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STUDIES OF A TREE SWALLOW COLONY

(Second Paper)

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DATA covering four more breeding seasons have been secured at the Tree Swallow (*Iridoprocne bicolor*) colony at Princeton, Massachusetts, since my first paper was published.¹

Complete data for the colony covering the seasons 1931 to 1937 inclusive, are given in tabular form in Table I. As shown by the data in the second line of this table, the number of breeding birds increased up to 1935, when 36 pairs bred, and then began to decrease, reaching 26 pairs in 1937, and 20 pairs in 1938.

SEASON OF 1935

The breeding season of 1935 was a successful one, although the average number of eggs per nest (4.86) was smaller than usual.² The average number of fledglings raised per nest in 1935 was 3.39. Despite a somewhat rainy May, there was little cold and windy weather and at no time did insects appear scarce. Excellent weather prevailed between June 24 and July 6 when the fledglings were leaving the nests.

A plan giving the location of the boxes in 1934 and 1935 is shown in Figure 1. No new boxes were put up in 1935, although box No. 23, which had only a 1¼-inch hole and was intended for Chickadees, was occupied by a pair of Tree Swallows. Boxes nos. 22, 43 and 58 were empty; boxes nos. 15, 20 and 48 were occupied by Bluebirds; and box No. 37 was occupied by House Wrens. All the rest of the boxes were occupied by Tree Swallows. Tree Swallows also nested in box no. 15 in July, after the Bluebirds had left, and Bluebirds nested in box no. 11 after the Swallows had deserted it.

Thirty-seven of the adults breeding in 1934 returned to nest in the colony in 1935. This is a return of 57 per cent, the highest for any year.³ Five of the 1934 mated pairs returned to the same

¹ *Bird-Banding*, 6, pp. 45-57.

² In 1933 the average number of eggs per nest was 5.62 and in 1934 the average was 5.68.

³ See Note No. 8 in Table I.

house they used last year and were mated pairs again in 1935. Ten birds of five other mated pairs returned but took new mates. Of these ten birds, four males were breeding in the same house as in 1934 and the fifth male was nesting in an adjacent house. Four of the females returned to adjacent houses and the fifth to a box 800 feet distant. None of these five females returned to the box used in 1934.

The 37 adults breeding in 1934 which returned in 1935, consisted of 19 males and 18 females. They were distributed as follows in 1935:

To the same box as 1934.....	18 (12♂ and 6♀)
To adjacent boxes.....	9 (6♂ and 3♀)
To nearby boxes.....	5 (1♂ and 4♀)
To distant boxes.....	5 (1♂ and 4♀)

The above data apparently indicate a greater attachment to last year's territory by the males than by the females.

In 1935 there were six complete nest failures due to the following causes:

Nest deserted just after eggs hatched.....	2 nests
Nest robbed of fledglings.....	1 nest
Eggs stolen.....	1 nest
Fledglings found dead after a rainy period.....	2 nests

SEASON OF 1936

In the fall of 1935 boxes 29, 52, 53, 58 and 59 which had been located at nearby points surrounding the main colony (Fig. 1) were removed and placed within the colony.

The season of 1936 showed high percentages for complete nest failures (48.2%) and fledgling mortality (45.5%), due largely to cold and rainy weather while the fledglings were being fed in the nests. On the afternoon of June 25, the temperature dropped to 55° F. The adult birds were apparently finding great difficulty in securing insects to feed their young. Several nests were under observation during the afternoon and the adult birds were away for long intervals between feedings and practically no swallows were seen flying over the colony in contrast to the large numbers generally in sight. The birds were apparently going long distances to secure insects, probably to some ponds or marshes at lower altitudes. The next morning, all the young in four boxes were dead and many in other boxes. The apparent reasons for the fourteen complete nest failures were as follows:

Eggs failed to hatch.....	1 nest
Eggs deserted.....	3 nests
Four days of rain and <i>Protocalliphora</i>	4 nests
Cold spell (55° F.).....	4 nests
Nests robbed of fledglings.....	2 nests

