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Efficiency of two methods for monitoring bird population levels: Breeding bird censuses contra counts of migrating birds

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It has been suggested that counts of migrating birds (visible migration or trapping totals) may serve as a substitute for breeding bird censuses in monitoring population trends. Using data from south Sweden, counts of breeding birds were compared with trapping (ringing) totals and counts of visible migration at bird observatories. Ringing totals showed a much higher between-year variation than breeding bird counts, and counts of visible migration showed a still higher variation. Some correlation between breeding population size and trapping totals was observed in intra-European migrants but not among tropical migrants. In terms of costs a population monitoring programme based on breeding bird counts will be considerably more efficient in detecting trends than a programme using trapping totals. It is supposed that the high variation in the migration counts is caused by weather factors.

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Было установлено, что учеты мигрирующих птиц (визуальные наблюдения миграций или тотальный отлов) должны заменить перепись гнездящихся птиц при мониторинге популяционных тенденций. На основе материалов из южной Швеции, сравнивали результаты учетов гнездящихся птиц с количеством пойманных (окольцованных) и визуальных учетов мигрантов на орнитологических обсерваториях. Тотальное кольцевание выявило более широкие вариации в разные годы, чем учет гнездящихся птиц, а визуальные учеты мигрантов также обнаружили большие колебания. Наблюдалась корреляция между размерами гнездящихся популяций и результатом тотального отлова внутриевропейских мигрантов, но она не установлена у тропических мигрантов. Программа мониторинга, основанная на учетах гнездящихся птиц более эффективна, чем программа, основанная на учетах тотального отлова. Предполагается, что большие колебания в количестве мигрантов вызваны погодными факторами.

1. Introduction

A rapidly increasing demand for knowledge of changes in the size of bird populations is apparent all over the world. One reason for this is the need for primary data in the study of avian population and community dynamics where theory construction has advanced faster than the collection of suitable data for testing the theories. Another reason is that bird communities and bird species populations are assumed to constitute particularly efficient monitors of environmental quality and health. Changes in the abundance of single species or in the dynamic equilibrium of whole communities depend not only upon natural events such as climatic change but also upon different forms of man-induced environmental impacts such as toxic chemicals, over-hunting, disturbance, shortage of food or shelter caused by herbicide application, new forestry or farming policies, and other forms of land exploitation. Lastly, proper formulation and implementation of conservation and management plans depend largely on accurate knowledge of current trends in population levels.

The design of a monitoring programme for such trends involves among other things a choice between different methods for estimating absolute or relative abundances of birds. And such a choice should have the character of a cost and benefit analysis because both man-power and money are in short supply and the sources of variation in nature, concealing true trends, are numerous.

The methodological approach chosen in most countries for monitoring trends in bird population levels has been to operate different kinds of breeding bird census programmes (normally on a sample basis in common birds with a 'diffuse' distribution, and as total counts in colonial breeders and rare species), or counts at the wintering grounds (normally total counts of species that concentrate to a few restricted areas, e.g. ducks, geese, waders). The details of the methods have varied but the general aim has remained the same: a direct estimate of the changes in the number of breeding or wintering birds from one year to another in selected species or – more often – in as many species as feasible. Country-wide programmes for breeding birds are presently active on the British isles (Williamson and Homes 1964, Williamson 1970, Batten and Marchant 1976), in North America (Robbins and Van Velzen 1970, Van Velzen 1972, Erskine 1976), in Sweden (Svensson 1974, 1977), and presumably elsewhere, and for wintering waterfowl in much of West Palearctic (Atkinson-Willes 1969, 1972).

It has been suggested that other indicators than the number of breeding or wintering birds should be used for monitoring population trends. It is trivial that on the average the long-term trends in the size of a population must be paralleled by trends in the number of young produced, the number of individuals taking part in migrations, the number of birds ringed, and other similar

indirect variables causally related to the size of the breeding population.

Ginn (1969) analysed in detail the annual variation of young produced by using ringing totals and nest-record card returns in order to see whether these variations mirrored the fluctuations in population size. Migration counts were discussed by for example Svärdsson (1951) and Edelstam and Ramel (1956). Spofford (1969) analysed the possible connections between the number of birds of prey counted on passage at Hawk Mountains and the size of their recruiting populations. Stolt and Österlöf (1975) used ringing totals mainly based on birds trapped during migration, in an analysis of recent changes of some Swedish migratory species populations.

It seems that most studies provide a rather weak support for the hypothesis that migration counts, whether of visible migration or of birds trapped for ringing, should be able to monitor short-term population changes efficiently. This is not unexpected in the light of the many factors, listed and discussed by Edelstam (1972: 23–28), assumed to affect the number of birds counted on visible migration.

Assuming that a major source of variation in migration counts based on trapping totals is the trapping effort Berthold and Schlenker (1975) announced the launching of a bird population monitoring programme for the working areas of the Vogelwarte Radolfzell and the Vogelwarte Helgoland in Austria and the German Federal Republic, to be based on counts of migrating birds trapped with a strictly standardized system of mist-nets at three localities, the so called MRI-programme.

It seems a priori obvious that the direct estimate of the changes in the breeding populations are to be preferred, and that indirect methods should be chosen only when direct breeding population estimates cannot be made without excessive difficulty or costs. Berthold and Schlenker (1975), however, argue strongly that migration counts will monitor population changes more efficiently than breeding bird censuses. A consequence of this, if it were true, would be that time and money ought to be spent on counting migrating birds instead of performing breeding bird censuses. But Berthold and Schlenker do not provide any conclusive information in support of their statement.

This paper is an effort to investigate whether breeding bird censuses or migration counts are to be preferred for bird population level monitoring. This will be done by comparing the population changes suggested by breeding bird censuses in southern Sweden with changes in the number of birds trapped at bird stations at the coast of southern Sweden.

