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THE MOURNING DOVE ON CAPE COD[1]

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The emphasis currently being placed by Fish and Wildlife Service personnel on investigations of the Eastern Mourning Dove, *Zenaidura macroura carolinensis* (Linné), because of its importance as a game bird, and the concentration of their efforts in the southern states where the species is hunted, suggest the desirability of analyzing the data we have obtained from 21 years of banding this species on Cape Cod, Massachusetts, where it is protected the year round.

It is 16 years since Low (1935) published his study of our first four years of dove banding at North Eastham. Since then the number of birds handled, and returns and recoveries therefrom, has increased five-fold. Study of this more adequate sample verifies the conclusions reached tentatively by Low, and suggests additional trends not apparent from his smaller totals.

SOURCES OF DATA

All the doves banded at North Eastham have been obtained through routine trapping operations when time and personnel have permitted general sampling of the upland bird population. Most of our doves are captured in 15 large house-traps located semi-permanently in fixed positions on the research station grounds. Birds enter these traps at ground level through funnel entrances on all four sides. For bait we use a standard chicken scratch feed for bulk, and add to it smaller quantities of millet, canary, buckwheat, and sunflower seed to increase its attractiveness.

No attempt has been made to be specifically selective in this trapping, and no special effort has ever been made to concentrate on doves. Whenever the trap line is operated, all individuals of all species that the bait attracts into the traps are duly banded, recorded, and released. Doves are present in the trapping area continuously in spring, summer, and autumn, and intermittently in winter. When present they frequently make up less than five percent and rarely more than ten percent of the individual birds handled daily.

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Although we have handled 2690 individual doves an impressive 6870 times in our 21 years of trapping, the species does not trap too well. A few individuals overcome their natural timidity enough to form the "trap habit," though not as satisfactorily as some of the bolder fringillids and icterids. One of our "trap-happy" doves was handled 64 times in a six-week period, and others have repeated from 30 to 50 times in a season. But most doves feed so warily around the traps before entering that only about half the individuals present at any one time are taken. For birds remaining in the vicinity the proportion eventually entering the traps is much higher, so perhaps 90% of our resident doves wear bands before leaving.

The variations in the numbers of doves handled annually (see Table I) in no way reflects the presence or absence of birds, but is the result of variations in the trapping effort and efficiency from year to year. In only a few years has the trapping been consistent and comparable, either in number of traps in operation, number of days of trapping, exact location of traps, times of day operated, or efficiency of baiting and tending, all and any of which affect the numbers of birds taken. As no adequate compensation can be made for these variables, the banding figures can in no way be made to show any fluctuations in the numbers of birds present. The peak year of dove banding, 1934, resulted from intensive and careful trapping by Seth H. Low, aided by a field planted to buckwheat that summer only, which attracted the August flocks from the surrounding area and held them near the traps during their stay.

The percentage of repeats varies so greatly with the manner of working the trap line that its deviations reflect the abilities of the trappers rather than any change in the behavior of the birds. The maximum 60% of individuals that repeated during the banner 1934 season resulted from Low's operating the traps with a skill and diligence never before or since equalled at the station. As a whole the proportion of doves repeating is not high, averaging only 39% in the 21 years of trapping. Thus 61% of the doves we have trapped failed to enter the traps again the same season. As absence from the traps does not necessarily mean absence from the vicinity, this factor of relatively poor trapability must be kept in mind when interpreting the banding figures.

The trap line has been operated over the years by some 30 different persons. Consequently the quality of the data recorded for individual birds varies considerably. For some seasons the age determination is not too satisfactory. We have never banded any doves as nestlings, and not all the operators have been capable of differentiating between adults and immatures, especially in the autumn after the young of the year have outgrown their more obvious juvenal characteristics. Nor have we as yet learned to tell the sexes apart with any certainty, even in spring adults.

The limited staff and the pressure of off-station work during the tern season often has forced us to forego all trapping of upland birds during June and July, making an unfortunate gap in our records for

this critical period in the doves' life cycle. For five years, however, 1931, 1932, 1934, 1936, and 1937, the trap line was operated continuously from March through November by competent volunteer personnel. The results for these five years are most significant, and are used alone in the analysis of seasonal trends.

It is also regrettable that we have never been able to study the Mourning Dove's life history and ecology on Cape Cod, except in the most general way. Time and personnel to do the necessary field work for such a study have never been available, particularly in the breeding season when terns take priority on the station's agenda. Hence our exact knowledge of the species' local habits contains many blanks which, if filled, would help greatly in interpreting the banding figures.

Despite these obvious limitations in the data, enough doves have been banded, and with sufficient regularity, to be of significance as a fair sample for statistical study. These basic data are summarized in Table I.

TABLE I

Column:	1	2	3	4	5	6	7	8	9	10
Year	New bandings	Returns[1]	Total individuals captured	Repeats	Total captures	Individuals repeating	Percent of individuals repeating	Ratio of returns to individuals present	Recoveries[2]	Percent recoveries
1930	74	.....	74	39	113	22	29.8	.....	3	4.0
1931	110	10	120	161	281	56	46.6	8.4	5	4.5
1932	175	27	202	231	433	94	46.5	13.4	13	7.4
1933	178	34	212	379	591	105	49.5	16.0	11	6.2
1934	316	33	349	1035	1384	209	60.0	9.5	16	5.1
1935	32	30	62	35	97	15	24.2	48.5	2	6.2
1936	98	17	115	222	337	46	40.0	14.8	4	4.1
1937	126	20	146	216	362	54	37.0	13.7	6	4.8
1938	127	25	152	86	238	44	29.0	16.5	8	6.3
1939	168	14	182	139	321	72	39.5	7.7	6	3.6
1940	129	29	158	73	231	42	26.6	18.3	7	5.4
1941	128	31	159	148	307	59	37.0	19.5	4	3.1
1942	129	28	157	126	283	54	34.4	17.8	1	0.8
1943	51	18	69	25	94	15	21.8	26.0	2	3.9
1944	153	16	169	80	249	38	22.5	9.5	2	1.3
1945	66	18	84	38	122	19	22.6	21.4	1	1.5
1946	95	16	111	111	222	36	32.5	14.4	2	2.1
1947	65	8	73	33	106	22	30.2	11.0	1	1.5
1948	167	15	182	117	299	63	34.6	8.3	2	1.2
1949	114	20	134	70	204	40	29.8	15.0	5	4.4
1950	189	31	220	376	596	110	50.0	14.1	4	2.1
Totals	2690	440	3130	3740	6870	1215			105	
Averages							39%	14%		3.9%

[1]From previous years only. Within-season returns based on the arbitrary rule of three months' absence from the traps have no significance without additional evidence of absence from the vicinity.

[2]Totals reported to date of each year's new bandings captured elsewhere. We have never recaptured a dove banded elsewhere.

STATUS ON CAPE COD

The turn of the present century found the Mourning Dove a comparatively rare species throughout New England. Uncontrolled over-shooting in this essentially breeding territory, following urban development during the late 19th century, had reduced the population almost to the vanishing point. Massachusetts, by her Act of 1908, became one of the first states to give the dove permanent protection. During the ensuing decade the effects of this beneficial legislation were most gratifying. The species made a rapid recovery, and soon re-occupied its former breeding range in safer numbers.

