Short-distance dispersal in the Reed Bunting *Emberiza schoeniclus*

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A computer method is described which, using observed movements, corrects bias caused by heterogeneity of terrain, and patchy distribution of marking and recapturing.

Adult Reed Buntings were observed to return to their earlier breeding sites, males more accurately than females. Adult males stay in the immediate vicinity of the breeding place until the onset of migration. Females exhibit the same tendency, although in their case it is somewhat weaker.

Young Reed Buntings begin to disperse from their birth-place within a week or two of becoming independent. Young males disperse sooner than young females. In following years Reed Buntings largely return to the neighbourhood of their birth-place. This is probably because they return to the place where they spent the pre-migratory period. This was usually quite near the birth-place. An experiment throwing light on the situation is described.

1. Introduction

A little known characteristic in bird populations is dispersal, by which it is generally meant movements leading to dispersion. In determining density in a population, however, dispersal, together with mortality and reproductive rates, is one of the most important factors. Therefore to understand how various population phenomena, especially those relating to density regulation, operate, exact knowledge of dispersal rates at all periods of a bird's life is needed. Although this is generally accepted, relatively few studies have been published on this topic. Several obvious reasons are to be found. First of all, study of dispersal requires an object which can be caught, marked, and recaught in large numbers. Recoveries of ringed birds make such studies possible, and many studies have been published using such data (see v. HAARTMAN 1949). Another, in some ways more accurate, method is to use recaptures of birds. Combining both methods is, of course, possible (RHEINWALD & GUTSCHER 1969). Further difficulties arise in processing the data, and also in assessing the role played in observed movements by (a) the spatial catching efficiency distribution of man and (b) the dispersal of the birds. If the former effect can be eliminated, the latter can then be determined.

Most studies published on the topic of dispersal only report the distribution of *found* birds. BERNDT & STERNBERG (1966) have taken into account that at a greater distance more space is available for birds and therefore those moving greater distances will be under-represented in catching files. These authors did not allow for the bias caused by the fact that, in general, the recovery activity of observers also diminishes greatly as distances increase. RHEINWALD & GUTSCHER (1969), however, have taken this into account in their study of the House Martin *Delichon urbica.* They calculated the proportion of nests which it was possible to inspect, over a range of varying distances from the place of marking.

In this paper short-distance dispersal in a Reed Bunting *Emberiza schoeniclus* population at different periods of summer and from year to year is analysed. The idea is basicly the same as that described by RHEINWALD & GUTSCHER (1969) but a different method is used.

2. Materials and preliminary procedures

Data for the present study were collected during the years 1966—1970 while studying the local Reed Bunting population of the mouth of Kokemäki River (ca. 61°32'N, 21°44'E) in south-western Finland. The study area and details of the field methods used are described elsewhere (HAUKIOJA 1968, 1970). Reed Buntings were caught using mist-nets throughout the period during which the birds are to be found in the area. Months with the most intense netting were, in order of priority, August, July and May.

For the present analysis the area was divided into 0.5 × 0.5 km squares, which covered the whole delta-area (Fig. 1). The number of squares was 390 (30 × 13). All place determinations used during computations were expressed using two subscripts, i.e. the column and the row of the map; e.g. the square in the top lefthand corner is (1,1) and that in the bottom righthand corner (30,13).

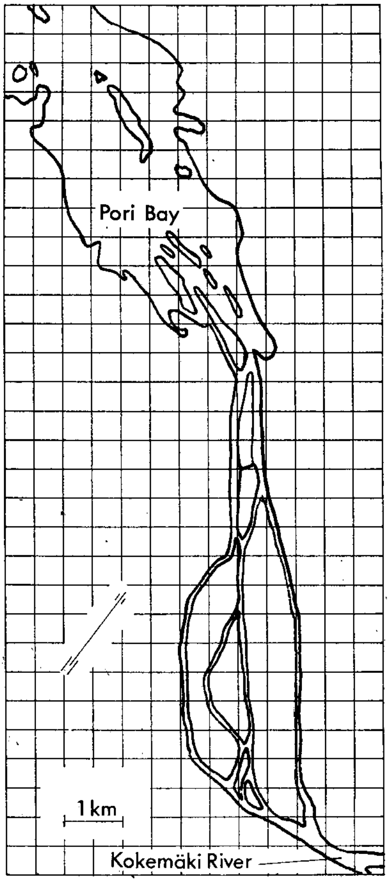


FIG. 1. Study area at the mouth of Kokemäki River, south-western Finland.

For the computer analysis the following data cards were punched:

1. The suitability of the terrain for the Reed Bunting was indicated using a value between 0 and 1, which was given for every square. 0 means that the square is probably not used by the Reed Bunting; eg. woods, fields and open water fell into this category. The value 1 means that the terrain was very suitable for the Reed Bunting. The values for squares were decided using knowledge of the delta-area and subjective reasoning. 109 nonzero values were punched (Table 1).
2. Records of catching efficiency. As a measurement of the catching intensity I used netting hours; one hour of catching birds using a six metre long net was used as the

TABLE 1. Suitability of the terrain for the Reed Bunting at the mouth of Kokemäki River. 0 means that the species probably does not settle to the place and 1 means a very suitable habitat.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.10	0.00	0.00	0.00	0.50	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00
3	0.25	0.00	0.00	0.25	0.50	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.00
4	0.25	0.00	0.00	0.25	0.50	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00
5	0.00	0.25	0.00	0.25	0.50	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.25	0.25	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.00
7	0.00	0.00	0.25	0.25	0.25	0.25	0.25	0.25	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.00	0.00	0.00	0.00
9	0.00	0.00	0.25	0.25	0.25	0.75	0.75	0.25	0.25	0.00	0.00	0.00	0.00
10	0.00	0.00	0.00	0.00	0.25	0.75	0.75	0.50	0.25	0.00	0.00	0.00	0.00
11	0.00	0.00	0.00	0.00	0.25	0.50	0.75	0.75	0.50	0.00	0.00	0.00	0.00
12	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.25	0.25	0.00	0.00	0.00
13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.25	0.00	0.00	0.00
14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.00
15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.00	0.00	0.00	0.00
16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.75	0.00	0.00	0.00	0.00
17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.75	0.10	0.00	0.00	0.00
18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	1.00	0.25	0.00	0.00	0.00
19	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.25	0.75	0.25	0.25	0.00	0.00
20	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.75	0.50	0.25	0.25	0.00	0.00
21	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.25	0.25	0.25	0.00	0.00
22	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.25	0.25	0.00	0.10	0.00	0.00
23	0.00	0.00	0.00	0.00	0.00	0.10	0.10	0.10	0.00	0.00	0.10	0.00	0.00
24	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.10	0.00	0.00
25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.10	0.10	0.00	0.00
26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.10	0.10	0.10	0.00	0.00
27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.25	0.10	0.10	0.00	0.00
28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.10	0.00	0.00	0.00
29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

basic unit. Cards punched contained the place, date and the number of netting hours in a square per day. The sum of the days on which netting took place in different squares was 591. The total netting hours per square are shown in Table 2.

3. Records for every individual caught. The number of these cards amounts to 3300 with information for 2235 different individuals, the distribution of which is given in Table 3. Although some individuals were caught more than once during a day, only one record per day was accepted. No sight records were included although there were some thousand records of colour-ringed individuals. The cards contained the following information: age and sex of the bird, place where it was caught and the date.

4. Records for every nest from which young were ringed. Altogether there were 932 Reed Bunting nestlings; their local distribution is given in Table 4. The above numbers do not include records where the destruction of a brood was confirmed after ringing. The cards contained the following information: place, number of young and the date when the young were ringed. Reed Buntings recaught after being ringed as nestling in the delta-area were recorded on the cards of group 3. A card giving the marking place and time they were ringed as nestlings was also punched. There were altogether 210 such birds and thus the total number of individual records on cards of group 3 was 3510.

All data from note-books were first coded and cards were punched. Because the reliability of results depends on the correctness of input data, considerable care was taken to minimize errors. Cards punched were run through a computer (IBM 1130) using a programme which revealed improbable punchings and listed cards. Listings were checked against original note-books and all errors detected were corrected. Most of the errors which had occurred in coding and punching were thus found. The data cards for individual

TABLE 2. Spatial distribution of netting efficiency (netting hours/100) for catching Reed Buntings in 1966—1970 in Pori.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	0.00	0.00	0.00	0.00	0.00	0.70	1.30	0.00	0.00	0.00	0.00	0.00	0.00
10	0.00	0.00	0.00	0.00	2.25	5.55	3.25	0.00	0.00	0.00	0.00	0.00	0.00
11	0.00	0.00	0.00	0.00	0.00	2.25	28.65	21.90	0.20	0.00	0.00	0.00	0.00
12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.10	0.00	0.00	0.00	0.00	0.00
13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.60	9.20	0.00	0.00	0.00	0.00
14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.75	0.30	0.00	0.00	0.00	0.00
15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	3.00	0.00	0.00	0.00	0.00
16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	15.70	0.00	0.00	0.00	0.00
17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	19.95	0.00	0.00	0.00	0.00
18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	42.45	0.25	0.00	0.00	0.00
19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75	10.00	0.00	0.00	0.00	0.00
20	0.00	0.00	0.00	0.00	0.00	0.00	0.80	34.35	0.00	0.00	0.00	0.00	0.00
21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.75	0.00	0.00	0.00	0.00	0.00
22	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

TABLE 3. Middle parts of a matrics giving spatial distribution of young and adult Reed Buntings caught in 1966—1970 in Pori.

