## INTERRELATIONS BETWEEN CLUTCH-SIZE, BROOD-SIZE, PREFLEDGING SURVIVAL, AND WEIGHT IN KENT ISLAND TREE SWALLOWS (continued)

## BY RAYMOND A. PAYNTER, JR.

## FLEDGING SUCCESS

Only five nestlings died in the nests producing fledged young. In addition, one nest with two young, one nest with three young, and one nest with five young failed to produce any birds that fledged. Most of the young died about one week after hatching with the earliest death at five days and the latest at 12 days. There was a heavy storm the night before the young in the nest with two birds died but the nest was dry and there was no indication that death was caused by the storm. In the nest with five nestlings, two birds died on one day and one bird on each of the following days. In the three-bird nest one died seven days before the other two. Although the cause of the mortality is unknown, it is fairly certain that gradual starvation did not take place because the young gained weight at the normal rate. Injury may be excluded since there were no visible indications of it and the direct influence of adverse weather seems to be ruled out, but, of course, the adults may have deserted the nest with the two nestlings as a result of the storm. Austin and Low (1932) state that crowding caused some of the young in their study to be suffocated. While it is not impossible, it is difficult to understand how they could be certain that the young were not weak and unable to compete with the other nestlings for food and were not gradually overwhelmed by their siblings. Suffocation seems hardly possible unless the birds were already weakened. Even starvation of a single bird or two seems unlikely unless it were initially smaller or weaker than the rest.

The causes of death of the five young in the nests that produced fledged birds are equally obscure except for one three-day-old bird that disappeared from the nest. Half of the shell was stuck to the lower portion of its body and the bird was noticeably smaller than the others in the nest. It lost weight until it weighed only 0.8 grams on the third day. Presumably it died and was easily removed from the nest by the adults.

The question now arises, Is there a difference between the over-all success of various size clutches? To test this, Table XII has been constructed and a chi-square test applied to the observed frequencies for 1948. The test indicates very clearly (P < 0.001) that there is a relationship between clutch-size and the over-all fledging success. Except for the single three-egg nest, which was completely successful, there is a trend toward greater nesting success in larger clutches. Since no relationship has been found between hatchability and clutch-size the critical period would be expected to be between hatching and fledging. However, when a chi-square test is applied to the frequencies presented in Table XIII, if the two-, three-, and four-young broods are grouped and tested against the five-, six-, and seven-young broods, survival is found to be independent of brood-size. Why does a relationship show up when the egg and nestling mortality are amalgamated? The most

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obvious explanation is that the data are too few to allow subdivision and a true picture is obtained only when the over-all survival is considered. In an attempt to clarify the situation, the survival rate was computed for only the nests hatching all of their eggs. This reduced the total number of nests from 24 to 12. The data are too poorly distributed within the sample to give results with any degree of accuracy, although the same positive relationship between clutch-size and survival seems evident.

The over-all success at Kent Island in 1947 has been ascertained from Winn's data (1949) and is presented in Table XII. Again the nest with the smallest clutch was completely successful, only that time it was a two-egg clutch rather than a three-egg clutch as in 1948. Since in both years there was only one nest in the lowest category, the value of this observation is questionable. Nevertheless, again there is a trend toward greater success in larger clutches. A chi-square test applied to the frequencies given in Table XII for 1947 fails to show so clear-cut a relation between clutch-size and success (0.05 > P > 0.02) but there seems little doubt that it does exist. As with the data from 1948, a relationship cannot be proved between clutch-size and hatchability or between brood-size and fledging success, but the fact that the over-all success in both years is so similar appears to be highly significant and strongly suggests that we are dealing with a natural phenomenon rather than a sampling error.

The data from Cape Cod and Connecticut cannot be treated in the same manner because the eggs deserted have been included in the samples with no regard for the fact that the adults frequently renest. However, it is interesting that in Connecticut there was greater egg mortality than at Cape Cod but much lower nestling mortality. Kuerzi (1941) has computed the egg and nestling mortality rates for both areas and found that approximately 28 per cent of the eggs failed to hatch in Connecticut in the three-year period of study whereas at Cape Cod only approximately 19 per cent were failures in a three-year period. In Connecticut 2.5 per cent of the nestlings died in the same period against slightly more than 36 per cent at Cape Cod. Only 50 per cent of the eggs produced fledged young at Cape Cod but slightly over 70 per cent were fledged in Connecticut. These figures are not exactly comparable with those from Kent Island, owing to differences in the handling of the data, but they do serve as general indications of the variability in the reproductive efficiency in various regions.

