BREEDING BIOLOGY OF PURPLE MARTINS AT THE NORTHERN LIMIT OF THEIR RANGE

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Purple Martins (*Progne subis*), North America's largest swallows, nest from southern Canada to northern Mexico and winter in South America (Peterson, 1961). In primeval times their distribution within this range, during the breeding season, was presumably dependent upon the presence of available abandoned cavities in forest trees which served as nest sites. Today, however, they nest almost exclusively in artificial nest boxes.

Early Alberta naturalists reported martins nesting in small colonies in burned-over forests of central Alberta (K. Wood, pers. comm.). My observations taken from central Alberta northward to the Arctic coast indicate that Edmonton, which has about 2,000 nesting pairs, is near the northern limit of the breeding range. Scattered pairs are found north of this city for about 150 miles. The available nest boxes and abandoned cavities, created mainly by woodpeckers, which occur along the Mackenzie River to the Arctic are not used by Purple Martins.

The breeding biology data reported here were gathered during a study of the influence of weather upon Purple Martin activity, the results of which will be published elsewhere. The objective of this study was to determine the characteristics of the breeding biology of this species at the northern limits of its breeding range.

Changes in climate occur with changes in latitude which are reflected in the biology of species with wide latitudinal ranges. Lack (1947) has stated that productivity as a function of clutch size increased from the tropics towards the poles for individual species nesting over a wide latitude. Since Allen and Nice (1952) have documented the breeding biology of Purple Martins in Michigan, it was appropriate to compare their findings with the situation at Edmonton.

MATERIALS AND METHODS

The breeding cycle was subdivided into seven arbitrarily selected stages to facilitate comparison of weather factors with activity. This subdivision was made on the basis of observations at the nest boxes together with entrance-departure activity recorded by an Esterline Angus recorder. These stages included: arrival, nest-cavity defense and pair-bond formation; nest building; nest completion; laying; incubation; nestling; and post-breeding defense of nest cavity. The activity data were obtained using photoelectric sensing devices and light sources attached to nest boxes and connected to the event recorder. When a bird passed through the light beam on entering or leaving the nest, the impulse was recorded. The method of recording and the use of these activity data are described in a paper to be published shortly.

Breeding biology data for each of the seven stages were recorded at all nests under study. Locations were in or near Edmonton, Alberta. In 1965, breeding data were collected from eight electronically equipped nests, hereafter called experimental nests, and thirteen nests not so hooked up and hereafter called control nests. The experimental nests were on one site, the others were located from 30 feet to 7.5 miles away from this location. In 1966, data were gathered from 18 electronically equipped nests and 14 unequipped nests at the same site and four others 22 miles southwest. The 1965 experimental nests were examined almost daily until all young fledged. Of the control nests, three were examined every third day, and three once a week. At five of the control nests, each young upon hatching was individually marked by painting its claws with nail polish. Later each nestling was banded with a U.S. Fish and Wildlife aluminum band. The wing chords of each marked nestling were measured daily from hatching until fledging. In 1966, all nests were checked at least every other day until just before the nestlings began to hatch, then daily until hatching was completed. Subsequent observations were made every second to fourth day until fledging.

Male Purple Martins may be separated into two age categories; those in adult plumage which are black in color, and those in first nuptial plumage which are similar to females and brown in color (Bent, 1942). Males in adult plumage will henceforth be called "adults" and males in first nuptial plumage will be called "yearlings." Both are sexually mature.

RESULTS AND DISCUSSION

Arrival, Nest-cavity Defense and Pair-bond Formation.—The first stage in the breeding cycle of Purple Martins was arbitrarily taken from the time of first defense of the nest cavity until nest building began. This stage is equivalent to the first three stages described by Allen and Nice (1952). I was unable to use their subdivision because of insufficient observational data and no significant variation of the mechanical recorded data during their three stages.

Martins begin arriving at Edmonton in mid-April. The mean first arrival date over a 17-year period (1948–1965) was 23 April (M. Fisher, pers. comm.). By 20 May most adult birds have returned. Yearling males begin arriving in late May and are generally quite abundant by early June. The first yearling males were noted 26 May 1965 and 25 May 1966 at the experimental sites.