	5	6	7	8	9	10
9	0	6	15	0	0	0
10	42	20	23	0	0	0
11	0	4	326	168	0	0
12	0	0	0	51	0	0
13	0	0	0	7	66	0
14	0	0	0	44	0	0
15	0	0	0	1	24	0
16	0	0	0	14	153	0
17	0	0	0	3	210	0
18	0	0	0	0	481	15
19	0	0	0	17	68	0
20	0	0	13	450	0	0
21	0	0	0	14	0	0
22	0	0	0	0	0	0

TABLE 4. Middle parts of a matrics giving spatial distribution of nestling Reed Buntings ringed in 1966—1970 in Pori.

	5	6	7	8	9	10
9	0	5	14	0	0	0
10	0	5	6	0	0	0
11	0	0	40	1	0	0
12	0	0	0	45	0	0
13	0	0	0	5	0	0
14	0	0	0	6	0	0
15	0	0	0	0	20	0
16	0	0	0	5	105	0
17	0	0	0	5	235	0
18	0	0	0	0	96	0
19	0	0	1	18	96	0
20	0	0	0	210	0	0
21	0	0	0	14	0	0
22	0	0	0	0	0	0

birds were sorted and listed anew using another programme made for tracing errors. When the data had been stored in a disc memory of the computer a programme was used which checked that no bird had been reported caught in a square where no netting had been conducted. Some errors were found and the corresponding files were corrected.

3. **Methods used in computations**

The distances which birds have been observed to move are on many occasions used as a measurement of dispersal rates. The distribution arrived at depends, however, not only on the movements of birds, but also on the spatial distribution of the observer's marking and netting points. In addition, the terrain where the investigation is carried out, is on many occasions such that there is no similarity in the probability with which the species studied settles in each square. Very often the species does not settle in some squares at all. This means that some movements from a given point (square) are more likely to be discovered than others. To correct this bias an expected distribution pattern was computed on the following lines.

Let us consider the situation where *n* birds are marked in a square *B* and later netting is conducted in a square *C* at a distance *a* from *B*. If some birds originating from *B* disperse just the distance *a* then the probability *p* that they will settle in square *C* is that proportion that the terrain suitability value in *C* represents of the sum of suitability values of squares at distance *a* from *B*. We can therefore expect the number of birds observed to disperse the distance *a* from *B* to *C* is determined according to the following equation:

(1) $\text{expected}_{(a)} = n_B \cdot h_C \cdot p$

where h_C shows the netting efficiency in square *C*.

In order to find an equation giving the expected numbers of birds netted the values in Fig. 2 were plotted. On the basis of the observed netting efficiencies the following equation was computed and used as h_C.

(2) $Y = 0.890 + 9.208X - 0.283X^2$

where Y is the expected number of birds netted for the netting efficiency X (given in terms of hundreds of netting hours) per square per day. Table 5 gives the computed numbers for each square using the number of netting hours and the equation (2). The number of birds actually caught are given in Table 3.

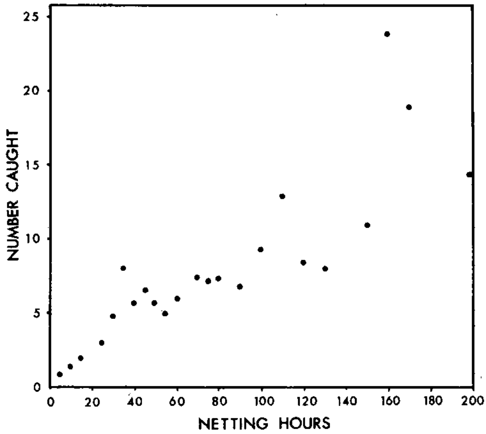


FIG. 2. Mean catches of Reed Buntings in relation to daily catching efficiency.

TABLE 5. Middle parts of a matrics giving spatial distribution of expected catches of Reed Buntings in 1966—1970 in Pori.

	5	6	7	8	9	10
9	0	8	13	0	0	0
10	26	59	40	0	0	0
11	0	26	308	225	3	0
12	0	0	0	97	0	0
13	0	0	0	33	96	0
14	0	0	0	75	4	0
15	0	0	0	1	40	0
16	0	0	0	6	173	0
17	0	0	0	4	252	0
18	0	0	0	0	489	5
19	0	0	0	15	113	0
20	0	0	14	401	0	0
21	0	0	0	28	0	0
22	0	0	1	0	0	0

By adding together the values of equation (1) for every square at distance *a* from square *C*, an expected value for this distance and this recapture square was arrived at. By computing the same figure for each recapture square and adding these together the final expected value for the distance *a* was arrived at.

When relative expected values were computed for each distance at intervals of 0.5 kilometres, the expected distribution in such a situation where movements of all distances are equally probable, was found. The expected value for distance 0.0 km, i.e. the same square where the bird was marked, was halved, because the length of movements to the following distance-category is, on average, half of that in other distances.

By comparing the expected distribution with that actually observed, biases caused by uneven marking and catching intensity and the heterogeneity of the terrain can be corrected to a large degree. Because actual numbers of recaught Reed Buntings were rather small, I only presented the expected and observed distributions without statistical treatment. Thus results and conclusions presented are only tentative.

Two variations of a programme were used in computing, both of which used the pertinent data on the disc, i.e. the catching files for birds, the netting efficiency file and the file giving values of the suitability of terrain for the Reed Bunting.

The first programme proceeded in the following way: a card was read which gave the following information needed in selecting the data on the disc: age, sex, limits of a marking period and limits for 1—3 recapturing periods. First of all a matrix showing the suitability of terrain was formed on the basis of the data contained in disc storage. Then the file containing records for individual birds was gone through, all 3510 records each time. If a record satisfied the conditions given on the card mentioned above, that is sex and age were those asked, and the date fell within the marking period, the record was taken into account in forming the matrix containing marking totals for each square. If an individual caught during the marking period (was it ringed then or earlier) was recaught a check was made to see if the recapturing date fell within one of the recapturing periods. If so, the distance the bird had travelled was computed and the movement was taken into account. If an individual was caught more than once during a recapturing period, only the first record was accepted.

After this the file containing netting efficiency data was searched. If a record satisfied the given conditions, i.e. the date fell within a netting period, a netting efficiency figure was computed using equation (2). The value arrived at was used in forming the netting efficiency matrix. Depending on how many catching periods were given on the card, one, two or three netting efficiency matrices were formed.

The expected values were computed using the method described earlier, and one — three tables were printed; as an example see Table 6.

Another programme, used when carrying out computations with the nestling data (or in general with grouped data), was in other respects the same but a marking matrix was formed from the file where brood markings were stored. The netting records of individuals were then checked and records which satisfied given conditions (the bird was a nestling and

TABLE 6. A table giving dispersal indices for each distance. An example.

Emberiza schoeniclus, Pori

Age (when marked)	Pull
Sex	Both
Marking period	25.5.1968—31.7.1968
Recapturing period	1.8.1968—25.9.1968
Sample size (marked)	314
Recaptured	48
Efficiency of recapturing (Hundreds of netting hours)	22.10

Dist. Km	Possib. Quadr.	Indices		
		Expected	Observed	
			No	Per cent
0.0	6	4567.76	11	0.24
0.5	9	3941.80	10	0.25
1.0	9	2462.75	6	0.24
1.5	9	2466.14	9	0.36
2.0	9	767.62	7	0.91
2.5	9	1005.25	1	0.09
3.0	8	3525.70	2	0.05
3.5	6	1419.98	1	0.07
4.0	6	1448.47	0	0.00
4.5	4	1419.68	1	0.07
5.0	2	236.28	0	0.00

the marking date fell within given limits) were sought. Later records for these individuals were examined and if these satisfied conditions for a recapture period and the sex of the bird was that asked, the record was accepted as a recapture and the distance was computed. The numbers ringed and expected values for males and females were always the same because these had to be computed from marked nestlings and their sexing was not carried out until the first recapture. For criteria, see HAUKIOJA (1969).