14 nests

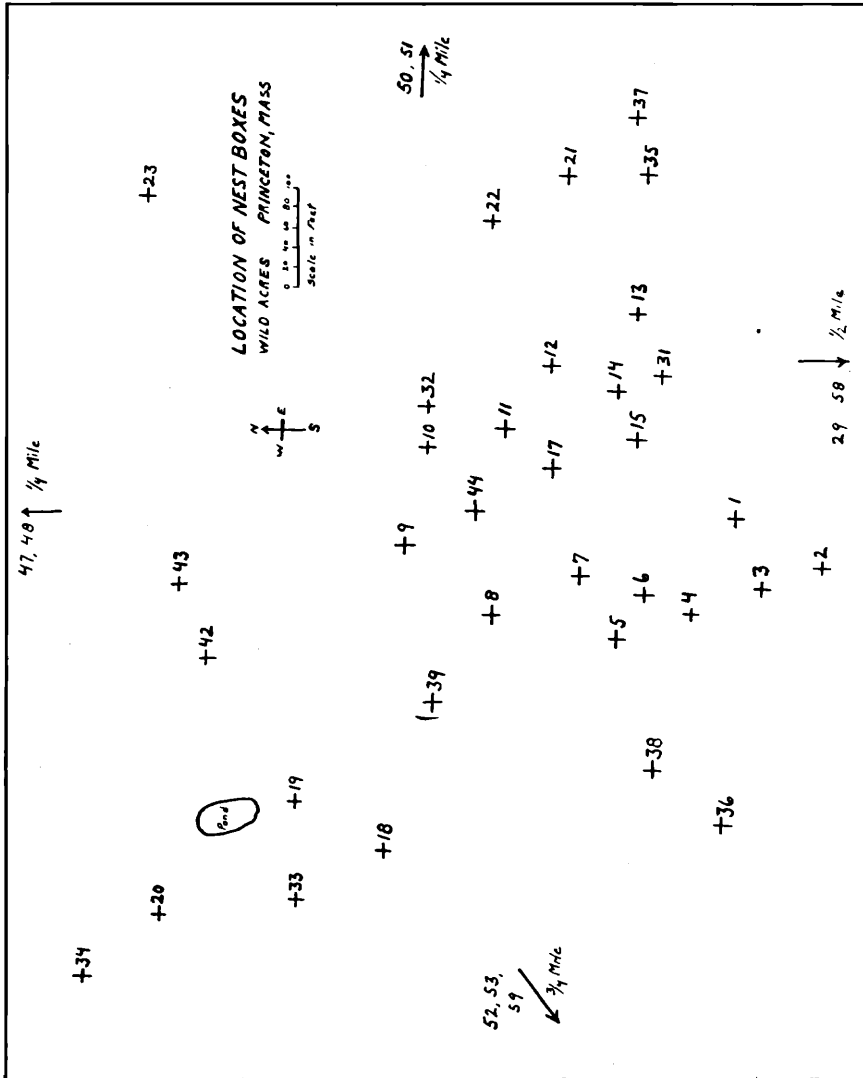


Figure 1. Location of nest boxes for Seasons of 1934 and 1935

In 1936 four pairs of swallows which were mated in 1935 remated again. Three other pairs which were mated in 1935 returned but took new mates. The adults breeding in 1935 which returned in 1936 were distributed as follows:

To same nest box as in 1935	10 (7♂ and 3♀)
To nearby nest boxes	10 (4♂ and 6♀)
To colony, but to a box at a considerable distance from one used the previous year	5 (1♂ and 4♀)