The level of entrance-departure activity is quite high at a martin colony during the first stage. Males are continually entering and leaving the nest cavity, while defending it against other males and attempting to attract females (Gaunt, 1959; Johnston and Hardy, 1962). Entrance-departure activity was generally greater in the morning than in the afternoon, given optimum weather conditions.

Based on the data for 21 pairs, the first stage in the breeding cycle lasted 6.5 ± 7.1 days, with a range of less than one day to 30 days. In 1966, birds that arrived before 25 May took a mean time of 5.4 days, whereas later arrivals spent a mean time of 2.0 days in this stage. The pair that spent 30 days in this stage were the first to arrive at the colony in 1965. After the first day, 28 April, they remained associated with one cavity and were apparently mated. They did not begin building a nest until six of the eight pairs in the colony had arrived and three other pairs had begun nest building. This pair began laying about the same time as did the others.

It appeared that, after martins arrived, some time was spent defending the nest cavity prior to building a nest. This period was shortened after about 25 May. Late arriving pairs acquired a cavity and very shortly began nest building.

Nest Building.—The nest building stage commences with the appearance of material in the cavity and terminates when the nest cup is lined with green leaves. This period is equivalent to the first part of "Stage 4" of Allen and Nice (1952).

Nest building took a mean of 11.8 days (sample size 30) in 1965 and 1966, with a minimum of five and a maximum of 27 days. These periods compare favorably to those reported by Allen and Nice (op. cit.). Birds that were late in acquiring a cavity built their nests in the shortest time. Almost all late nesters were yearlings. A mean of 7.6 days was shown for yearling birds, whereas adults took a mean of 13.6 days to build the nest. The long period of 27 days was by a relatively early nesting pair.

The influence of the electronic equipment, including the photoelectric sensing devices, on the time involved in the nesting stage, was investigated by comparing the control and experimental nests. No significant difference was found.

Observations indicated that most nest building took place in the morning. The birds were generally not around the colony in the afternoon. Activity at the nest entrance during the nest-building stage was characterized by periods of nest construction lasting a few minutes and then periods with no activity when birds were away from the colony. Entrance-departure activity recorded during the nest-building stage was only exceeded by activity in the previous stage.

Nest Completion.—The nest completion stage covers the time interval between the day the nest cup is lined with leaves and the day laying begins. This period corresponds to the latter part of Allen and Nice's (1952) "Stage 4."

Nest completion lasted a mean of 3.2 days with a range of 0 to 9 days (sample size 27). This time interval compares favorably with the three days reported by Purchon (1948) for Barn Swallows (*Hirundo rustica*) in Europe and from 3.5 to 5.5 days for Rough-winged Swallows (*Stelgidopteryx ruficollis*) noted by Lunk (1962). The shorter periods of time generally involved late