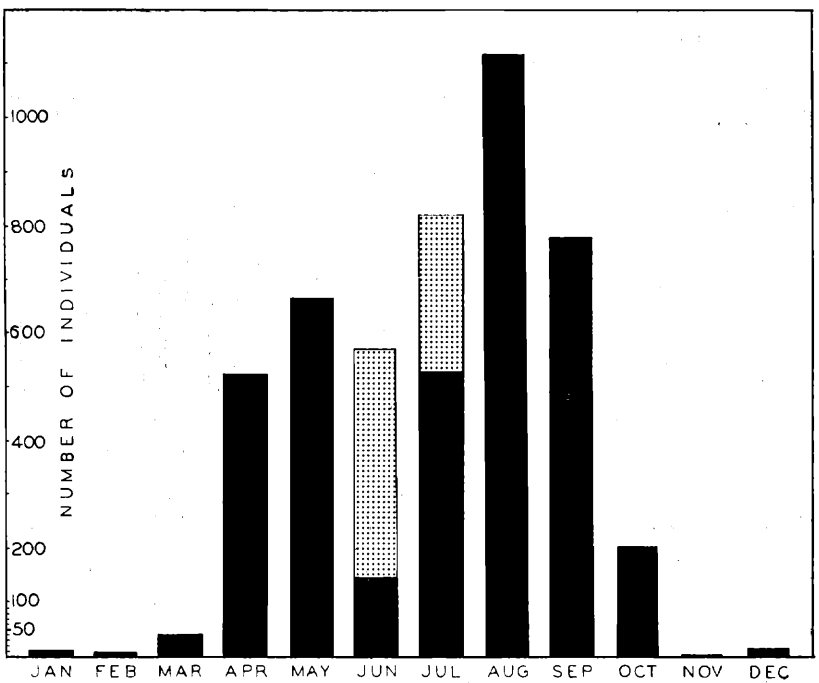


Figure 1.

Monthly abundance of Mourning Doves at North Eastham as shown by total individuals trapped from 1930 through 1950. The stippled additions to the bars for June and July are estimates to compensate for varying periods of no trapping during these months 16 of the 21 years (see p. 151).

The dove seems to have reached its ecological saturation point on the outer Cape in the early 1920's. At least our field observations, which started on Cape Cod in 1925, have not remarked any changes in the relative annual abundance of the species since that time. Judging from contemporary literature (Forbush, 1912, 394-396, 1927, 82-87; and seasonal reports in the Audubon journals) the bird has continued to increase slowly in abundance elsewhere in New England. It seems still to be extending its breeding range on the northern peripheries, and to

be wintering more often in more northerly areas (Palmer, 1949, 296-298).

Because a few doves winter annually on Cape Cod, and the species can be found here throughout the year, it is often regarded as a permanent resident. While this is true in a limited sense for the species as a whole, it is not strictly correct. The banding evidence reveals that all individuals of the species are migratory, and that certainly two and probably three distinct populations of Mourning Doves visit Cape Cod annually. In the commonly accepted parlance for defining occurrence, the species is on Cape Cod essentially a common summer resident, an uncommon and irregular winter visitor, and a not uncommon spring and autumn transient.

THE WINTER POPULATION

The winter population is so small in comparison to the large numbers of doves present from April to October (Figure 1) that the individuals comprising it might almost be regarded as of only accidental occurrence. However, these wintering individuals shift about so rapidly and at random, and, strangely enough trap so poorly, that the banding figures are not commensurate with their relative abundance. The few that discover the food bounty in the traps never avail themselves of it more than a week or two before moving on. While doves are reported on the outer Cape practically every winter, we have noted their presence at or near the station only 12 of the 21 winters, and have trapped them only in five.

The 40 individuals we have recorded in our traps between November 1 and March 20 are admittedly a very small sample. Nevertheless they should yield, by the same percentages resulting from birds banded at other seasons, about one recovery and five returns. That we have not received a single recovery or return from them to date is understandable. As these birds winter where there is no open hunting season, shooting recoveries are not to be expected. Because the rigors of the northern winter must exact a higher non-human-induced mortality than in doves wintering in more favorable southern latitudes, fewer of them are available to return in subsequent winters. Returns to a wintering ground are seldom as high as those to a breeding ground in any species, but from the decline in the numbers of doves from December through February, it is doubtful if many of these birds survive except in the mildest winters. Other factors being equal, the total absence of returns emphasizes the uncertain behavior of these doves that winter in the north.

Not one of our wintering doves has been taken earlier than September 25, nor later than April 3. Even more significant, not one of our much more adequate summer-banded sample has been captured later than October 31, or earlier than March 25. Thus the wintering population, though small and erratic in its comings and goings, is apparently a distinct, discrete group of individuals from the summering population.

Where these birds come from, or where they go, remains for more

adequate banding to reveal. All we can say of them from the data at hand is that they apparently do not breed on the Cape, but arrive irregularly any time from late September through early December, and depart during February and March, never remaining later than early April.

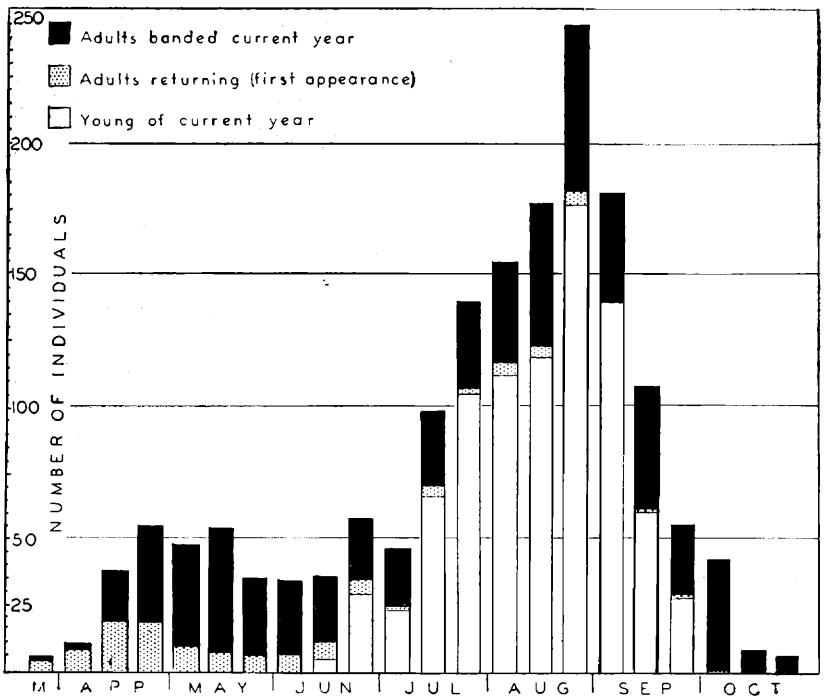
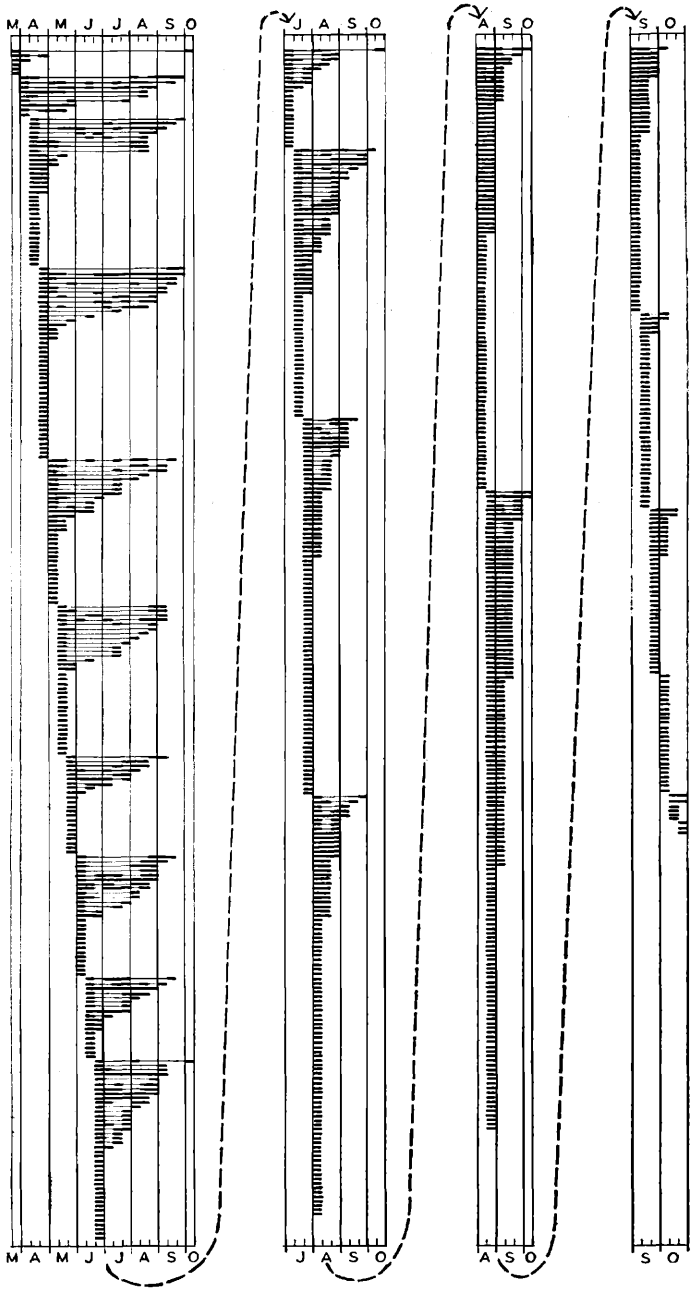