The programmes used were tested by using a 5 × 3 matrix and by counting the correct values by hand.

Figures given in this paper were combined from about 250 different tables, the computing of which, using the IBM 1130 (a comparatively slow computer) took about ten hours.

4. Dispersal of adult birds

4.1. Site tenacity during breeding period

Results of computations showing the return distances of adults in relation to the former year are given in Figs. 3—4.

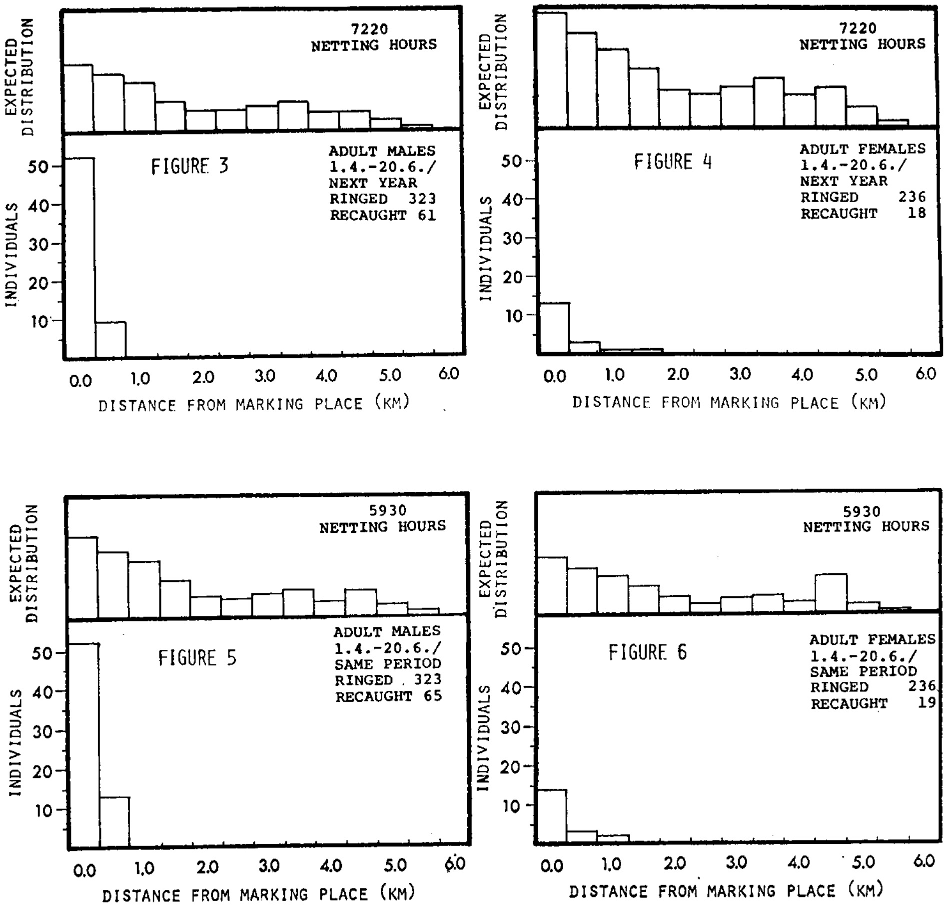
Males seem to be very *ortstreu*; most returning birds settled in the same square in which they were marked. Movements to adjacent squares are mainly of birds which were caught at the boundaries of squares. In such cases the computed distances are often too great because merely crossing a square boundary means that birds are allotted to the next distance category, that is 0.5 km. My experience with colour-ringed birds indicates that Reed Bunting males usually settle in the same territory as the preceding year. Field experience with colour-ringed females indicates that they are less loyal to their breeding place of the preceding year than males. Fig. 4 confirms this but also shows that they too settle mainly in the immediate vicinity of the former nesting site. For both sexes expected values are rather high up to a distance of four to five kilometres but the greatest distance verified was only 1.5 km.

Because breeding Reed Buntings stray rather a lot even in the course of a breeding season, especially in the afternoon, I have computed their movements in relation to the marking place for the same season (Figs. 5—6). The accuracy of the expected distribution is quite low because netting efficiencies have been computed for the whole period. It was therefore not possible for late marked birds to be caught during early catching periods although these were used in computations. Figs. 5 and 6 indicate that even in the course of a breeding season (even in May) Reed Buntings stray a lot, males less than females. Figs. 3 and 4 therefore depict, not only movements to other breeding places, but also that adults may have been caught while outside their territories. The greatest distance I found a colour-ringed female to change its breeding place from one season to another, was about 1 km; the same distance for males was about 0.5 km.

4.2. Movements during summer and early autumn

In the following section the places at which adult Reed Buntings were netted during summer months are compared with their breeding place (i.e. the place where they were caught during 1.4.—20.6.).

Figs. 7 and 8 show movements of adult Reed Buntings from the breeding season to the period 21.6.—10.7. This is a period when many individuals, especially females, are still breeding, but also many birds have begun their annual moult. Fig. 7 shows that moulting birds are still found in the neighbourhood of their nests. Fig. 8 shows that some females moved considerable distances (approx. three kilometres from their breeding place) but the majority of the females were caught near their breeding place. It was verified that a male also travelled three kilometres,



FIGS. 3—6. Computed and observed distance distribution from the marking place in recaught Reed Buntings.

but this is not shown in Fig. 7 because the first time it was encountered during the recapture period (21.6.—10.7.) it was in the same square where it was marked, and the programmes used took account only of the first observation during a recovery period.

These few wanderers are a somewhat puzzling feature. They show that birds travel such distances but it is not necessarily indicative of a change their permanent living place. E.g. two birds found at a distance of about three kilometres from the breeding place at the end of June and the beginning of July were later caught in the same square where they were marked during the breeding period.

FIGS. 7—12. Computed and observed distance distribution from the marking place in recaught Reed Buntings. →

