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An analysis of the recovery distribution based on finding probabilities

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The paper presents a method which enables us to estimate the number of ringed birds migrating to each destination area. The method is applicable for birds which can be divided into groups migrating to various destination areas in different proportions. The number of ringed birds from each group has to be known. The concept of a ringing-recovery ratio is introduced.

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INTRODUCTION

One of the most important tasks of ringing is to determine the distribution of the birds after migration (*e.g.* from breeding to winter grounds). It is often done by showing the recoveries on the map, assuming that their distribution corresponds to that of the ringed birds. But such an assumption is not usually true (*e.g.* BUSSE and KANIA 1977, PERDECK 1977), as the detection coefficient (ratio of number of the recoveries to the number of ringed birds present in the area, BUSSE and KANIA 1977) is changeable in time and space. Time changes can refer to years (*e.g.* the reporting rate of White Storks *Ciconia ciconia* in the middle-east Africa was higher during the colonial time than now, KANIA 1985), seasons or even shorter periods (*e.g.* rings found on waterfowl are reported much more often during the hunting season than beyond it). It is also known (*e.g.* PAYEVSKY 1973) that the detection coefficient varies from area to area. It can be 0 in an area uninhabited by man and close to 100% in the case of birds carrying rings readable by binoculars and staying for a longer time in the restricted area which is densely populated by ornithologists (*e.g.* arctic geese and swans wintering in some parts of Western Europe).

The detection coefficient depends on many factors (*e.g.* density, hunting customs and cultural level of people, place where the ring is fitted – tibia or tarsus, kind of address written on it – SALES 1973, habitat, predator pressure) which are hard or impossible to quantify. Thus the calculation of their influence seems to be impossible. But an approximate picture of the distribution of the ringed birds can sometimes be obtained in another way, by means of a method presented below.

The method gives a point estimate. The problem of estimating its confidence limit is still open. But just as direct inspection of the recovery map is, in spite of above criticism, a proper preliminary approach, an application of the method may sometimes be very useful in closer examination of the data.

The method was published in the Notatki Ornitologiczne (Busse and Kania 1977), used in two papers by Busse and Maksalon (1978) and Kania (1981) and next presented (together with an application) in the bulletin The Ring (Busse 1981). In the present paper the method is described in a simpler manner than in the original publication, but with all the details important to its user included.

THE METHOD

A basic question in the spatial analysis of ring recovery data can be formulated as follows. How many ringed birds, potentially, of the species or population under investigation, migrate to each destination area, *e.g.* wintering area? That is, for instance, what are the values of N_{1A}, N_{1B}, ..., N_{1K}* for group 1 in Fig. 1?

When all the birds under investigation are treated as a whole, the answer to the question seems to be impossible. But if they can be divided into groups (*e.g.* groups 1, 2, ..., n in Fig. 1), migrating in different proportions to various destination areas (*e.g.* areas A, B, ..., K in Fig. 1), the answer is obtainable. Those groups may be, for instance, sex-age groups, successive waves of migration, geographical populations *etc.* We take into consideration potential migrants to the destination areas – that is, including the birds which would migrate there if they were not killed, caught or exhausted before starting migration or during it.

The number of ringed birds from group G, potentially migrating to the area T, (N_{GT}) can be calculated from the formula:

$$N_{GT} = V_{GT} \cdot x_T \quad (1)$$

where V_{GT} is the number of recoveries of birds belonging to the group G, found in the destination area T; x_T, the ringing-recovery ratio** for area T, is the number of birds potentially migrating to area T, which, on average, have to be ringed to receive one recovery from that area. The ringing-recovery ratio is specific for every area and, as for the detection coefficient, is practically impossible to assess by evaluation of the influence of the natural environment and human activity. However, a set of equations can be constructed, which makes it possible to find values of x_T for each area. In the set there is one equation for each group. Each equation is an expansion of the formula from Fig. 1:

$$N_{GA} + N_{GB} + \ldots + N_{GK} = N_G \quad (2)$$

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* Indices 1, 2, ..., n, generally G, denote bird groups. Indices A, B, ..., K, generally T, denote destination areas.