Figure 2 (above).

Total individual Mourning Doves trapped at North Eastham from March 21 through October 31 in 1931, 1932, 1934, 1936, and 1937, the only years the traps were operated continuously throughout this period. The horizontal scale is in successive 10-day periods, March 21-31, April 1-10, 11-20, 21-30, etc. As the vertical scale shows the 5-year total of individuals divide it by five to obtain the annual average. Because the identity of immatures becomes progressively more uncertain after mid-September, no young of the years are indicated for October (see p. 164).

Figure 3 (on right-hand page).

Banding and repeat data for figure 2 graphed to show first appearance and duration of stay of each individual dove. The horizontal scale is in the same successive 10-day periods. The presence of each bird is indicated by a heavy bar in the appropriate period. The five-year totals are combined and grouped vertically by annual arrival dates, with individuals of longest stay at the top of each group.


M A M J J A S O
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THE SUMMER POPULATION

Using only the banding data for those years the trap line was operated continuously, Figure 2 shows the total individuals trapped during successive ten-day periods from the first appearance of returning migrants in late March to the last departure of summering and transient birds in late October. Interpreting this graph from our daily banding records and field notes, the first non-wintering doves may appear any time between March 25 and April 5. The arrival date varies somewhat each year, but so far we have been unable to correlate it with any meteorological or other environmental factors.

The vanguard of the spring flight is small, and composed predominantly of returns. The flight increases in volume in mid April and continues through mid May when the numbers of doves attending the traps fall off. The adult population of the trapping area in the breeding period varies annually from three to five pairs of doves, and remains fairly stable from late May to early August. The increasing number of adults appearing in mid August signals the start of the post-nuptial flocking preparatory to migration.

The summer population of both adults and young starts to diminish with the first marked departure of doves, usually during the last few days of August. The reduction of the ranks progresses steadily through September. The last pronounced wave of departees disappears during the first week of October, but a few stragglers usually linger on through the month. The last summer and/or transient bird is always gone by the first of November.

THE TRANSIENT POPULATION

The movements of all land birds in migration on the outer Cape are still a matter of conjecture on which neither years of field observation nor banding have as yet shed much light. The absence of northern species in passage during spring is remarkable. A few Canadian and Hudsonian Zone land birds appear irregularly in April and May, but in nothing approaching the numbers of individuals or of species that pass through the nearby mainland at this season. Our spring flights are composed almost entirely of the species which breed here.

Most of our breeding species, our Robins, Red-wings, Grackles, Cowbirds, Song and Chipping sparrows, as well as our Mourning Doves, first appear each spring in larger numbers than are observed at nesting time. It seems unlikely that all these individuals find breeding space on the Cape. Whether the unsuccessful surplus back-tracks over the land to the mainland, or hops off boldly across Massachusetts Bay or the Gulf of Maine to find suitable unoccupied territory we do not know. The available evidence indicates that the outer Cape in spring is essentially a migration terminus for land birds.

In the autumn, on the other hand, the appearance of passage birds is pronounced. Some, particularly those species breeding to the west and northwest which appear every late summer and early autumn, probably work their way out along the land in a post-nuptial wandering rather than in definite migration. Most of the true migrants seem

to reach the Cape directly from over the water rather than by following the circuitous path around the shore. Their flights correlate with the direction and intensity of the autumn winds. Strong easterlies during the fall flights reduce their numbers. Periods of calms or light westerlies invariably increase them.

The Mourning Dove movements in spring and autumn seem to fall into this general pattern, although the banding evidence is not as definite as one could wish. We have enough recoveries only to sketch in the southward flight to the wintering grounds, and the repeat record is in some respects negative rather than positive evidence. Nevertheless the repeats do suggest the existence on the Cape of populations of spring and autumn transients, distinct from the summer and winter populations. As portrayed in Figure 3 they reveal a pronounced fluidity of individuals throughout the season. Part of this reflects the species' poor trapability. It is unlikely, for instance, that all the individuals appearing for the first time during the height of the nesting season in June were new arrivals, or that all those appearing for the last time in early summer had left the area. Figure 3 does reveal during the expected flight periods, and more pronounced in autumn than in spring, an increase of the individuals that appear only once or twice.

The decrease of individuals noted the end of May in Figure 2 now is seen to result from the disappearance of those birds of brief attendance which we assume to be spring transients. Many of these departing birds probably nest near by on the Cape, particularly the large numbers which appear in April and May, are absent through June and July, and reappear in August, September, and even October. Nevertheless some of them are "passage" birds in the more exact sense, en route through to more distant nesting grounds. Only one of our doves banded in spring has been recaptured elsewhere before the autumn flight. An adult banded April 24, 1939 and which never repeated, was found dead 11 days later on May 5, 1939 at Brockton, Massachusetts, 52 miles west-northwestward across the Bay on the mainland. This is our only proof that some individuals which arrive here during the spring flight leave the Cape before the nesting season.

The presence of an autumn transient population is suggested more strongly by the increase of individuals which appear only briefly in the periods after late July. Figure 2 shows the total number of individuals present to remain fairly stable from late July through mid August, increasing slowly as more young leave the nest and the resident birds flock before migrating. Figure 3 shows an increasing fluidity in the composition of the flocks at this period, reflecting the transiency of the restless young of the year which now comprise two-thirds of the birds trapped.

The striking increase in the population to its late August peak in Figure 2 probably marks the appearance of the final broods with their parents, simultaneously with the arrival of the first wave of transient non-residents, which gathers with it many of the resident birds as it passes through. A few of the known resident birds, those which are trapped regularly through the breeding season, may linger as late as October, but Figure 3 shows that most of them disappear in late August

or early September with this first wave of departees. The ten-day intervals in which the data are assembled are too long to reveal it, but a dearth of doves in the area is always apparent for a short period between August 25 and September 5 after this first wave leaves and before more transients arrive.

The rapidly declining population is even more fluid through September. A few of the transients may remain in the vicinity for 20 or more days, but most of them stop barely long enough to be trapped and banded before pushing on southward. Still to be discovered is the source of these autumn flight birds. We have yet to capture a dove banded elsewhere to give us a clue, but they probably come from the north and/or west. More summer banding of doves elsewhere in New England may eventually tell us.

