STUDIES OF LONG-TERM POPULATION DYNAMICS BASED ON RINGING DATA

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ABSTRACT

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In the papers devoted to monitoring of population dynamics two kinds of ringing data are used: national ringing totals and station ringing data. The first type of data should usually be avoided. The latter one can be used for monitoring purposes with care. These data are influenced by the level of standardisation of catching effort and catching conditions, but also by the position of a station in relation to the migration pattern of the species. During analysis of data some allowance can be made, when the raw data are incomplete. Population dynamics information can be studied as raw data presenting year-to-year fluctuations of population level or as a smoothed curve showing a more general trend "clean" of part of the variation in the raw data noise. The noise can, however, be studied as a separate parameter of the population dynamics, but the coefficient of variation commonly used for this purpose is not adequate for the problem.

Interpretation of the results should be cautious because of a few pitfalls waiting for students trying to use regression analysis and for those comparing their data with breeding bird censuses. Complex bird migration studies may be helpful in the interpretation of population dynamics patterns.

KEYWORDS: long-term population dynamics; ringing data; migration count; field methods; evaluation methods.

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INTRODUCTION

Ringing data can be a source of information on population dynamics. This type of material is two-sided: ringing recoveries can be used in the evaluation of survival rates – a very important parameter of population dynamics – while ringing totals can be used to describe long term population trends and to analyse yearly fluctuations of bird numbers. Most papers presented at both the EURING/MEG Technical Meetings (at Wageningen and at Sempach) have been devoted to survival analyses, while long-term population dynamics studies based on ringing data are dispersed elsewhere (*e.g*, Berthold 1972, Busse 1973, Dalberg-Petersen 1976, Hjort and Lindholm 1978, Berthold and Querner 1979, Lindholm *et al*. 1983, Busse 1984, Baumanis and Rute 1986, Berthold *et al*. 1986, Busse and Cofta 1986, Petterson and Hedenström 1986, Svensson *et al*. 1986, Rabøl and Lyngs 1988). This separation is a very unfortunate phenomenon, as the results of these studies should be used together, being two aspects of the same process. In survival studies different assumptions are adopted and in many cases they determine the results. These should be, however, related to real data on long-term dynamics of a population. It is possible that an apparently correct assumption causes results which do not fit a real population at all. This is one reason for the present discussion of methodological problems in the evaluation of population dynamics based on ringing data. The problems are different for the evaluation of national and station ringing totals.

NATIONAL RINGING TOTALS

This kind of data has been used in monitoring evaluations a few times (*e.g.* Stolt and Österlöf 1975, O'Connor and Mead 1984, Tiainen 1985). Although these authors have found some reasonable results, it should be stressed that such totals may be very biased, especially when they contain both pulli and full-grown birds. The most obvious source of bias – the variable number of ringers – could be, theoretically, corrected by recalculation of the number of ringed birds per ringer, but one should keep in mind that apart from the number of ringers, their ringing preferences, as well as popular ringing programmes and general ringing politics of the scheme, could influence the ringing of different species very much. The implict assumption of an equal interest among ringers in the ringing of different bird groups or species may be wrong, so the presentation of species data as a percentage of the total ringing (Stolt and Österlöf 1975, O'Connor and Mead 1984) seems to be doubtful. Additionally, apart from the conscious activity of ringers, long-term changes in the standard of living and social development of a country play an important role in the ringing activity by changing the amount of free time and money spent on ringing as a hobby. It can be concluded that national ringing totals should be avoided as a source of monitoring data or, at least, treated with extreme caution.

STATION RINGING DATA

When a study is based on this kind of ringing data the problem of control of biases seems to be simpler than in the case of the national ringing totals, but numerous biases could still be expected. These are of very different origin: they depend on the locality of a station in relation to the migration pattern of a species, methods of data collection and evaluation.

Looking from the point of view of monitoring problems, one can imagine an ideal ringing station: (1) located inside a large area covered by homogenous and stable habitat, where broad front migration occurs, and having (2) highly standardised methods of data collection. A real European bird ringing station is, however, generally far from this ideal model.