## WEIGHT

In the course of the investigation, over 1600 weighings were made. The samples for a given age range from three for 21-day-old birds to 103 for 7-day-old birds. The mean weight for each age is given in Table XIV. The weight curve (Fig. II), when plotted simply with the daily mean weight against age, shows a slight drop near the end not usually found in vertebrate logistic growth. However, it is not uncommon in birds for there to be a peak in weight a short time before fledging and then a gradual loss until the nestling approaches the weight of the adult and is ready to leave the nest. This has been re-

		TABLE XII	. OVER-ALL	NESTING SI	UCCESS AT KEN	t Island in	1947 AND ]	1948.		
YEAR			1947			_		1948		
Source			WINN 1949	-				THIS PAPER	~	
Clutch- Size	No. of Nests	No. or Eccs	No. Not Fledging	No. of Fledged Young	Per Cent Successful	No. of Nests	No. of Eccs	No. Not Fledging	No. of Fledced Young	Per Cent Successful
2	1	2	0	2	100.00		:	:	:	:
က	1	ŝ	1	2	99:99	1	ŝ	0	er.	100.00
4	5	8	ŝ	S	62.50	4	16	10	9	37.50
5	2	35	2	28	80.00	ŝ	15	9	6	60.00
9	11	99	4	62	93.93	13	28	16	62	79.48
2	:	:	:	:	:	ę	21	£	18	85.71
Total	22	114	15	66	86.84	24	133	35	98	73.68
		T	ABLE XIII.	FLEDGING F	AILURES AT KI	ent Island i	N 1948.			
		Broo Size a Hatchi	D- NT NO. ING NE	. OF STS	No. of Nestlings	No. Fledcing	PER Succi	<b>CENT</b> ESSFUL		
		07 FO		1	2 18	051	83 35	0 *		
		41		5	ဆန္	~ ?	100.00			
		100	2	0 00 -	0 89 r	44 44	80.00 91.00	0.00		
	1	~	"	-	,	,	10.001			
		TOTAL	24	Ŧ	113	98	86.75	3		

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# PAYNTER, Kent Island Tree Swallows

Bird-Banding July

		TABLE XI	IV. MEAN	DAILY WEIG	CHT OF NE	STLINGS AT	Kent Isla	ND IN 1948.			
Š	ISTS			0	NLY NESTS	FLEDGING	SAME NUMI	ber as Hatc	HED		
		3-Bird 1	NESTS	4-Bird	NESTS	5-Bird ]	NESTS	6-Bird	NESTS	7-Bird	NESTS
	MEAN	No. of	MEAN	No. oF	MEAN	No. of	MEAN	No. of	MEAN	No. of	MEAN
	WT.	OBSER.	WT.	OBSER.	WT.	OBSER.	<b>W</b> τ.	OBSER.	WT.	OBSER.	WT.
	1.62	4	1.87			5	1.40	16	1.33	6	2.10
	2.24	6	2.38	4	2.70	9	2.25	30	2.10		:
	3.38	6	3.60	8	3.35	15	3.51	36	3.16	2	3.80
	5.00	9	5.78	8	4.80	15	5.20	30	4.81	2	5.54
	7.49	6	7.54	4	6.00	10	7.70	24	7.02	2	6.94
	9.44	15	9.98	4	10.30	15	9.12	30	6.70	2	9.90
	12.52	15	12.88	8	11.85	20	12.92	36	12.40	7	12.68
	15.28	12	15.88	8	13.60	20	16.42	36	15.25	7	16.55
	17.80	12	18.43	8	17.15	15	18.72	36	17.41	•	:
	19.41	15	21.05	8	19.27	20	20.15	36	19.00	2	18.00
	20.74	12	21.68	8	20.82	20	21.16	30	20.16	2	19.36
	21.40	6	23.06	4	21.35	15	20.97	24	21.01	7	20.60
	21.75	12	23.31	:	:	10	20.88	18	20.98	7	21.67
	21.78	15	22.94	8	22.26	15	21.17	30	20.94	2	21.11
	21.55	12	22.32	œ	21.71	20	21.27	36	21.23	7	21.85
	21.71	6	22.02	8	21.62	15	20.99	36	21.61	2	21.50
	21.28	12	21.02	8	21.05	15	20.84	36	21.17	7	21.10
	20.96	13	20.84	8	20.53	17	20.07	35	21.04	2	20.88
	20.52	ഹ	21.34	2	20.46	15	19.82	33	20.12	2	20.50
	19.95	-	19.20	9	20.00	6	19.44	17	19.79	5	20.43
	18.00			:		ŝ	18.80				