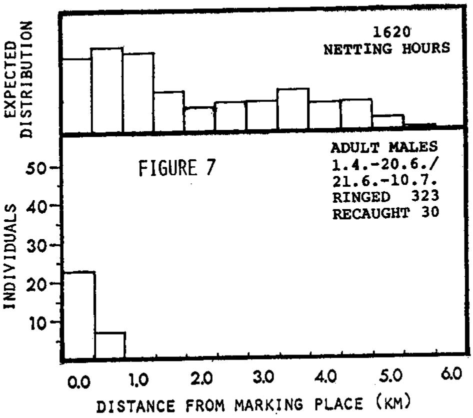


FIGURE 7

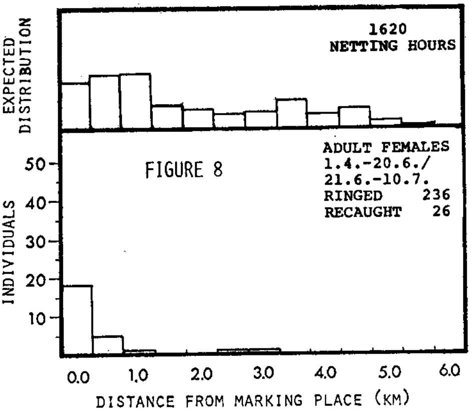


FIGURE 8

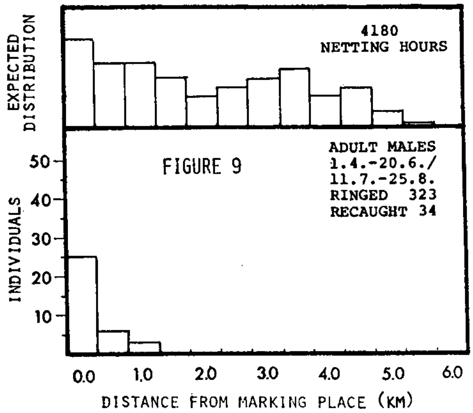


FIGURE 9

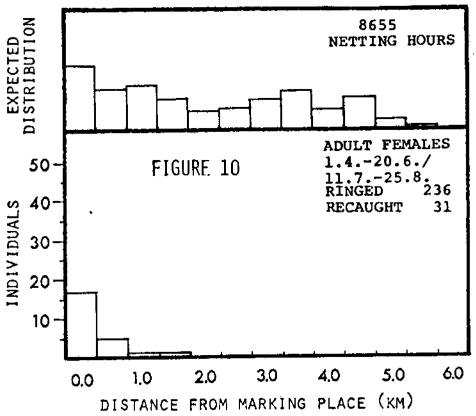


FIGURE 10

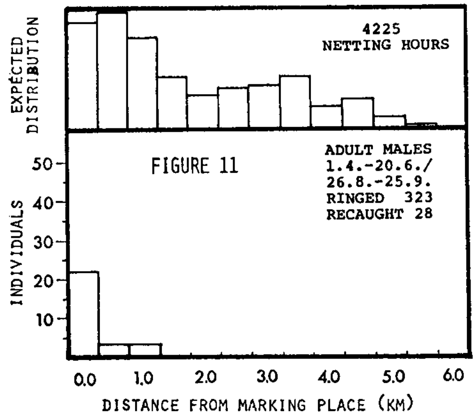


FIGURE 11

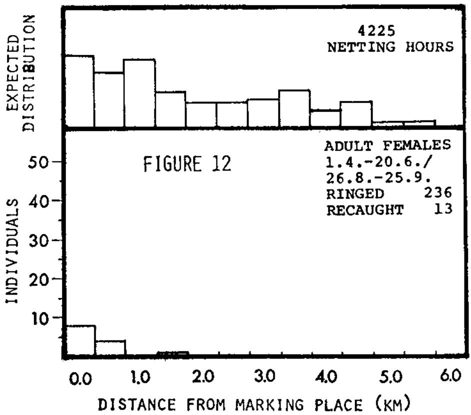


FIGURE 12

Figs. 9 and 10 give the distances from the breeding place at which Reed Buntings were caught during the period 11.7.—25.8., i.e. during the period when practically all adults undergo their post-nuptial moult. These figures show that adult Reed Buntings moult near their breeding place, most birds having been found less than 0.5 km from their breeding place. It is worth noting that in the expected distribution rather high values occur even at a distance of 3—4 km from the breeding place, but no birds were actually caught there.

Figs. 11 and 12 give the distances from the breeding place during the premigratory phase, that is from 26.8. to 25.9. Most individuals finish their moult at the beginning of this period. Even during this period Reed Bunting males were found only in the neighbourhood of their territories. Also females, most of which begin their migration during this period, are found mainly near their breeding sites. Once again their fidelity to the marking place was not as strong as the males.

4.3. **Discussion**

The results presented above refer only to local dispersal; the possibility cannot be denied that some individuals might change their breeding sites over greater distances although in practice the bulk of the population shows strong territory fidelity. What has been said above and what follows about dispersal refers only to local dispersal unless otherwise specified.

The Reed Bunting has been shown to exhibit the general site tenacity characteristic of many passerines (v. HAARTMAN 1949). Also the fact that males are more attached to their territories than females is a well-known phenomenon (v. HAARTMAN 1949).

Adult Reed Buntings are probably even more *ortstreu* than shown in Figs. 3—12 because evidently many individuals are not trapped in nets which are often put out in the same place in their territories. The numbers recaught in the same square where birds were marked are therefore too small, but I have not found any reasonable method of correcting the error caused by this behavioural bias.

The fact that some males may defend more than one territory at the same period has been revealed e.g. in the Pied Flycatcher *Ficedula hypoleuca* by v. HAARTMAN (1949). The fact that individuals of a territorial species, as the Reed Bunting is said to be (HOWARD, 1929, used the Reed Bunting as a classic example), wander greatly in the course of a breeding season (Figs. 5—6) may be rather uncommon. On the other hand, it is also very difficult to verify this without netting birds over large areas.

Where adult passerines live immediately after the end of their breeding activities is, on many occasions, difficult to determine in practice. Therefore it is understandable that few data are available about this period. As far as I know, such keen site-tenacity after breeding has been observed in only a very few passerines. LACK's (1946) example of the Robin *Erithacus rubecula* is the best-known. Aspects relating to this topic are probably the most remarkable feature about adults found during the present study.

KALELA (1958), starting from observations of autumnal display and also the fact that (partially) migratory birds sometimes are observed in their former territories in the autumn, developed a hypothesis that territoriality is the primary mode of life in birds. Only the refractory period after breeding, when most species moult, and migration result in the abandonment of territories.

Although migration causes Reed Buntings to move away from their breeding sites, the effect of the moult is not very significant in this respect. It must also be stressed that instances of passerines disappearing from their territories during moult, may only mean that the observer does not find them. I have never identified a moulting colour-ringed Reed Bunting in the field except in those few cases where male parents began to moult while feeding a late brood. Figs. 9—10 show, however, that adults moult near their territories but, because of their skulking behaviour, they are extremely difficult to find without using nets.

On cool autumn mornings, especially in September, the singing of Reed Buntings is rather often heard in my study area. I have never succeeded in identifying an adult colour-ringed male while singing in autumn. As indirect proof that adults probably sing just in their own territories is the fact that in the middle of September, when most individuals present in the study area are adults, many singing places are situated on the same bushes that were preferred in the spring. BELL (1967) has reported two cases where English Reed Buntings have been observed to sing in September in their former territories.

KALELA (1958) has concluded that, since autumnal territoriality and aggressiveness are such widespread phenomena, they cannot be a sign of non-adaptability. The opinions presented earlier must therefore be regarded as misinterpretations. I agree with this and a more detailed discussion of the matter is presented later in this paper.

5. Dispersal of young birds

5.1. Tendency to return to the birthplace

In the last chapter it was found that adult Reed Buntings stay practically the whole period they are in Finland near the territory where they bred the former spring. When discussing Reed Buntings ringed as nestlings or young and recovered in a later year at the mouth of Kokemäki River, it is therefore possible to take into account all birds recaught some later year at the study area whether they were recaught during the breeding season or outside it. In any case they provide a rather good picture of the place where birds were breeding.

Because, in small passerines, about half of the adult population dies annually the expected values used in all analyses, where returns of different years were combined, were determined by dividing the expected value for the x:th year after ringing by 2^{x-1} and adding these values together.

Figs. 13 and 14 show the distance distribution of birds ringed as nestlings and recaught in a later year in the study area. It is evident that returning individuals of neither sex show any clear tendency to return to the exact place of birth. The distribution of returning males has no obvious peak when compared with the expected distribution; females evidently have a peak at a distance of about 1.5 kilometres.

Earlier I have shown (HAUKIOJA 1969, 1970) that the development of early and late broods differs. Therefore Figs. 15—18 were computed to check whether there was any difference in the dispersal of late and early broods in following years, but no clear difference was found to exist. If anything, however, the young from late broods disperse more.

5.2. Dispersal during the first summer

Reed Bunting young from first broods become independent at the end of June-beginning of July. In the first half of July young from the first broods remain mainly in the vicinity of the birthplace (Figs. 19—20), females more so than males. In spite of rather high expected values at a distance of 3—4 kilometres, none has yet been observed at this distance. The postjuvenile moult of

