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Interpretation of recovery patterns – contradictory points of view

EXTENDED ABSTRACT

Careful analysis of contemporary evaluations of recovery patterns shows that they are frequently methodologically primitive and traditional ever since the first papers devoted to the problem of spatial distribution of birds. This situation has encouraged the author to a theoretical discussion of methods of interpretation of recovery patterns. The problem was partially discussed in some publications (Busse 1969, 1986a, 1987a, b; Busse and Maksalon 1986) and summarised in the most recent publication (Busse 1986b), where details of the discussion can be found.

The most complicated recovery patterns can be found if a study contains analysis of birds ringed within a wide breeding area or at a number of bird stations. In this case, results of the analysis frequently depend on hidden assumptions underlying the basis of the interpretation but not explicitly discussed in a paper. The most common assumption which is usually not stated is that of the homogeneity of the sample under study. This assumption is a basis for one of the models of migration, while if heterogeneity is suspected a quite different interpretation may result.

Different pictures of migration extracted from recovery evaluations can be reduced to two essential models defined by the assumptions which are the basis of the model construction.

CLINE MODEL

Assumptions

1. The breeding area and wintering area are occupied by a homogeneous bird population, within which all its characters (both morphological and behavioural) are changing clinally.

2. The birds are forced into seasonal movements by existing environmental circumstances, which define destination area, route and timing of migration.

3. The problem of inheritance of orientation and navigation is ignored.

Conclusions

1. The word "population" used in the context of this model can be treated as a shortened form of an expression: "a group of individuals inhabiting a defined study area". It does not mean that any genetic differences between such "populations" exist.

2. The winter recovery pattern shows the wintering area, which is not differentiated into separable winter-quarters.

3. Any differences in recovery patterns of birds originating from neighbouring areas is due to a cline-type change of environment at the breeding or wintering areas or by migratory barriers.

4. Any differences in recovery patterns of birds migrating through a bird station in subsequent periods of migration are due to a cline-type change of migration time of birds originating from a number of subareas localised side by side at the breeding grounds.

Methodological consequences

1. Migration patterns can be sufficiently presented as maps of recovery places of birds originating from breeding subareas, ringed at some bird stations or migrating in different periods of migration.

2. The migration pattern of birds originating from one study area or migration period can be described by an average direction of migration (the mean direction being calculated from all data from the defined period) and by average co-ordinates of recoveries.

3. Wide-angle recovery patterns should be specially explained by the occurrence of actual barriers or instability of orientation mechanisms of migrants, as such patterns are not generally explained by the model.

4. Curved migration routes found in some species must be explained by the actual circumstances of migration.

POPULATION MODEL

Assumptions

1. The wintering area of European migrants can be divided into separate winter-quarters localised at late ice-period refuges of the species or created from them by shortening of the migration route (secondary winter-quarter); for long-distance migrants these areas are the first parts of Europe occupied in the past by the populations invading the continent from the south – this determines the actual pattern of migration.

2. Winter-quarters are occupied at winter-time by a defined population, members of which are genetic descendants of birds which started their dispersion from this area to central and northern Europe in the period after the ice age.

3. Wintering at defined winter-quarters is genetically coded; individuals which are hybrids of parents of different populational origin have genetic possibilities to migrate towards different winter-quarters.

4. Actual migration routes are inherited and repeat history of dispersion of populations from refuges to central and northern Europe – they can be, however, modified continuously by a selection pressure of natural or human origin.

5. If a population winters at secondary winter-quarters or migrates by a modified migration route the recovery pattern of first year birds reflects older migration customs of the population, while the recovery pattern of adults shows the most recent wintering area.

CONCLUSIONS

1. The word "population" in the context of this model has a defined genetic meaning: "A group of individuals which are descendants of birds originating from a specified ice age refuge and having inherited migration behaviour involving wintering at the same winter-quarter and migration by a historically evolved migration route". Population members can breed at separated areas or at mixed zones (these are interpopulational hybrids). As membership of the population is defined by genetic characteristics of an individual, hybrids can demonstrate membership of two or even more populations.

2. Winter-quarters are homogeneous regarding the population of wintering birds, while breeding areas can be occupied by a pure population or by individuals of mixed population origin.

3. The shape and localisation of pure population areas and/or mixed zones and actual migration routes can be a basis for hypotheses describing the post ice age history of the species.

4. Differences in recovery patterns of migrants ringed at a bird station in subsequent periods of migration are due to the differentiated populational composition of migrants in these periods, in which case individuals can migrate from pure population areas, from mixed zones or there can be crossing of migration routes of populations originating from quite different breeding areas.

5. It is not necessary to explain curved migration routes by actual environmental conditions.

Methodological consequences

1. The migration pattern should define winter-quarters, migration routes and breeding areas of populations.

2. After a preliminary analysis of the distribution of winter-quarters it is necessary to map the ringing localities in the breeding grounds of those birds wintering within specified winter-quarters as a basis for the delimitation of pure population areas and mixed zones.

3. A wide-angle recovery pattern means that the studied area lies at a mixed zone of two or more populations, so calculation of mean direction and/or co-ordinates is not allowed.

4. A curved migration route can be explained by a history of population dispersion, if there are no other clear causes.

5. A shift of recovery patterns of birds ringed at a station in subsequent periods of migration means that there is population mixture and calculation of average directions and/or co-ordinates is not allowed; the population structure of migration waves can be reconstructed from the changing relations between numbers of recoveries at defined winter-quarters.

6. If there is the suggestion that the studied sample is composed of members of a number of different populations (because of a shift in the recovery patterns of the migrants), then it is necessary to use special methods of analysis when the biometrical data are being evaluated.

The second model is suggested as much more useful for evaluations, explaining observed migration patterns better and encouraging complex studies of the migration of birds.

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DISCUSSION OF THE PAPER BY P. BUSSE

REG noted that with Redwings, for example, the same individual may winter in different areas, and questioned whether this in any way weakened the arguments that had been put forward in the paper.

PB suggested that migration by an individual to different winter quarters could be explained by the individual being a hybrid of parents with different genetic make-up. It may be that the individual can then choose its direction of migration. This could possibly be, for example, in response to the weather conditions. He noted that there is a similar pattern with Rooks, which may be as a result of social conditions.

REG suggested that it is strange that, if a choice of migration direction is admitted, then birds should not, in general, choose their migration direction by the economics of feeding conditions near the breeding ground. PB responded by quoting the example of the Robin. For this species the migration direction may be imposed by the October winds, but the curved route used by this species is repeated year after year, so that the explanation breaks down.

This part of the discussion was therefore rather inconclusive.

GF noted that many of the results described in the paper were not objective, but subjective, especially the boundaries that had been drawn. Boundaries are not so clearly defined, and different researchers working with the same data would

almost certainly obtain different results. He noted that for his work on Starlings cluster analysis had been used as a more objective approach.

(Ed.) Cluster analysis is clearly a statistical technique that can be used with such data to lend the analysis a greater degree of objectivity. In a somewhat similar situation, NORTH (1977, 1979a) used cluster analysis methods in attempts to develop an objective approach to the estimation of territory numbers from field records in the Common Birds Census. Of course, even when using a cluster analysis method a decision has to be made regarding the level of clustering to use.

PB responded by agreeing that if more information could be obtained we would probably find that strip areas exist around the boundaries where mixing occurs. He felt that the problem of exact borders is not important at present, nor is the question of which technique should be used to delineate the boundaries.

ACP remarked that sometimes the distributions of groups may look bounded, rather than continuous, but that this may be an effect due to the greater ringing effort in some countries than in others.