Attention should be drawn to one pair of birds that have been mated for four consecutive seasons, namely F-81853(♂) and H-80104(♀). This pair has occupied box no. 1 for three consecutive seasons but this year they nested in an adjacent box (no. 2). Another pair of birds which were mated in 1935 were again mated in 1936 but in an adjacent house. These two cases would appear to indicate that tree swallows at times are attracted to last year's mate instead of to the nest box used the previous year. H-80104 returned again to box no. 2 in 1937 but had a new unbanded mate; her mate of four seasons (a bird at least five years old) failed to return.¹

SEASON OF 1937

In the fall of 1936 boxes nos. 1, 7, 48, 50 and 51 were removed (Fig. 1) hence they were not available in 1937; no. 47 was moved to a position within the colony. The season of 1937 was a successful one with good weather during the period the fledglings were in the nests. There were five complete nest failures and one nest in which four of the five fledglings died. In five of these six cases the cause of the failure was apparently due to the disappearance of the male bird. No male bird was seen around any of these five nests during the last of the incubation period nor after the fledglings were hatched. In no case did he enter the box to feed the young. In the sixth case of nest failure the eggs were deserted.

The twenty-six adults breeding in 1935 or 1936 which returned in 1937 were distributed as follows:

To same nest box	9 (5♂ and 4♀)
To nearby nest boxes	10 (6♂ and 4♀)
To colony but to a box at considerable distance from one used previous year	2 (2♀)
To or from box outside of colony (one or two miles away)	3 (3♀)
To Kraus colony (4 miles away)	2 (2♀)
Total adults returns	26

(Four of the above birds were not captured in 1936 and the date in these cases refers to 1935).

¹ H-80104 returned to box No. 2 in 1938 and hence she is at least 6 years old.

In 1937 none of the breeding birds which were captured had the same mate as in 1936, although four pairs that were mated in 1936 returned. In this respect the results of the 1937 breeding seasons do not correspond to those of the three previous years. As all the males were not captured in 1936 and 1937 there appear to be three possible cases where the birds might have been mated for two seasons, *i.e.* box 5 where the male was not captured in 1936 or 1937, box 11 where the male was not captured in 1937 and box 17 where the 1937 male was a 1935 fledgling trapped for the first time in 1937.

SEASON OF 1938

The results of the 1938 breeding season were the worst ever experienced at the colony. A hard northeast storm began the 26th of June and it rained steadily for three days. During this time the weather was cool, but not cold. On the morning of the 29th a check-up of the nest boxes showed that out of eighty-two fledglings that were alive when the rain began, forty-one were dead. Eight boxes lost their entire broods. Most of the deaths were in the boxes in which the eggs had recently hatched or in which the birds were about half fledged. The boxes in which the fledglings were nearly ready to fly came through safely. Twelve fledglings (3 boxes) left the nests during the storm.

One interesting result of the storm was that a fledgling hatched in box 11 and which left the nest during the heavy rainfall was found dead in box 38, four hundred feet away. At this time there were in box 38, two other dead fledglings and three living ones.

The percentage of eggs hatched in 1938 was 81 per cent, the fledging mortality was 52.8 per cent and the reproductive efficiency was 38.8 per cent.

The distribution of the returns in 1938 was as follows:

<i>Age</i>	<i>No.</i>	<i>Date Banded</i>	<i>Per cent of banded birds known to be alive</i>
7 years	1	1932, adult	4.76 per cent
6 years	1	1933, adult	3.56 per cent
4 years	4	1934, fledglings	2.7 per cent
4 years	2	1935, adults	7.4 per cent
3 years	2	1935, fledglings	1.6 per cent
3 years	5	1936, adults	35.8 per cent
2 years	3	1937, adults	18.7 per cent
2 years	2	1936, fledglings	3.13 per cent
1 year	1	1937, fledgling	1.16 per cent

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It should be noted in connection with the above data that eight breeding adults in 1938 were not captured.