THE SOUTHWARD FLIGHT

The points of recovery of our Cape Cod Mourning Doves plotted in Figure 4 reaffirm the facts pointed out by Low (1935) from his smaller sample of recoveries. The wintering ground of the Cape Cod doves extends through the coastal plain from southern Virginia to central Florida, westward through the gulf lowlands to Alabama, and occasionally to Louisiana and and east Texas. Very few individuals stray beyond the land-rise into the piedmont, and only one has straggled to the Appalachian Mountains, an immature taken far off its course in Tennessee on November 21.

The winter range centers in the coastal plain belt from South Carolina to northern Florida and eastern Alabama. The semi-circle from the edge of the land-rise embracing this area contains two-thirds of the winter recoveries. Possible bias in this distribution because dove hunting may be more intense within this perimeter as suggested by Taber (1930) is unlikely. Potential hunting pressures must be fairly even throughout the southern states, and the concentration of recoveries of Cape Cod doves within this area over a 21-year period establishes it as the population's preferred wintering ground.

After leaving the Cape the doves seem to make a rapid flight southward. As they are not shot in quantity until they are well south of the Mason-Dixon line, the more northerly recoveries mark their passage very sketchily. The lone New Jersey recovery, banded May 5, 1936 and never handled again until it was found dead August 16, 1940, was probably not a flight bird. The Delaware and Maryland recoveries, however, were in passage; the former was shot October 9, the latter three in late September. One of the Virginia birds was killed November 14, the other December 14, indicating that some of our birds do winter that far northward.

Three birds taken with the concentration perimeter, two in South Carolina on September 28 and "late September," the other in Georgia on September 28, probably mark the earliest southern arrivals. The latter bird still holds our dove time-distance record (Low, 1935) with its 43.8 miles per day average flight.

Except for one bird picked up dead after hitting a power line in

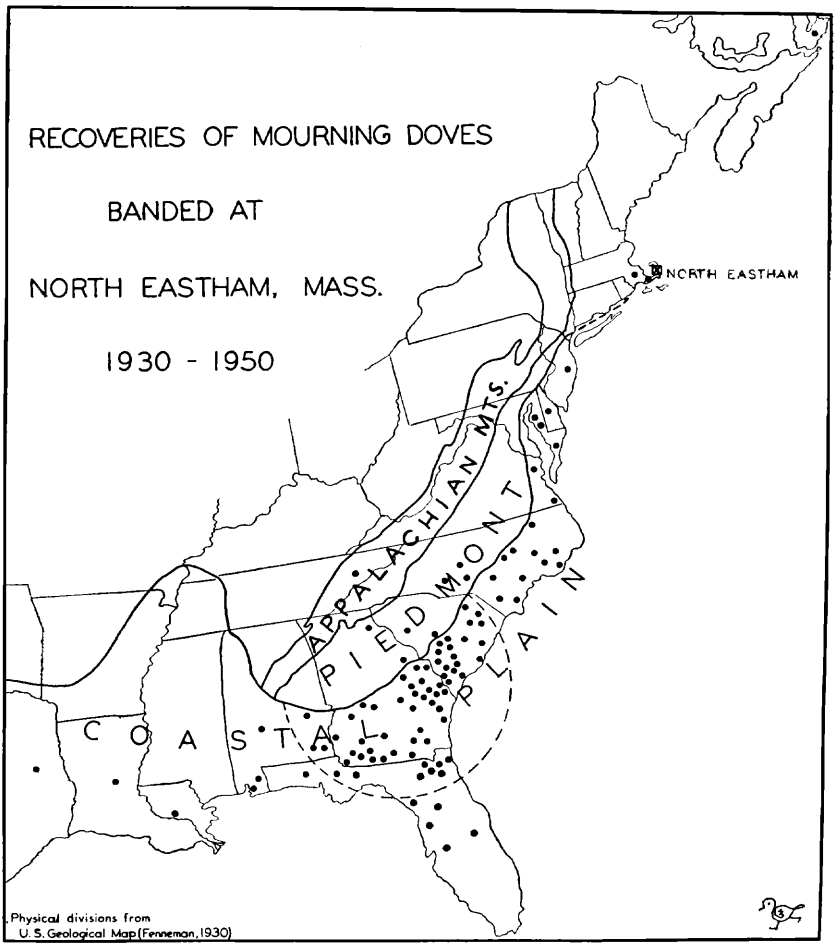

Figure 4.

Farmville October 23, all the North Carolina recoveries were shot in December and January. In addition to the three September records mentioned above we have one South Carolina recovery on November 24, and from Georgia one on October 9 and three in late November. The earliest Florida bird was shot November 9 at Plant City, the next on November 20 at Sanderson. Two Alabama doves were shot November 11 and 14 respectively. All the rest of the southern recoveries were shot after December 1, most of them in December and January. A few birds have been reported from Georgia and South Carolina in February. One South Carolina bird was shot March 5, long after the hunting season closed, and probably as the first migrants were leaving for the north.

We have no banding data on the northward flight in spring.

SITE TENACITY AND GROUP ADHERENCE

Bird banders have long been aware that in many migratory species the percentages of returns to the place of banding are highest at stations on the breeding grounds, lower on the wintering grounds, and lowest on migration routes between the two. This tendency of individual birds to return to the same territory year after year, called site tenacity (Austin, Sr., 1949), has never been evaluated precisely. It can be measured only by appraising the returns of banded birds. Methods for doing this have not yet been standardized.

The trait is most important to old-age, ultra-specialized forms so limited by their ecological needs they may have difficulty finding suitable territory, and less so to birds contending with no shortage of favorable habitat. It is evinced least by youthful, plastic, aggressive species able to adapt themselves to a wide range of environmental conditions. The degree of site tenacity a migratory species displays thus is indicative of its relative adaptability, and as such is a potential measure of its evolutionary age.

The Mourning Dove exhibits site tenacity more strongly than is suggested at first glance by the average 14% return to the trapping area of our Cape Cod population (Table 1, column 8). Evaluated in relation to the total numbers of individuals handled, the return ratio varies excessively each year according to the seasons the traps were operated most intensively. The high percentages in 1935, 1943, and 1945 resulted from heavy trapping of the adult population in April and May, and comparatively little later in the year. The low percentages in 1934, 1939, 1944, and 1948 reflect the opposite situation, light trapping in spring, and/or heavier sampling in the late summer when most of the captures are young of the year. While the 14% average for the 21 years is a fair approximation, it is an unsatisfactory measure of site tenacity because the young of each current year which predominate in the annual totals are an irrelevant factor reducing the percentage unnecessarily.

Preferably the returns should be appraised either in proportion to the numbers of adults present, which is unfeasible because of the lack of age-determination for a large part of our sample, or else related to the numbers of banded birds available to return, which is difficult on an annual basis because of inequalities in the yearly trapping. The fairest and most realistic standard available for judging the significance of the dove returns is an estimate of the numbers of banded doves surviving from year to year over the 21-year period.

The total number of individual doves handled annually prior to 1950 is 2910 (Table 1, column 3). As the mean annual mortality in our dove population (to be shown later) averages 69%, only about 903 of these birds could have been available to return in later years, or slightly more than twice the 440 returns taken through 1950 (Table I, column 2). In view of the species' poor trapability, and particularly the age bias in the trapping (also to be discussed later), considerably more than half the surviving doves must return to the trapping area each summer season.

Site tenacity to the breeding grounds may therefore be considered

a major behavior trait in the Mourning Dove. Our data are inadequate to show adherence to individual nesting territories, but a return to the natal area is exhibited by young doves coming back to nest for the first time. The tendency probably becomes stronger and more pronounced with age as demonstrated in the terns (Austin, Sr., 1949).