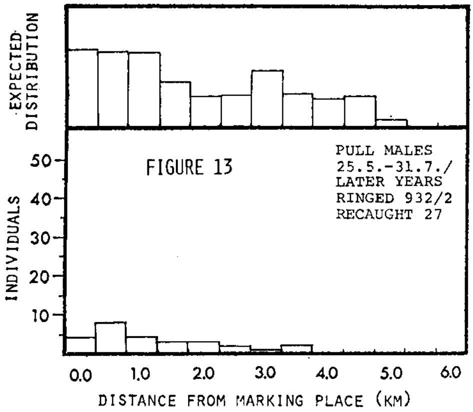


FIGURE 13

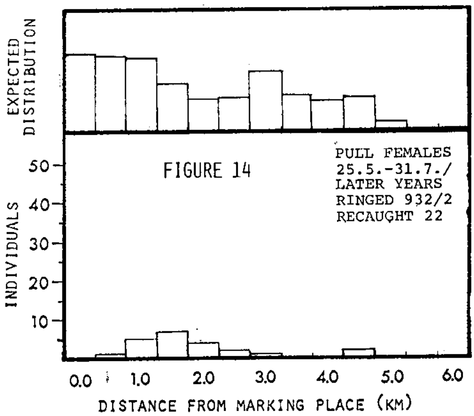


FIGURE 14

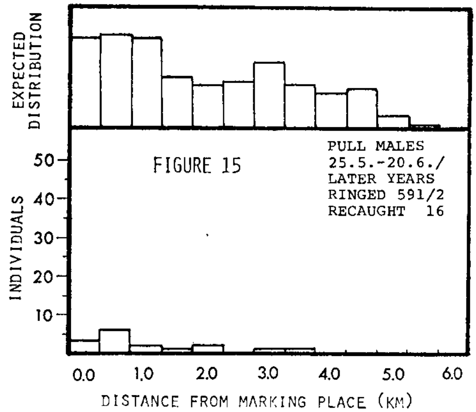


FIGURE 15

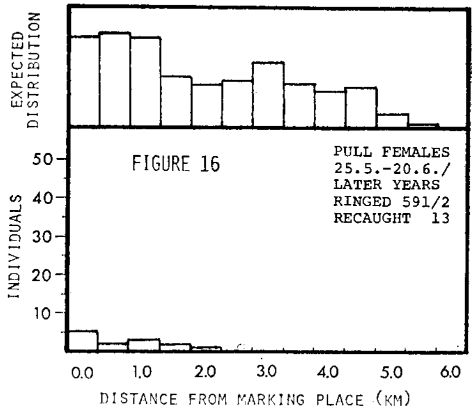


FIGURE 16

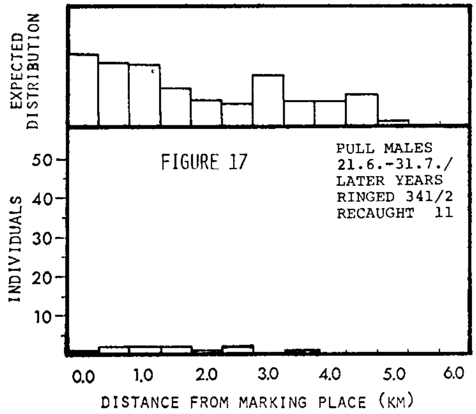


FIGURE 17

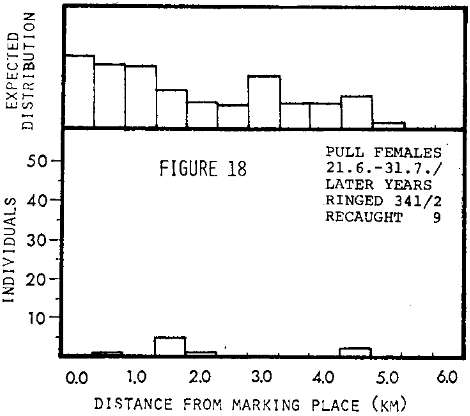


FIGURE 18

young from first broods lasts from the latter half of July to the latter half of August. Therefore, 16.7.—25.8. was used as the next period. During this time young birds dispersed more (Figs. 21 and 22) and still females concentrated nearer the birthplace than males.

Because young birds remain rather near their birth-place in the first half of July, dispersal from the birthplace can also be measured by computing the distances of recaptures from the period 1.7.—15.7. onwards to the period 16.7.—25.8. (Figs. 23 and 24). These give very much the same picture as Figs. 21 and 22.

After moulting (period after 25.8.) birds are found, during the period when they stay in the delta area, in small numbers at varying distances from the birthplace (Figs. 25—28).

Young Reed Buntings stray a lot during late summer months (Figs. 29 and 30). These movements probably lead some birds away from the delta area although most birds are found only rather short distances away. Movements during July and August may also result from another factor, that is, young from late broods may then have the same dispersive phase shown for early young in Figs. 21—24.

Figs. 31—34 depict the summer dispersal of ringed young from late broods. Up to the 25th August they have been found not farther than two kilometres from the nest. Again males seem to disperse more than females. At the end of August and in September the young ringed from late broods seem to have dispersed much more (Figs. 33 and 34). Consequently, some of the movements observed in Figs. 29 and 30 result from the dispersive behaviour of late broods after independence.

5.3. Tendency of young Reed Buntings to return

Figs. 13 and 14 gave the distribution of adult Reed Buntings in relation to their birthplace. It may indicate that the Reed Bunting shows tenacity to the birthplace, or that some kind of imprinting occurs in the course of the first summer or early autumn when birds still remain comparatively near their birthplace.

In order to test this, computations were performed where each period during the first summer was used in turn as the marking period and the recapturing period was in every case formed by following years. In so doing it was expected that the period which, when computed in relation to later years, gave the nearest concentration of recaptured birds to the marking place, would be the period when selection of the future breeding place most probably occurs.

Figs. 13 and 14 gave a distribution which might reasonably be studied first as a source of basic information. Expected and observed distributions for males were very similar, showing that males disperse comparatively greatly. In females a concentration to 1—3 kilometres from the breeding place was observed.

Figs. 35 and 36 give the same information for the period 1.7.—15.7. Because it was earlier found that during this period young stay mainly in the neighbourhood of the birthplace, it is reasonable to expect that the distribution of birds closely resembles the distribution observed in Figs. 13 and 14. Taking into account the small amount of data this seems to hold true.

Figs. 37 and 38 give the tendency to return in relation to the place where

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FIGS. 13—18. Computed and observed distance distribution from the marking place in recaught Reed Buntings. ←

FIGS. 19—30. Computed and observed distance distribution from the marking place in recaught Reed Buntings. →