Localisation of the station

The location of the station is very rarely so ideal: most stations are situated in places where concentration of migrants is expected – on islands, at the sea coast or on mountain passes. Such places allow more birds to be caught, but the number of migrants occuring is more sensitive to random fluctuations due to weather conditions. These fluctuations are not the same at the typical locations listed above: they are biggest on islands (*e.g.* Heligoland – Germany, Ottenby – Sweden, Christiansø – Denmark), smaller at the sea coast, where migrants land after oversea flight (*e.g.* Dutch coast, Hel Peninsula – Poland) and on mountain passes (*e.g.* Col de Bretolet – Switzerland); the smallest influences of the weather can be expected at those coastal sites which are guiding lines for diurnal migrants (*e.g.* Rybatchy – USSR, Mierzeja Wislana – Poland). It should be stressed here that some inland stations are ecologically the equivalent of island stations (*e.g.* an isolated lake for reed birds) with all the consequences of belonging to that type. Generally, the type of station must be considered when monitoring data are interpreted. This is because weather fluctuations cause part of the between-year number variation. However, these fluctuations will not change long-term trends.

The important requirement of the location of the station in homogenous and stable habitat is very rarely fulfilled. Homogeneity of habitat allows us to assume the equal capture efficiency of all nets used at the station, which is helpful when, due to organisation of the station work, the number of nets is not exactly stable. Nets located in varied habitat are not of equal capture value and will vary for different species (this was clearly shown in a paper of Berthold *et al.* 1976), so recalculation of catching results per net or per standard length of nets is necesarily biased and, moreover, biased to different extents for various species. The second mentioned parameter of the habitat – its stability – would be fulfilled only at a station located in climax stage habitat. This is practically never the case, as such habitats are very unsuitable for catching birds. In most habitats where the stations are situated, the habitat is in the succesion stage: reedbeds become dryer and more bushy, while bushes and young forest plantations grow up and become more dense. It is clear that these processes lead to changes in the suitability of the habitat for different bird species, which can cause substantial bias in long-term trend estimation. The problem is solved at the stations in two different ways: (1) artifical standardisation of plant cover at the station area (*e.g.* MRI Program – Berthold and Schlenker 1975), or (2) movement of the catching area inside a bigger area of similar habitat according to succession (*e.g.* Operation Baltic stations – Busse and Kania 1967). Both types of solutions have their own advantages and disadvantages. The first method is applicable in special conditions, when the habitat can be easily managed, *e.g.* "catching gardens" at a few stations (*e.g.* Heligoland, Ottenby) or willow shrubs at borders of lakes. Discussing this method of management of the station area one must have in mind that an elimination of habitat bias is apparent only – the bias can extend further as an area around the station may strongly alter its attraction for birds, which could concentrate at the places out of the station area or *vice versa*. This bias is, in practice, uncalculable. The second solution - adaptation of the catching area and location of nets according to habitat succession reduces "habitat bias", but its effectiveness depends on local conditions and the experience of the station staff. The best results are at stations situated at clear guiding lines of migration when experienced staff carefully choose new catching places taking into consideration the local traditions of migrants. However, in that case the bias is uncalculable too.

Methods of data collection

The most important elements of the field methods are as follows:

1. Sufficiently long, standard and continuous period of work,

2. Standard number and quality of catching devices,

3. Enough numerate and qualified staff.

The requirements listed will be clear and obvious, when one looks at Figure 1, where an example of the seasonal migration dynamics of a typical migrant, the Robin, is presented. A two month long period of work is necessary to cover the time of migration of the species in any particular year. Yearly fluctuations in migration time are at the level of ten days (*e.g.* Song Thrush – Maksalon 1983), so a two and a half month period of work is sufficient for

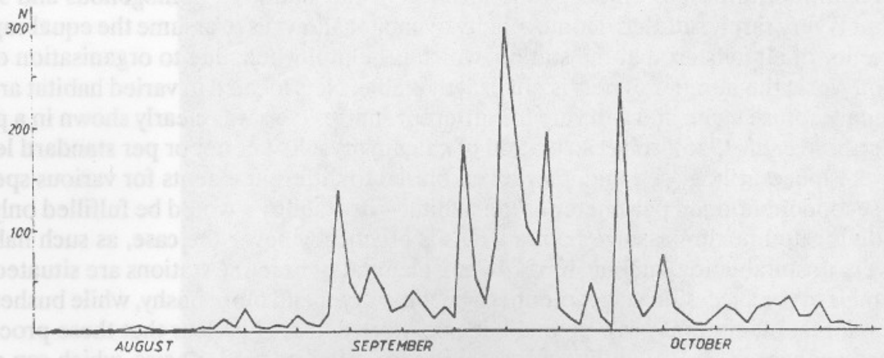

Fig. 1. Example of seasonal migration dynamics of the Robin (*Erithacus rubecula*) at Bukowo station (Poland) autumn 1981.

the species. When more species, and usually this is the case, are studied simultaneously this period would be insufficient, as a number of species would migrate earlier or later than the example species mentioned and their data would be biased because of variation in migration time. Few such species can be found, when the period of autumn work of the station is limited to August 17th - October 31st (Busse and Halastra 1981). If the work of the station is carried out every year throughout the standard period the data are directly comparabole. In practice there are, however, some deviations from the standard time – for different reasons the station starts to work later or is closed earlier. In such cases the resultant data are not directly comparabole to other years and it is necessary to make an extrapolation of bird numbers to the standard time. This can be done on the basis of the average cumulative curve of migration of the species (Busse 1973).