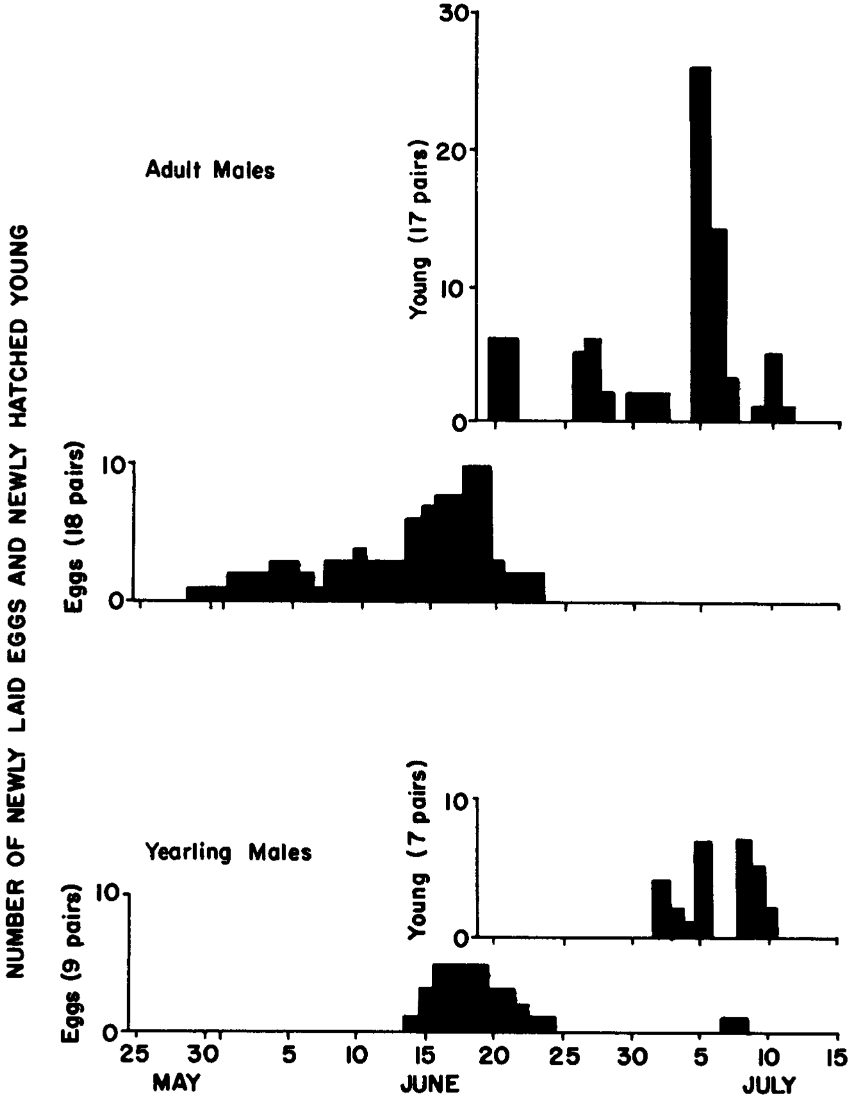

FIG. 1. A comparison of the laying and hatching dates between female Purple Martins mated to males in adult plumage and those in yearling plumage in the same colony, Edmonton area, Alberta.

nesting birds. The period of nine days was shown by a pair which took early possession of a nest cavity and began nest building within a week. Presumably the nest was finished before the female was physiologically ready to lay. There was no significant difference between experimental and control nests for the time spent in the nest completion stage. Total entrance-departure activity during the nest completion stage was slightly less than during the previous stages. At this time, males continued to defend the nest, but observations indicated there was little competition for nest sites.

A foreshortening of the nest building and nest completion stages occurred as the season progressed. Five pairs that terminated these stages after 19 June took a mean of 7.6 days for these two stages. Birds that finished this stage the week before, took 14.9 days (sample size 16). The mean for both seasons in the stages was 15.0 days. This may be an adaptation to assure that young hatch, fledge, and become strong on the wing when aerial insects are most abundant in Edmonton in late June and July.

Laying.—Purple martins generally lay in the early morning on successive days (Allen and Nice, 1952). Female martins mated to adult males began laying up to two weeks before those mated to yearling males (Fig. 1). This reduction in time explains the close agreement of peak laying for both age groups as shown in Figure 1. The skewed distribution for adults may be explained by some birds arriving early and beginning to nest immediately. The curves for hatching differ from those for laying because all eggs in a clutch hatch nearly synchronously.

Martins, in the Edmonton area, laid 4.8 ± 0.6 eggs (sample size 54) with a range of three to eight. This number of eggs approaches closely that reported by Widmann (1922) of 4.9 and Allen and Nice (1952) of 4.9 ± 0.7. It appears that Purple Martins, nesting near the northern limits of their range, have not changed their clutch size. MacArthur (1961:196) claims that "if, due to severe climate and the hazards of longer migration, mortality is always greater at high latitude, then so must clutch size be higher, or the species won't live there." Either the Purple Martin is a relative "newcomer" to these northern latitudes and has not yet adapted its clutch size, or MacArthur's assumption is not valid for these birds.

The mean number of eggs was nearly the same for both years. Larger clutches of seven and eight eggs were laid in 1966. The pair laying seven eggs was first to arrive, nest and begin laying in 1966. Eight eggs were laid by the third pair to begin laying the same season. There was no evidence to suggest that these larger clutches were laid by other than single birds. The pair with seven eggs fledged seven young, and seven of the eight young fledged from the other nest. It appears from this very small sample that should a female Purple Martin lay a greater than average number of eggs, the parents can raise at least seven young, given conditions similar to those experienced in 1966.

Female martins mated to yearling males, produced a mean of 4.29 ± 0.67 (sample size 14) eggs as compared to females mated to adults which layed

TABLE 1

CLUTCH SIZE IN PURPLE MARTINS, IN RELATION TO THE ONSET OF LAYING IN THE EDMONTON AREA, ALBERTA.