WANDERING FEMALES

The trappings of the past three seasons have shown seven cases in which adult females have nested at points at a considerable

distance from that of the previous year. L-42744 banded as an adult in 1934 has bred in four different boxes, three of which were about a mile from each other. L-74810, a 1934 fledgling, was captured in 1935 and again in 1937 at places two miles apart. She was not captured in 1936. L-42712 banded as an adult in 1934 has been trapped three times, twice in the colony and once four miles away. 36-18542 banded as an adult in the colony in 1936 was captured in 1937 breeding at a point four miles away. 36-18526 banded as an adult in 1936 was trapped in 1937 in a box two miles away. H-69733 nested twice at the colony and the third nesting was at the Kraus colony four miles away. L-74847 nested twice at the Kraus colony and the third time at the Chapman colony four miles from the Kraus colony. No males have been observed wandering in this manner.

BIRDS RETURNING FOR SEVERAL SEASONS

Each year a number of birds are trapped which have nested in Princeton for more than one season. The distribution of the returns of the Chapman colony to Princeton for the year 1937 are given in the following table:

	<i>Year banded</i>	<i>No. of birds known to be living</i>	<i>Percentage of birds known to be living in 1937</i>
Adult Return—1.....	1936	10	71.5
Adult Return—2.....	1935	2	7.4
Adult Return—3.....	1934	5	11.6
Adult Return—4.....	1933	3	10.7
Adult Return—5.....	1932	1	4.8
		21	
Fledgling Return—1.....	1936	3	
Fledgling Return—2.....	1935	2	
Fledgling Return—3.....	1934	7	
Fledgling Return—5.....	1932	1	

One bird of this group, F-81855(♂), was at least six years old in 1937 as he was banded as an adult in 1932.¹ Another bird, F-76398 (♂) was hatched in the colony in 1932 and has apparently occupied the same box (no. 35) for 5 consecutive years. The male in box 35 was not trapped in 1933, however, and whether this bird was breeding there in 1933 or was one of the males breeding for the first time when two years old is not known.

FLEDGLING RETURNS

As recorded in my previous paper, the percentage of returns for the fledglings has been very small. From 1931 to 1936 inclusive a total of 605 fledgling Tree Swallows have been banded by Dr.

¹ This bird returned again in 1938 and hence is at least 7 years old. He has occupied the same box (no. 34) except in 1933 and 1938, when this box was occupied by Bluebirds before he arrived. In 1933 and 1938 he bred in the adjacent box (no. 20).

Douglas Kraus and the author at the two colonies in Princeton. These were therefore available as returns up to 1937. Of these, 27 have been recovered in Princeton and one in Hubbardston within four miles of the banding station. This is a return of 4.6 per cent.

It is interesting to note that six of the fledglings from the Chapman colony were recovered in the Kraus colony four miles south, and one was recovered in Hubbardston four miles west. These recoveries make one suspect that many more fledglings might be breeding within the fifty square miles enclosed by this four miles radius. Unfortunately no time has been available to trap the isolated pairs of birds breeding within this area, although as recorded in my 1935 paper, six isolated boxes have been under observation at distances from the colony varying between one and four miles.

As previously recorded, two fledglings were recovered a month after banding at points in Connecticut and New Jersey. The only other fledgling recovered at a distance from the banding station was at New Ipswich, N. H. This bird was banded in June, 1933, and was recovered dead in June, 1934. This is a very interesting recovery as the bird was apparently breeding in New Ipswich which is 21 miles almost due north of Princeton.

An analysis of the fledgling returns has brought out some very interesting facts. Twelve of the 26 fledglings which were recovered alive in Princeton were not trapped until they were two years old and eleven of these twelve two-year old birds were males. This apparently indicates that many of the males do not breed until they are two years old. This same fact has been reported by Kluivjer (1935) in connection with his study of starlings (*Sturnus vulgaris*) in Holland.