2. Material and methods

The material used in the analysis consists of trapping totals and counts of visible migration at Falsterbo, Tor-

hamn, and Ottenby bird observatories (locations: 55°23'N, 12°48'E; 56°04'N, 15°50'E; 56°12'N, 16°24'E), ringing totals for the whole of Sweden, and breeding bird census data from Sweden south of about 62°N. The trapping data from Falsterbo and Ottenby were kindly put at my disposal by the boards of these stations. The trapping data from Torhamn were extracted from the annual reports of that station (Möllersten and Tägtström 1971, 1972, 1973, 1974, 1975). The data on visible migration were taken from Edelstam (1972) and Ulfstrand et al. (1974). Ringing totals for Sweden were obtained from Stolt and Österlöf (1975) and the census data from the Swedish Breeding Bird Census (Svensson 1974, 1975b, 1976, and unpubl.).

The period for the analysis had to be restricted to 1969–1975 (shorter in some cases) because data from the breeding bird census were not available for earlier years.

Nineteen species were selected for the study mainly on the basis of the criteria that they should be migratory and be represented with fair numbers both at the bird stations and in the breeding census. Even for the species selected some comparisons could not be made because of too small sample size: a mean of at least 15 birds per year for the period of comparison was set as a minimum limit.

The nineteen species represent different categories in terms of migration habits. In Tab. 1 all species have been listed and divided into groups according to the diel pattern of migratory activity and the location of their winter quarters. Most of them migrate during the night and about half of them go to Africa south of the Sahara, the other half to southern and western Europe.

The counts at Ottenby included the whole migration seasons for the species selected for this study (only a small proportion of *Turdus merula* passed in early spring before the trapping activity began). Trapping was carried out from sunrise to sunset between the following dates: 5 Apr–7 Nov 1970, 16 Mar–28 Nov 1971, 26 Mar–27 Nov 1972, 24 Mar–27 Nov 1973, 27 Mar–9 Nov 1974, and 1 Apr–6 Nov 1975. The counts were divided into a spring and an autumn sample with 30 June/1 July as dividing dates.

The trapping conditions at Ottenby remained almost constant over the period considered here. A few stationary traps of the Heligoland type were operated continuously, and mist-nets were used, their number and location being fairly constant but sometimes modified by wind conditions and the number of birds present in the small lighthouse garden where all trapping was carried out.

At Falsterbo trapping was not carried out over such an extended period every year as at Ottenby and furthermore the time when ringing started and ended varied from year to year. Therefore the totals for two restricted calendar periods were selected for the present analysis instead of the annual totals. These periods were a spring period between 20 April and 31 May and an

Tab. 1. List of species treated in the present study. They are divided into categories according to the location of their winter quarters and their diel migration pattern.

I. Intra-European migrants (winter quarters in western and southwestern Europe and in Africa north of Sahara)	
A. Day migrant:	<i>Fringilla coelebs</i>
B. Day and night migrants:	<i>Prunella modularis</i> <i>Emberiza schoeniclus</i> <i>Turdus iliacus</i>
C. Night migrants:	<i>Troglodytes troglodytes</i> <i>Turdus philomelos</i> <i>Turdus merula</i> <i>Erithacus rubecula</i> <i>Regulus regulus</i>
II. Trans-Sahara migrants (winter quarters in subtropical and tropical Africa)	
A. Day and night migrant:	<i>Anthus trivialis</i>
B. Night migrants:	<i>Phoenicurus phoenicurus</i> <i>Hippolais icterina</i> <i>Sylvia atricapilla</i> <i>Sylvia borin</i> <i>Sylvia communis</i> <i>Sylvia curruca</i> <i>Phylloscopus trochilus</i> <i>Muscicapa striata</i> <i>Lanius colorado</i>

autumn period between 25 August and 25 October. This means that for most species only a part of the migrants actually trapped were included in the samples. Since the timing of migration may have varied somewhat from year to year this truncation of the sample periods may have introduced increased variability into the counts.

At Falsterbo only mist-nets were used. All trapping was performed in a very small area around the lighthouse. The trapping effort was modified in accordance with wind conditions and the number of birds available for catch. Normally birds were trapped from sunrise until there were few or no birds remaining later in the morning.

Torhamn bird station was operated in a more erratic manner. There was no permanent personnel working with ringing except during parts of June, July, and August. Over the rest of the year trapping was carried out only during weekends and in some other periods. Besides, trapping occurred at several localities, the most important ones being the southern point of the Torhamn peninsula and the island of Utklippan. Little standardization was applied.

The data of the Swedish Breeding Bird Census were collected by a territory mapping method identical with the standard recommended by the International Bird Census Committee (Anon. 1970, Oelke 1970, Svensson 1975a) in a large number of sample plots spread over the southern half of Sweden.

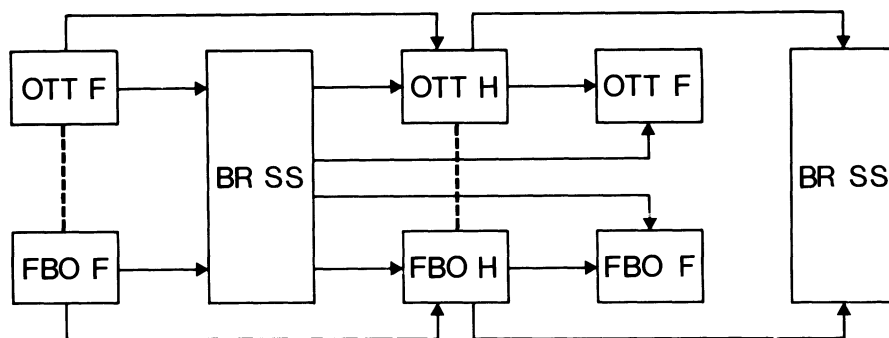


Fig. 1. The fourteen comparisons between migration and breeding population counts studied in this investigation. The diagram covers a period from one spring of a first year to the breeding season of a second year. Ott = Ottenby, Fbo = Falsterbo, Br SS = Breeding population of South Sweden, F = Spring, H = Autumn.