** The term has been proposed by Philip M. North.

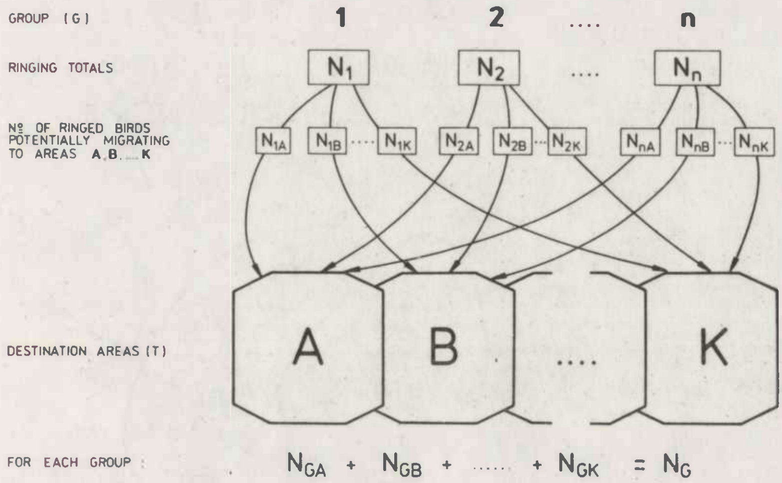

Fig. 1. The model of the migration of some groups of ringed birds to some destination areas

N – number of ringed birds. Other symbols – see footnote on the opposite page

obtained by substitution of N_{GT} (*i.e.* N_{GA}, N_{GB}, ..., N_{GK}) according to formula (1). The set is as follows:

$$\begin{cases} V_{1A}\cdot x_A + V_{1B}\cdot x_B + \ldots + V_{1K}\cdot x_K = N_1 \\ V_{2A}\cdot x_A + V_{2B}\cdot x_B + \ldots + V_{2K}\cdot x_K = N_2 \\ \cdot \\ \cdot \\ \cdot \\ V_{nA}\cdot x_A + V_{nB}\cdot x_B + \ldots + V_{nK}\cdot x_K = N_n \end{cases} \tag{3}$$

AN EXAMPLE

Let us examine a hypothetical example of the application of the method (Fig. 2). There are two groups of birds numbered 1 and 2. The total numbers of birds ringed are known (N_1 and N_2). Those birds migrate to two wintering areas, called A and B. The numbers of birds recovered there (V_{1A}, V_{1B}, V_{2A}, V_{2B}) are also known. Our question is how many of ringed birds from both groups potentially choose each of those two areas, *i.e.* what are the values of N_{1A}, N_{1B}, N_{2A}, and N_{2B}? To obtain those, first the values of x_T have to be calculated, using set (3):

$$\begin{cases} 100\cdot x_A + 10\cdot x_B = 10\,000 \\ 60\cdot x_A + 24\cdot x_B = 15\,000 \end{cases}$$

These give: $x_A = 50$, $x_B = 500$.