The age and sex of the 28 fledglings banded by Chapman and Kraus recovered in Princeton¹ in 1931-1937 is shown in the following table:

♂♂ returning to breed for 1st time, 1st year after hatching	5
♂♂ returning to breed for 1st time, 2nd year after hatching	11 ²
♀♀ returning to breed for 1st time, 1st year after hatching	8
♀♀ returning to breed for 1st time, 2nd year after hatching	1
Sex undetermined (2 dead)	3
Total fledgling returns	28

$$\text{Per cent returns} = \frac{28}{605} = 4.6\%$$

¹ One 1934 fledgling recovered in April, 1938, in the adjacent town of Hubbardston, four miles from the colony, has been included in this table.

² One of these (F-76398), mentioned previously, may have been breeding in box 35 the preceding year.

FLEDGLING RETURNS FROM CHAPMAN COLONY TO
TOWN OF PRINCETON

<i>Year of Banding</i>	<i>Returns</i>	<i>Total Fledglings Banded</i>	<i>% Return</i>
1931	1	7	—
1932	3	48	6.3
1933	3	61	4.9
1934	10	148	6.8
1935	2	125	1.6
1936	3	64	4.7
	<hr style="width: 50%; margin: 0 auto;"/> 22	<hr style="width: 50%; margin: 0 auto;"/> 453	<hr style="width: 50%; margin: 0 auto;"/> 4.85

An analysis of the fledgling returns showed that only in two cases did more than one fledgling from the same brood return. In 1935, two fledglings hatched in box no. 33 the previous year returned and two from box no. 4.

Another interesting fact brought out by an analysis of the fledglings recovered in or within four miles of the colony, is that in every case except one, one or both of the parents also returned. In seven cases both of the parents returned, in seven cases only the female and in six cases only the male. The one exception where neither parent returned was for a fledgling hatched in 1936 which returned in 1937. However, as all of the adults were not captured in 1937, one of the parents may have returned. It seems rather doubtful if parents and fledglings remain together through the winter or migrate north together in the spring and the above facts probably have no significance. It is, however, an interesting observation obtained from an analysis of the returns.

No interbreeding has taken place in the colony during the six years of its existence. In only one case has a bird of the third generation (grand daughter) returned to the colony and none of the young of this bird returned the following year. It is interesting to note that two 1934 fledglings, a male from box 4 and a female from box 31 mated in box 44 in 1935.

DISPERSAL OF FLEDGLINGS

The most interesting fact brought out in the study of this colony is the disappearance of the fledglings. This of course, is the experience also of other banders. No data have been published to the author's knowledge showing the distribution of fledgling recoveries of any species of birds banded in the United States. Considerable data, however, have been published on the distribution of European Swallows (*Hirundo rustica rustica*). Some of these data were mentioned in my 1935 paper. Additional information on this subject is recorded by Pfromm (1931) and by Boyd and Thomson (1937).

Pfromm records the recovery of eight birds banded as fledglings the previous year. The distances of these from the points of hatching

were as follows: two at 300 meters, one at 400 meters, two at 700 meters, one at 1500 meters and two at 3000 meters.

Boyd and Thomson (1937) analyzed the records of the swallows banded under the British Birds marking scheme which have been recovered in the British Isles. The exact number of fledglings banded is not recorded but the 125 birds recovered in subsequent years that were banded as nestlings are of the order of about one-half of one per cent of those banded. Of these 125 recoveries, 103 were in the British Isles and 22 abroad (not breeding, however). Of these 103 birds, 18 were recovered at or very near the place of banding, 72 at distances varying from one hundred yards to 13 miles and 13 at distances varying from 29 to 350 miles. It appears from the discussion that few of these birds were actually breeding when recovered.

The authors of this paper point out that while few of the nestlings were recovered at the exact place of banding, many of them were recovered close by and several of those captured at a distance had probably not completed their migration and may have been on the way to their natal area. Several were recovered north of the place of banding as was the case with one Princeton fledgling.

