeks (Fig. 8) thereafter changing less on a percentage basis. However, the maximum amount of actual weight change occurs during the 2nd through 8th weeks (Fig. 7), with an unexplained drop in the 7th week.

FOOD INTAKE BY CAPTIVE BROWN PELICANS

Feeding of nestling. I was unable to measure directly the amount of food consumed by nestling Brown Pelicans in the field. However, I did measure food intake, weight, and culmen and wing length in three chicks raised in captivity (Table 3, one chick illustrated in Fig. 9). Data from known-age nestlings indicate that one chick rescued in 1970 was 17-19 days old when captured. This chick consumed a variable amount of fish daily that consisted of a

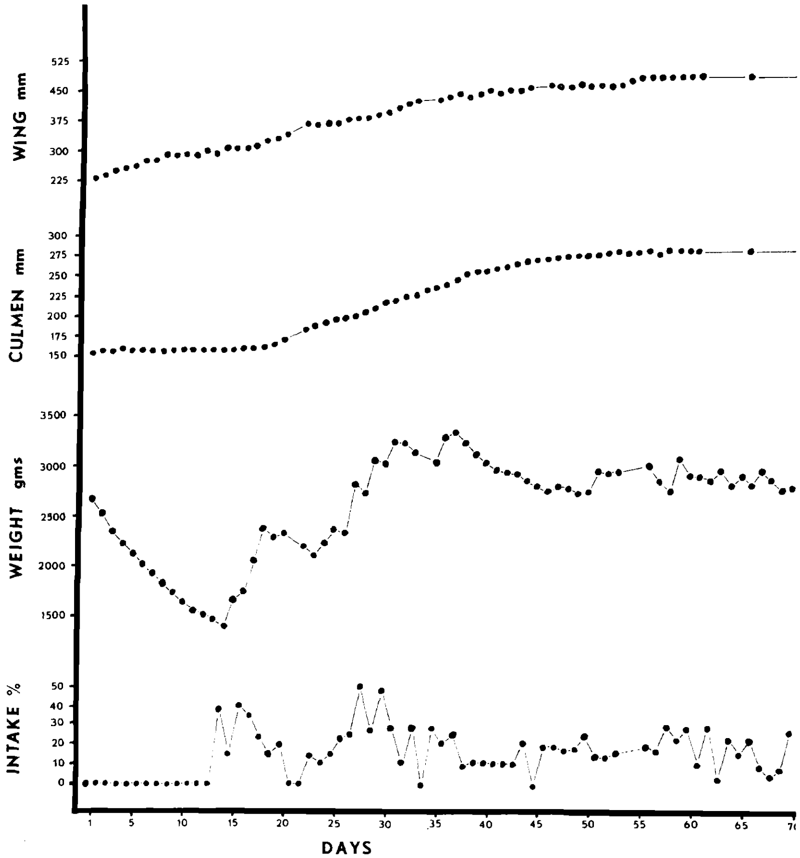

FIGURE 9. Changes in weight, culmen and wing length, along with food intake calculated as percentage of daily body weight for a nestling Brown Pelican that was 30-34 days old when captured.

remarkably constant 35-40% of its daily body weight as its weight increased steadily from 800 to 2,500 g during an initial 25 days. Between 25 and 45 days in captivity the increase to an asymptotic weight of ca 3,200 g was less regular and food intake fluctuated between 25 and 40% of daily body weight. During the next 15-

Table 3.

Food intake and weight changes in captive Brown Pelicans.

Notes on individual	Time period	Total intake (g)	Weight changes (g)	Average intake (g/day)	Intake as percent of daily body weight
17-19 days old on capture, found below nest; estimated to have been out of nest not more than 1-2 days.	initial 50 days (to asymptote)	33,960	800 to 3,200	679	29%
	additional 94 days (maintenance)	52,733	2,800-3,100	561	17.3%
30-34 days old on capture, found below nest; estimated to have been out of nest for several days. Upon capture weighed 2,660 g. Deprived of food for 13 days, lost 1,260 g, or 47 percent of initial weight at rate of 3 percent per day.	initial 25 days (to asymptote)	15,390	1,400 to 3,000	615	22%
	additional 50 days (maintenance)	23,185	2,700-3,000	464	16.8%
38-42 days old on capture, found below nest; estimated to have been out of nest for several days. Upon capture weighed 3,200 g. Deprived of food for 13 days, lost 1,430 g, or 45 percent of initial weight at rate of 3 percent per day.	initial 31 days	18,147	1,770 to 4,000	585	18.7%
	additional 63 days (maintenance)	34,587	3,200-3,400	549	16.1%
adult captured at a fishing pier on 16 July and held until 22 November 1971. Healthy when captured and underwent molt while in captivity.	129 days	76,166	3,300-3,500	590	17.5%
	fed 103 times during the 129 days	same	same	739 per feeding	21.8%