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ported before in pelicans, parrots, hawks, owls, etc. (Portmann 1937), and in some passerines including the tree swallow (Low 1933). Portmann (1938) has explained this peak in weight as being due to the very rapid development of the liver and the intestines which reach a maximum size and then decrease. Stevenson (1933) has shown for the house wren (*Troglodytes aedon*) that the length of the small intestine reaches its maximum on the 11th day and then appears to shorten slightly. Whether the shortening of the intestine is caused by an increase in its diameter rather than to a loss of material is unknown, but in the light of Portmann's work for other species a decrease in the total amount of material is to be expected.

There are at hand interesting comparative data for the house wren (Huggins 1940) and the barn swallow (*Hirundo rustica erythrogaster*) (Stoner 1935), both species which have a peak in weight before fledg-



Fig. II. Arithmetic growth curve for all nestlings at Kent Island in 1948.

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ing, and which also show the same general growth pattern as found in the tree swallow. Although the data for the wren and barn swallow are not very abundant, which accounts for the irregularities in their curves, when plotted on a semi-logarithmic graph, to show the rate of growth, several fruitful comparisons may be made with the tree swallow growth rate curve (Fig. III).

The first third of each curve is nearly a straight line. This is known as the "logarithmic phase" of growth, or, in other words, the nestlings are growing at a constant rate. In the three or four days before the maximum weight is attained the rate declines. This is undoubtedly due to a change in metabolism and probably is correlated with the development of feathers. Baldwin and Kendeigh (1932) have demonstrated in the house wren that feathers in all areas begin rapid growth on the sixth day and this is approximately the day on which the daily increment in weight begins a slower rate. Stoner (1935) found that the outer tail feathers and the outer primaries appear on the fourth day in the barn swallow and, although he presents no data for the other tracts, it is known that the rectrices and the primaries appear several days before the other feathers in psilopaedic birds. Therefore, general feather growth might be expected on the sixth day or the seventh day, which again is the age at which the first change in the



Fig. III. Semi-logarithmic growth curves for the House Wren (Huggins 1940), the Barn Swallow (Stoner 1935), and the Tree Swallow.

rate of weight increase is found. Unfortunately, there are no data on feather growth in the tree swallow, but because of the close phyletic relationship between the two swallows and the similarity in their growth plots, it may be assumed that the same relationship exists between weight and feather growth in both species.

There are no temperature data for the young tree swallows but the semi-logarithmic plots reveal an interesting relationship between weight and temperature control in the house wren and the barn swallow. Baldwin and Kendeigh (1932:112) state, "The temperature control mechanism is more or less functional when the bird becomes 9 days old." It will be noted that it is at about this age when the bird reaches its maximum weight. In the barn swallow, Stoner (1935:407) has found, "The temperature control mechanism apparently becomes established at about the 9th to 10th day . . ." Again this is approximately the time of the greatest weight and also when growth (total mass) tapers off. Presumably the same relationship between weight and growth and temperature control exists in the tree swallow.

These data naturally raise the question, Is there a relationship between brood-size and the weight of the young, or their rate of growth? In Table XIV there have been listed the mean weights for the various brood-sizes at each age. Only the nests fledging all of the young that were hatched are considered in order to eliminate difficulties owing to nestling mortality. These data have been plotted in Figure IV. It will be seen that there is considerable overlapping until about four days before the birds reach their maximum weight, but then the birds in the nests with three young pass through this period weighing substantially more than the other nestlings, although later the curves again converge. The birds in nests of four young also seem to weigh more than those in larger broods at this period but, unfortunately, there are no data for the 13th day, a most critical time. The sample for the seven-bird nests is made up of only one nest and although the young appear to weigh slightly more at their maximum than the five- and sixbird broods, this may be an artifact of the data.

These data were plotted on a semi-logarithmic graph to discover any variations between broods in the rate of the gain and the loss of weight. Little was learned from these plots because of the difficulty in fitting the curves to the observed points, but the decline in weight is slightly more rapid for the three- and four-bird broods. This is not unexpected because these broods have greater maximum weights and the three-bird broods fledge earlier than the other broods. If all of the birds are to weigh roughly the same when they fledge, as they do, it is "necessary" for the birds in the small broods to lose weight more rapidly. No clear-cut pattern is discernible for the other sections of the curve. This may be due to the small size of the samples as well as to the difficulty in plotting the curve.