For comparative purposes the original figures (both migration and breeding counts) were recalculated to a common datum: the mean for all years included in each case was set to an index value of 100 and the annual figures were transformed accordingly.

The variation between different years during the period of investigation was expressed by the coefficient of variation. This coefficient was calculated for the trapping totals at the bird stations for spring and autumn separately (except for Torhamn), for the ringing totals of all Sweden, and for the breeding census results. For comparison I also calculated the coefficient of variation for certain counts of visible migration at Ottenby and Falsterbo, though not for the same period as for the other counts (1947–56 at Ottenby, 1949–60 at Falsterbo), and also for both ringing totals and migration counts at three Polish observatories.

It is reasonable to assume that a number of positive correlations should be obtained between different counts since they are causally linked with each other. The most important of these relations are shown in Fig. 1. Each arrow in this diagram goes from one count to another. The one to which the arrow points is expected to depend, at least partly, on the one from which it originates. Also one would expect to find a positive correlation between the counts at the two bird stations (dotted lines without arrows). The strongest positive correlation should be expected to exist between the number of birds trapped in the spring and the breeding population size in the summer following that spring since very little mortality and no reproduction will have occurred in the short intervening period.

To test these assumptions correlation coefficients were calculated for all the fourteen combinations of two different count series indicated in Fig. 1. Throughout the paper 'significance' means significance at the 95% level of probability.

3. Results

3.1. The variation between years

The annual indices of migration at Ottenby and Falsterbo, with spring and autumn values separated, and the annual breeding abundance index for south Sweden are shown for six species in Fig. 2. One can easily observe that the relative variation in the counts at the bird stations are much higher than in the counts of the breeding populations, although the annual sample size is of the same magnitude or even greater in the former.

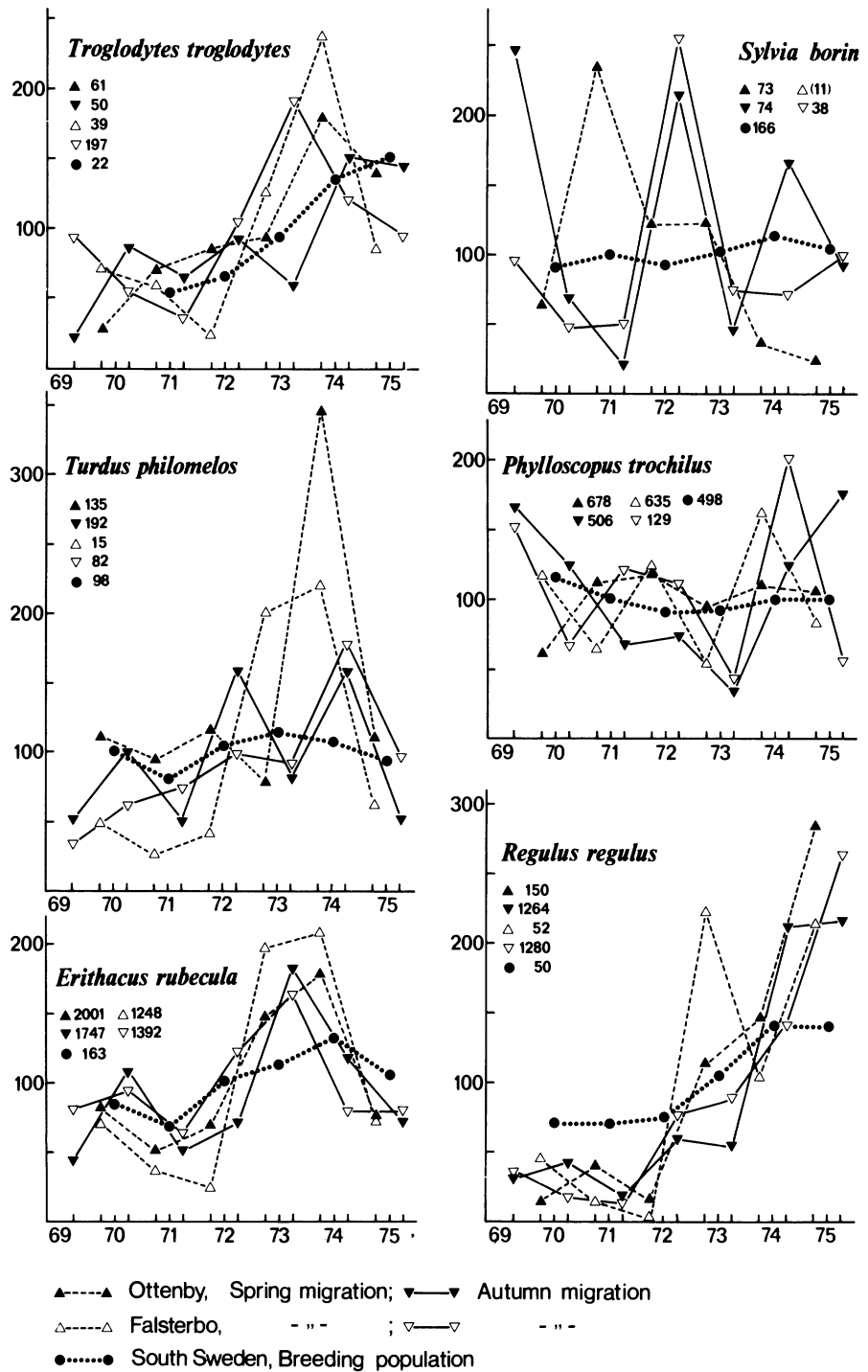
Fig. 3 shows for all species and for all different methods and localities that the coefficient of variation of the breeding bird census totals almost invariably is lower than the corresponding coefficient for the migration counts (trapping and ringing totals). The former coefficients fall mainly below the lower dotted line in the figure, the latter mainly above the same line. The coefficients for the counts of visible migration are still higher, usually to be found above the upper dotted line or around 100%.