As ecological requirements are more exacting during the reproductive period than at any other part of the avian life cycle, and as birds are more restricted in their movements then than at any other time, site tenacity is understandably strongest and most manifest on the breeding grounds. Birds are most free from territorial limitations while migrating, but the low percentage of returns to banding stations on flight routes is not necessarily indicative of failure to follow the same path. Individuals may stop over at different points on the route as the exigencies of the journey demand.

Site tenacity must influence the selection of the wintering grounds to some degree. The ecological requirements in winter, although possibly less exacting than those at nesting time, may be equally restrictive and quite as limiting to the species' survival. Unfortunately we do not have access to Mourning Dove data from banding stations in the south, and the few that have been published are inadequate for evaluation of the annual return. The recoveries of our Cape Cod doves indicate a return to the same general area by the population as a whole each winter, but without as close individual adherence to particular restricted territories as in summer.

The recoveries suggest that doves do not remain in close-knit groups either on migration or in winter. Their time-spread over the area intimates that the birds move individually or in loosely-connected small units. Nor do our summer returns and repeats warrant any assumption of the grouping of individuals other than that incident to fidelity to the nesting territory. Group adherence, the attachment of individual birds to each other as demonstrated in the terns, is thought to be the outcome of lasting family ties (Austin, Sr., 1951). If this be so, the trait can hardly be expected to be strong in a multi-brooded species like the dove, where early separation of adults from their offspring is the rule.

NESTING AND DISSEMINATION OF YOUNG

In the absence of any information from direct observation of the nesting habits of the Mourning Dove on Cape Cod, the summer banding figures may be explored to see what they reflect of the local nesting phenomena. These should not differ materially from those studied and reported in detail elsewhere in the range of the species. From the pertinent literature (cf. Nice, 1922-1923, 1926, 1943; Tyler, 1932; McClure, 1942, 1943, 1946; Kendeigh, 1942; Young, 1949; Quay, 1951) the following generalizations may be drawn:

The nesting period varies with the latitude, being longer in the south and shorter in the north.

The normal clutch is two eggs, with very few and inconsequential variations.

The incubation period is about 15 days, perhaps slightly shorter; the fledgling period averages 14 days; the brood cycle 31 days.

The species is multi-brooded, each pair raising at least two clutches, often three, and in southern latitudes sometimes four or more.

The nesting success, figured as percent of eggs laid which produce young that leave the nest, varies from 15% to 70%, with a well authenticated average of 47% in observed samples.

Referring again to Figure 2, the first young appear in the traps at North Eastham in mid June (earliest record June 16). Allowing 31 days for the brood cycle, and a few more days for the young to find the traps, the first eggs are laid early in mid May. Undoubtedly the exact dates of first layings vary somewhat, perhaps from about May 5 to 20.

By late June the entire first hatch is on the wing, and the parents are engaged with incubating the second clutch. A second increase in young shown in Figure 2 for mid July betokens the appearance of the second brood in the traps on schedule. The succession of broods is not so distinct after mid July for, as McClure has noted (1942, 68), the broods now begin to overlap. The sharp increase of young in late August suggests the appearance of the final broods at that time, but the figures are then confused by the simultaneous premigratory flocking of the local birds and the arrival of early migrants.

The observed brood cycle of 31 days (Nice 1923, 54) which is corroborated so nicely by the trapping evidence in June and July, implies that each hatch of young is abandoned by its parents as soon as or shortly after it leaves the nest. Indeed, the doves are seldom observed in family groups of parents with young on the wing. The latter most frequently appear at first in the traps alone or with another immature, unaccompanied by guiding adults.

The young being "on their own" so early in life may account in large part for their high degree of mobility during the post-brooding period. The haphazard scattering of young before the southward migration that has been found in herons and terns is suggested by the fluidity of individuals at this period, but only one of our young doves has been reported off the regular southward path. An immature not long out of the nest when banded August 25, 1950 and which never repeated, was found dead October 28, 1950 at Mabou, Inverness County, Cape Breton, Nova Scotia. The finder, Angus S. Cameron, reported the bird was "fat and must have been dead only a short time." Other than its interest as a possible example of the "grenade" effect in the premigratory scattering of young, this recovery is of added import in that it is well beyond the normal north-eastern periphery of the species' range.

PRODUCTION OF YOUNG

The percentages of young present in the dove population during the summer and early autumn are an index to the species' annual replacement, and as such of significance both to practical game management and to theoretical ornithological demography.

Figure 5 is based on samples of doves aged as captured by the more capable and careful of our operators during the five years of continuous summer banding. Comparison of Figures 5 and 2 reveals that although the trappings in late June and early July are half young and half adults, the total number of individuals present has not doubled. As nesting success cannot have been perfect, the balance between the numbers of adults and young taken requires explanation.

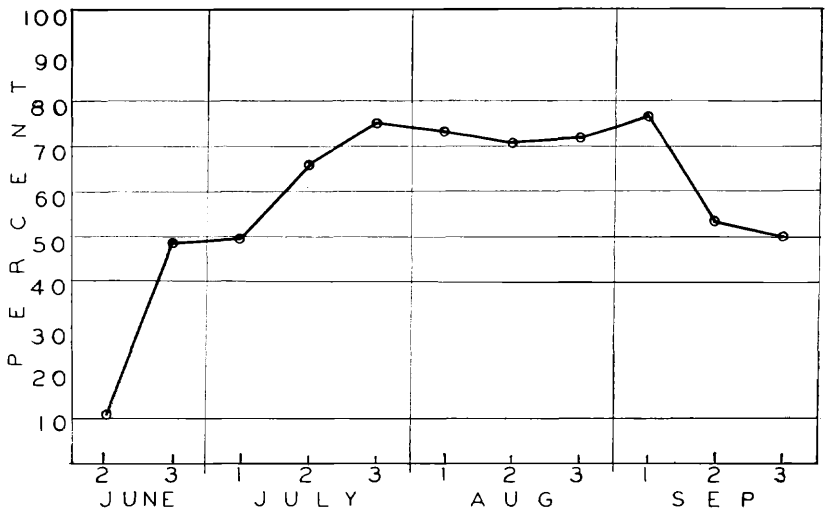

Figure 5.

Percentages of young of the year among the Mourning Doves trapped at North Eastham during the summer months. Data are for the same five years used in Figures 2 and 3, and the horizontal scale represents the same successive 10-day periods.

Figure 2 shows the number of young trapped in late June to be slightly less than the late May-early June adult captures, which also have now declined slightly. In early July the numbers of both adults and young decline still farther, which cannot reflect a mortality because both have lessened in proportion. The decrease in adult takes suggests their closer restriction to individual breeding territories as the nesting approaches its height. The more mobile young of the first brood are at the same time straggling out of the trapping area faster for the moment than others are coming in from elsewhere to replace them.

Figure 5 shows the percentage of young to increase with the first appearance of the second brood in mid July, and to reach a peak in late July when most of this hatch is probably on the wing. From Figure 2 we see the number of adults has not yet increased signally, though there is a small increment in early August. While the adults are still limited in their movements by nesting territorial restrictions, the young have begun to flock in from elsewhere out of all proportion to the possible productivity of the first two nestings. Their numbers

are now more than double the original breeding population, which could not possibly have produced them in two broods even with perfect survival, and as yet there has been neither time enough for nor any indication of the third brood. An age bias in the trapping is clearly manifest, the less timid young entering the traps more readily than the shyer adults.