Each year a large number of unbanded breeding adults appear at the Princeton colony. As the Princeton data seem to indicate that breeding adults usually return to the same place to breed in subsequent years, these new adults presumably are fledglings of the previous year. Obviously they could not all have been hatched in Princeton. The appearance of these new adults each year and the disappearance of so many fledglings apparently points to a wider dispersal of the fledglings of Tree Swallows than that indicated for European Swallows in Boyd and Thomson's paper.

In my 1935 paper I suggested that the young swallows might spread out after leaving the nest and in this way become acquainted with new territory in which they would breed the following year. No information covering the summer and fall dispersal of Tree Swallows is known to the author and the two fledgling recoveries at points south of the station would appear to indicate a southerly migration to the sea coast in July.

Drost and Desselberger (1932) and Boyd and Thomson (1937) both give interesting data showing the dispersal of the young swallows during the same year in which they were hatched. One young Danish martin (*Delichon urbica*) was recovered the same season 220 miles north east of the banding point and many swallows (*Hirundo rustica rustica*) were recovered in a general northerly direction at distances varying between 32 and 63 miles from point of hatching. The fall dispersal of British swallows was in all directions but the distance was not great. While the data for Continental birds indicate a general northerly dispersal in the fall, the data for the British birds do not.

If our bird banders would give more attention to Tree Swallows

(which are very easy birds to capture) more swallows which were banded as fledglings would probably be recovered and hence a better knowledge of the dispersal of fledglings obtained.

BLUEBIRDS AND HOUSE WRENS

Each season a few pairs of Bluebirds (*Sialia sialis sialis*) and House Wrens (*Troglodytes ædon ædon*) nest within the area occupied by the Tree Swallow colony. No fighting was observed between Tree Swallows and Bluebirds during the season of 1935, 1936, and 1937 which is contrary to the experience of previous years. In 1935 and 1936, one pair of Bluebirds nested within the colony and two pairs nested on the edge of the colony. In 1937, three pairs of Bluebirds nested within the colony although one nest was deserted just after the eggs hatched. In several cases after Bluebirds had built a nest and laid eggs, Tree Swallows frequently looked in or attempted to enter the boxes but in every case the Bluebirds were able to hold possession of the box.

In 1935, 1936, and 1937, two pairs of House Wrens nested within the colony during the breeding season of the Tree Swallows and each year a number of additional boxes had nests built in them by males which were not used by breeding birds. The wrens did not molest the Tree Swallows except in one case. In 1937 a pair of Tree Swallows nested in box 36 after all the other swallows had left the area. A wren was observed singing around this box soon after the fledglings hatched and a few days later the young Tree Swallows were found on the ground under the box. This obviously was the work of the male House Wren.

PROTOCOLLIPHORA

In 1937, the Protocalliphora larvæ and pupæ were counted in a few selected nest boxes. Data for these are given in Table II. Very careful counts were made immediately after the fledglings left the boxes and the pupæ cases were placed in screened containers. The counts while the fledglings were in the nests were not always accurately made and no doubt a number were overlooked in each case. About two weeks after the larvæ and pupæ were collected a large number of the flies and secondary parasites emerged. Careful observations indicate that few, if any, of the fledgling Tree Swallows or Bluebirds were killed by the Protocalliphora.