For the purpose of facilitating a comparison I have calculated the linear regression lines for trapping and breeding census data separately. The regression parameter estimates are given in Tab. 2. With these estimates I have calculated the expected mean coefficients of variation for three selected levels of sample size. These coefficients are also given in Tab. 2. Three species, *Erithacus rubecula*, *Phylloscopus trochilus*, and *Regulus regulus*, were treated separately because a visual inspection of Fig. 3 suggested that the data points for these species fell above those of other species both for migration and breeding counts.

We can conclude from Tab. 2 that for small sample size there is a fairly small difference between the variability of migration and breeding counts. But when the sample size increases the variation decreases very steeply for the breeding counts but much more slowly for migration counts.

Exactly the same trend is revealed when we inspect Fig. 4 where the results for the three deviating species

Fig. 2. Changes in the number of trapped birds of six species at Ottenby and Falsterbo bird stations and in the breeding population levels in South Sweden. Along the ordinate the relative numbers are given as percentages of the mean for the whole period. Sample size (mean for the whole period) is given with figures for each species. The different symbols are explained in the figure.



are shown. The coefficients of the breeding counts fall in all three species far below those of the migration counts.

3.2. Co-variation between different counts

To obtain a first impression of how the counts with

different methods, in different seasons, and at different localities varied with or against each other we can examine the six species of Fig. 2. In some cases the trend of the breeding population is reflected by the migration counts whereas in other cases no apparent agreement exists.

Correlation coefficients for all fourteen comparisons

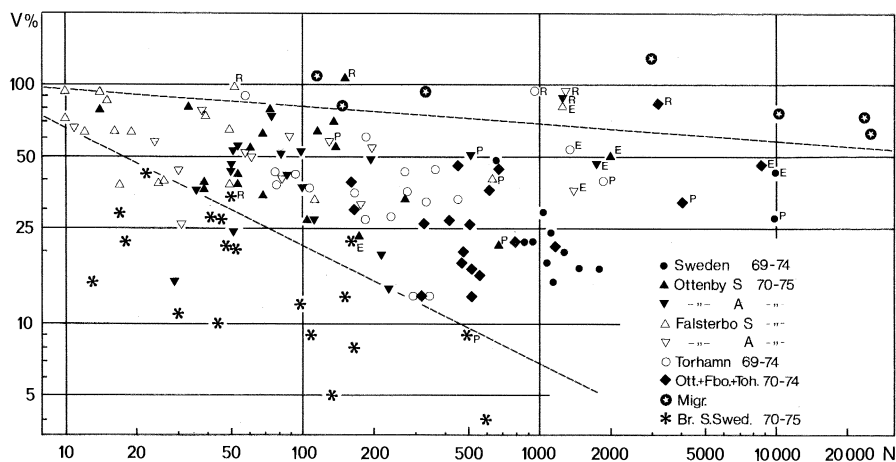


Fig. 3. The coefficient of variation (V %) plotted against annual average sample size (N). The variables included are listed in the figure. S = spring; A = autumn. Migr. = counts of visible migration at the bird stations for *Fringilla coelebs*, *Anthus trivialis*, *Emberiza schoeniclus*, and *Prunella modularis*. Br. S. Swed. = breeding population level of South Sweden. Three species are specially indicated: E = *Erithacus rubecula*, P = *Phylloscopus trochilus*, and R = *Regulus regulus*.

of Fig. 1 are given in Tabs 3 and 4. Tab. 3 indicates that there is a difference between different kinds of species. Species that stay in Europe in the winter are, with one exception, mostly positively correlated, whereas species that migrate to south of the Sahara mostly produce weak correlations or even negative ones. *Fringilla coelebs*, the only true day migrant among the intra-European migrants, is an exception. It is also interesting to note that *Phoenicurus phoenicurus* and *Sylvia atricapilla* have more positive correlations than the other species. These two species are border-cases since

probably even Scandinavian birds may winter north of the Sahara.

Considering particularly the correlation coefficients between the Falsterbo and Ottenby spring counts and the breeding population counts we can see (Tab. 3) that 5 of 15 coefficients are very high and significantly different from zero in the group of intra-European migrants whereas this figure is only one out of 16 in the trans-Sahara group. The average coefficient for the two groups also differ considerably, being clearly positive in the former, and close to zero in the latter.

Tab. 2. Comparison of the between-year variation for the two sampling methods: trapping count and breeding census; and between different trapping stations. The variation is expressed by the coefficient of variation for three selected sample sizes. The regression parameter estimates with which the coefficients of variation were calculated are also given. Equation: $\log V = b \log N + \log A$.

Locality	Sampling method	Coefficient of variation for different sample size (N)			Regression parameter estimates	
		N = 10	100	1000	slope (b)	log (intercept A)
Ottenby, spring	trapping	79	43	23	-0.267	2.165
Ottenby, autumn	trapping	40	37	34	-0.0313	1.627
Falsterbo, spring	trapping	69	45	29	-0.185	2.021
Falsterbo, autumn	trapping	56	48	41	-0.0696	1.817
Ottenby and Falsterbo, autumn and spring	trapping	65	42	27	-0.190	2.000
SBBC	breeding census	31	12	4.3	-0.430	1.924
Ratio Ott + Fbo/SBBC	trapping/census	2	3.5	6		
Mierzeja Wiślana	trapping	97	61	39	-0.197	2.182
Hel	trapping	72	51	36	-0.150	2.009
Bukowo	trapping	83	62	47	-0.124	2.040
All three stations	trapping	81	59	42	-0.140	2.048
<i>E. rubecula</i> and <i>R. regulus</i> , all stations	trapping	132	98	73	-0.127	2.246

Tab. 3. Number of positive and negative correlation coefficients among the fourteen comparisons shown in Fig. 1, and the correlation coefficients obtained between spring migration and breeding population size. The figures in parenthesis are the number of significant coefficients. B = breeding census.