Year	First egg laid in week ending	Number of clutches	Cumulative sum % of total	Clutch size Mean ± SD
1965	4 June	2	8.3	6.00 ± 0
	11 June	5	29.1	5.20 ± 0.40
	18 June	9	66.6	4.78 ± 0.42
	25 June	5*	87.4	4.20 ± 0.75
	2 July	0		
	9 July	1*	91.6	4.00
	16 July	2*	100.0	3.50 ± 0.50
	All pairs	24*		4.71 ±0.79
1966	4 June	4	13.3	6.25 ± 0.42
	11 June	3	23.3	5.33 ± 0.15
	18 June	19	86.7	4.63 ± 1.00
	25 June	3	96.7	4.33 ± 0.15
	2 July	1	100.0	5.00
	All pairs	30		4.90 ± 0.99

* Includes replacement clutches.

5.00 ± 0.63 (sample size 40). These results compare with those reported by Meyer (1957) for Cliff Swallows (*Petrochelidon pyrrhonota*); Kuroda (1964) for Starlings (*Sturnus*) and Perrins (1965) for Great Tits (*Parus major*); and Lee (1967) for Purple Martins. Presumably the reduction in clutch size by female martins mated to yearlings, which generally begin nesting later than those mated to adults, would shorten the total time for the breeding cycle and hence nestlings would hatch out one or two days earlier than if the clutch had been of larger size. There was no evidence that the females mated to yearling males were also not yearling birds.

A comparison between the date of onset of laying and clutch size is shown in Table 1. It is apparent that clutch size was diminished as the season progressed. In addition, the daily number of newly-laid eggs and newly-hatched young are presented for the years 1965 and 1966 in Figure 2. It is apparent that the majority of Purple Martins at Edmonton laid eggs during the second and third week of June in both years. By 25 June 87 per cent had begun laying in 1965, and 97 per cent in 1966. Consequently, the majority of young were hatched by early July (Fig. 2) near the peak of insect abundance. Lack and Lack (1951) found a similar correlation between the breeding season of European Swifts (*Apus apus*) and food availability. The two females that re-nested, each laid four eggs. One had earlier