TABLE I
SUMMARY OF TREE SWALLOW DATA

	1931	1932	1933	1934	1935	1936	1937
1. Number of boxes available for tree swallows, bluebirds and house wrens	8	19	31	41+6 ³	42+4	42+6	40+6
2. Number of boxes occupied by tree swallows	4	13	21	31+3	36+3	29+3	26+0
3. Number of boxes occupied by bluebirds	1	3	3	1	3+1	3+1	3+0
4. Number of boxes occupied by house wrens	0	0	0	0	2+0	2+0	3+0
5. Percentage of boxes occupied by tree swallows, bluebirds and house wrens	62.5%	84.5%	77.5%	78.0%	88.5%	81.0%	80.0%
6. Number of adults banded	2	21	28	43	27	14	16
7. Number of fledglings banded	7	48	61	148	125	64	86
8. Number of adults breeding in colony previous year which returned to colony	—	—	12	20	37	25	20 ⁸
9. Percentage of banded adults breeding in colony previous year which returned to colony	—	—	50.0%	47.6%	57%	36.2%	51.5% ³
10. Number of adults banded previous year which returned (Return-1)	—	2	11	11	21	7	10 ¹
11. Percentage of adults banded previous year which returned (Return-1)	—	—	52.5%	39.4%	48.8%	27%	71.5% ¹
12. Number of adults and fledglings banded 2 years ago which returned (Return-2)	—	—	1	9	10	18	4
13. Number of adults and fledglings banded 3 years ago which returned (Return-3)	—	—	0	1	6	6	12
14. Number of fledglings banded previous year which returned to colony	—	1	1 ⁹	2	3 ⁹	2	3
15. Percentage of fledglings banded previous year which returned to colony	—	—	2.1%	3.3%	2.0%	1.6%	4.7%
16. Number of adults not banded	6	2	1	3	3	19+4	7
17. Number of fledglings not banded	0	0	0	0 ²	0	0	0
18. Number of birds leaving at end of breeding period	15	74	103	216	196	122	138
19. Number of banded birds leaving at end of breeding period	9	72	102	214	193	99	133
20. Number of eggs laid	—	—	118	176 ⁴	175 ⁴	—	—
21. Number of eggs hatched	—	—	108	158 ⁴	155 ⁴	—	—
22. Percentage of eggs hatched	—	—	92%	89.9%	88.5%	—	—
23. Fledgling mortality	—	—	47	10	33	—	—
24. Percentage of fledgling mortality at colony	—	—	43.5%	6.3%	21.3%	45.5%	21.1%
25. Number of complete nest failures at colony	2	1	7	2	6	14	5
26. Percentage of nest failures	—	7.7%	33.3%	5.9%	16.7%	48.2%	19.2%
27. Number of fledglings leaving boxes	7	48	61	148	125	64	86
28. Reproductive efficiency	—	67.5% ⁶	51.5%	84%	69.8%	—	—

¹ In this case nine birds returned to Chapman colony and one to Kraus colony.
² Fledglings in three outlying boxes were not banded.
³ First figure refers to boxes in or near colony; second figure to outlying boxes—i.e. more than one mile away. Two of the outlying boxes were occupied by red squirrels in 1935 and hence were not available for Tree Swallows.
⁴ Excluding outlying boxes.
⁵ Based on nine boxes for which accurate data were kept.
⁶ Twenty-two Swallows (56.4 per cent) banded as adults in 1936 returned to the Town of Princeton in 1937. Four Swallows that were breeding in 1935, but not captured in 1936, were breeding in Princeton in 1937, making twenty-six adult returns for 1937. If these birds were breeding in 1936 the returns of breeding adults to Princeton were 66.6 per cent, instead of 51.5 per cent.
⁷ Two additional fledglings were recovered for the first time the following year.

TABLE II
PROTOCOLIPHORA LARVÆ AND PUPÆ IN A SELECTED NUMBER OF NESTS

Nest Box No.	Number of Fledglings	% Fledgling leaving nest	Number of larvae found and removed before fledglings flew	Number of larvae and pupae removed after fledglings had flown
2	5	100%	—	102
3	5	100%	—	112
5	5	20%	94	— ¹
6	3	0%	0	— ²
10	6	100%	0	—
11	6	0%	52	— ²
14	5	100%	47	66
17	5	100%	—	135
18	3	0%	30	— ²
33	4	100%	41	21
34	6	83.3%	106	—
38	6	100%	75	30
48	3	100%	—	74
52	5	100%	62	34
53	5	80%	—	61

A blank in the 4th column indicates no count was made.

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¹ No male seen at nest box after eggs hatched.

² Nest deserted by female. No male seen at nest box after eggs hatched.

³ See also Bibliography in Chapman, 1935.