A puzzling feature of the arithmetic curves is that there seems to be no definite day on which a peak in the weight may be said to occur, except for the three-bird broods and possibly for the four-bird broods, although data for the 13th day, which may be very important, are lacking. Simply on the basis of the observed weights, the peaks for the three-, four-, five-, six-, and seven-bird broods are the 13th, 14th, 15th, 16th, and 17th days, respectively. In several instances it was merely a matter of a few tenths of a gram which placed the maximum on one day rather than on another and probably the differences are not significant.

Naturally, there is an upper limit to the amount of food that the adults are able to bring to the nest. Moreau (1944) found that the quantity of food brought to the nest is greater for large broods than for small broods, but it does not increase in proportion to the number of young. Lack and Silva (1948) confirmed this in the English robin *(Erithacus rubecula)*. Therefore, the rounding-off in the weights of the larger broods may be highly significant. It may indicate that these broods are not receiving all of the food that they are capable of utilizing and if the adults were able to increase the supply of food a peak in weight would be clearly attained. If this is the correct interpretation, which does not seem improbable, the earlier fledging of the three-bird brood seems even more certain. Because the smallest broods are receiving all of the food that they can utilize, it is presumed that they must be growing under optimum conditions and therefore



Fig. IV. Arithmetic growth curves for each brood-size at Kent Island in 1948.

fledge earlier than birds whose growth may be retarded by less sufficient food.

Although the semi-logarithmic plots fail to show it, probably the rate of growth for the smallest broods differs from that of the larger broods when the young are large enough to begin to tax their food supply. The ninth or tenth day is probably that time since it is at this period that the variations in weights become apparent. The rate of the increase in weight probably then begins to decline and continues to do so until the maximum weight is reached. After this the food demands of the young may remain high, but probably do not go higher, since the mass of the bird has been attained and the form is essentially the same as in the adult except for the feathers which continue to grow at a more or less constant rate.

#### [To be concluded]

#### **GENERAL NOTES**

Some Banding Notes on Purple Grackles.—During the nineteen-year period from 1932 to 1950 inclusive, my wife and I have banded 2,689 Purple Grackles, (Quiscalus quiscala). All of these birds were caught in traps in our own garden and none were banded as nestlings.

Purple Grackles usually arrive in Huntington, Long Island, New York, during the last week in February or early in March, depending upon the weather. The northern shore of Long Island Sound, a few miles north of our banding station, is considered the northern limit of their breeding range. Previous to 1940, Grackles were seldom taken in the traps before the first week in May. However, due to better trapping technique and earlier warm weather they have been taken in April and often in March during the past decade.

The bulk of these birds move westward and southward in September and October. A few stragglers, sick, crippled or recovering from shotgun wounds pass through our station in November and December of each year. These are banded if it is possible that they will survive. Spring and Autumn are usually the best seasons in which to trap this species, when they move around in large flocks. However, any month, with the exception of the four winter months, may be the high month. In 1940, the August catch numbered 155 of these birds and is the biggest total for any single month we have recorded.

In large catches taken at one time, a great variation in the plumages can be noted. Among such birds are brilliant blues; bright greens, along with intermediates and dull brownish individuals in the same flock. It is probable that Bronzed and Purple intermix. No attempt was made to differentiate.

Of the 2,689 Grackles banded, 1,993 were recorded as adults and 696 were birds of the year. The larger and more brilliantly colored adults were considered males while the smaller duller adults were considered females. Adults were judged on the basis of three factors: The quality and state of the plumage, glossy in Spring, worn or molting in the post-breeding months and smooth and bright in Autumn; the season of the year; and a cream-colored iris in comparison with the murky brownish-gray iris of the young birds.

Of the total adults banded, 933 were considered males, 711 were considered females and the sex was not noted in the case of 349. It is believed that the number of each sex is about equal throughout the years despite the larger number of males banded. Early in each season the male is very dominant and often prevents a female from entering a trap, while if a female does get caught in a three-cell trap she usually attracts two males in the other parts of the same trap. Early in the summer the female does most of the nest building and incubation, hence has less time to become involved in a trap.

In subsequent years 225 adults or about 11 percent of all adults returned or were recovered. Of these 115 or 12 percent were males while 100 or 14 percent were females. Of the 696 immatures banded 44 returned or were recovered. This is less than 7 percent of the immatures.