20 days body weight declined slightly and the culmen and wing reached full length at about 65 days whereas food intake declined and remained between 10 and 25% of body weight per day.

During the initial 50 days in captivity while weight increased and the culmen and wings grew steadily, this chick consumed 33,960 g of fish, or 679 g per day at a rate of 29% of daily body weight. During an additional 94 days while weight decreased to and then remained at a maintenance level of 2,800 to 3,100 g and the culmen and wing lengths remained constant, this chick consumed 52,733 g of fish, or 561 g per day at a rate of 17.3% of daily body weight.

Feeding of nestlings preceded by starvation. In 1971 on the same day I obtained two chicks which had been out of their respective nests 3-5 days. I estimated their ages at between 30-34 days for one chick and 38-42 for the other. Both were maintained without food or water for 13 days (Fig. 9 illustrates data for the 30-34 day-old-bird). Neither bird showed any obvious behavioral aberrations during the starvation period but they did intensify begging when I approached the cages late in the period. Both chicks lost weight at 3% per day, the younger losing 1,260 g or 47% of its initial weight and the elder losing 1,430 g or 45% of its initial weight. On the first day of feeding the smaller chick consumed fish totaling 38% and the larger chick 28% of their weights on that day. The next day they only ate 10% and 15%, perhaps as a reaction to the large intake on the previous day after so long a period of starvation. On the 3rd day of feeding, they took 35% and 40% respectively, then intake of the smaller chick declined steadily for four days; intake of the larger remained at 32% and 36% and then declined to 18% and 16%. During this period the weights increased rapidly and both chicks almost doubled in weight. Neither chick was fed for two days, after which food intake increased rather erratically, as did body weight. After asymptotic weight was achieved and the body weight was decreasing to a maintenance level, food intake remained between 10% and 20%.

The culmen and wing achieved full length at approximately 50 days in captivity (37 days after feeding began) and about 20 days after asymptotic weight was reached and the same time that maintenance weight was achieved. During the period of starvation, the wing (and thus the primary feathers) of both birds continued to grow although body weight decreased. However, the culmen stopped growing during this period. This information presents problems as regards the use of these parameters to age nestlings in the field and will be discussed more fully below.

During the period that the chicks were growing to asymptotic weight, the younger individual consumed 15,390 g while its weight increased from 1,400 to 3,000 g, or 624 g per day at a rate of 22% of daily body weight. During an additional 50 days after maintenance weight was reached the chick consumed 23,185 g, or 464 g per day at a rate of 16.8% per day. The larger chick consumed 18,147 g of fish while its weight increased from 1,770 to 4,000 g, or 585 g per day at a rate of 18.7% per day. During an additional 63 days after maintenance weight was reached the chick consumed 34,587 g, or 549 g per day at a rate of 16.1% of its daily body weight.

Feeding of captive adult. An adult was also maintained in captivity from 16 July to 22 November 1971. This adult underwent much of a complete molt during this time and maintained its body weight at 3,000 to 3,500 g. It consumed 76,166 g during this period of 129 days, or 590 g per day at a rate of 17.5% of daily body weight.

Food intake summary. I must emphasize that these birds were maintained in cages that prohibited complete wing flapping, allowed only some walking movements, and were at a relatively constant temperature of 72° F, considerably lower than ambient temperatures in nesting colonies in Florida. Thus, food consumption of 16-18% of daily body weight during maintenance of weight for all four birds reported here must be considered a minimal figure. With our present knowledge, it is impossible to estimate food consumption of wild pelicans, but it probably is somewhat higher than the 16-18% figure of daily body weight recorded here.

