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PURPLE FINCHES AT HILLSBOROUGH, N. C., 1961-65

By Charles H. Blake

Another four year's experience with *Carpodacus purpureus* at Hillsborough, N. C. since my earlier paper (Blake, 1962, p. 173) has served to refine some of my conclusions.

Figure 1 of this paper is a continuation of Fig. 1 of the previous paper. The bandings in each season have still shown an alternation between 'good' years and 'off' years. There is some evidence for a fall migration. Only in good years is there s substantial but brief spring migration around 1 April. Even the rather abnormal off year 1964/5 shows only the midwinter peak in February. This suggests that in off years the number of wintering finches in South Carolina and Georgia is relatively lower than in good years. (Compare Blake, 1962, Table II.) Before looking further at population variation we must consider the construction of Table I.

Table I. Population Known to be Banded and Alive in Given Season

Season	Season Total	Season Input	Carryover	Actual Returns
1957/8	117	117	—	—
58/9	21	7	14	3
59/60	337	325	12	12
60/1	41	21	20	8
61/2	205	185	20	11
62/3	30	2	28	2
63/4	385	358	27	25
64/5	126	121	5	5

"Season Total" is, for each season, the sum of the corresponding entries in the next two columns. "Season Input" is the total of birds newly banded and foreign birds newly recovered in the given season. "Carryover" shows the number of birds banded in some previous season but provably alive in the given season whether actually captured in that season or not. Returns actually handled in a given season are shown in the last column.

Table I offers some intriguing problems. The alternation of good and off years is quite clear and appears to be related to the biennial production of tree seeds in the North. There is also an indication of a fluctuation with a four-year period. For this apparent cycle I can suggest no cause. Note also that the input in off years varies

Fig. 1. Numbers of banded Purple Finches present at Hillsborough, N. C. during each third of a month in the months and years stated.