Species	No. of correl. coeff.		Correl. coeff.	
	positive	negative	Ottenby spring/B	Falsterbo spring/B
<i>Troglodytes troglodytes</i>	14 (2)	0	+0.88*	+0.61
<i>Turdus philomelos</i>	8	1	+0.26	—
<i>Turdus iliacus</i>	4 (1)	2	−0.13	—
<i>Turdus merula</i>	8	1	+0.61	+0.74
<i>Erithacus rubecula</i>	14 (4)	0	+0.85*	+0.77
<i>Prunella modularis</i>	10 (1)	3	+0.75	+0.93*
<i>Regulus regulus</i>	14 (10)	0	+0.90*	+0.72
<i>Emberiza schoeniclus</i>	8 (1)	1	+0.94*	—
Total/Average	80 (19)	8	+0.63	+0.75
<i>Fringilla coelebs</i>	2 (1)	12 (2)	−0.36	−0.66
<i>Phoenicurus phoenicurus</i>	10	4	+0.57	−0.16
<i>Hippolais icterina</i>	4 (1)	2	+0.21	—
<i>Sylvia atricapilla</i>	9 (1)	5	+0.47	+0.25
<i>Sylvia borin</i>	3	6	−0.25	—
<i>Sylvia communis</i>	5	4	+0.53	−0.25
<i>Sylvia curruca</i>	4 (1)	5 (1)	+0.08	+0.92*
<i>Phylloscopus trochilus</i>	8	6	−0.79	+0.20
<i>Muscicapa striata</i>	3	6	+0.09	—
<i>Lanius collurio</i>	5 (1)	4	−0.56	+0.13
<i>Anthus trivialis</i>	4	5 (2)	−0.17	—
Total/Average	55 (4)	47 (3)	+0.02	+0.18

Tab. 4 shows largely the same picture. As we could expect *Erithacus rubecula* and *Regulus regulus* almost consistently produce high positive coefficients. The other species in the intra-European group produce lower but still positive values. The trans-Sahara migrants, however, show values close to zero or even negative values.

The expectation that the highest positive correlations should be produced in the comparisons between the spring count at the bird stations and the breeding pop-

ulation count is not met; several of the other comparisons give as high or higher values.

4. Discussion

4.1. The high variation in the migration counts

There are many factors that may disturb the strength of the relationship between changes in population size in a breeding or recruiting area and changes in the number of migrating birds counted at a bird observatory, thus explaining the much higher variation in counts of the latter type. A first provision for a strong positive correlation is that the migrating birds emanate from the population with which it is compared or from a population with the same fluctuation pattern. If this condition is satisfied a good correlation between breeding and migrating numbers can be expected, but only when also the following factors are kept constant: 1) productivity, 2) proportion of the breeding population taking part in the migration (valid for partial migrants), 3) proportion of the migrating birds passing the bird observatory, 4) proportion of the passing birds that interrupt migration and settle down (or in the case of counts of visible migration: fly low enough), thus becoming trappable and possible to count, and 5) proportion of the trappable birds actually trapped (proportion actually seen of those passing within visibility range).

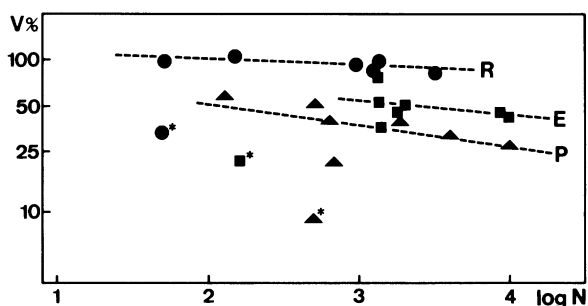


Fig. 4. The coefficient of variation (V) against annual sample size (N) for the three most abundant species *Regulus regulus* (R), *Erithacus rubecula* (E), and *Phylloscopus trochilus* (P). The linear regression lines were: $\log V_R = -0.04 \log N_R + 2.09$, $\log V_E = -0.10 \log N_E + 2.02$, and $\log V_P = -0.14 \log N_P + 1.99$. The regression calculations did not include the data points for the breeding populations (the asterisks).

Tab. 4. Correlation coefficients for the fourteen pair-wise comparisons indicated in fig. 1. Only coefficients based on a sample size of 15 or more birds per year were included. E.r. = *Erithacus rubecula*, R.r. = *Regulus regulus*, Ott = Ottenby, Fbo = Falsterbo, S = Spring, A = Autumn, NS = Next spring, BBC = Breeding bird census, D.f. = degrees of freedom. No. of species with positive and negative coefficients within parenthesis.