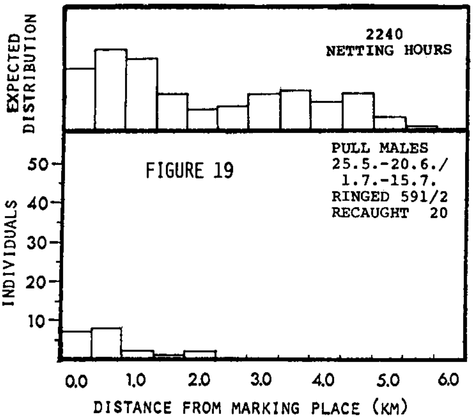


FIGURE 19

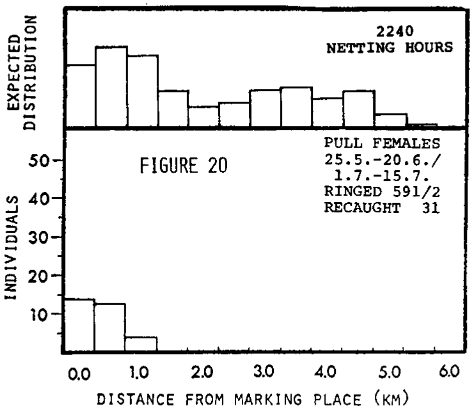


FIGURE 20

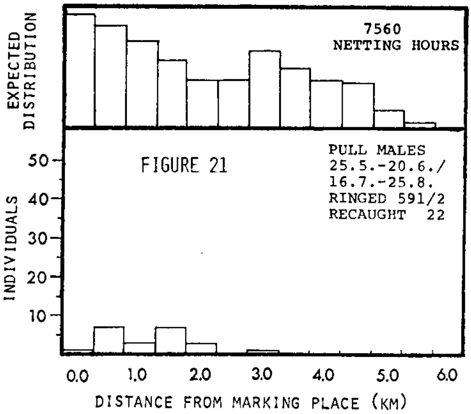


FIGURE 21

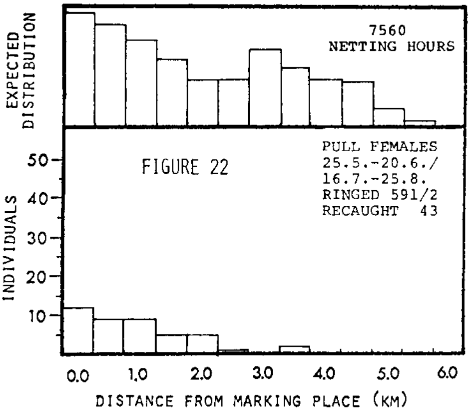


FIGURE 22

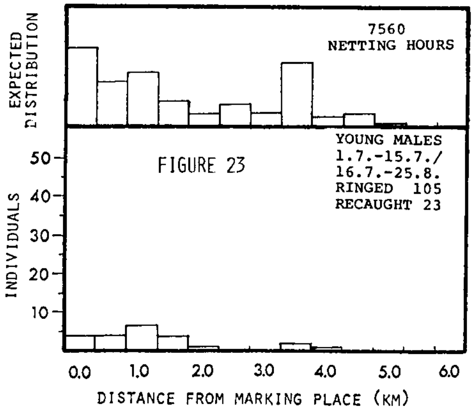


FIGURE 23

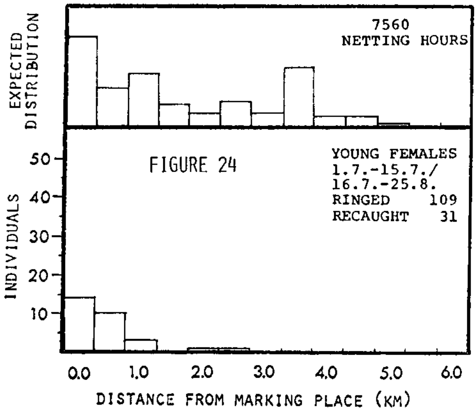


FIGURE 24

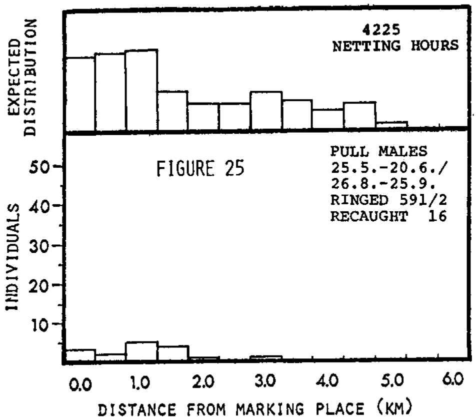


FIGURE 25

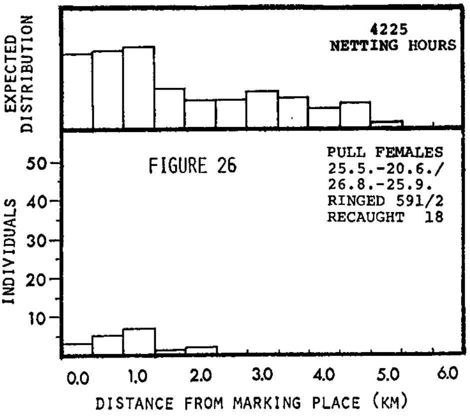


FIGURE 26

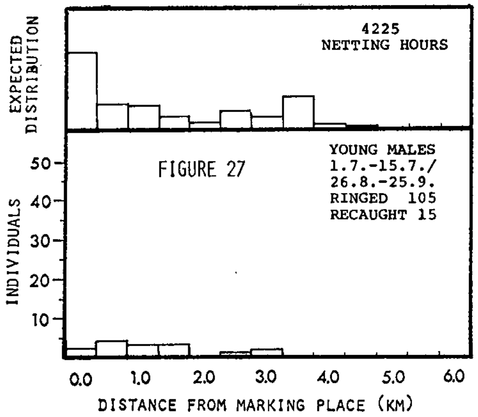


FIGURE 27

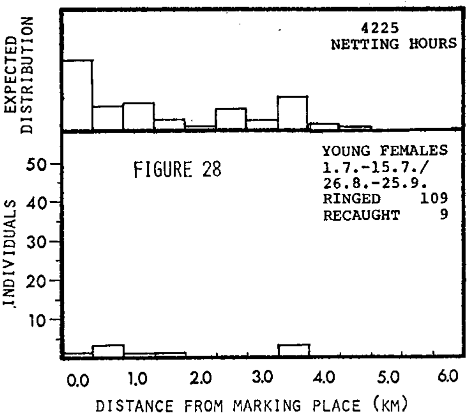


FIGURE 28

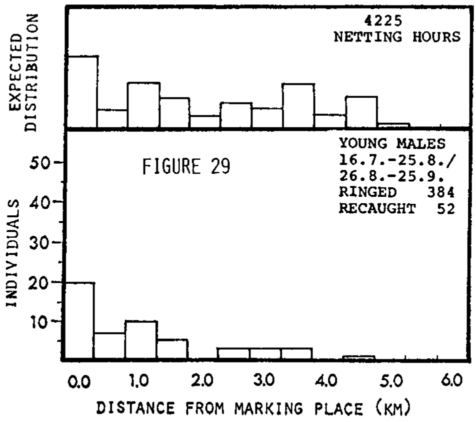


FIGURE 29

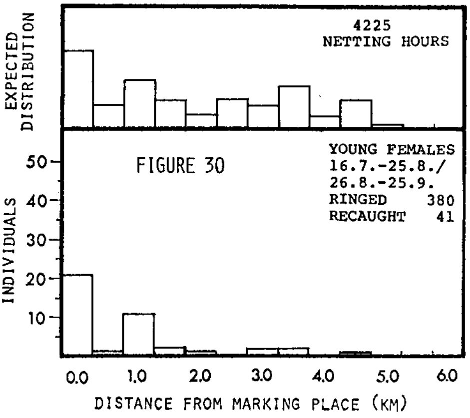
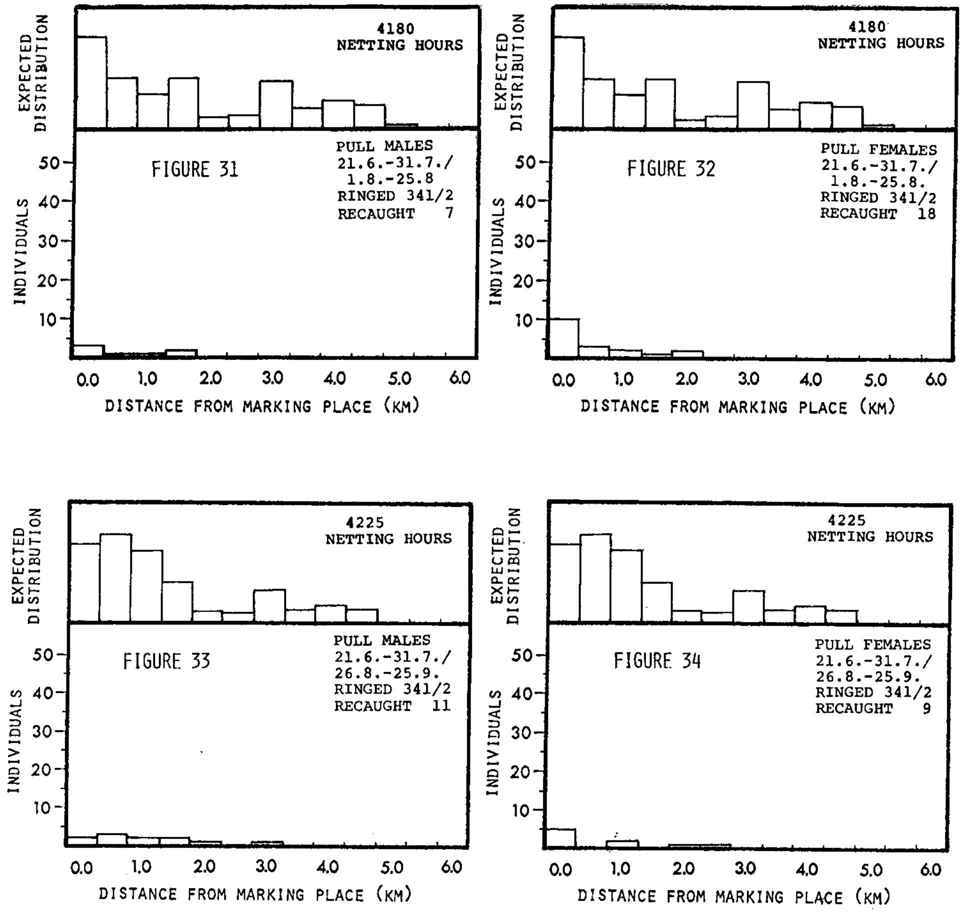


FIGURE 30



FIGS. 31—34. Computed and observed distance distribution from the marking place in recaught Reed Buntings.

young birds were caught during the period when they usually undergo their postjuvenal moult.

Returning birds marked after the period of the postjuvenal moult, i.e. from the end of August- beginning of September onwards, are given in Figs. 39 and 40.

5.4. Discussion

Studying the summer dispersal of juvenile birds, as has been done for the Reed Bunting in this paper is in practice impossible for many species of birds because of the difficulty in catching large numbers of young birds in the period between their becoming independent and migration. Therefore, very few studies exist about this topic (KALE & JENNINGS 1966, HIRTH *et al.* 1969).

However, several authors have come to the conclusion that some kind of imprinting must occur between the time of leaving the nest and the beginning

FIGS. 35—40. Computed and observed distance distribution from the marking place in recaught Reed Buntings. →