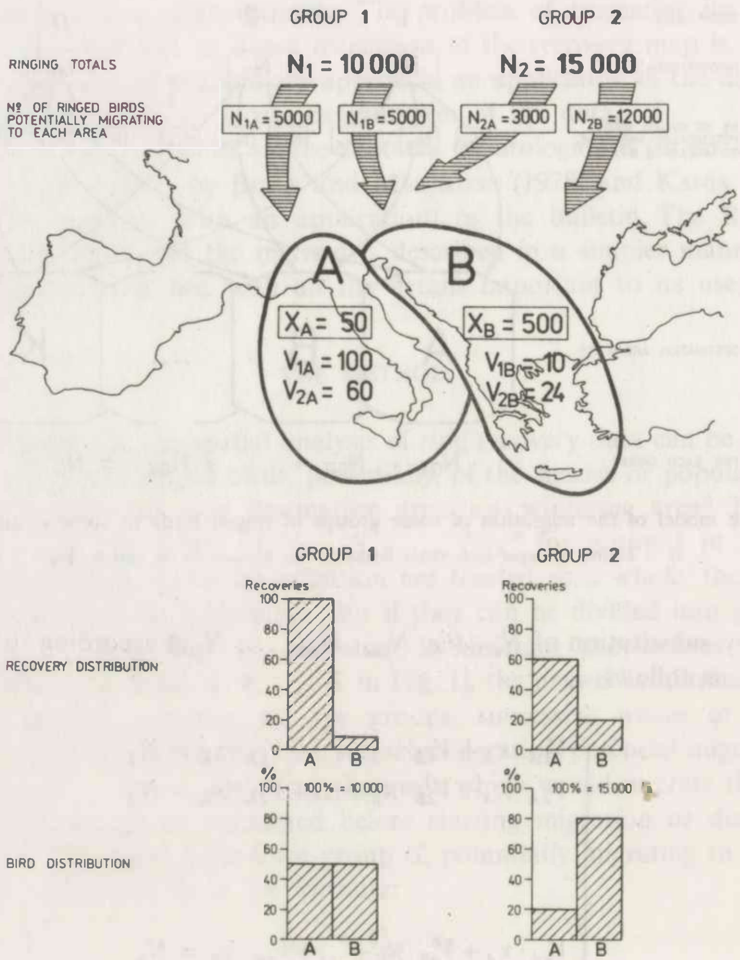

Fig. 2. Schematic diagram of the distribution on wintering areas of two hypothetical groups of ringed birds, each of them migrating to both destination (wintering) areas, but in different proportions. In the upper part of the Figure the unframed numbers denote known data, the numbers with the frames denote calculated values

Knowing x_T, the values of N_{GT} can be calculated from the formula (1), as follows:

$$N_{1A} = 100 \cdot 50 = 5000, \quad N_{1B} = 10 \cdot 500 = 5000,$$
$$N_{2A} = 60 \cdot 50 = 3000, \quad N_{2B} = 24 \cdot 500 = 12000.$$

The picture of winter distribution of birds from both groups, obtained in this way (lower part of Fig. 2) is quite different from the one obtained when assuming that the recovery distribution corresponds to the ringed birds distribution (middle part of Fig. 2).

THE REQUIREMENTS

It is possible to obtain the point estimate of the bird distribution over the destination areas by means of the method presented only if the following requirements are met:

1. The investigated birds can be divided into groups.

2. The total area, to which the birds migrate, can be divided into some destination areas.

3. No destination area is omitted (which can be the case when the area has an extremely low, near-zero recovery rate).

4. The number of groups (or equations in the set) is not smaller than the number of destination areas (or unknown variables). If the number of groups is bigger than the number of destination areas (the number of equations is bigger than the number of unknowns), the set of equations is insoluble, because the requirements (6) and (7) are never fully met and (9) is only sometimes fully met. Then one has to look for the values probably closest to the real one. Such values can be the numbers which, after substituting the unknowns, will yield the lowest possible sum of the squared differences between the right and left members of the equations of the set (3). This is achieved by differentiation (see Appendix).

5. If the numbers of groups and destination areas are equal (number of equations = number of unknowns) none of the equations can be identical with another, because it reduces the number of equations used in the calculation of the unknown variables (x_T) below the required minimum.

6. The ringing-recovery ratio is the same for each part of any destination area or the distribution of each group over any area is the same.

7. Birds from each group have the same probability of being reported. When the groups represent geographical populations, their breeding grounds have to lie close to each other and have to be small, when compared with the distance to destination areas, so that it can be assumed that factors influencing mortality of birds from those populations after ringing, and before reaching the destination area, operate with equal power. When destination areas are arranged in such an order that to reach some of them birds have to cross the others, a problem arises with the recoveries from the migration period. In the case of those destination areas through which some birds migrate farther, the only recoveries that can be included are those which are found after the end of the migration to the furthest destination areas, and before the beginning of the migration from there. Of course, all recoveries with an uncertain date of death or capture should be excluded, as well as those concerning the birds weak or injured when found, as they could stay in the finding place only because they were unable to continue migration. In the case of furthest destination areas all the recoveries can be included. However, then the values of x_T are lower and can be used only to calculate the values of N_{GT}, and not to compare with x_T from areas closer to the ringing place.

8. The number of recoveries is not too small.

9. The recoveries are from the period during which any ringing-recovery ratio does not alter. The alterations can be due to the effect of modifications in the hunting season or quota, political changes, wars *etc.* Such alterations have no impact on the results received only when the proportions of birds, ringed before and after their occurrence, are the same for each group.