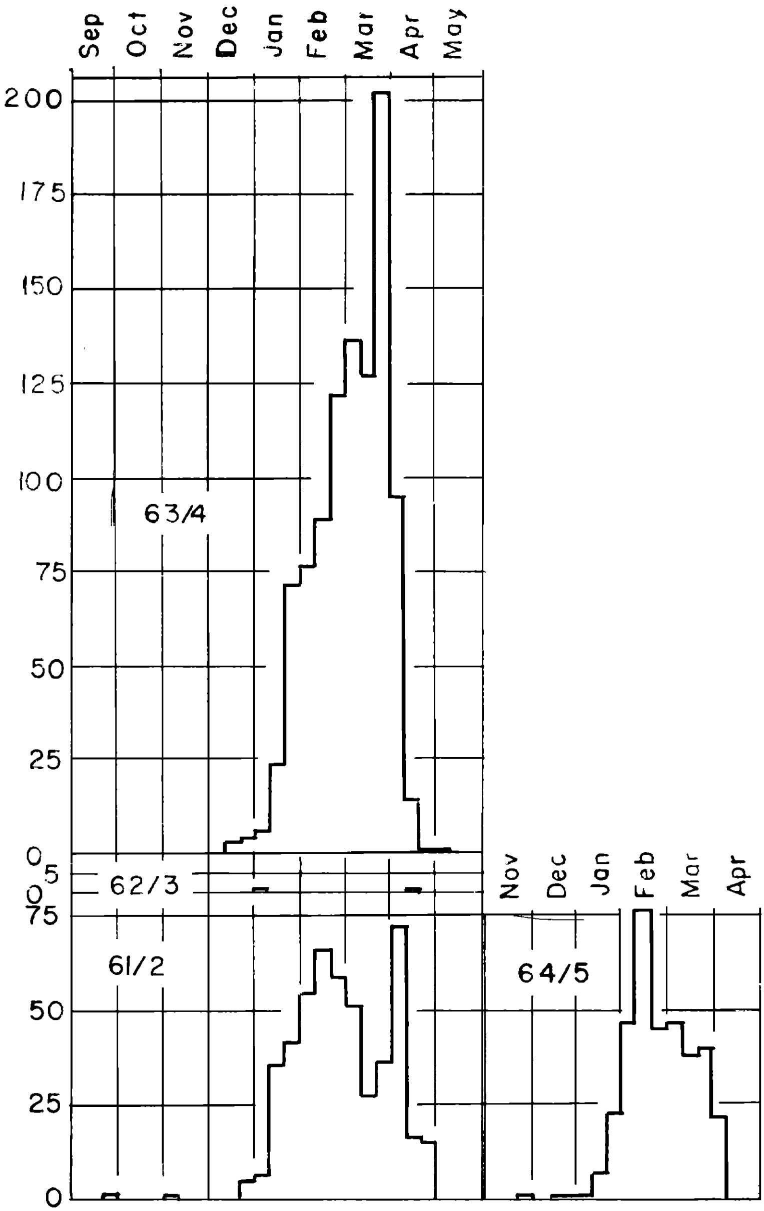
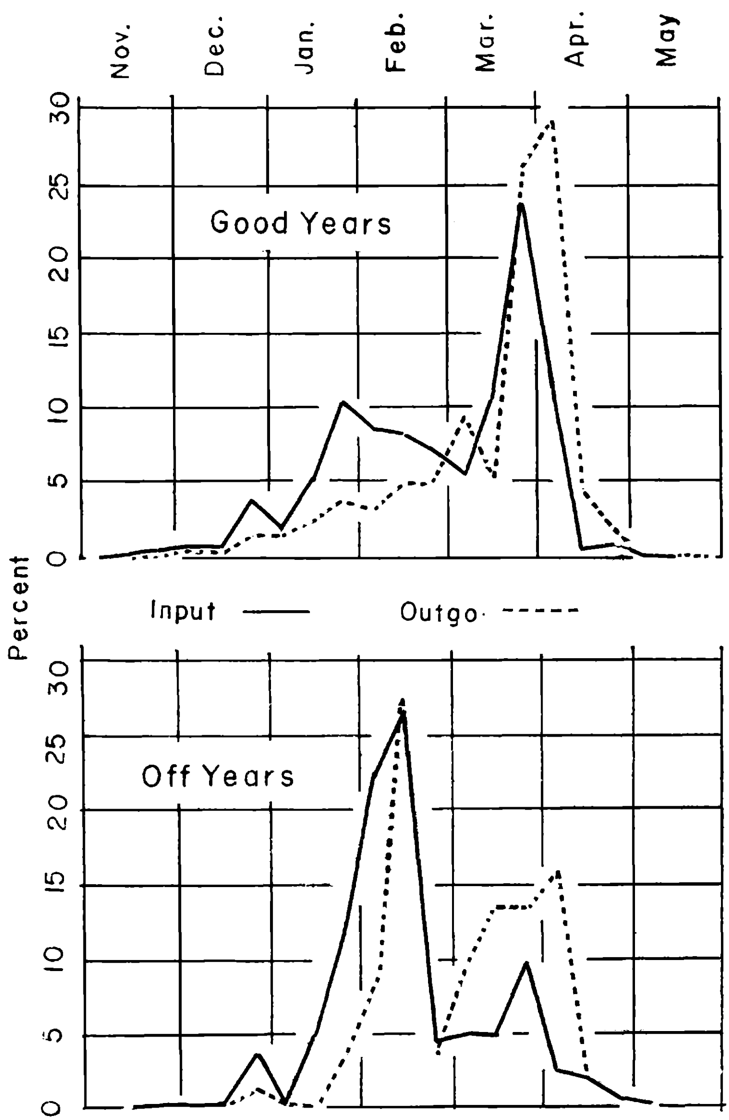


Fig. 2. Percentage of total Purple Finches first captured (Input) or last captured (Outgo) in each third of a month in the months stated.



in parallel with the input in good years. It is possible that fluctuations with still longer periods exist. With only 8 years in the record it would be footless to attempt any further analysis. I content myself with two expressions of opinion: First, that even a mathematically ascertainable cycle is rather meaningless unless it can be linked to a physical cause, and second, that the general increase in the carryover registered in good years suggests an overall increase in the total population related to this banding station. This second point will be touched on later with independent evidence.

The differences between good and off years may be examined by another technique illustrated by Fig. 2. In each third of a month is shown the percentage of the total number of birds handled in the four years of a category which either first appeared or last appeared (as the case may be) in the given period. Foreign birds and returns are treated the same as new bandings. For practical purposes we find a net input through February and a net outgo from March on. Only the second third of March in good years may be considered exceptional.

There are three input peaks, a small one in the last third of December, another in January or February, and finally one in the last third of March. The December peak seems to be the meager fall migration. Two causes which may act at about the same time appear to produce the mid-winter peak (or peaks). It has been evident that snowfalls force the birds in to feeding stations. Our snow cover does not last long but it is often wet at the beginning so it clings to trees and may hide the natural food. It is also probable that natural food supplies have been reduced by mid-winter. The final peak near the end of March is clearly the spring migration. It may be reasonably concluded that, in off years, the number of finches south of Hillsborough is both relatively and absolutely smaller than in good years.