Though no juvenal mortality has been observed, and no estimate can be made of how many young have died since leaving the nest, no doubt some deaths occur, but become fewer as the fledglings gain experience. This post-fledgling mortality probably contributes partly to the slight decline in the percentages of young present throughout August. Another factor in the decline is the increasing number of adults Figure 2 shows coming to the traps in August as their mobility increases with the waning nesting season. Both these effects are offset by the continual appearance of more young from the staggered third broods.

The slight rise in the proportion of young to 77% the first of September when many of the resident doves have left and transients have begun to pass through may be caused in part by age bias in the trapping of the early transients. Coupled with the sharp decrease in the proportion of young later in the month, it suggests the possibility intimated by Ginn (1950, 381) that the immatures may precede the adults in the southward flight. However, by mid September the early-hatched young resemble the adults so closely that many of them are perhaps not recognized as such in the hustle of handling the number of birds our traps produce at this season, and the apparent drop in percentages of young from mid September on may not be real. The peak proportion of young in the early September samples probably signifies the advent of young from the final local broods simultaneously with the flocking in of immatures produced earlier elsewhere, increased somewhat by age bias in the trapping.

These various influences affecting the relative numbers of adults and young in the trapped sample hinder any accurate estimate of the percentage of young actually produced. Nevertheless the sample does provide some indication of its order of magnitude. Although we cannot determine the exact weight of age bias in the trapped sample, we may reasonably assume that the net summer replacement in the total population is not greater than 70%, or slightly less than the average percentage of young present in the sample trapped in August and early September. Disregarding the comparatively slight adult mortality during the breeding season, this implies that every 30 adult doves has produced 70 young, an average of 4.6 per pair, yielding a birth rate of 233 young per 100 adults.

The breeding biology and the timing and periodicity in the increase of young doves during the season indicate the species rears three broods each summer on Cape Cod. The production of 4.6 young per pair in three broods of two eggs each requires a nesting success of 77%. While only slightly higher than the maximum 70% reported by McClure (1946), this is considerably in excess of the 50% success obtained by averaging the results of all observers (Young, 1949, 44; Quay, 1951, 85).

If we assume a minimum breeding success of 50%, the three two-egg broods would produce only 3 young per pair, or 150 young per 100 adults. In this case the replacement rate is 60%, which we may adopt as its lowest probable limit in accord with the evidence.

Because all our Cape Cod pairs, particularly those frustrated in late nesting attempts, may not have time to produce a third brood in the 14- to 15-week nesting season, nesting successes may average even higher than the estimated 77%. The nesting mortalities reported by Nice, McClure, Kendeigh, Young, and Quay, while unquestionably accurate for the samples observed, cannot satisfy the species' production requirements indicated by the survival figures. Scrupulously heedful of the birds' welfare as these workers undoubtedly were, their very actions in observing the nests could not help but contribute to the mortality, especially that portion of it resulting from predators and from desertion by the parents which caused most of the observed nesting failures. Survival may therefore be considerably higher in unwatched nests, and the actual nesting success nearer the 77% estimated from the banding evidence than the observed average of 50%. It follows that the annual replacement rate is probably closer to the assumed maximum 70% than to the postulated minimum 60%.

MORTALITY AND SURVIVAL

Except for seasonal and minor temporary fluctuations the Mourning Dove population of Cape Cod has neither increased nor decreased during the 21 years covered by this study. The population may therefore be considered to be maintaining itself in balance, and the annual replacement and mortality rates, theoretically at least, should be about equal. It will be of significance to see how well the replacement rates as estimated above agree with the annual mortality rates shown by the recoveries and returns.

The most reliable estimates of avian mortality are those based on the recoveries of banded birds. Following the methods of Lack, Farner, and others[3], the recoveries may be regarded as a fair sample in themselves, irrespective of the numbers of birds banded to produce them. This eliminates possible discrepancies resulting from age or regional bias in banding, but does not rule out biased selection in the recoveries, particularly from human interference, a major influence in all game birds. For our Cape Cod doves 89.5% of the recoveries were reported as shot or "killed."

It is most convenient in analyzing these recovery and return records to make all calculations for each year as of November 1, immediately after all the resident and migrant doves have departed southward. Much of the age bias could be eliminated by making all calculations from January 1 as recommended by Lack, and all of it by using March 25, the date of first return of the adult population to the nesting

[3]For details of the statistical methods employed see Pearl (1940), Lack (1943, 1946, 1949), and Farner (1945, 1949). Other recent studies of mortality from banding data may also be consulted, notably those of Marshall (1947), Paynter (1947), and Hann (1948).

grounds. This would preclude any possible correlation between the annual birth and death rates, and prevent consideration of the first year mortality which is not only much greater than in subsequent years, but of vital concern in a short-lived species.

In this analysis where there is no evidence to the contrary all birds handled between March 25 and October 31 are assumed to be alive on November 1 the same year. The mortality among adults during the breeding season and the possibly greater death rate among the young between the time of banding and the time of departure are disregarded. Neither can be estimated from the data at hand. The few recoveries shot in the south before November 1 are included in the first year totals, their shorter life spans averaged with those killed or dying later in calculating the mean survival after November 1.

As we are interested first in the mean annual mortality exhibited by the entire population, which must be balanced each year by the replacement if the species is to maintain itself, let us first examine all the recoveries without regard to their ages when banded or their causes of death. From these may be derived the most trustworthy mean death rate for the population as a whole, and from that an estimate of the amount of further life our birds may expect. The 105 recoveries we have received to date (June 1, 1951) from all doves banded prior to November 1, 1950, may be arranged in a life table as follows:

TABLE II

Year after banding	Number dying each year (recoveries)	Number alive at start of each year	% of total alive at start of each year	% of year's population dying each year (annual mortality rate)	Expectation of further life on Nov. 1[4]
0-1	79	105	100.0%	75.4%	0.51 years
1-2	15	26	24.8	57.8	0.91 "
2-3	5	11	10.5	45.6	1.38 "
3-4	3	6	5.7	50.0	1.18 "
4-5	2	3	2.9	66.6	—
5-6	1	1	.9	100.0	—

Mean annual mortality, 0-6 years: 69%[5]

Mean annual mortality, 1-6 years: 55%

[4]Using Farner's (1949) formula:

$$Y = \frac{1}{M} - (1\text{-}p)$$

where Y is the mean longevity, M the mortality, and p the mean period lived during the year in which death occurs, in this case 0.18 years.

[5]Using Lack's formula:

$$M = \frac{D1 + D2 + D3}{D1 + 2D2 + 3D3}$$

where M is the mean annual mortality, and D1, D2, D3 the numbers dying in successive years.

The 69% mean annual mortality yielded by these recoveries is very close to the upper limit of the replacement rate as estimated previously.

The mean life expectancy of the entire population, adults and

young[4], is .63 years, or 7½ months after November 1. This estimate is influenced by the high age-biased mortality in the first year after banding, and by the preponderance of recoveries during the shooting season in mid winter. The mean duration of life of the 26 birds which survived after the first year is just one year, but the small sample is not sufficiently random after the second year to fall into a normal frequency curve. Hence it does not show whether the adult mortality levels off immediately or continues to decline with age.