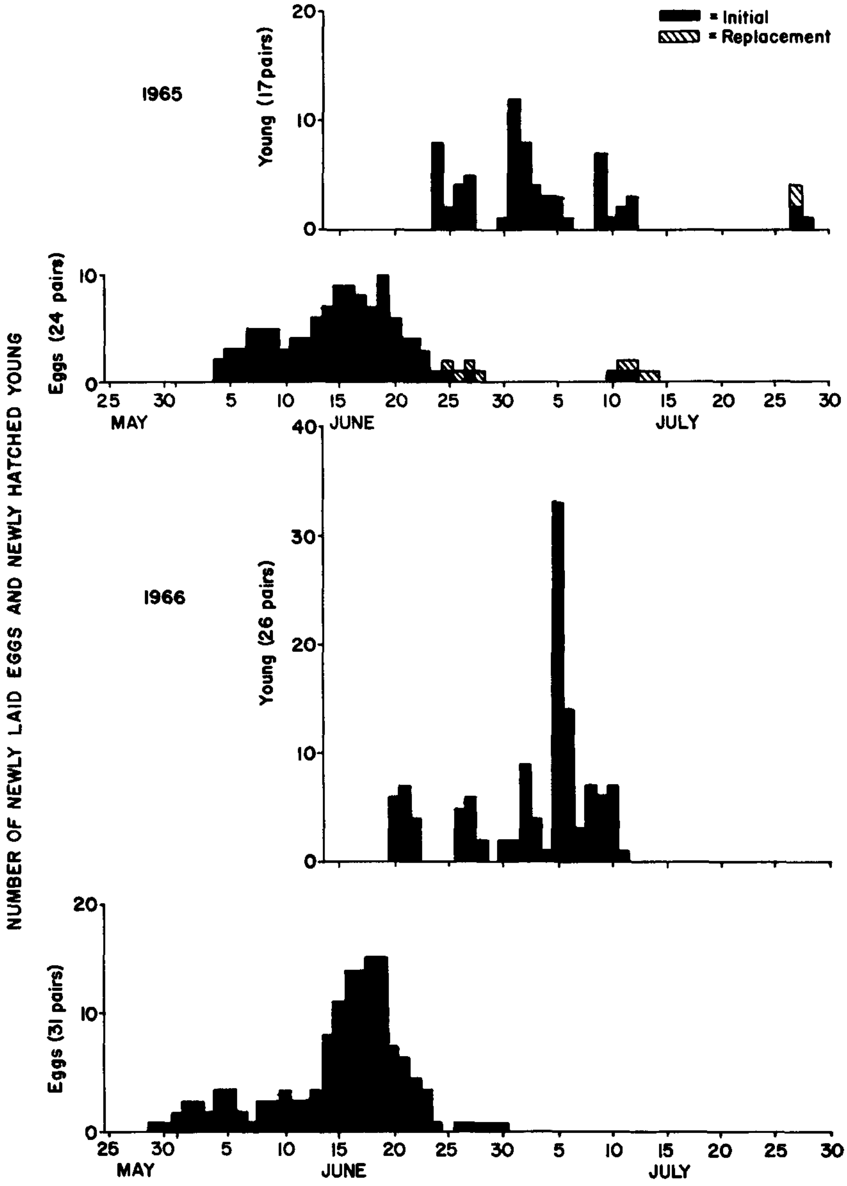

FIG. 2. Laying and hatching frequencies for Purple Martins in the Edmonton area, Alberta.

laid six eggs, the other five. Allen and Nice (1952) reported that martins, which re-nested always laid four eggs in the second clutch.

The possible influence of the continuous light source at the nest entrance on the timing of laying in Purple Martins was investigated. No significant difference in the timing between control and experimental nests was found in either year.

Entrance-departure activity during the laying stage remained relatively constant throughout the day. I suggest that this was because martins stayed closer to the nest, ready to defend the recently deposited eggs from possible predation. This greater tendency to defend the nest, once they began to deposit eggs, was noted while checking the nests each day.

Incubation.—The period of incubation is the time from the laying of the last egg in a clutch until it hatches (Thomson, 1964). To determine this time, I selected, in 1965, 11 nests and numbered each egg on the day it was laid. In one nest, the last egg hatched at the same time as the others; in two nests it hatched with the last part of the clutch; and in eight nests it was the last egg to hatch. These results are similar to that found by Lunk (1962) for Rough-winged Swallows.

The mean incubation time for the marked eggs was 16.6 days, with a range of 16–18, the same mean as that for all nests in both seasons, which ranged from 15–18 days. This time is slightly in excess of that of 15 to 16 days reported by Allen and Nice (1952). I presume the greater length of time is due to the cooler climate of the more northern latitude at Edmonton. Edmonton has a mean temperature in June of 57.8° F, whereas, at Ann Arbor, Michigan, it is 67.9° F. When a female departs to feed while incubating, she allows the eggs to cool and embryo development is retarded.

There was no correlation between either clutch size or age of males and length of incubation time. The mean incubation time for clutches in control and experimental nests was not significantly different. There was little variance in the entrance-departure activity levels throughout this period. It appeared that female birds have certain sessions and recesses, while incubating, and unless there is extremely inclement weather, activity remains relatively constant.

Nestling.—The nestling stage extends from hatching of the last egg to fledging of the last young. Purple Martins remained in the nest approximately four weeks. The mean departure time for 15 broods studied was 27.4 days (sample size 15) ranging from 26 to 31 days. In one nest not included in this analysis, a nestling remained 37 days in the cavity. The four siblings from this nest had left an unknown number of days earlier. This individual was examined and showed no observable defects. The parents continued to feed it until it departed. Reports in the literature indicate that martins re-