While the outgo seems to follow the input fairly well, including a slight rise coinciding with the December peak, there is a small peak or rise in early March which anticipates the spring migrant outgo. This peak also shows in Fig. 5. I interpret this as departure of some wintering birds in advance of the main spring arrival.

ANNUAL MORTALITY

Estimating the annual mortality presents the peculiar problem of allowing for the effect of off years on the ascertained survival in those years. We can illustrate this by using the survival obtained below to compute a column of theoretical carryovers corresponding to the proved carryover column of Table I.

This implies that a number of birds are alive but unrecorded in off years. Regardless of the precise number this must, in fact, be so. A cogent reason for this conclusion is that a considerable fraction of returning birds in good years are birds whose actual returns are registered only in good years (Blake, 1964, p. 126).

The procedure is to tally, for each cohort, the birds provably alive in each subsequent good year. A cohort, in the present usage, is the birds banded in a particular season.

TABLE II

Season	Theoretical Carryover	Season	Theoretical Carryover
1957/8	—	61/2	20
58/9	16.7	62/3	37.6
59/60	12	63/4	27
60/1	27.8		

TABLE III. DATA FOR CALCULATION OF SURVIVAL

Cohort Season	1957/8 No.	1959/60 No.
1959/60	13	
61/2	6	12
63/4	2	8

We now add all prior year's numbers from the above and also all subsequent year's numbers.

Prior	Subsequent
13	6
6	2
12	8
31	16

The ratio 16/31 = .516 is the weighted survival for two years. The corresponding survival for one year is the square root of 0.516, or 0.718. The amount of raw data is rather small but the calculated survival is not inconsistent with other data. The "expectation of life" from any date later than about the first December 1 of life may be taken as three years. This, of course, assumes an age-independent survival rate. It is obvious that we cannot use the initial size of the cohort because it includes a large fraction of transmigrants which will not furnish returns. Eventually we may find that the survival in one season differs from that in another season but is independent of the age of the birds.

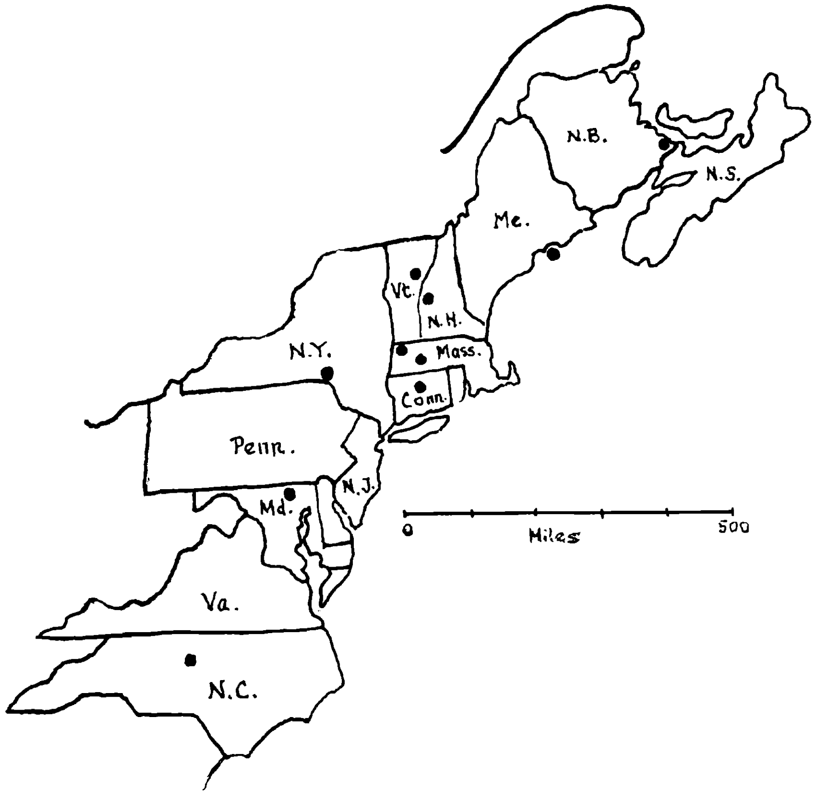
TRANSMIGRATION AND WINTERING RATES

It is already evident (compare Fig. 2) that a considerable proportion of the birds handled, even in off years, are transmigrants which cannot be expected to show returns. For good years the calculation of a wintering rate is not difficult. As an example the

TABLE IV. CARRYOVER AND TOTAL POPULATION BASED ON DEDUCED SURVIVAL AND WINTERING RATES. SURVIVAL OF 0.718, WINTERING RATES AS SHOWN. ALTERNATE TOTALS BASED ON OFF YEAR CARRYOVERS FROM TABLE II. SEE ALSO TABLE I.