DISCUSSION AND CONCLUSIONS

The substantial difficulty in showing the exact distribution of ringed birds on the basis of the recovery distribution lies in the fact that recoveries almost never constitute random samples of ringed birds.

The presented method accepts these uneven weights of recoveries, but not wholly, as it is practically impossible to divide a total destination area into small and numerous areas which really are uniform with respect to the ringing-recovery ratio, thus to entirely fulfil requirement (6).

Also requirement (7) cannot be fully met. Requirement (8) could be stated more precisely only after experimentation with hypothetical sets containing the totals of recoveries and ringings for different numbers of bird groups and destination areas and for various values of the ringing-recovery ratio.

In spite of these shortcomings, in some cases the method enables us to obtain a more correct picture of the spatial distribution of the ringed birds than the methods which assume that recoveries are random samples of ringed birds. However it should be stressed that the results obtained by the method presented here should not be fully accepted without checking them against other approaches, *e.g.* analyses of bird measurements and population trends (Busse 1981).

APPENDIX

An example of using the differentiation method to find the lowest possible of sum the squared differences between the right and left members of the equations of the hypothetical set of three equations with two unknowns

Data:

Group (G)	N_G	V_{GA}	V_{GB}
1	30 000	65	203
2	25 000	35	297
3	20 000	34	202

From the formula (3) and the data in the table, the following initial set of equations can be constructed:

$$\begin{cases} 65x_A + 203x_B = 30\,000 \\ 35x_A + 297x_B = 25\,000 \\ 34x_A + 202x_B = 20\,000 \end{cases}$$

A least squares approach is now adopted to optimise the x_A and x_B. The squares of the differences are: $(65x_A + 203x_B - 30\,000)^2$, $(35x_A + 297x_B - 25\,000)^2$, $(34x_A + 202x_B - 20\,000)^2$, with sum $\sum$, and the partial derivatives of the sum of squared differences, calculated with respect to variables x_A and x_B are as follows:

$$\frac{\partial\sum}{\partial x_A} = 2\,[65\,(65x_A + 203x_B - 30\,000) + 35\,(35x_A + 297x_B - 25\,000)$$
$$+ 34\,(34x_A + 202x_B - 20\,000)],$$
$$\frac{\partial\sum}{\partial x_B} = 2\,[203\,(65x_A + 203x_B - 30\,000) + 297\,(35x_A + 297x_B - 25\,000)$$
$$+ 202\,(34x_A + 202x_B - 20\,000)].$$

As the smallest sum of squares will occur only when both the partial derivatives equal 0, the values x_T closest to the real ones can be obtained by equating the above derivatives to 0; *i.e.* $\frac{\partial\sum}{\partial x_A} = 0$, $\frac{\partial\sum}{\partial x_B} = 0$, which again yields a set of equations with a number of unknowns. However, the number of equations in this set is now equal to the number of the unknowns. After some reordering, the above set is as follows:

$$\begin{cases} 6606x_A + 30\,458x_B - 3\,505\,000 = 0 \\ 30\,458x_A + 170\,222x_B - 17\,555\,000 = 0. \end{cases}$$

The solution of this set is: $x_A = 314.7$, $x_B = 46.8$.

DISCUSSION OF THE PAPER BY W. KANIA AND P. BUSSE

GF requested clarification of what was meant by "recovery rate"*. WK replied that there were two possibilities, namely:

1. The number of birds found compared with the number ringed.
2. The number of recovered birds compared with the total of the part of the population that goes to the destination area in question.

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* (Ed.) The term "recovery ratio" has now been used in the critten paper to replace "recovery rate", where appropriate.

GF commented that it is important to use such words in just a single sense, and WK confirmed that in the formulae "recovery rate" had been used in the second of the two senses described.

PMN questioned whether the different modes of recovery were accounted for, and WK confirmed that account of these was taken by the X values.

KHL commented on the probably differential ringing effort in the recovery areas, but WK pointed out that the method does not require knowledge of this.

CJM noted that the only way that the basic assumptions are likely to be violated may be in differential reporting rates for, *e.g.*, political reasons.