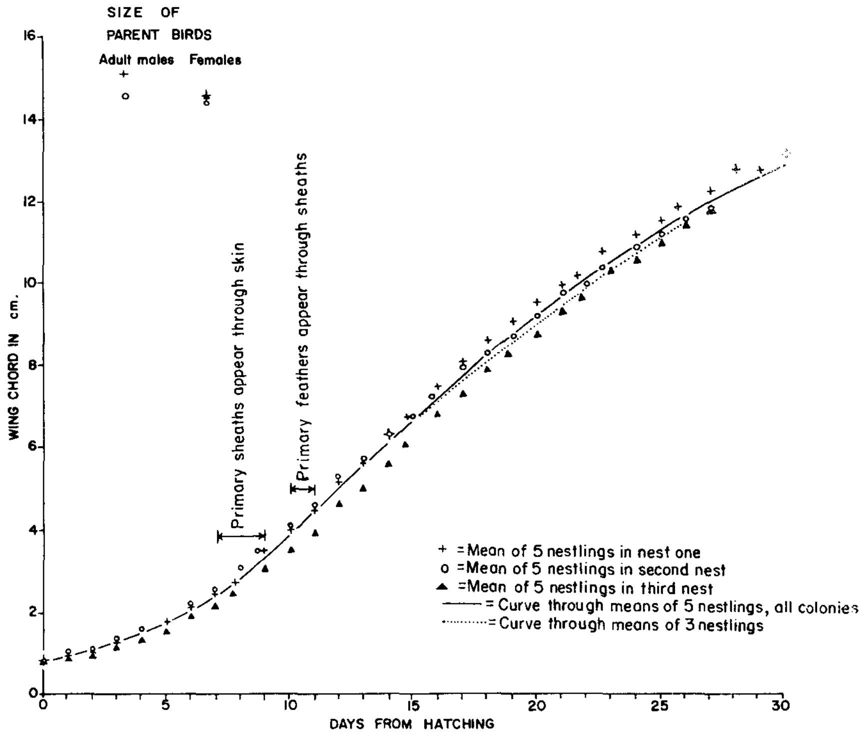

Fig. 3. A growth curve of wing lengths in Purple Martin nestlings based on three nests each containing five nestlings in 1965 at Edmonton, Alberta. Curve was drawn by inspection.

mained in the nest elsewhere slightly longer than at Edmonton. Forbush (1929) stated that martins sometimes remained in the nest for six weeks. Allen and Nice (1952) found martins fledged at between 27 and 35 days, usually about 28. The earlier fledging at Edmonton may be due to more hours of sunlight at this northern latitude which would provide more feeding time and presumably faster growth.

Between day 17 and 21 of the nestling stage, the young came to the nest entrance to beg and accept food. A mean of 19.6 days (sample size 26) was calculated for this time with a range of 14 to 24 days. There was no difference between control and experimental nests. The data were consequently combined.

To follow growth of the young, wing chord measurements were made of nestlings in two nests with three young, and three nests with five (Fig. 3). The curves were prepared using the known age of each young in the nest.

TABLE 2

MEASUREMENT OF ADULT PURPLE MARTINS FROM THE EDMONTON AREA TAKEN IN 1964 COMPARED TO BIRDS IN THE EASTERN UNITED STATES.

Measurements made according to Pettingill (1961) and are presented in millimeters.

	Edmonton			
	Male (Adult and Yearling)	Female	Both sexes	Eastern U.S.A.* Both sexes
Sample Size	15	19	34	–
Wing Chord				
Mean	152.5	150.0	151.1	–
Range	145–161	143–157	143–161	129–157
Tail				
Mean	76.5	71.2	73.7	–
Range	71–91	66–78	66–91	70–88
Tarsus				
Mean	15.9	15.5	15.7	–
Range	14–18	13–18	13–18	11–16
Bill				
Mean	11.4	11.4	11.4	–
Range	10–12	10–13	10–13	11–13

* Data from Forbush (1929).

Nestlings had been individually marked on hatching. From about the 5th day onward, one or more nestlings had longer wings than the others. These larger nestlings were assumed to be males as adult and yearling males were found to be the same size, and were larger than females as shown in Table 2 and Bent (1942). Willson (1966) showed that the sex of nestling Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) could be determined on the basis of weight, at six days of age. A comparison of the growth for the nests with three nestlings with those of five nestlings indicates no difference until day 17. Subsequently, the curve for five nestlings showed larger nestlings present. This could be explained by more males per brood in the nests with five young. It was observed that the appearance of the primary feather sheaths and later the primary feathers had no influence on the growth curves as shown in Figure 3. Various measurements of parent birds, were taken, according to Pettingill (1961), while banding Purple Martins in the same area in 1964. Results are presented in Table 2. There was no difference between adult and yearling males. Females had slightly shorter wing chords, tail lengths and tarsus lengths. The length of the bill was the same in both

TABLE 3

A COMPARISON OF PURPLE MARTIN PRODUCTIVITY AT EDMONTON, ALBERTA WITH THAT REPORTED AT THREE COLONIES IN THE UNITED STATES AS REPORTED BY ALLEN AND NICE (1952).