In an example diagram (Figure 2) it can be seen that, due to fluctuations of migration time, variation around the average curve is rather large, especially in the central part of the migration time, so the extrapolation is allowed only for a few marginal five-day periods. An example of the results of such extrapolation is given in Table 1 and in Figure 3.

The considerations presented as above are based on an assumption of continuous work at the station – the work is carried out each day throughout the whole standard period. Figure 1 shows clearly that any sampling (*e.g.* one day of catching per week, or five or ten day periods *etc.*) cannot give reasonable data for monitoring purposes – accidental and uncalculable deviations would be much too big. The same is true for any uncontrolled gap in the period of work – analysis of Robin migration at Bukowo station (1971-1982) shows that a single peak day of migration contains on average 14.4% of birds caught in a particular year (but as much as 28%). Similar observations were made by many students at different bird stations. That fact leads some of them (*e.g.* Rabøl and Lyngs 1988) to conclude that peak day values are accidental (depending on the weather) and that they should be damped mathematically before calculation of indices of true population size. However, study of

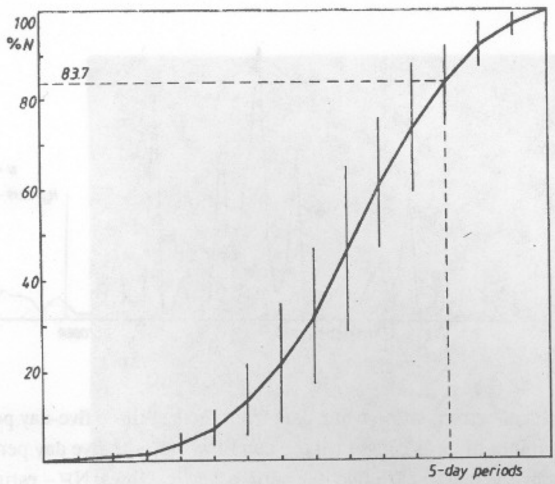

Fig. 2. Average cumulative curve of migration of the Robin (*E. rubecula*) for Bukowo station (1971-1982). Vertical lines – ± 2 S.D.

Table 1

Result of extrapolation of the number of Robins (*E. rubecula*) at Bukowo station, when data from the last three five-day periods are treated as "unknown". Extrapolation based on Figure 2. N57 - number of birds caught by the end of 57th five-day period, NE - estimated number of birds for the end of work (60th five-day period), N - real number of the birds caught till the end of 60 th five-day period, Δ - NE-N difference in percent.

Year	N57	NE± 2S. D.	N	D%
1971	1054	1259±166	1149	+9.6
1972	1097	1310±174	1158	+13.1
1973	1100	1314±174	1206	+8.9
1974	-	-	-	-
1975	788	941±153	887	+6.1
1976	535	639±85	690	–7.4
1977	596	712±94	781	–8.8
1978	478	571±76	682	–16.3
1979	481	575±76	555	+3.6
1980	517	618±82	653	–5.3
1981	2339	2674±355	2574	+3.9
1982	852	1018±135	1100	–7.4

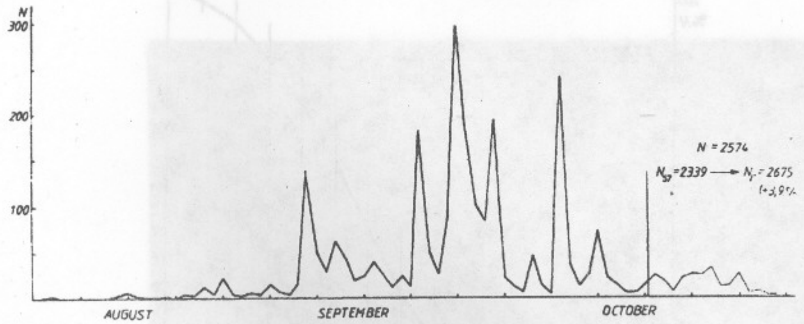

Fig. 3. Example of the results of extrapolation when data from the last three five-day periods are "unknown". N – real number of birds caught till the end of work (60th five day period), N57 – number of birds caught by the end of 57th five-day period (vertical line), NE – estimated number of birds for the end of the 60th five-day period. Extrapolation based on Figure 2.