The actual first year mortality of the young of the year must be higher than the 75.4% indicated by Table II, for it is reduced in the recovery sample by the longer survival of those birds which were at least one year old when banded. These comprise an indeterminate portion of the sample, probably not more than 40%, possibly less. A life table based on recoveries of doves banded as fledglings would illuminate this point, but the age determination at banding of most of our recoveries was so unsatisfactory that those known beyond question to have been young of the year are too few to be of significance. However, we can segregate the 27 recoveries banded in spring before the first young appear, and five more banded after June 15 which were reliably aged as adults. We thus have two groups, one entirely of birds banded as adults, the other with a much higher proportion of young than the original sample. These tabulate as follows:

TABLE III

a. Banded as adults				b. Age unknown, but fewer adults		
Recoveries	Alive at start	Annual mort. rate	Year	Recoveries	Alive at start	Annual mort. rate
21	32	65.5%	0-1	58	73	79.5%
5	11	45.5	1-2	10	15	66.8
3	6	50.0	2-3	2	5	40.0
2	3	66.6	3-4	1	3	33.3
1	1	100.0	4-5	1	2	50.0
			5-6	1	1	100.0
Mean annual mortality: 60.6%				Mean annual mortality: 73.8%		

As expected, both the first year and the mean annual mortalities are lower in the adult group and higher in the predominantly young sample. Both groups are so small their significance after the second year is negligible, but it is interesting to note the closeness of the second year mortality in Table III-b to the first year rate in Table III-a.

A similar life table may be constructed from the returns. Here the basic data are not those birds known to have died, but those known to have survived. To arrive at the mortality we must assume all those not known to be alive are dead, which is not precise because it is impossible to retrap all the birds remaining alive of any given sample. This is of no moment in estimating the *rate* of decline except in the first year, where age bias increases the size of the original trapped sample. Age bias apparently does not affect the trapping of returns. A first year return for all we can see is neither more nor less wary or easier to trap than one five or more years old. As all the older birds are caught with about equal facility, the figures from the second

year on are relatively unaffected by any change in trapability, and the rates they indicate should be representative of the actual adult mortality for the entire population.

The vagaries of shooting and the uncertain cooperation of the public which so greatly influence the reporting of recoveries do not affect the capture and recording of the returns, which should therefore yield a fairer reflection of the mortality from all causes. And as the sample of returns is larger and more adequate, better frequency distribution and greater significance for the later years of life may be expected.

Many doves banded during the last few years have not yet completed their life spans. Possibly some birds ten or more years old are still carrying our bands. The total of these more than six years old is so small, about half of one percent of the original sample, that they may be disregarded. Discarding the bandings of the past six years eliminates for practical purposes all the doves that might still be alive. The following life table is built on the returns to November 1, 1950 of all doves banded between 1930 and 1944:

TABLE IV[6]

Year after banding	Number dying each year	Number alive at start of each year	% of total alive at start of each year	Annual mortality rate
0-1	1724	1994	100.0%	86.5%
1-2	141	269	13.5	52.5
2-3	65	128	6.4	50.7
3-4	31	63	3.3	49.2
4-5	19	32	1.6	59.5
5-6	9	13	.6	69.2
6-7	2	4	.2	50.0
7-8	0	2	.1	.....
8-9	0	2	.1	.....
9-10	1	2	.1	.....
10-11	1	1	.05	.....

Mean annual mortality, 0-11 years: 81.5%[5]
Mean annual mortality, 1-11 years: 52.0%

[6]Every individual known to be alive from captures in later years is counted as alive in earlier years when it may not have been trapped. In Table I only those returns actually handled are listed for each year.

The mean annual mortality for the entire population shown by these returns is, as foretold, somewhat higher than that shown by the recoveries alone where age bias in the trapping is not a factor. As age bias affects the trapping of the original sample only, the unduly high mortality and correspondingly low survival for the first year are the only other rates it alters. The actual death rate for the first year of life in the Mourning Dove is probably very close to 79.5% indicated in Table III-b, or in round numbers about 80%.

The mean annual mortality in adults shown by the returns is three percent lower than that calculated from the recoveries. At first glance this suggests that shooting, on which the recoveries are largely based, takes a higher toll of adults than other causes. However, the difference

is almost entirely accounted for by the four individuals that lived beyond six years. If these four birds, less than one-fourth of one percent of the original sample be disregarded, the mean annual death rate of adults from their second through their sixth years is 54.7%, remarkably close to the rate shown by the recoveries, 55%.

Table IV shows the adult mortalities to be fairly stable. The death rates for the second, third, and fourth years are very close together. Though they do decline slightly, the differences between them are within the normal variation to be expected in the frequency distribution. That the mortality is indeed constant after the first year is shown most clearly by plotting the returns themselves on a logarithmic grid (Figure 6) which allows us to analyze changes in their rate of decrease. In logarithmic plotting any regular geometric progression appears as a straight line. Once established, this line may be continued indefinitely in either direction, and variations in the progression are at once perceptible by their divergence from it.

Figure 6 shows that the rate of decline of the population is greater in the first than in any subsequent year, and that it levels out immediately at the end of the first year. A straight line drawn from the first through the second and third year points gives the best "fit" for all the other points. The returns for the fourth year are slightly above this line, those for the fifth not far below it. The remainder of the sample (the four old birds again) is so small that some aberration is to be expected. As these points fall almost equally on both sides of the continuation of the first-to-third-year line, no later shift in the rate is indicated. Indeed, that so small a sample fits so well is conclusive evidence of its validity.

It is obvious from these statistics that doves in the wild live but a small fraction of their potential life span. The greatest age reached by any of our banded doves is ten years, but we have no indication that this approaches the physiological age limit for the species, whatever that may prove eventually to be. The individual dove's chances of longer survival are easily computed from Table IV, or read directly from Figure 6. Only one bird in 150 can expect to live five years, and one in 500 to six. The one ten-year-old bird in our sample of almost 2000 was "living on borrowed time," for the chances are that only one bird in 3750 will live that long. At the same rate of survival only one dove in 7500 will live 11 years, and only one in 15,000 may survive to the ripe old age of 12.

For practical purposes we may assume that the first year mortality in our Cape Cod Mourning Doves from all causes after leaving the nest is about 80%, and that the adult death rate, reached at the end of the first year, is about 55%. The life expectancy of each dove that leaves the nest is thus less than one year, and for each bird that survives the first year, slightly less than one year more. As the population's "turnover" is almost complete every four years, replacement must be rapid and continuous if the population is to be maintained.