	Michigan	Missouri	Pennsylvania*	Alberta
Years of study	3	1	7	2
No. of nests	29	45	294	55
No. of eggs laid				
Total	143	220	1380?	262
Mean per nest	4.9	4.9	4.7?	4.8
Eggs hatched	119	129	1100?	198
Per cent	83.2	58.2	80.0?	76
Nestlings fledged				
Number	55	110	850?	185
Per cent	31.5	50.0	61.6?	70.7
Fledge per pair	1.9	2.4	2.9?	3.4

* The Pennsylvania figures are estimates.

sexes. A size comparison of the Edmonton birds to those in eastern North America indicated the northwestern ones are larger (Table 2).

The number of young martins fledged at Edmonton was greater than found in other studies, even though the clutch size was the same (Table 3). Martins studied at more southern latitudes were influenced by rain and cold weather which reduced their numbers. One period of bad weather at Edmonton occurred when most birds were incubating. Of the four nests with young at the time, all lost at least one chick and one lost three of five. I presume that if weather conditions during this study had been as detrimental as described in the reports from more southern areas, then martin productivity would have been substantially reduced.

Entrance-departure activity, together with observations, indicated that nestling feeding began in the early morning, continued at a steady rate all day, and fell off at or near sunset. There did not appear to be any major peaks or troughs in levels of activity. Once the adults begin feeding nestlings they apparently continue at about the same rate, whereas Lunk (1962) in a study of Rough-winged Swallows, reported a very marked spurt in feeding nestlings before dark. Allen and Nice (1952:635) had stated, "It seems evident that both age and number of young influence the rate of feeding although we are hampered by lack of exact information on both these points."

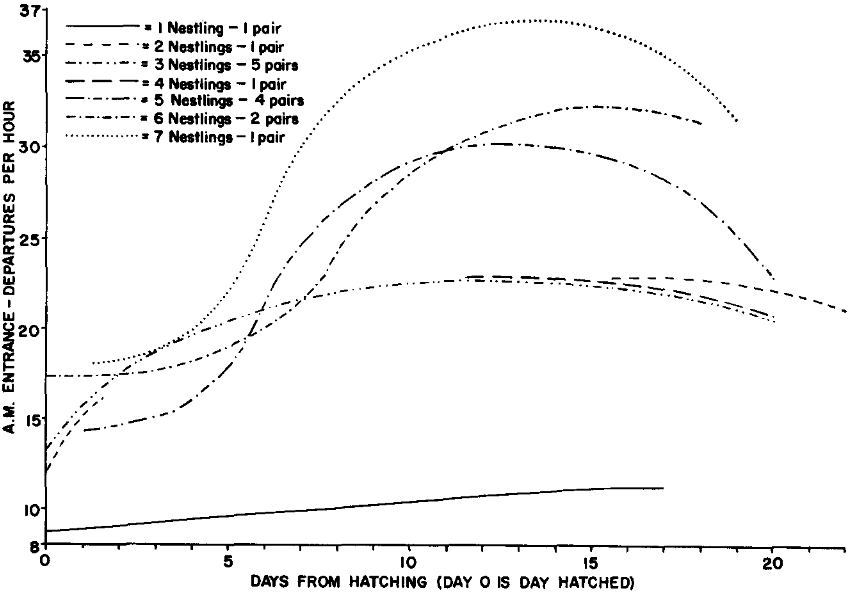

FIG. 4. Mean morning activity on a per hour basis for each day during the nestling stage for nests containing one to seven young. Curves were drawn by inspection and were prepared, ignoring data recorded on days with very cold, windy, rainy weather.

This speculation was investigated. It appears from Figure 4 that entrance-departure activity, presumably the rate of feeding, increased both with the age of young and the number per nest. The activity curve, for all broods with more than one nestling rose to a plateau at about day 10 and remained at this level until day 14, when activity began to decrease. An increase in number of trips per hour as the nestlings aged was similarly reported for other swallow species (Moreau, 1939, 1940; Purchon, 1948; Lunk, 1962).