daily fluctuations of Robin migration at Bukowo station (above) suggests that this conclusion is doubtful and should be further checked. It was found that years with a high total of birds also showed a high variance in daily catches ($r = 0.98$, the same for variance calculated with and without peak days), so these peak catches are a natural consequence of high variance connected with high population level. The other test of the latter hypothesis is presented in Figures 4 and 5. The cumulative curves of birds caught in separate years were constructed as follows: out of forty days of the main period of migration a day was found with the smallest catch, then to that number of birds there was added the next smallest catch and so on to the highest peak day. The curves never crosses each other, which means that the distribution of days with low and moderate catches, as well as the highest ones, is determined by the total number of migrants. The average curve (Fig. 5) can be used for extrapolation of the total number of birds when for a few peak days the number of birds cannot be fixed (Fig. 6), *e.g.* in a case when too small a number of staff and/or inexperienced staff of the station excluded some of the standard set of nets from the data collection. The bias caused by the estimation is surprisingly low: the coefficient of variation is only about 7%, when estimation is based on thirty five out of forty catching days.

Extrapolation of catches, when the number of nets varies between days or seasons, is in common use, *e.g.* Busse (1973) recalculated the yearly catches per net of standard length, using the average number of nets operated in a season (a stable number of nets were generally in operation and they were open continuously), while Rabøl and Lyngs (1988) recalculated the catches every day per total length of nets in use on a particular day (a different number of nets was operated on different days and they were open during varying parts of a day). However, everybody using such recalculations must be aware that this operation may generate biases, which could be substancial and difficult to estimate. Especially dangerous are frequent changes in the number of nets and placement of those in use – these can lead to gross disturbances of the migration dynamics curve and enlarge biases of other extrapolations. Because of this sampling with a fixed number of nets and continuous catching is strongly recommended. The latter is important because of the different diurnal activity pattern of migrants during low, moderate and peak migration days.

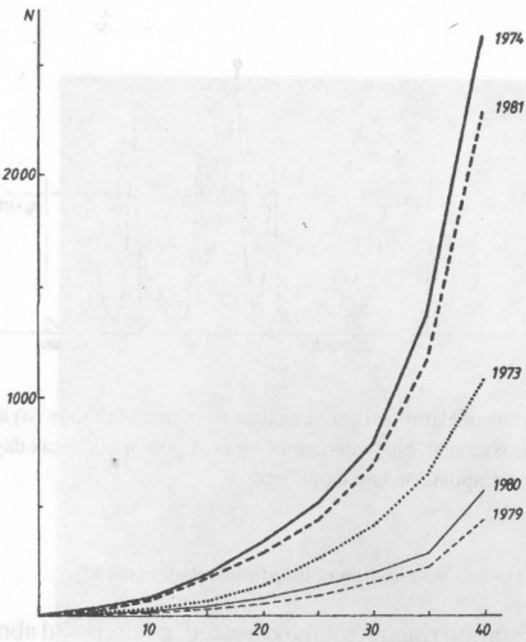

Fig. 4. Cumulative curves of catches in the main period of migration of the Robin (*E. rubecula*) at Bukowo station. Explanation in the text.

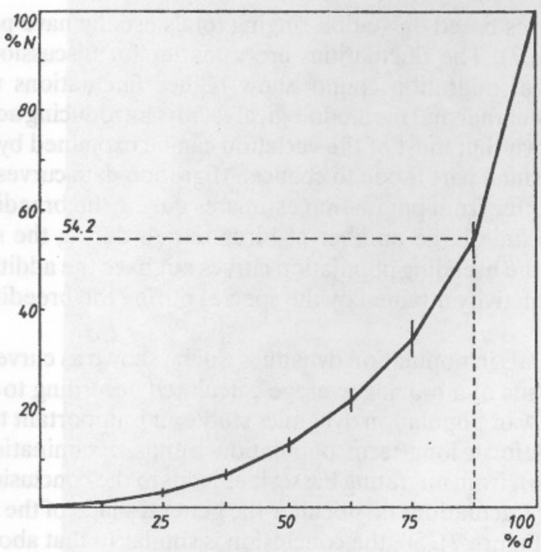

Fig. 5. Average cumulative curve calculated from data presented in Figure 4. Vertical lines – ± 2 S.D. Forty day period is treated as 100%.