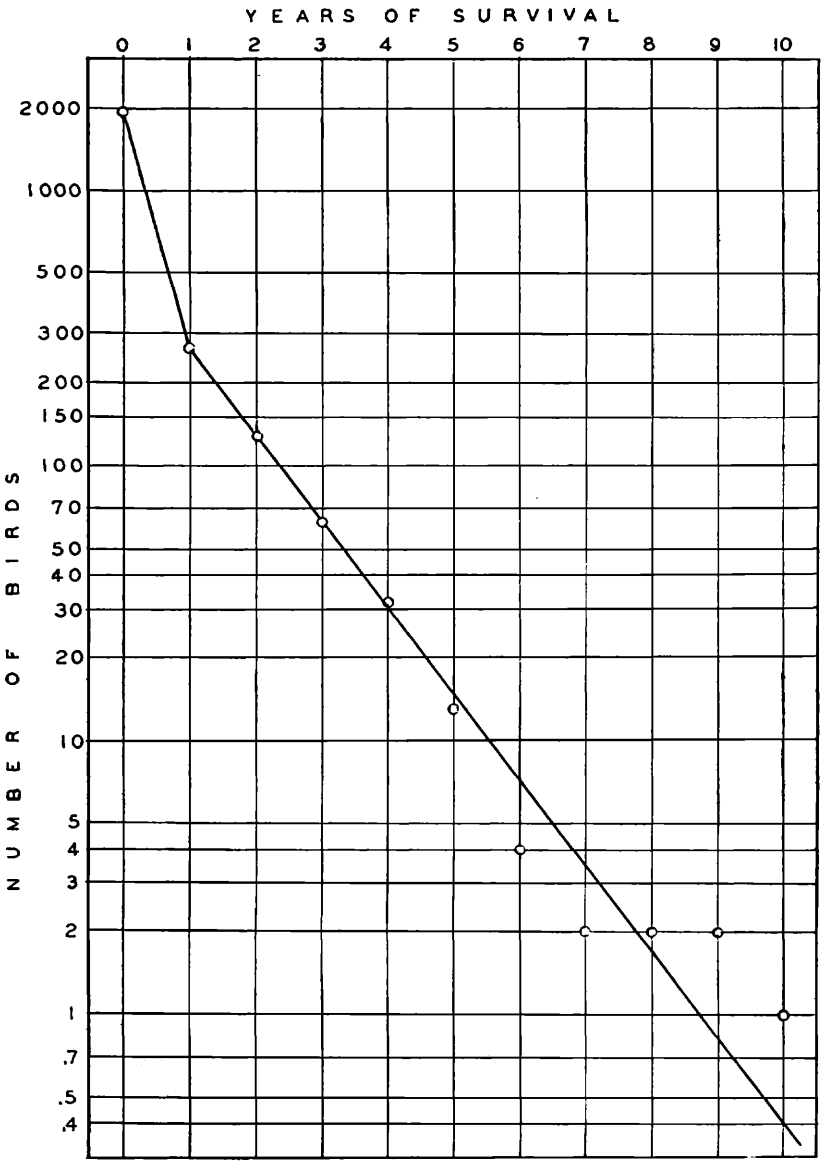

Figure 6: Logarithmic plot of returns listed in Table IV, column 3 (p. 168).

SHOOTING VERSUS "NATURAL" MORTALITY

No adequate study of the relative mortalities from shooting as distinct from "natural" causes in a migratory game bird subject to heavy hunting pressure has yet been published. The few analyses that have been made from the statistics available in non-game groups that

are shot occasionally are somewhat indefinite and contradictory. Some show no essential differences, others, such as those of Lack (1943) and Paynter (1947) in the gulls, indicate a significantly higher mortality from shooting in the first year of life than from other causes. Our sample of dove recoveries is much too small to be reliable when subdivided according to causes of death as follows:

TABLE V

a. shot				b. "found dead"		
Recoveries	Alive at start	Annual mort. rate	Year	Recoveries	Alive at start	Annual mort. rate
75	94	79.5%	0-1	4	11	36.5%
12	19	63.0	1-2	3	7	43.0
5	7	71.5	2-3	0	4	.....
0	2	.....	3-4	3	4	75.0
2	0	100.0	4-5	0	1	.....
0	0		5-6	1	0	100.0
Mean annual mortality: 77%				Mean annual mortality: 41%		

These two samples are greatly disproportionate in size, and the strikingly illogical distribution of the "found dead" group shows it is not a random, fair sample. A much larger group of recoveries, particularly of those resulting from sources other than shooting, will have to be analyzed to prove any actual differences. The close conformity of the annual mortality rates calculated from our recoveries, most of which were shot, to those based on the returns which are not influenced by the reporting of shot birds, suggests that the hunting deaths are not disproportionate to those from other causes in our Cape Cod population.

It is tempting to argue that as the recovery sample shows 89.5% of our doves shot, hunting accounts for nine-tenths of the current dove mortality. It is just as fallacious to argue the other extreme, that as less than four percent of the doves banded are reported shot, hunting is of no significance to dove survival. We have no way of estimating the ostensible discrepancy between the numbers of banded doves shot and the numbers reported, but the ratio of recovery of bands from birds killed by man must be much higher than the ratio from those which die "naturally," because so few of the latter come to human notice. With an annual mortality of 69% and a reported recovery of less than 4% of our banded doves, we are ignorant of the fate of 95% of the birds that disappear each year. This allows ample scope for increase in both categories.

History shows the Mourning Dove was almost extirpated in New England by unrestricted hunting before this was curbed. As the dove population is now maintaining itself successfully in this section of the country, and even increasing slowly in some localities, *current* hunting pressures on the wintering grounds cannot be considered excessive for the welfare of the doves nesting in New England. Whether more doves might return here each spring if they were not shot in the south, or whether the same number would die each winter anyway, hunting having replaced some "natural" cause of death and accounting

only for what is conveniently termed "the expendable surplus," we cannot say. And if more doves were to return each spring, whether or not Cape Cod could support a larger breeding population and produce a larger supply of birds for the southern hunters each year, is equally uncertain.

The fact remains that although shooting is unquestionably a major cause of death in our dove population, it cannot be demonstrated from the available evidence to be either more or less important than deaths from predators, disease, malnutrition, accidents, or any other causes, all of which must be balanced by the replacement rate to perpetuate the species.

We have seen that the annual replacement and death rates are roughly of the order of magnitude of 70% in our Cape Cod population. As 95% of the deaths on which these mortality rates are calculated occur in the south before the birds return to nest, the chances are that for every 100 birds flying south in the autumn only about 15 pairs will be available to start the following nesting season, provided of course the sex ratio remains in balance. These 15 pairs can restore the population to its original 100 only with a nesting success of 77%. A lower nesting success demands a higher winter survival if the population level is to be sustained. If the nesting success is 50% the return of 20 pairs of adults is needed to restore the population to its previous level by autumn.

The balance between the winter mortality and the summer breeding success is exceedingly fine. The difference between indefinite survival and rapid extermination is in a precarious equilibrium, for the maximum potential replacement rate is not sufficiently greater than the mean annual mortality to allow a comfortable margin of safety. Obviously it would not take much more hunting pressure, or a few successive poor breeding seasons, or an unlucky combination of both, very long to exterminate so short-lived a bird.

SUMMARY

From analysis of data obtained by banding 2690 Mourning Doves at North Eastham from 1930 through 1950 the following conclusions are drawn:

The Mourning Dove on Cape Cod is a common summer resident, a not uncommon spring and autumn transient, and an uncommon and erratic winter visitor. Each category is composed of a discrete group of individual birds.

The Cape Cod breeding and transient populations winter through the southern coastal plain from Virginia to Florida, westward to Alabama, and occasionally to Louisiana and Texas, centering in Georgia and South Carolina.

Site tenacity is strong to the nesting area, less so to the wintering ground. No evidence of group adherence as distinct from site tenacity is manifest.

Three broods of young are produced annually on Cape Cod, with a nesting success probably in excess of 70%. The maximum possible annual replacement rate of 70% is very little in excess of the 69%

mean annual mortality demonstrated by the recovery and return figures.

The oldest dove known to date reached 10 years of age.

The annual mortality is about 80% the first year of life, at the end of which it declines to about 55%, where it remains constant for the next 10 years.

The life expectancy of all doves at time of leaving the nest is less than one year, and for those which survive the first year, slightly less than one additional year.

The population "turnover" is practically complete every four years.

Deaths from shooting cannot be demonstrated from the evidence to be of greater or lesser importance than deaths from "natural" causes.

The Cape Cod population is now maintaining itself, but the maximum potential replacement rate is so little in excess of the demonstrated mortality that any slight adverse change in either could result in rapid extermination.

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MOURNING DOVE TRAPPING IN THE SOUTHEAST

A COOPERATIVE DOVE STUDY

BY J. E. KEELER AND FRANK WINSTON

INTRODUCTION

Migration of birds is an interesting type of behavior as well as one of the most important factors in management of game birds. Federal and State wildlife administrators must know where game birds rear their young, where they spend their lives during different seasons and the direction and extent of movements during fall and spring migration before good management is possible. It is necessary to have this information so regulations may be formulated that will give the hunter optimum hunting, yet afford adequate protection to the species.

In 1948 the Association of Southeastern Game and Fish Commissioners voted to undertake a cooperative Mourning Dove study. One important phase of this study was to learn as much as possible regarding the movements of this dove. The best method known was to