Season	Wintering Rate	Numbers alive								Carryover	Totals	Totals ex Table II
57/8	.216	117.								—	117.	
58/9	.154	18.1	7.							18.1	25.1	23.7
59/60	.089	13.0	1.1	325.						14.1	339.1	
60/1	.154	9.3	0.8	20.9	21.					31.0	52.0	48.8
61/2	.157	6.7	0.6	15.0	3.2	185.				25.5	210.5	
62/3	.154	4.8	0.4	10.8	2.3	20.9	2.			39.2	41.2	39.6
63/4	.089	3.5	0.3	7.7	1.7	15.0	0.3	358.		28.5	386.5	
64/5		2.5	0.2	5.5	1.2	10.8	0.2	31.9	121.	52.3	173.3	

Fig. 3. Northeastern America, showing Hillsborough and other points of banding or recovery.



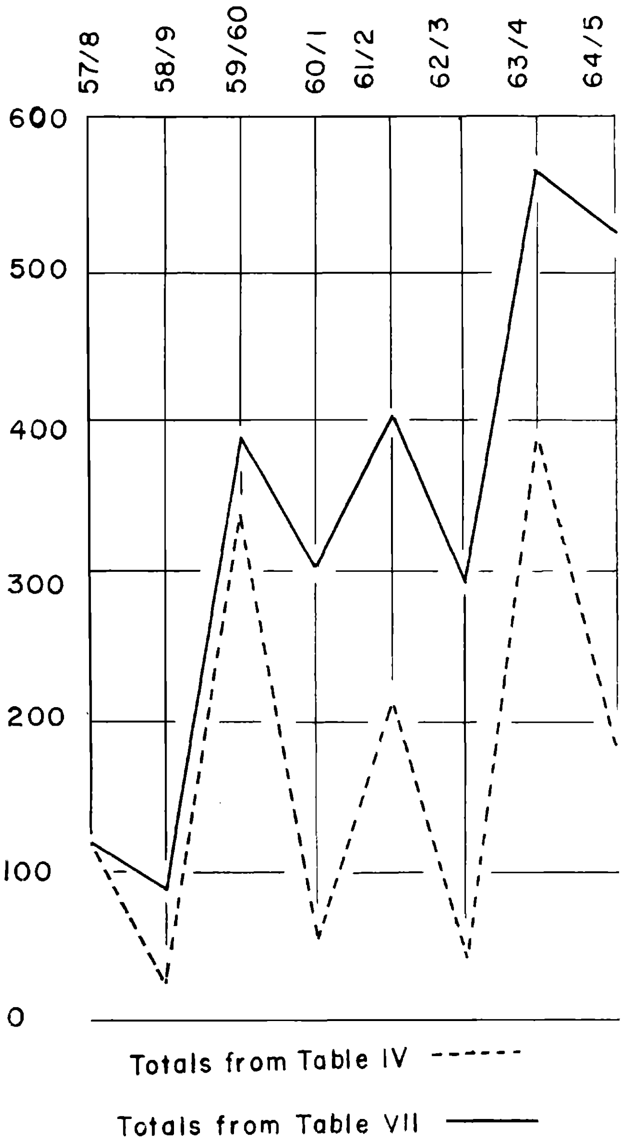
birds of the season 1957/8 showed 13.0 returns two years later. We already know that the mean survival over two years is 0.516. Dividing 13.0 by this figure yields 25.2, the number of birds which had to be alive in 1957/8 to yield 13.0 survivors in 1959/60. If we regard these 25.2 birds as the wintering birds in the population of 117 birds, then 25.2/117.0 gives a wintering rate of 0.216 and a transmigration rate of 0.784.

The available wintering rates are:

1957/8	0.216
1959/60	0.089
1961/2	0.157

The data from off years is non-existent or too scanty to be of use. It will be noted that the figures given suggest that the wintering rate varies inversely with the total population. The mean of these wintering rates is 0.154.

Fig. 4. Comparison of the observable population (from Table IV) and the calculated total living (from Table VIII) for the stated seasons.



These wintering rates and the survival rate are used to derive Table IV.