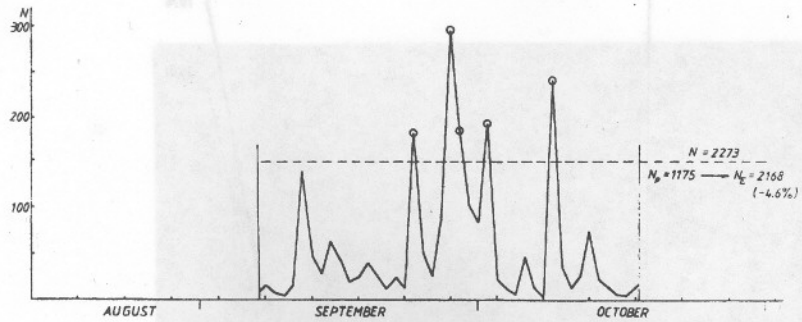

Fig. 6. Example of the results of extrapolation when data from five peak-days (o) are "unknown". N – real number of birds caught, Np – number of birds caught in non-peak days, N_E – estimated number of birds. Extrapolation based on Figure 5.

Evaluation of the station ringing data

Yearly (seasonal) station ringing totals corrected, as discussed above, can be presented as raw data curves, where they are plotted against the years of the study. The other method of presenting the data is a plot of percentage indices of population size, calculated from the raw data in relation to a datum level. When comparisons of the curves from different stations or populations are expected the latter method is recommended, especially when mean population level is accepted as a basis for calculations.

The raw data curves based on station ringing totals usually have pronounced year-to-year fluctuations (Fig.7). The fluctuations are a matter for discussion. Whilst Svensson (1978) considered that migration counts show higher fluctuations than breeding bird censuses, because of weather and methodological factors introducing accidental deviations. Busse (1980) has shown that most of the variation can be explained by natural population processes and only a small part is due to chance. Migration data curves during the autumn are clearly likely to differ from population estimates during the breeding season since the migrant birds will include large number of birds reared during the summer. Thus such curves not only trace the breeding population curves but have the additional (and variable) influence of the productivity attained by the species during the breeding season.

More general trends in population dynamics can be shown as curves based on raw data but smoothed by means of a moving average calculated according to different formulae. From the point of view of population dynamics studies it is important to know whether the yearly fluctuations deform long-term population trends. Examination of some tens of smoothed curves drawn from migrating Passerines leads to the conclusion that in most cases even big year-to-year fluctuations do not alter the general shape of the smoothed curve (an example is shown in Figure 7). So, the conclusion is similar to that about the value of peak day catches for yearly number indices – usually even the most extreme values are based on the real size of the population studied.

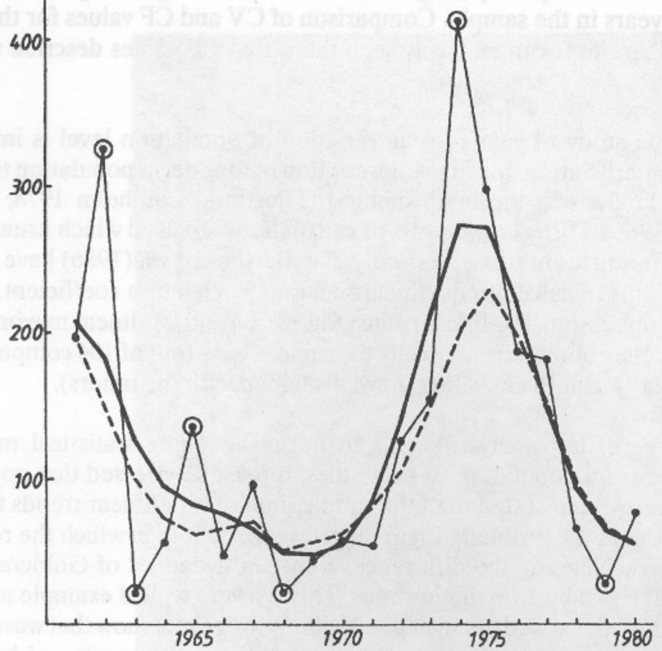

Fig. 7. Presentation of the station ringing data: Goldcrest (*Regulus regulus*), Mierzeja Wiślana station •–• – raw data curve, — – smoothed curve, all years included, --- – smoothed curve, extreme yearly totals (o) excluded.