Samples compared	D.f.	Intra-European migrants			Trans-Sahara migrants
		E.r.	R.r.	Other species	
Ott S/Fbo S	4	0.97	0.82	0.19 (3+ 1-)	0.10 (4+ 2-)
Ott A/Fbo A	5	0.76	0.90	0.26 (4+ 1-)	0.24 (5+ 1-)
Ott S/BBC	4	0.85	0.90	0.42 (5+ 2-)	0.02 (6+ 4-)
BBC/Ott A	4	0.53	0.94	0.38 (6+ 1-)	-0.02 (5+ 5-)
Ott S/Ott A	4	0.76	0.85	0.36 (5+ 2-)	0.07 (4+ 6-)
Ott A/Ott NS	4	0.52	0.92	0.11 (4+ 3-)	-0.15 (5+ 5-)
Ott A/BBC N	4	0.51	0.68	0.11 (5+ 2-)	0.30 (7+ 3-)
Fbo S/BBC	4	0.77	0.72	0.40 (3+ 1-)	0.18 (4+ 2-)
BBC/Fbo A	4	0.33	0.88	0.01 (2+ 3-)	-0.28 (0+ 6-)
Fbo S/Fbo A	4	0.37	0.70	0.02 (2+ 1-)	+0.00 (2+ 1-)
Fbo A/Fbo NS	4	0.90	0.87	0.64 (3+ 0-)	-0.33 (0+ 3-)
Fbo A/BBC N	4	0.64	0.92	0.27 (4+ 1-)	-0.03 (3+ 3-)
BBC/Ott NS	3	0.36	0.95	0.31 (6+ 1-)	-0.01 (6+ 4-)
BBC/Fbo NS	3	0.47	0.58	0.06 (2+ 2-)	0.19 (4+ 2-)

Productivity. It is well known that productivity may vary from year to year. Among passerines such variation may have considerable effects on the number of birds leaving a breeding area since the number of young produced in a season is rather high. The autumn populations of our common passerines are generally from two to three times higher than the breeding populations. Therefore changes in productivity can be expected to be of some importance as a source of variation in autumn counts. On the other hand migrating birds are recruited from vast areas and it is perhaps not very probable that failure or unusual success will occur simultaneously over the whole recruiting region. Regrettably little is known about temporal synchronization of the geographical variation of breeding success, i.e. whether ups and downs in breeding success occur simultaneously over vast areas or not, and therefore it is not possible to determine positively that variation in productivity is a significant factor. So much can be concluded from general knowledge of population dynamics, however, that for evaluating long-term trends in population size variation in productivity cannot introduce any serious bias.

Partial migration. Some species are only partially migratory. Among the species treated in this paper this is valid for the Swedish populations of *Regulus regulus* and *Turdus merula*. Especially the former stays in south Sweden over the winter in considerable numbers. On the European continent or on the British isles quite a number of species show this pattern. For such species it is obvious that weather, food conditions, and population density may cause a variable proportion of the autumn population to leave the country, thus increasing the variation of the migration counts very much. If there are long-term cycles or trends of climate change the proportion of migrants in a population may change accordingly, introducing a systematic error in a count.

Migration routes. The proportion of the migrating birds that pass a bird observatory is affected by changes in the migration routes. Visual observations as well as recovery data have shown that migrating birds may travel along quite different routes in different years. Most famous in this respect are perhaps some arctic waders, particularly the *Calidris* species. In some years they appear in great numbers at for example Ottenby whereas they may be almost absent another year (Edelstam 1972). Recoveries of *Calidris alpina* have shown that birds of this species may use several alternative routes: they may travel along the south Baltic coast, cross the Baltic via Öland and southernmost Sweden, or travel along the Arctic and Atlantic coasts (Svårdson 1952, Jenning 1954, Danielsson 1956). An increase of *Branta leucopsis* at Ottenby has been interpreted as an effect of a migration route shift after a change of resting grounds from Scania to the island of Gotland (Edelstam 1972), although in the light of new evidence on population increase in this species that interpretation may be questioned (Hjort 1976). Radar studies have also revealed similar large scale shifts in migration routes for species of several taxa, though most of them may be of short duration (see e.g. Bergman and Donner 1964, Hjort and Alerstam 1976).

Since migration routes in the strict sense (traditional flyways) probably are rare among species of the kind we are dealing with in this paper (most of them are broad-front migrants, particularly those flying in the night) changes of migration routes are not necessarily always of the same major importance as a source of variation as it is in species migrating along narrow flyways or corridors. Note, however, that Busse (1973a) argues that different populations of small passerines do migrate along narrow, discrete corridors, an interpretation of his data that I consider erroneous.

The day-migrating species are, however, affected by topographical features of the landscape, and may concentrate to places like Ottenby and Falsterbo. Even if this leading line effect does not in itself increase variability (on the contrary, if exactly the same leading lines were followed every year they would decrease variability) it may increase the sensitivity to other factors, primarily to the wind. The effects of wind strength and direction on the course of bird migration have been extensively studied (a recent review in Alerstam 1976), and it is beyond any doubt that the effects of the wind can be strong, causing whole cohorts of birds to travel along routes that they would not have chosen under other winds (cf. also Rudebeck 1950); even a small shift of a migration path in relation to a leading line (e.g. a coast) might cause the birds to pass beyond the range of the observer or the catchment area of a trapping station.

It is becoming appreciated that birds migrate in large numbers only during a small number of days or nights out of the many possible during the period of migratory readiness (Rudebeck 1950, Edelstam 1972, Ulfstrand et al. 1974) because, not too surprisingly, only certain weather types are favourable for migration. This means that the system is very sensitive. One single night or day with peak migration but with some wind-drift or a direction-shift caused by some other factor could then cause the total count for that season to be very heavily affected. I believe that differences in the weather conditions between years are of utmost importance in causing high variability in migration counts.

Numbers resting and feeding in vegetation. As important for the accuracy of a migration count as the stability of the migration routes or the gross migration pattern is the proportion of the migrating birds that descends to the ground level and begins to move in the vegetation. Only that proportion can be trapped.

It is well-known among ringers at bird stations that during the migration periods birds may be extremely abundant certain mornings but almost absent other mornings. This is of course partly an effect of the erratic pattern of migration discussed above: Birds can be common of ground level only when they are common in the air. After a night with heavy migration one would expect the terrain below to harbour a lot of birds and the same would be expected for a day-migrant after the morning travel activity has faded. But it is not that simple when it comes to understanding more precisely whether birds will be abundant just at the trapping site or elsewhere. Many local factors may determine this: weather, especially fog belts, and presence or absence of suitable feeding-sites and shelter.