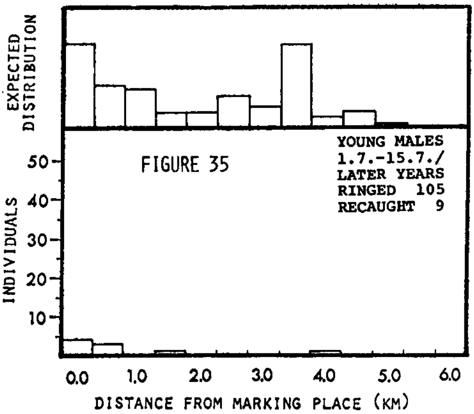


FIGURE 35

YOUNG MALES
1.7.-15.7./
LATER YEARS
RINGED 105
RECAUGHT 9

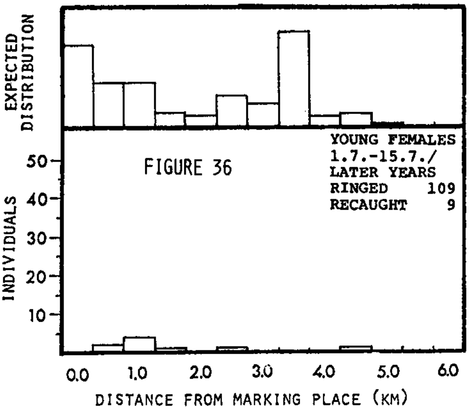


FIGURE 36

YOUNG FEMALES
1.7.-15.7./
LATER YEARS
RINGED 109
RECAUGHT 9

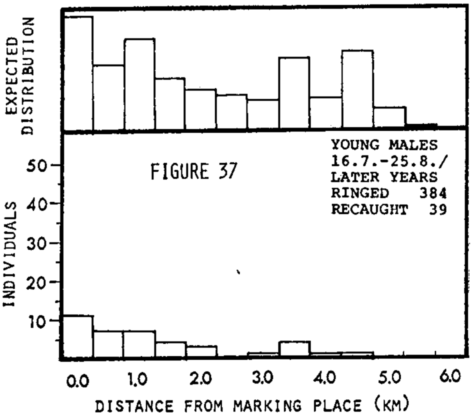


FIGURE 37

YOUNG MALES
16.7.-25.8./
LATER YEARS
RINGED 384
RECAUGHT 39

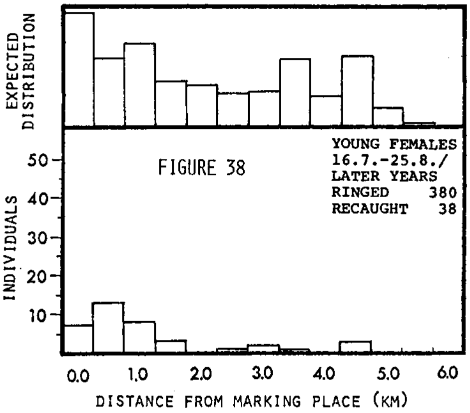


FIGURE 38

YOUNG FEMALES
16.7.-25.8./
LATER YEARS
RINGED 380
RECAUGHT 38

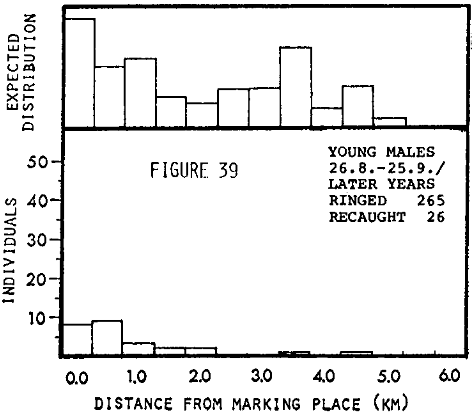


FIGURE 39

YOUNG MALES
26.8.-25.9./
LATER YEARS
RINGED 265
RECAUGHT 26

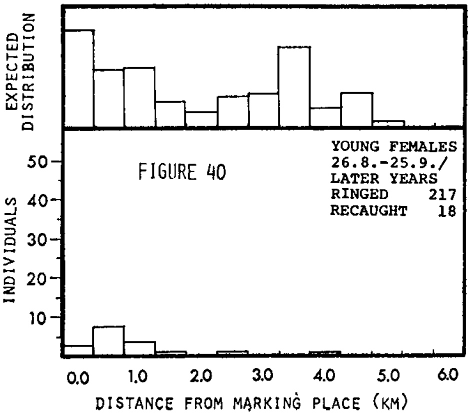


FIGURE 40

YOUNG FEMALES
26.8.-25.9./
LATER YEARS
RINGED 217
RECAUGHT 18

of migration. E.g. NICE (1937) and others (see KALELA, 1958, for further references) have given fragmentary field evidence that young birds may settle in their future breeding place even in the autumn. To study this more closely in the Reed Bunting, the information in Figs. 35—40 was combined in Table 7. This gives the numbers of birds recaptured in a later year in the same or adjacent squares, i.e. at a distance of up to half a kilometre and, on the other hand, farther than half a kilometre from the place where they were caught during a period of the first summer. In males it seems evident, although statistically not significant, that just before migration they concentrate more to the future breeding place than earlier during the same summer. This shows that imprinting has taken place up to this period. Even more interesting is the fact that when the concentration to the future breeding place is keenest, adult Reed Buntings also remain near or in their territories. I mentioned earlier that adult Reed Buntings may sing during this period, and this holds true also for young individuals. How closely this singing place lies to the territory the next year I do not know. However, I consider it improbable that they choose their territories accurately for the following year as early as the first summer. It seems more likely that young males choose a place to which or near to which they return the following spring. The fact that a large proportion of birds evidently dies each winter makes exact territory establishment the preceding autumn improbable.

The corresponding situation in females in Table 7 shows that although the migration of young Reed Bunting females begins in the first half of September (HAUKIOJA 1969) the concentration to the future breeding place is greatest during the period 25.8.—25.9. There is, however, no statistically significant deviation from preceding periods. This concentration suggests that the imprinting period occurs during late summer.

In considering the above situation it is well to keep the following sources of error in mind. Firstly, young and adult Reed Buntings range widely each day especially after the moult, although they probably use the same roosting site. This means that within the course of a day, they can be caught in widely separated places. Thus concentration to the marking place can not be expected to be very accurate the following spring. Secondly, young from first and second broods are combined in the material in Figs. 37—40, especially in Figs. 39 and 40. It is quite possible that late-born young settle in an area very late in the season, thus obscuring the relationship between autumn and spring localities. A more thorough investigation is impossible because of lack of recaught birds.

LÖHRL (1959) has studied the same problem experimentally in the Collared Flycatcher *Ficedula albicollis* and states that the period of moult determines the place where young birds settle to breed the next spring. The evident discrepancy in the period of imprinting between the Collared Flycatcher and the Reed Bunting is not surprising because the Reed Bunting and the Collared Flycatcher behave differently during the late summer. The Reed Bunting may linger in the same area for weeks after the moult, but, according to LÖHRL (1959), the Collared Flycatcher begins to migrate before the completion of the postjuvenal moult. This means that birds released in LÖHRL's (1959) experiments after moult should in normal conditions be migrating and it seems very reasonable that they do not choose their future breeding area at this stage. LÖHRL (1959) has thus experimentally proved the conclusion that the return tendency

TABLE 7. Numbers of adult Reed Buntings recaptured in a later year in Pori in relation to the distance from the place where they were caught in their first summer.

Marking period	Age	Males			Females		
		≦0.5 km		>0.5 km	≦0.5 km		>0.5 km
		N	%	N	N	%	N
25.5.—31.7. 1.7.—31.7.	pull. juv.	19	(53)	17	3	(10)	28
16.7.—25.8.	juv.	18	(46)	21	20	(52)	18
26.8.—25.9.	juv.	17	(65)	9	11	(61)	7

is based on some kind of imprinting mechanism after nest-leaving.

Computation from the first summer onwards show that male Reed Buntings concentrate more densely than females to the vicinity of the first summer marking place. This was evident in all periods although the recovery material used was sparse. DHONDT & HUBLÉ (1968) have reported the same thing in the Great Tit *Parus major*. This final state in the Reed Bunting, however, does not say anything about how dispersal occurs in both sexes, and the analysis showed that during the first summer the dispersive pattern is quite different from the final distribution; males disperse more intensively than females at this phase. With more material the above results would open possibilities for far-reaching conclusions about the nature of site-tenacity but it is pointless to speculate further about this problem with the present limited data.

6. On the role of autumnal territoriality in density regulation

The conclusion that young and old individuals stay near the future breeding place just before autumn migration was arrived at on the basis of the material presented earlier. Males have been observed to sing from the end of August onwards. During the field study no particular effort was made to detect signs of increased aggressiveness although this has been observed in many species during autumn (KALELA 1958). Autumn aggressiveness and displays have earlier been interpreted as signs of non-adaptability but, as KALELA (1958) has pointed out, such a widespread phenomenon must have some important function, and density regulation seems to be an attractive possibility (see KALELA p. 29).

In order to test if and how closely Reed Buntings choose their future breeding place as early as the autumn I carried out the following experiment.

In the southern part of island Välisanta there is a meadow where the following numbers of colour-ringed Reed Bunting pairs nested annually in 1966—1968. The numbers breeding in the study area of nearby Hevosluoto are given for comparison.

	Välisanta	Hevosluoto
1966	9	12
1967	7	13
1968	10	11

Both areas consist of marsh with low willow *Salix* bushes. These are areas of very dense Reed Bunting populations, and thus are evidently optimum habitats for the Reed Bunting. In the spring of 1969 I removed from the area every old male (5 individuals) returning to its former territory and kept them in captivity in the town of Pori. The first male was caught on April 17th, the first day it was seen, the following was removed April 21st (first observed April 19th), and others April 23rd (April 23rd), April 23rd (April 23rd) and May 1st (April 25th). Also the first young bird was removed April 25th (April 21st). Four young birds settled in the vacant territories. One was observed fod the first time on April 23rd and the others on April 25th. After that no new male settled in the area until the evening of May 4th, by which time each of the males had paired and the number of breeding pairs was four, about half of the number in previous years. The number of pairs in Hevosluoto in the same year was 12, in other words the same level as in earlier years. On the evening of May 4th I released in Välisanta the males which had been kept in captivity; of these at least four and possibly all five old birds and the single young bird nested in the area. The total number of pairs was thus ten; the identity of one male was not quite clear.