It will be noted that all the totals in the first total column (except that for 1957/8) are slightly higher than the totals which are observed or may be inferred from other data. If we compare the above figures for good years with the corresponding season totals in Table I, we find an average difference of 1.2 per cent. I conclude that for these years the estimates of transmigration and survival rates are satisfactory. For off years the mean difference is either 26.3 per cent or 21.5 per cent, depending on which set of totals is used. A possible explanation of this greater difference is that it represents the deficit in spring migrants already noted. See Fig. 4.

A STANDARD POPULATION FOR HILLSBOROUGH

There are situations in which it is convenient to estimate the probable age composition of a group of Purple Finches. For this purpose we need to know the composition over a span of ages of a given population based on an average survival rate. We must assume that the annual survival rate is constant throughout life. Under that condition the calculation of such a population is simple. If we desire a population totalling 1000 individuals, we multiply 1000 by 1 minus the survival rate to secure the first item in our table. It is a matter of judgment how we designate this item. In the present case it may be called the number at the first December 1 of life or more simply the number of first winter birds or those of age 1. To complete the table each item is multiplied by the survival rate to obtain the number of birds one year older. For the present population we have the subjoined table.

TABLE V. STANDARD HILLSBOROUGH POPULATION OF PURPLE FINCHES

Age	Number	Cumulative No.	Age	Number	Cumulative No.
1	282	1000	11	10.3	37.8
2	202	718	12	7.4	27.5
3	145	516	13	5.3	20.1
4	104	371	14	3.8	14.8
5	74.9	267	15	2.7	11.0
6	53.8	192	16	2.0	8.3
7	38.6	138	17	1.4	6.3
8	27.7	99.7	18	1.0	4.9
9	19.9	72.0	19	0.7	3.9
10	14.3	52.1	20	0.5	3.2
			Older	2.7	2.7

The cumulative number shows the number of birds of the stated age or older. The number older than age 20 arises from the fact that, in theory, the table goes to an infinite age.

It is important to keep in mind the assumption that the annual survival rate is the same regardless of age. This assumption is not likely to be true for birds younger than about the first December 1 of life and it may not be true of very old birds. It is the only practical assumption that can be made for most birds. This is because the available samples from a given area are too small to give us confidence in the necessarily small changes in survival rate over the first few years of life. To illustrate this let us look at the variation with age in human survival rates where the enormous populations at hand do give us confidence in the variation. I give the total changes over 10 year periods from the 1941 Commissioners Standard Ordinary Mortality Table.

Age span (years)	Total negative change in rate
10–20	0.00046
20–30	0.00113
30–40	0.00262
40–50	0.00614
50–60	0.01427
60–70	0.03271

The quoted table is stated in terms of an initial population of 1000000 at age 1. Our Purple Finch data is based on an initial sample estimated as 156. My more extensive data on the White-throated Sparrow suggests that a sampling variation as large as 0.1 is to be expected in the survival rate at a given age. I think it reasonable to conclude that, as the matter stands at present, sampling errors are large compared to any reasonably expectable real variation with age in the survival rate.

If the survival rate can be shown to vary with age then the method used above to find a standard population is inapplicable and an iterative method must be used.

PURPLE FINCHES AWAY FROM HILLSBOROUGH

Ten birds have either been banded here and taken elsewhere or vice-versa. So far as Hillsborough dates are concerned they range from 1 February to 4 April, hence within the period in which the largest number of finches are available here.

With two exceptions these foreign localities are from Hartford, Conn., north or northeast. One bird was banded in Maryland and one in southern New York. The only real conclusion is that our finches remain east of the Appalachians or just get into them in Vermont, New Hampshire, and New York. Other than this point the concentration in the Northeast may well represent the concentration of banders rather than the concentration of Purple Finches. See Fig. 3.

The elapsed time between apparent departure from the banding point and recovery varies from one month to almost six years. The average time is nearly three years, evidence not only of the longevity of finches but that transmigrants may move back and forth repeatedly without being captured at a particular point.

TABLE VI.

51-66298	Hillsborough	14-22 Feb '58	Granby, Mass.	4 Mar. '63	550 mi.
62-31495	Hartford, Conn.	31 Mar '59	Hillsborough	28 Mar '60	525 mi.
62-16141	Somesville, Me.	18 Apr '59	Hillsborough	23 Mar '64	775 mi.
61-36727	Deposit, N. Y.	26 Apr '59	Hillsborough	16 Feb-31 Mar '65	475 mi.
61-79094	Canaan, N. H.	23 Oct '59	Hillsborough	2-9 Apr '60	625 mi.
53-63155	Hillsborough	1 Feb.-31 Mar '60	Adams, Mass.	1 May '60	550 mi.
63383	Hillsborough	4-6 Apr '60	Plainfield, Vt.	2 Mar '63	675 mi.
64-18956	Sunnybrook, Md.	17 Apr '60	Hillsborough	24-27 Mar '64	275 mi.
63-77183	Somesville, Me.	8 Aug '60	Hillsborough	4 Apr '64	775 mi.
64-11260	Hillsborough	1 Apr. '62	Port Elgin, N. B.	Oct '62	1110 mi.