In population dynamics studies the level of year-to-year variation is an interesting parameter, which can be analysed as a special measure of population processes. Different bird species show different levels of variation (Busse 1973, Abraszewska-Kowalczyk 1974), spring time fluctuations are different from the autumn ones (Buse and Cofta 1986) and variation at one station can be different from fluctuations of the same species at another station. When this problem is studied one meets a methodological problem with the calculation of the measure of variation. Standard deviation and coefficient of variation are not good measures here as they depend not only on year-to-year variation but also on a long-term trend of population size (Busse and Cofta 1986, Rabøl and Lyngs 1988). Both parameters of the long-term trend – a shape of the curve and mean size of population – influence the value of these indices of variation. Busse and Cofta (1986) have proposed the calculation of another index of variation – the coefficient of oscillations (C.O.), based on the idea that variation should be expressed as a measure of deviations from the smoothed curve of long-term population dynamics. After further study the formula C.O. does not seem ideal and now, in current studies, I use a similar index of variation called the coefficient of fluctuations:

$$\mathrm{CF} = \frac{1}{M} * \frac{\sum (X_{oy} - X_y)^2}{N} * 100\% \ ,$$

where M – mean value of population size index for all studied years, X_y – the value of population size index for year "y", X_{oy} – local value of moving average for the year "y", and N – number of years in the sample. Comparison of CV and CF values for the same data is presented in Figure 8. It can be easily seen there that CF values describe the size of the variation better.

Although the study of year-to-year variation of population level is important, most students are primarily interested in the description of long-term population trends and they use regression analysis as the main method (Hjort and Lindholm 1978, Tiainen 1985, Berthold *et al.* 1986). Different variants of calculations are used which usually give similar results, with differencies in robustness only. *E.g.* Berthold *et al.* (1986) have used the same data in five variants of calculations (Spearman rank correlation coefficient, linear regression, log-linear regression, log-linear robust regression and log-linear maximum likelihood estimation) and they obtained practically the same effects (out of 104 comparisons only six, and not statistically significant values, have disagreed with the others).

Although regression analysis seems to be an adequate statistical method for the problem of long-term population trend studies, it must be stressed that population dynamics is much more complicated than the simple linear or log-linear trends to which use of that method reduces the problem. Figure 9 gives an example in which the regression lines do not describe sufficiently the differences between dynamics of Goldcrest populations migrating through two bird ringing stations. This is a very typical example as most population dynamics studies, carried out over a sufficiently long time, show that wave-like, or cyclic population dynamics patterns, predominate among studied species of birds. This very common phenomenon forces caution in the interpretation of the results of regression analyses based on short-term studies. In population dynamics studies even ten years' data seem to represent too small a sample for general conclusions on the welfare of the species. Local, short term trends can be drastically different from a really long-term trend, as illustrated in Figure 10. The twenty-eight year trend shown there as a "real long-term trend" should be, however, treated with caution too, as there are reports on population cycles as long as fifty years in birds (Machalska *et al.* 1967).

Interpretation of the results

It could be generally agreed, that station ringing data collected and evaluated with all the cautions discussed above give sufficiently good information about the real number dynamics of migrants passing through the station. However, there is a further methodological problem: "what population is represented by the studied group of migrants?". The problem is important, as looking for causes of year-to year variation in population level and interpretation of whole population dynamics needs the fixing of the breeding and wintering areas of the population studied. In some cases it is possible to find them by ringing recoveries analysis alone, in other more complex bird migration studies must be included. It should be stressed here that apparently natural assumptions on native areas of migrants taken as a basis for correlation analyses are frequently dubious, which leads to poor correlations between ringing station data and breeding bird censuses (Svensson 1978, Rabøl and Lyngs 1988). Migration patterns of various species are very different and hardly any between-species extrapolations can be accepted. There are examples which show that quite different birds migrate through stations situated relatively close to each other – Busse (1972) for the Redstarts migrating through Mierzeja Wislana and Nowa Pasleka,Operation