The decrease in number of feeding trips per hour after day 14, coincided with observations of adults bringing to the young much larger insects, including Odonata and Lepidoptera of unknown species. Observations indicate that the number of trips with larger insects increased as the young become older. I postulate that parental feeding trips, hence, could be reduced and yet still provide the same amount of potential energy per nestling.

Various workers have reported that the number of feeding trips was greater in larger broods but not proportional to the brood size (Nice, 1943; Moreau, 1947; Lack, 1948, 1954; Gibb, 1955; Royama, 1966; Willson, 1966). My results agree with these findings (Fig. 4). Each young in larger broods presumably would not have received as much food as in smaller ones. Possibly the decrease in quantity of food brought per nestling in the larger broods may be compensated by heat conservation. Gibb (1955) suggested such a compensatory relationship in his study of Great Tits (*Parus major*). He mentioned that reduction of heat loss will reduce to some extent the demand for heat production and energy intake.

In both seasons, six young fledged from some nests. In 1966, two pairs each fledged seven young. Since a pair of martins can successfully fledge a larger number of chicks, I assume that those pairs feeding one, two, and three nestlings are not feeding at maximum rates. I suggest that martins would adapt to produce an ideal number of young, which can be fed at near maximum efficiency. If too many young are in the clutch, then according to Perrins (1965) the nestlings fledge underweight and die; if too few, maximum feeding rates are not approached and a loss of productivity occurs. I presume that the productivity of three to four per nest found in this study is the optimum number at this northern latitude. Two birds, each from a different 1966 nest of seven young, all of which were banded, returned, one in 1968 to the birth site and the other 23 miles southwest of the birth site in 1969, indicating that some of the nestlings from such large families will survive two and three years.

Yearling males were breeding for the first time. Data from three pairs of yearling birds obtained during three three-hour observation periods a week apart with young about one, two and then three weeks of age, indicated that the yearling males fed nestlings 45 per cent as often as did females at the same nest, whereas data from seven pairs with adult males, obtained at the same time and with young about the same age, indicated trips by adult males to the nest equalled those of the females at the same nest. Kendeigh (1952) reported similar results for one pair of adult martins.

Post-Breeding, Nest-Cavity Defense.—The post-breeding nest-cavity defense stage lasts from the time nestlings begin to fledge until birds depart on fall migration.

While studying martins in 1964 and later during this project, I noted these birds were quite active around the nest boxes shortly after young fledged. Allen and Nice (1952) in their detailed study do not mention such activity. Olmstead (1955:8) briefly discussed this stage: "After the young are fledged, adult males engage in short decisive flights and sing short bursts of song from the ledge of the box. A few mated pairs linger near the nest, but females and young are in the minority." Johnston and Hardy (1962) note groups of three or more individual martins participate as social units in investigating neighboring colonies in the spring and after breeding was complete. Based on data for 14 males, the final stage in the breeding cycle lasted 5.9 ± 4.6 days with a range of one to 19 days. Nearly all birds participating in this stage were yearling males. A detailed discussion of this stage will be published elsewhere.

SUMMARY

A study of Purple Martins was undertaken to determine the characteristics of this bird's breeding biology near the northern limits of its breeding range. Research was conducted during the summers of 1965 and 1966 in the vicinity of Edmonton, Alberta.

The breeding cycle was divided into seven stages. These stages and the mean duration of each were: arrival, nest-cavity defense and pair-bond formation—6.5 days; nest building—11.8 days; nest completion—3.2 days; laying—4.8 days; incubation—16.6 days; nestling—27.4 days; post-breeding defense of nest cavity—5.9 days. Clutches laid later in the season were smaller. The number of young fledged varied from one to seven with a mean of 3.4 for 55 nests. These breeding statistics are not significantly different from those reported by Allen and Nice (1952), except that incubation was longer, and fledging success greater at the latitude of Edmonton. During the nestling stage, activity at the nest entrance, presumably reflecting the rate of feeding of nestlings, increased to day 10, was maintained through day 13, and decreased after day 14. As brood size increased, the nest entrance and departure activity decreased per nestling. Males in adult plumage were observed to feed young at a rate similar to females, whereas males in first nuptial plumage fed young at half this rate. Males in first nuptial plumage were the main participants in the post-breeding defense of the nest-cavity.

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