POPULATION NECESSARY TO YIELD BIRDS PRESENT AT HILLSBOROUGH

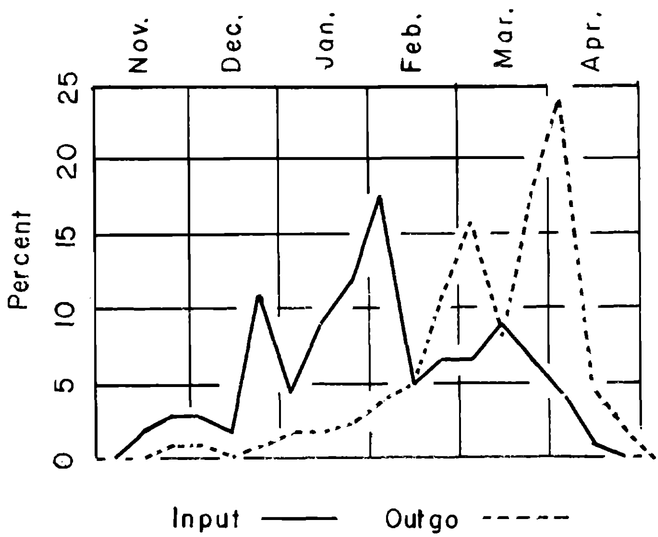
Of the grand total of 1136 Purple Finches handled at Hillsborough six, or 0.53 per cent, have been banded elsewhere. This suggests that about half a per cent of the population that furnishes finches to Hillsborough is banded. Hence its total size over the eight years has amounted to a fifth-million (214,000) birds. The number alive in a given season is much less than this. To arrive at a figure for the average season we need to look at the total of living and banded birds in a season. Here we assume no transmigration and the mean survival rate of 0.718. See Fig. 4.

TABLE VII. TOTAL LIVING BIRDS

Season	Total	Season	Total
57/8	117.	61/2	401.8
58/9	91.	62/3	291.0
59/60	390.3	63/4	566.6
60/1	301.9	64/5	527.8

We now see further evidence of the point made earlier that there is an overall increase in the number of birds related to the banding station. This increase is not to be taken at face value. The word "population" is used here to subsume all those individual finches which are available to be eventually taken at Hillsborough pro-

Fig. 5. Input and outgo of finches showing returns. Construction as in Fig. 2.



vided they live long enough. This means that the "population" need not be confined to any definite breeding or wintering range and that the increase does not imply that there is any necessary increase in the total number of living finches in any part of the species' breeding range. My present view of the situation is that finches produced in a given year and frequently wintering south of here are gradually banded over a period of years. This is especially likely in a species that shows such a large proportion of transmigrants. Two points bear this out: First, the average time between banding and recovery of the birds in Table VI is 2.8 years, and second, we shall see that an abnormal number of returning males were more than a year old at banding. Apropos of Table VI, if we reject the three recoveries at six months or less, the mean elapsed time for the remainder is 3.8 years.

The average annual number of living and banded birds is 336 and we suppose this figure to be 0.53 per cent of the population alive in an average year. The population is 63,400.

RETURNS

There have been available to yield returns 1,015 individuals. Of these 51 have actually returned in later years. This is a crude return rate of 5.02 per cent. Because some birds have returned more than once the average result is 1.37 returns per returning bird.

We have already seen that a large number of finches are transmigrants and have a general estimate of 15.4 per cent of winterers. This suggests that only 156 wintering finches have been handled. On this basis the return rate is 32.7 per cent. However, we must

Fig. 6. Tabulation of lengths of stay of finches showing returns; distributed by half-months.