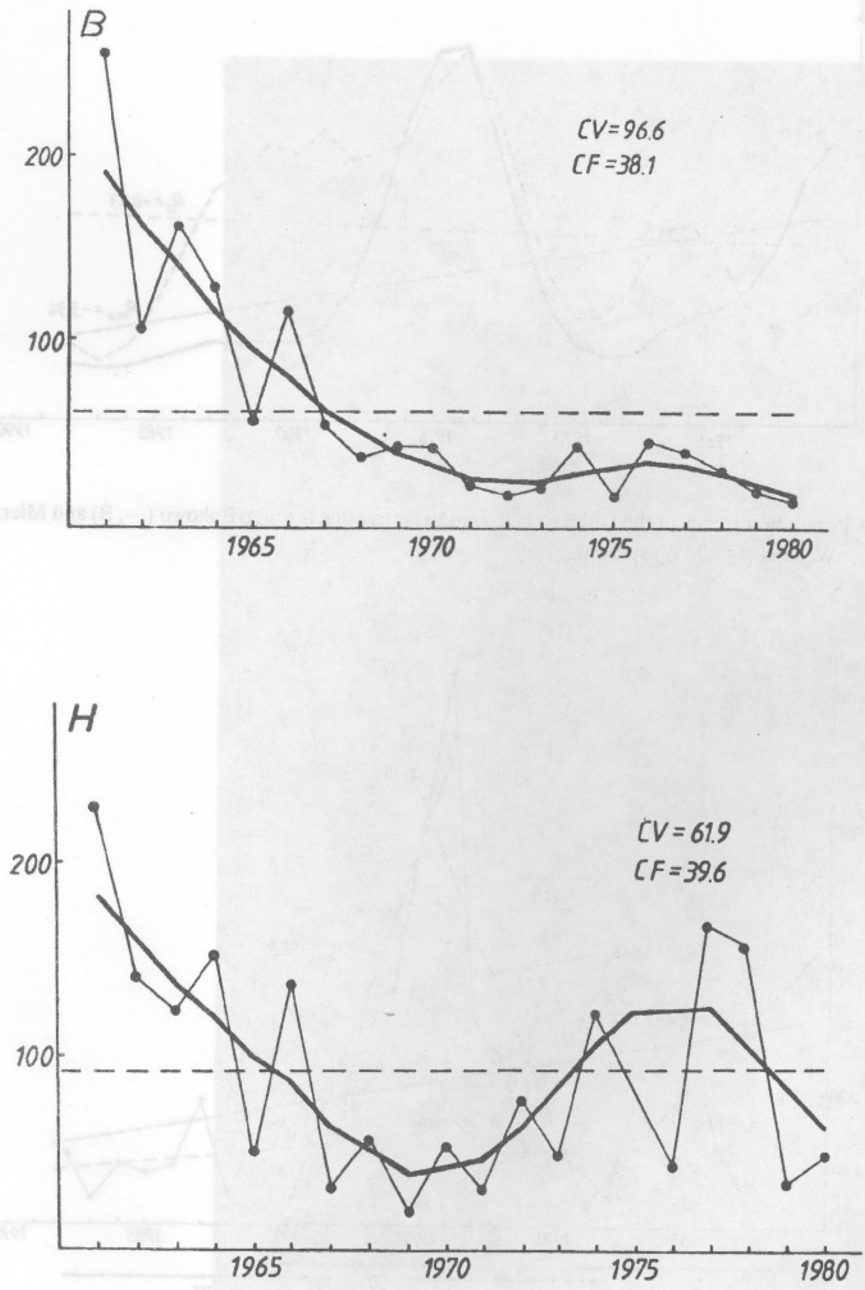

Fig. 8. Two measures of variation (CV – coefficient of variation, CF – coefficient of fluctuations) calculated for the Blackbird (*Turdus merula*) – data from Bukowo (B) and Hel (H) stations. •—• – raw data curve, — – smoothed curves, --- – mean population level for the station.

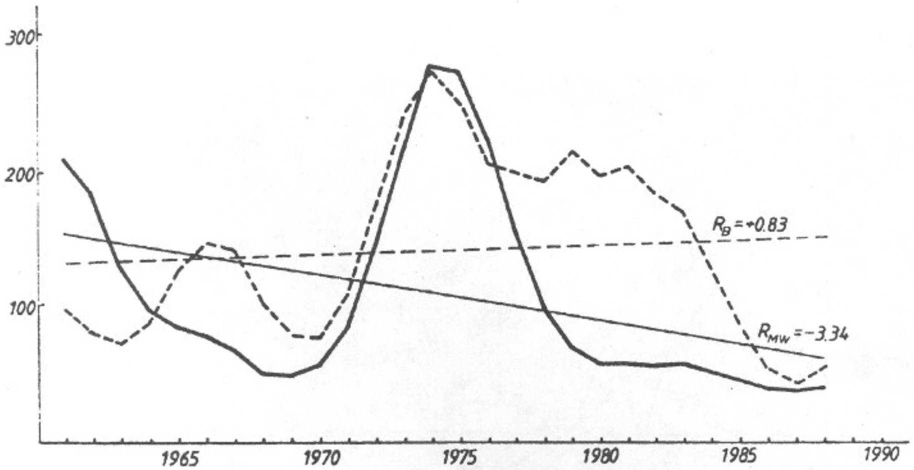

Fig. 9. Population trends of the Goldcrest (*R. regulus*) migrating through Bukowo (---, B) and Mierzeja Wiślana (—, MW) stations.