So far I have assumed that the vegetational conditions at the trapping site remained constant from year to year. This is rarely the case, and this fact was one of the reasons why Berthold and Schlenker (1975) so strongly stressed the importance of keeping the vegetation unchanged along the mistnet lines in their MRI-program. I

do not think, however, that vegetational changes have been of significant importance for the counts made at Falsterbo and Ottenby, since, even if there have been some long-term changes, there have been no drastic changes from year to year of the order of size of the annual fluctuations in the trapping totals.

The proportion of birds potentially available that are actually trapped is also determined by the trapping strategy: kind of traps, location of traps, when and for how long they are in operation, trapping method (active or passive), and quality and number of personnel. I will not dwell long on these factors: they can all be standardized if desirable. On the contrary, I will argue that at certain localities and under certain conditions it is not desirable to enforce complete standardization. At localities such as Ottenby and Falsterbo where all trapping is carried out in small gardens and bush areas surrounded by more or less extensive areas of open grassland or sea a very high proportion of the birds available is actually trapped. This is shown by a successively higher proportion of birds already ringed as the hours pass. Those days it would not help to standardize the trapping system any further. But of course it is not always like this. Some mornings it seems to be a considerable movement going on. Birds that arrived early in the morning leave the trapping site rapidly. Such days the number of birds trapped would be affected by the trapping effort. Actually, under such conditions standardization of the trapping effort could lead to a smaller proportion of the birds being trapped than under other conditions. Hence it seems even preferable to be able to vary the trapping effort with the number of birds in order to keep the trapping ratio constant. But this problem is probably less prominent at an inland locality than at a coastal plot or on an island.

Finally it is necessary to distinguish between the increased variability caused by random fluctuations in the above sources of variation and systematic trends in the mean count caused by continuous shifts in the same variables. Thus, long-term weather cycles or slow changes in the vegetation around a trapping site may cause trends in the mean count of birds that are erroneously interpreted as population size trends.

4.2. The generality of the results

Three different methods for obtaining estimates of population change are considered in this paper: Counts of breeding populations, migrating birds by trapping, and visible migration. It is important to know if the data obtained in southern Sweden for the breeding population changes are representative for equivalent species in other geographical areas and if the counts of migrating birds at bird stations in the same area are representative for bird stations in general.

The first method can be tested by comparing the Swedish data with those given by Batten and Marchant (1976) for Britain. I have extracted from their table VII

the population level indices from 1969–74 for the species treated in the present study. It was found that the coefficients of variation fell close to or well below the lower dotted line in Fig. 3, thus indicating that the variation between years is the same in Britain as in Sweden. Only *Troglodytes troglodytes* and *Regulus regulus* fell appreciably above, because they increased enormously during the period 1969–74, giving the variation estimate a strong systematic component.

The second method can be tested by using trapping data from other stations. Such data are, however, rather scarce since most stations have not applied a standardized trapping effort over many years.

Vauk and Hornberger (1972) and Vauk and Schröder (1972) have presented migration data from Heligoland where trapping occurred with almost the same method and intensity over the period of study. *Sylvia communis* produced a coefficient of variation of 51% in spring ($n = 195$ birds per year) and 118% in autumn ($n = 287$ birds) in the period of 1958–1969. *Phoenicurus phoenicurus* gave a coefficient of variation of 49% in spring ($n = 363$) and 78% in autumn ($n = 471$) for the years 1958–68. Winkler (1974) gave in a diagram the number of *Fringilla coelebs* trapped in 1957–1972 at Col de Bretolet. Excluding the totals for 1957 and 1967 (years with incomplete trapping seasons) the coefficient of variation was 53% ($n = 5600$).

The most extensive data have been produced in the 'Operation Baltic' (Busse 1973a), summarized in his table 1 (for details see also Busse 1973b). The coefficients of variation of Busse's data are given in Tab. 2.

In spite of the fact that the available information is scanty and the trapping strategies have not always been fully standardized it seems that my conjecture that the c.v.-values from the Swedish bird stations are typical for variability in trapping totals has not been refuted, in fact not even weakened.

The third method, counts of visible migration, is not of major importance in this study, but I have referred to it several times and I have also included data for four species in Fig. 3. Therefore, I also plotted the coefficient of variation against the annual mean total for a greater number of species at four stations (Falsterbo and Ottenby in contrast with Bukowo and Hel on the Polish coast of the Baltic) (Fig. 5). When the annual count was less than about 1000 birds the coefficient of variation was normally above 100% and not even with very large annual samples did the c.v. decline below about 50%. The situation was the same for all four stations.

It seems in fact that a coefficient of variation of about 50% is a minimum value that only exceptionally can be improved in counts of visible migration. All the species included in the comparison of the four stations are small or medium sized passerines (the filled symbols in Fig. 5). To test whether the same high variability occurs also in larger and more longlived birds some birds of prey were also included in Fig. 5. We can see that their variability is smaller than that of the passerine species or