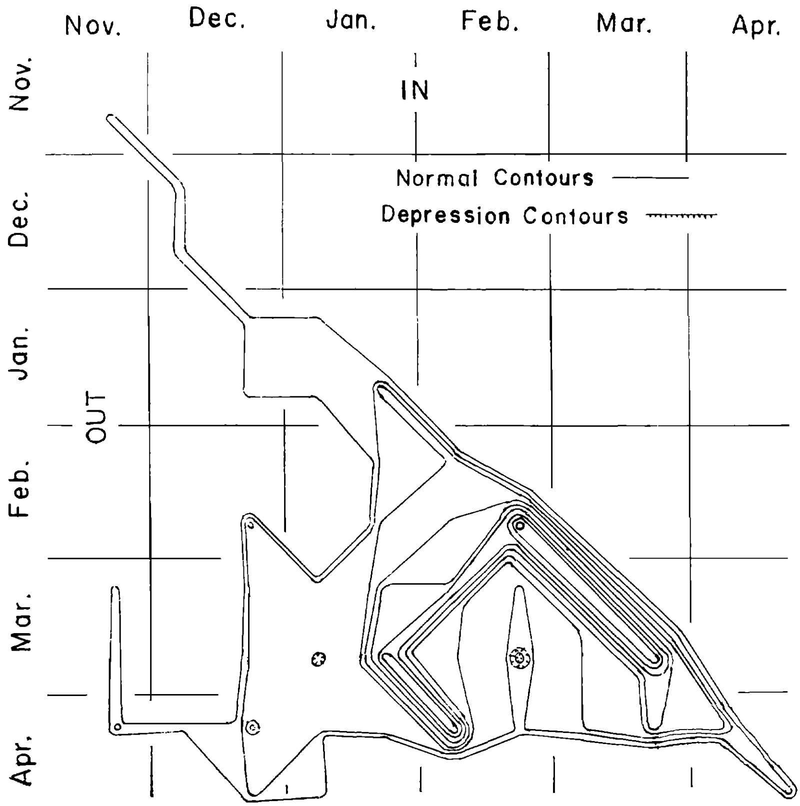
Half-month of capture

Half-month of stay	Nov.	Dec.		Jan.		Feb.		Mar.		Apr.	
0	1	1		1	3	3	9	8	8	4	2
1		1	1	1	2	4	2	3	5		
2			1		3	6		3			
3					5	3	2				
4			3	2	7	7					
5			2	1	2						
6			2	2							
7	1		4	1							
8	1	1	2								
9	2										

also take account of the fact that there is mortality between the original banding and the possible time of return. The mean elapsed time is 1.96 years. It is easily determined that, for an annual survival rate of 0.718, this means an overall survival of 0.523. The expression to be evaluated is $0.718^{1.96}$ The best estimate of the actual number of finches available to yield returns is only 81.5. We may conclude that the real rate for first returns is 62.6 per cent. By a similar calculation 44.5 per cent of birds available for second returns have actually returned a second time.

We may use the same construction as in Fig. 2 to display the input and outgo of the finches that have shown returns. The original stay as well as all returns have been used in Fig. 5. It will be noticed that the fall migration and midwinter peaks are especially prominent. The outgo peaks again represent the early outgo of some wintering birds in March and the main departure in April. These are offset relative to the input peaks, much more than in Fig. 2, which shows a higher proportion of long stay birds. The length of stay may be shown in another way (Fig. 6). The unit of time is a half month. Those birds leaving in the same half month as their arrival are counted as having zero stay, leaving in the following half month as having one half-month stay. This is not

Fig. 7. Contour map of input and outgo of finches showing returns; distributed by half-months.



an exact measure of length of stay but it does quite simply give a satisfactory picture of the situation. It is clear that the earlier birds in this group arrive the longer they tend to stay. A third procedure is to construct a contour map from the numbers of Fig. 6. These numbers may also be arranged to show half month of departure or of stay. (Fig. 7)

Fig. 7 is constructed by tallying birds first taken in a given half-month (and hence occurring on the same vertical line) on the horizontal line which represents the half-month when last taken. The diagram results from connecting identical numbers by lines (contour lines). An essential rule is that no contour line may cross either itself or any other contour line. With data of this sort, there may be more than one way of contouring. In such cases we resort to Occam's Razor and select the method which yields the simplest result. One avoids depression contours as far as possible. A depression contour arises when we have a pit whose wall extends at least one contour interval below any part of the surrounding area. Other contours are normal or elevation contours. Contours on a vertical surface should coincide but, by convention, they are merely drawn as close together as possible. For some interesting remarks on the mathematics of contours, see Ball (1939, p. 101).

FEMALE FINCHES

There are 14 individuals on record whose history indicates that they are females. The number of provable postnuptial molts at last appearance is distributed as follows:

1 postnuptial molt,	2 birds
2 "	, 9 "
4 "	, 3 "
5 "	, 1 "

We have 11 birds banded here. At banding we must consider these as having undergone no provable postnuptial molt. Nine of these showed normal plumage, that is, no noticeable departure toward yellow or red areas. One had a yellowish rump. (# 66273) and one had head, throat, breast, rump yellowish (# 66257).