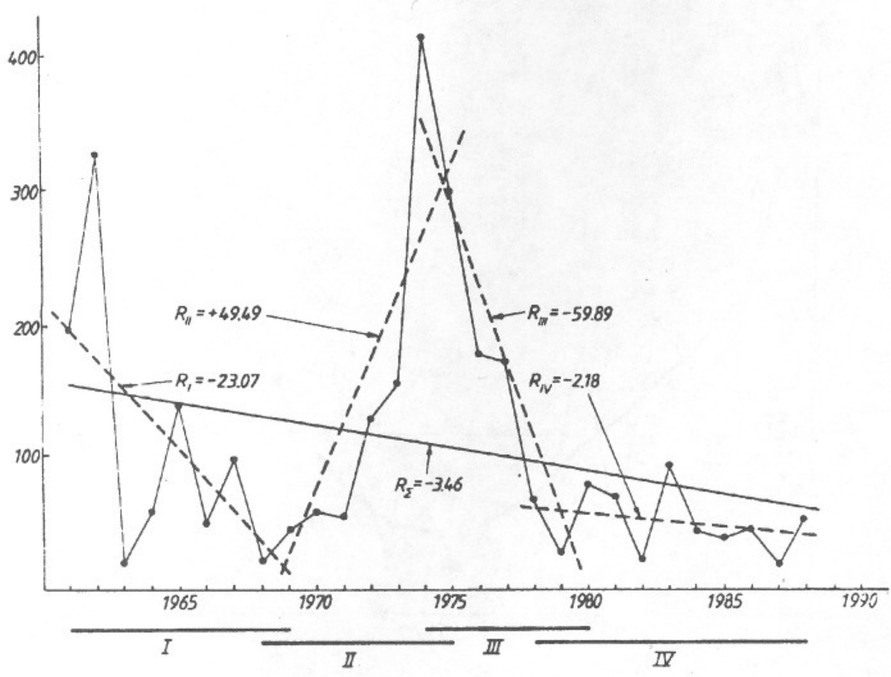

Fig. 10. Comparison of local, few year trends, calculated for four periods (I-IV) and long-term trend of population of Goldcrests (*R. regulus*) migrating through Mierzeja Wiślana station, •–• – raw data, — – long term trend (Σ), --- – local trends for different periods.

Baltic stations, Maksalon (1983) for Song Thrushes passing Ottenby and Falsterbo stations. The case of the Song Thrush is especially apposite as it was shown that migrants through Polish Baltic coast stations include individuals differentiated both by the origin and destination of migration and, moreover, the numerical composition of these migrants is not the same at the stations (Busse and Maksalon 1978, Maksalon 1983). This is a situation when it is impossible to assign described numerical dynamics to any defined area. There is, however, another example, where the numerical dynamics of succesive waves of migrants is clearly differentiated as succesive waves come from separate breeding grounds (Meadow Pipit – Petryna 1976).

These few examples suggest that interpretation of the results of population dynamics studies, based on ringing station data, is very difficult if the migration pattern of the species is not well described.

DISCUSSION OF THE PAPER

H. Noer made a small correction, pointing out that the correlation between migration counts and population counts referred to Denmark, not Sweden.

P. Busse reiterated the point that, nevertheless, even if statistical significance is achieved, the results may not be biologically significant.

L. G. Underhill alerted the audience to the potential pitfalls of cross corelation when dealing with the long-term time series that will arise and noted that it is essential to use common software in the analyses. He suggested that to smooth data it might be better to use running medians than running means.

P. Busse expressed the hope that in the next meeting more attention will be paid to such problems, noting the need for statistical tools for analysing whole processes.

S. R. Baillie asked what weather factors cause large numbers of birds to be caught on small number of days.

P. Busse suggested that peak days are probably incorporated into the mechanism of migration (since similar patterns can be observed year by year).