An interesting pattern of daily food intake during maintenance of weight was also demonstrated by these captive birds. Figure 10 illustrates fluctuations of weight of the two 1971 captive chicks along with fluctuations of food intake measured as a percentage of body weight. Intake follows a definite pattern, varying from 10% to 30% on a 3 -to 4-day cycle. This pattern is most evident when the birds were being fed daily (days 83-110) but also is evident during a period when they were not fed every day, with no food available every 3rd to 5th day (days 70-86). Comparing the days of largest and least food intake with fluctuations in body weight indicates that the days of greatest food intake are days when body weight is low, usually after one or two days of stable weight and lowered intake. Days of least food intake are days when body weight is high. During periods when food is withheld the body weight fluctuates more than when food is available daily and food intake also fluctuates more dramatically.

DISCUSSION

My data are insufficient to calculate the total amount of fish necessary to raise a nestling pelican, however, ca 50,000 g is probably a close approximation. The rate of consumption of the three captives corresponds well with the growth rates of wild nestlings (Fig. 8): the smaller chicks consume a higher percentage of their daily body weight at the time when weight is increasing most rapidly.

A significant result of these feeding experiments was the demonstration of the ability of nestling Brown Pelicans to withstand starvation. Even after a minimum of 13 (and probably 17-19) days without food when fish were made available again, the starved chicks could still beg, eat, and, later, grow normally. This ability to withstand long periods of starvation has obvious survival value to a species whose food availability in the wild is often erratic. Long-term effects of starvation on the neurophysiological ability of chicks remains unknown. Additionally, long-term effects of

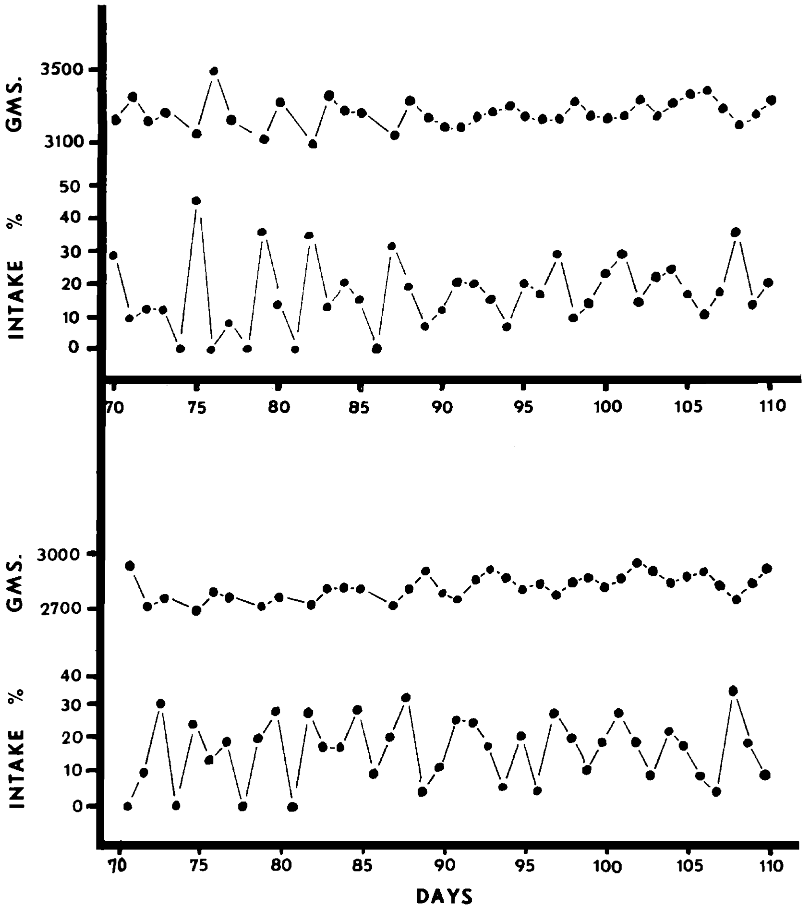

FIGURE 10. Fluctuations in weight and food intake calculated as percentage of daily body weight for two nestling Brown Pelicans.

starvation during the nestling period followed by successful fledging on postfledging survival also remain unknown.