Four birds were handled after one provable postnuptial molt. One (# 66273) had a slightly tawny rump, one (66318) had a yellowish rump, (31495) a yellowish throat, and (63113) some pink in the right malar area and a rusty rump.

After two provable postnuptial molts there were 10 birds handled. Two birds (66257, 66272) had head, throat, breast, and rump yellowish. (66274) had the quill margins slightly pinkish, (66280) had rump slightly yellowish, (63113) head and rump rather yellowish, (11226) throat and rump yellowish, and (66287) had the superciliary stripe and rear of crown ruddy, throat pale salmon, rump and lower back tawny. Three birds, including (66273) seemed normal.

One of the three birds handled after four postnuptial molts was normal. One (63113) had the rump yellowish and one (18956) had the upper parts and throat ruddy.

The single bird taken after at least five postnuptial molts (36727) was generally yellowish in color.

TABLE VIII. SUMMARY OF COLORING OF FEMALES

Molts	Brown	Yellow	Pink
0	9	2	—
1	—	3	1
2	3	5	2
4	1	1	1
5	—	1	—

Both Kennard (1962:90) and I (Blake, 1957: 26) have discussed the coloration of adult females. Table VIII indicates a greater proportion of yellow than Kennard found and probably more than I found. From Table VI we get a suggestion that the Hillsborough birds may breed in northern New England which tends to answer affirmatively Kennard's query as to whether the pink color is less frequent in northern New England.

PROPORTION OF RED MALES

A consideration of the percentages of red males in the present population raises questions as to the sex ratio of the population. The actual observations are, first that 30.0 per cent of 1,109 birds at banding were red males; second, that 51 returning birds are partitioned as follows: red males 22, brown males 18, females 11, as shown by their plumage at return.

From the set of figures for returning birds we find only 21.6 per cent of females. Out of 40 returning males 55.0 per cent were red at banding and of the 51 returning birds 43.1 per cent were red males at banding. If we assume a real 50:50 sex ratio there would have been but 27.5 per cent red males in the returning population. This latter figure is reasonably near the percentage observed at banding for the whole population.

If we assume a stable (50:50) population it is easy to deduce from a survival rate of 0.718 that the population should be 35.8 per cent red and 64.2 per cent brown. There is not yet any data adequate to assess the statistical significance of the differing percentages of red males. It does seem reasonable to suggest the likelihood that an insufficient number of females return to the banding point. This may not be due to a higher mortality but rather to a lower "Ortstreue" in females.

The figures for returning birds compared with a stable (50:50) population and the observed population are also consistent with the view that there may be, in reality, less than 50 percent of females in the population observed here.

SUMMARY

The alternation by years of high population (good years) and years of low population (off years) is confirmed. Spring migration is clearly deficient in off years.

The annual survival rate is 0.718. The expectation of life is three years.

The fraction of birds in good years which will yield returns (wintering rate) is 0.154 on the average but varies from 0.089 to 0.216. The calculated numbers alive indicate that the mean survival and wintering rates are reasonably correct, at least for good years.

The age composition of a standard population of a thousand finches is deduced.

The restriction to the Atlantic slope of Hillsborough Purple Finches also handled elsewhere is described.

It is estimated that the Hillsborough finches are a sample from a mean annual population of 63,400 birds. The general increase with time of the total of living birds in the banded population is discussed.

The real rate of first returns is estimated as 62.6 per cent of the available birds and for second returns 44.5 per cent.

Further evidence is given for the tendency of returning birds to be those which stay at Hillsborough a relatively long time. Three graphical displays of this are given.

The coloration of the known females is discussed. The relative scarcity of pink females is noted.

The proportion of red males is consistent with the view that the local population contains less than 50 per cent of females.

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AVIAN POPULATIONS IN A RECENTLY DISTURBED OLD FIELD SUCCESSION

By JOSEPH H. WATERS

Because of the rapid pace of house and road construction in southeastern Massachusetts and other areas, it seems desirable to determine effects of these activities on native bird and other animal populations. Only with this fund of information can effective measures be taken to ensure preservation and continuation of native animal species. Academically, it is of interest to determine succession of bird and other animal populations as formerly cultivated areas revert to woodland. Studies of succession of avian species populations have been made in other sections of the country, but have been generally lacking in southeastern New England. The study reported herein was conducted to determine effects of plant succession, and subsequent suburbanization, on avian populations.