If the classic concept of territory establishment were true, every vacant territory should have been filled by newcomers. These would have been able to settle in the area because aggressive territory owners had been removed. However, the number of pairs remained the same during nine days at a time when the last males were arriving. Consequently this hypothesis does not seem reasonable. Although the number of birds in the experiment was rather small, the result was consistent with KALELA's (1958) hypothesis.

STEWART & ALDRICH (1951) and HENLEY & COPE (1951) carried out the first experiments having something in common with mine in a small (40 acres) area during a budworm infestation. They reported that over a longer period territories from which adults had been removed were reoccupied, and thus many more adults could be shot in the area than had originally settled there. Vacant territories were also quickly filled in the experiments made by ORIANS (1961). The firstly quoted experiments, however, are not really comparable to my own. I have tried to determine whether arriving young birds have a rigidly determined goal in mind. The first experiments quoted prove little about this, and show that at a later phase of the breeding cycle birds at least visit or settle in foreign territories (STEWART & ALDRICH 1951, p. 473 state that "practically all of the adult males taken appeared to be on their breeding territories at the time they were collected"). I have data on the Reed Bunting which depicts a similar situation. When netting in May-June and especially in July, up to four adult Reed Bunting males were caught in the course of a single day in a territory where a male permanently sang. If I had carried out shooting experiments similar to those quoted above, the results would probably have been the same, i.e. large numbers of adults shot in the area in relation to the original breeding population. This, however, has, at least in the Reed Bunting, nothing to do with nesting in the area. Foreign males and females visit the area whether the territory owners are present or not. This happens even as early as the incubation period and more and more during the nestling period. It is, however, unrealistic to deny the possibility that different species and perhaps different populations of the same species may behave differently in choosing a place to breed, and in how tightly they are attached to the territory during the breeding season.

The concept that some kind of density regulatory phenomena occur during autumn also make it possible to understand another widespread phenomenon: why males stop feeding young much earlier in summer than females, even though this, at least partially, results in reduced production of young (HAUKIOJA 1970). If the idea is accepted that birds tend to produce as many young as possible, it is difficult to avoid the conclusion that males derive some benefit from doing so. Because the postnuptial moult lasts nearly two months they have to stop breeding activities in the middle of July at the latest in order to allow time to complete the moult before the autumnal territorial period.

7. General discussion

7.1. Theoretical aspects

The meaning of the word dispersal is ambiguous. In general it means processes leading to dispersion, and besides this it means "movements of an immature bird from its birthplace to its first breeding-place; or (of less frequent ocurrence) of older birds from the breeding-place of one year to the breeding-place of the next year. Such movements occur as a result of an innate mechanism leading to dispersion" (BERNDT & STERNBERG 1968). The other factor which, together with dispersal results in dispersion is spacing. According to the same authors this means "movement forced upon a bird by external circumstances, particularly inter- and intraspecific competition, which do not allow it to establish itself in the place first selected for settlement but force it to withdraw elsewhere". The term dismigration combines the above ways leading to dispersion.

Deciding which movements constitute dispersal and which constitute spacing is extremely difficult especially in migratory birds (RHEINWALD & GUTSCHER 1969). Spacing may also lead to very long movements as shown experimentally by BERNDT & STERNBERG (1968) and the difficulty normally arises in that it is impossible in practice to know whether a bird has visited its birthplace before settling in another place.

Taken literally the above definitions do not completely correspond to the situation in the Reed Bunting in this paper but it seems evident that movements leading to dispersion during the premigratory period basically have to be placed in the category of dispersal. When birds arrive in the spring near the place where they were before autumn migration, spacing is probably the pertinent term. The results of the removing experiment show that spacing did not lead males to move great distances. If dispersal had occurred in spring it would be expected that the best habitats would have been settled quickly. The same result might also be achieved if spacing in spring had resulted in long-distance movements in males.

It may be that there are basic differences between the sexes in the effects of dispersal and spacing, but my Reed Bunting material is not sufficient for wider discussions.

WYNNE-EDWARDS (1962) uses the term "epideictic" of the phenomena needed for density regulation and which he interprets as exhibitions of population size. As an example he uses e.g. the moult migration of the Shelduck *Tadorna tadorna* which has something in common with autumnal conditions in the Reed Bunting although the function is probably quite different. LACK (1966), in denying the plausibility of this interpretation, says, on page 307, "since this behaviour occurs after breeding, usually in an area remote from where the birds bred, and since it involves only the adults, not the young, and in some other species of ducks only the males, any epideictic function seems wildly improbable". It is easily observed that the situation in the Reed Bunting satisfies the criticism made by LACK (1966) and the phenomenon can thus be interpreted as epideictic. It is quite another thing whether group-selection need be invoked to account for it. WIENS (1966) has shown that many phenomena in WYNNE-EDWARDS' (1962) treatment can be understood in terms of individual selection.

7.2. Use of the method described

My aim in developing the programmes used in this paper was to find how large a proportion of an expected value was actually observed at each distance and to fit a curve showing this as made by RHEINWALD & GUTSCHER (1969). Such a function makes it possible to compute "the half-distance" birds disperse and is very useful in many aspects of studying population dynamics, e.g. in evaluation of population size, death rates at short intervals, and so on. The recapture-materials accumulated when studying the Reed Bunting, are however, so sparse that this kind of treatment does not seem possible. Materials like that in this paper are easily collected in some species. In such situations it is possible to obtain more far-reaching results although those aspects to which most attention was paid in this paper are among the most difficult to study.

The computations done, are in practice possible only by using an electronic computer, at least if the number of squares in the matrix is large (390 in this study) and there are several marking and recapturing squares. If the size of the matrices increases much, the speed of computers rather soon becomes a limiting factor, even if much faster machines are used than in this case. This also hinders correction of some evident sources of error, e.g. it is unlikely that birds start to disperse in each direction with a similar degree of probability. They probably start in proportions which reflect the suitability of the surrounding terrain. It is also probable that birds concentrate to squares which are boundered by unsuitable areas. Taking these into account in programmes is not difficult but results in an immense increase in the amount of computer time needed.

Probably the best way of studying this kind of phenomena is by simulation. It demands partly quite different data than those used in the present paper, e.g. knowledge of how birds behave when they meet unsuitable areas, how often they change their direction when wandering and so on. The field work needed in such a study is probably at least as laborious as in this study.

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Selostus: **Pajusirkun kiertelystä ja paikkauskollisuudesta**

Kirjoituksessa esitetään menetelmä, jolla merkittyjen yksilöiden pyynti- ja kontrollointiaineistoista saadaan esille eläinten omaa liikkumista kuvaavia arvoja. Todetuissa siirtymissähän kuvastuu yleensä myös pyydystäjän merkinnän ja uudelleenpyynnin epätasainen alueellinen jakautuma sekä maaston ominaisuudet. Menetelmä perustuu siihen, että merkinnän ja pyynnin tehokkuuden aluejakautumaa ja maaston laatua hyväksikäyttäen lasketaan eri etäisyyksille siirtyneille yksilöille suhteelliset odotusarvot ja verrataan tätä jakautumaa todettuun etäisyysjakautumaan. Menetelmää sovellettiin Porissa vuosina 1966—1970 pyydystettyihin pajusirkkuihin.

Pesivien pajusirkkujen todettiin palaavan varsin tarkasti edellisvuotisille pesimäpaikoilleen, koiraiden tarkemmin kuin naaraiden (kuvat 3—6). Vanhat pajusirkkukoiraat oleskelivat reviireillään tai niiden lähistöllä syysmuuton alkuun saakka (kuvat 7, 9 ja 11). Vastaava ilmiö esiintyi naaraillakin (kuvat 8, 10 ja 12), joskin heikompana.

Nuoret pajusirkut alkoivat hajaantua pesimäpaikoiltaan varsin nopeasti itsenäistymisensä jälkeen (kuvat 19—34). Nuoret koiraat levisivät ympäristöön nopeammin kuin nuoret naaraat. Seuraavina vuosina monet pajusirkut palasivat pesimään syntymäpaikkansa lähistölle (kuvat 13—18). Tämä johtunee etupäässä siitä, että ne pyrkivät muuttomatkan jälkeen palaamaan sille paikalle, missä olivat olleet ensimmäisen elinkesänsä lopulla (taulukko 7). Syntymäpaikkauskollisuus liittyisi täten siihen, että nuoret pajusirkut vaeltavat ensimmäisenä kesänään suhteellisen lyhyitä matkoja ja ovat täten syyskesällä yleensä vielä melko lähellä syntymäpaikkaansa. Kirjoituksessa kuvataan tilannetta valaiseva koe.

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