If a similar pattern of fluctuating food intake as in the captives also exists in wild, free-living birds, it would hold far reaching implications for daily activity cycles. I do not have data on daily activity patterns of individual birds in the wild but do know that in situations such as at fish processing plants or fishing piers where fish are superabundant, some pelicans will eat so much that they are unable to fly afterwards. Certainly days also exist when an individual pelican is unable to capture any fish. This ability to eat large amounts when food is available and then to exist for one or more days of food unavailability, for whatever reason, has obvious survival value to a fish-eating bird whose food supply may be erratic.

The results of these growth studies indicate that for the Brown Pelican, growth of nestlings occurs within certain limits, at least for those that fledge successfully. Furthermore, they confirm Ricklefs' (1972) view that growth rate occurs within rather "narrow limits" set by adult body size and the mode of development (altricial in this case). The advantages of being the first chick to hatch in a clutch are obvious from these studies (Table 1 and Fig. 5). Any nestling that receives sufficient food grows within certain bounds and at a rate that ensures fledging. Nestlings that do not receive sufficient food starve to death. The relation between the range of weights at which nestlings fledge and postfledging survival still must be investigated. Variations in growth of individual birds occur through a variety of factors such as annual fluctuations in food availability, differences in food gathering ability of individual adults, differences in position of the chick in the brood as determined by hatching sequence, and also probably the sex of the individual nestling.

Ricklefs (1972), using my data on nestling weights for 1969 and 1970, calculated a growth rate (K_g) of 0.071 for Brown Pelicans and has discussed growth rate relations to patterns of growth in other families of birds. While weight is obviously an important parameter to measure and manipulate, the growth of the extremities along with weight must also be considered. Presenting the actual growth curves for the extremities and weight along with calculation of the actual changes in linear and weight measures, the time needed to achieve asymptote and the rate function for different parts of the growth period present a comprehensive view of growth which is most biologically useful, and thus all these data allow comparison of allometry between species.

Brown Pelicans undergo a rapid growth of the tarsus, reaching full length within about 30 days or three-eighths of the nestling period. The survival advantages of having the legs develop rapidly are obvious, especially for nestlings hatched in an arboreal habitat. Young pelicans spend considerable time during the nestling stage actually destroying their own nests. Within about 5-6 weeks they must remain perched on just a branch near or on the site where the nest was located. This pulling, tearing, and tossing of nest material with the bill is probably an important aspect of the development stage as the young develop muscular coordination of the head and neck. However, sufficient development of the legs is required to maintain their perch.

The relationship between weight and the lengths of the appendages remains unclear from these field observations and laboratory experiementation is needed. Obviously, the culmen, wing, and tarsus are dependent on food intake to provide the energy for growth allocation. Weight appears to be the major factor determining the ability of the individual to develop the remainder of the body. The rate of change in weight is a maximum during the first 1 to 3 weeks of the nestling period. Then weight increases much less rapidly with an increase during the 5th week over the 4th but then with a continuing decline in rate of increase. During this period the wing and culmen are continuing to grow at approximately the same rate but after weight has leveled off, growth rate of the wing and culmen slows and steadily decreases. The decline in actual amount of increase in weight closely parallels the changes in length of the wing and culmen, especially during weeks 6 and 7. Weight begins to decrease in week 5 but this does not manifest itself in decreases in culmen and wing length until a week or so later. This relationship between weight and wing length and bill length is somewhat clarified by the conditions in starved nestlings.

During two weeks starvation by two chicks, their weights decreased, the culmens ceased growing, but the wings continued to grow (Fig. 9). When the birds were fed again the culmens required almost a week of weight increase prior to commencing growth. This probably indicates that once the feathers begin to grow, the amount of resource allocation necessary for continued growth of a feather is considerably lower than that necessary to form the bone and other materials involved in culmen growth.

This information also indicates that while wing length measurements may indicate age of nestlings, they are not an accurate indicator of the health of individual birds. Species' differences undoubtedly exist, but I question the use by Ricklefs and White (1975) of wing length as a growth indicator in Sooty Terns (*Sterna fuscata*). I strongly believe that to obtain an accurate measure of age of nestlings in a colony based on measurements made at lengthy intervals or with only one visit to a colony during the season, one must measure weight, tarsus length, wing length, and bill length. With these several measurements age can then be estimated. Tarsus length is useful only early in the growth stage because it reaches full length so rapidly. Certainly the roundness and firmness of the tarsus is a good indicator of the health of individual birds, as is the contour of the mandible. The weight-to-wing length and culmen length relationship is also valuable, and probably is the most accurate measure of age and condition of the birds. As an example, a pelican with a culmen of 200 mm and wing length of 300 mm (indicating age 50 $\pm$ days) and a weight of only 2,000 g (indicating age 22-35 days) is not a healthy individual, and it is probably impossible to age that bird accurately, although the estimate arrived at based on culmen and wing length would be most accurate.

I believe that the culmen and wing length approach full adult parameters near the end of the nestling stage is probably the factor that "triggers" fledging. With the wing fully grown the birds are able to support their body and fly. In fact, older nestlings spend considerable time flapping their wings prior to fledging. It is my impression that several individuals I have observed make their first take-off did so almost by accident and were "surprised" to find themselves in the air. Young birds spend considerable time immediately after leaving the nest "learning how to use" their bills. They pick up and toss debris, plunge and withdraw the bill from the water, hold water in the pouch, and bill other fledglings prior to actually attempting to catch fish. It may be an advantage to develop the neck and bill musculature at this time while the culmen is slightly short and to learn how to manipulate the slightly shorter bill than a more unwieldy full bill length. Since the wing continues to grow during this period, it undoubtedly has reached full length before the young leave the vicinity of the colony and begin to dive for fish.

Adults *rarely* feed young away from the nest and young birds do not return to the nest after having once flown (Schreiber, unpubl. data). We know young birds are less efficient at feeding than are adults (Orians, 1969; Schreiber et al, 1975, and unpubl. data). Thus, fledging at weights greater than those of adults obviously provides the energy needed for survival until the young become proficient at feeding themselves.

This paper clarifies many points in the growth and development of nestling Brown Pelicans. The data contained herein allow estimation of the ages of any given pelican nestling. This information is valuable for studies such as the determination of the seasonality of breeding in colonies to which access is difficult or in which disturbance seriously affects productivity, as it does with pelicans. While this paper delimits some of the aspects of growth and food intake in the Brown Pelican, further studies should involve laboratory experimentation on metabolic rates and caloric measurements.

SUMMARY

This paper presents data on the growth and development of nestling Brown Pelicans in Tampa Bay, Florida as measured in four years, 1969-1972. The increase in culmen, wing, and tarsus lengths and weight are described along with plumage characteristics at various ages, thus allowing any given nestling to be aged. Normal growth occurs within certain limits and chicks that do not develop within these bounds starve to death. The interactions between weight and growth of the extremities are examined. Food intake in captive chicks is described and these findings are related to growth of wild nestlings. The implications to survival of different growth rates of various parts of the body of the individual are discussed.

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LITERATURE CITED

LECROY, M., and S. LECROY. 1974. Growth and fledging in the Common Tern (*Sterna hirundo*). *Bird-Banding*, **45**: 326-340.

ORIANS, G. H. 1969. Age and hunting success in the Brown Pelican (*Pelecanus occidentalis*). *Anim. Behav.*, **17**: 316-319.

RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis*, **110**: 419-451.

———. 1972. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis*, **115**: 177-201.

———. 1974. Energetics of reproduction in birds. *In* Avian Energetics, Paynter, R. A., JR., ed. *Publ. Nuttall Ornithol. Club*. No. 15: 152-292.

RICKLEFS, R. E., AND S. C. WHITE. 1975. A method of constructing nestling growth curves from brief visits to seabird colonies. *Bird-Banding*, **46**: 135-140.

SCHREIBER, R. W., AND R. W. RISEBROUGH. 1972. Studies of the Brown Pelican. *Wilson Bull.*, **84**: 119-135.

SCHREIBER, R. W., G. E. WOOLFENDEN, AND W. E. CURTSINGER. 1975. Prey capture by the Brown Pelican. *Auk*, **92**: 649-654.

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