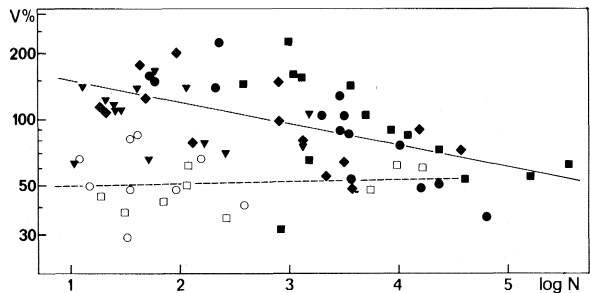


Fig. 5. Variation between years in counts of visible autumn migration. The coefficient of variation (V %) has been plotted against the average annual number of migrants counted (N). Data from four localities have been compared: Bukowo (◆), 9 years, Hel (▼), 8 years, Ottenby (●), 10 years, and Falsterbo (■, □), 11 years. The filled symbols refer to 14 passerines observed almost annually at all four stations: *Anthus trivialis*, *Alauda arvensis*, *Carduelis chloris*, *Loxia* sp., *Parus caeruleus*, *Fringilla coelebs* (incl. *F. montifringilla* at Falsterbo), *Sturnus vulgaris*, *Emberiza citrinella*, *Carduelis cannabina*, *C. spinus*, *Turdus pilaris*, *Parus major*, *Anthus pratensis*, *Motacilla alba*. The open symbols refer to 9 birds of prey: *Buteo buteo*, *B. lagopus*, *Accipiter nisus*, *Pernis apivorus*, *Circus aeruginosus*, *Pandion haliaetus*, *Falco subbuteo*, *Falco columbarius*, *Falco tinnunculus*. The slope of the regression line for the fourteen passerines was -0.08 at the two Polish stations combined and -0.21 and -0.13 at Ottenby and Falsterbo. The regression line in the figure for all passerine data combined has a slope of -0.09 and the line for the birds of prey a slope of $+0.01$.

about 50% for counts of less than 1000 birds (passerines above 100%). In contrast to the passerines, however, the coefficient of variation does not improve with increasing number of birds in the annual count. It is still about 50% for the species passing Falsterbo in numbers of about 10000 birds every autumn.

I propose that the observed facts can be explained by assuming that there is a fundamental variation of about 50% caused mainly by weather influences inherent in a migration count, and that this variation is independent of the degree of standardization (in fact the degree of standardization has been high or fairly high at all four stations).

In concluding the comparisons of the Swedish data with data from other areas and stations evidence is in support of the view that my estimates of variation are typical and ought to provide a satisfactory basis for rough predictions also elsewhere.

4.3. A comparative cost-benefit analysis of different methods

Knowing the residual variance of the regression of the annual count on time it is easy to calculate the number of years for which counts must be made before any specified linear trend can be detected with any desired confidence.

Assuming a desired confidence level of 95%, Tab. 5 gives the smallest number of years that has to elapse before a trend with a slope steeper than each of four

Tab. 5. Number of years during which counts must be made before a linear trend can be established with 95% confidence. A comparison between trapping counts at bird stations and censuses of breeding birds.

A. Relation between residual variation and slope of trend line							
Slope %	Variation: residual standard deviation in per cent						
	100	50	40	30	20	10	5
10	18	12	11	9	7	6	4
5	28	18	16	13	11	7	6
2	>40	32	28	23	18	12	8
1	>40	>40	>40	36	28	18	12

B. Comparison between breeding census, trapping count and visible count for some typical levels of variation							
Type of count	Slope of trend line	Approximate no of birds in sample					
		50	50–200	200–1000	1000		
Census of breeding birds	C.V.	20	10	5	–		
	10	17	6	4			
	5	11	7	6			
	2	18	12	8			
	1	28	18	12			
Trapping count	C.V.	60	40	30	20		
	10	14	11	9	7		
	5	20	16	13	11		
	2	>40	28	23	18		
	1	>40	>40	36	28		
Visible count	C.V.	–	100	100	100		
	10		18	18	18		
	5		28	28	28		
	2–1		>40	>40	>40		

selected levels (10, 5, 2, and 1% a year) under seven different levels of residual variation (coefficients of variation: 5, 10, 20, 30, 40, 50, and 100%).

It can be seen that rather weak trends can be detected within few years if the coefficient of variation is in the region of 5% or lower, but that very many years are required if the coefficient of variation appreciably exceeds 10%.

It can also be seen that with the same number of birds counted per year one needs more than twice as many years for detecting the same trend with trapping counts at bird stations as with breeding bird censuses with the territory mapping technique. The situation is still worse when counts of visible migration are to be used for monitoring purposes.

We can apply this theoretical information on the data of Fig. 3 using the coefficients of variation as approximations of the residual variance of the regressions. To

do so is fairly correct for those cases that do not show any trends but will overestimate the number of years required in those cases where a trend is apparent, such as for *Regulus regulus* and *Erithacus rubecula*. For comparisons between different levels of variance the procedure gives, however, sufficient accuracy.

For the same sample size we can see that approximately twice as many years are required before we can detect a trend of a certain slope if we use trapping counts compared with breeding bird censuses. For example, the coefficient of variation is about 10 and 40% for breeding and trapping counts, respectively, with sample size in the region of 50–200 individuals in the annual count. This gives 12 and 28 years for a 2% slope and 7 and 16 years for a 5% slope. In the sample size region of 200–1000 individuals typical coefficients of variation were about 5 and 30%. There we get 8 and 23 years at the 2% slope of the regression line for census and trapping counts.

Thus, in terms of 'alertness', an early warning system based on counts of breeding birds would be better and more than twice as fast as a similar system based on migration counts, depending on, as we have seen, the higher variability between the annual counts in the latter measure.

Another way of looking at the problem of sample size (in this case the number of years) required to determine a certain change with a specified significance is to consider a situation when a bird population level suddenly falls, e.g. in the way the *Sylvia communis* population did in Britain from 1968 to 1969 (Winstanley et al. 1974, Batten and Marchant 1976).

Beginning with the expression of Student's *t* for the difference between two means

$$t(n_1+n_2-2) = \frac{(m_1-m_2) - (M_1-M_2)}{s \sqrt{\frac{1}{n_1} + \frac{1}{n_2}}}$$

we assume that the population means (M_1 and M_2) are equal, $n_1 = n_2 = n$, i.e. we compare the same number of years before and after a change, and $s_1 = s_2 = s$. That will give us

$$t(2n-2) = \frac{(m_1-m_2)}{s \sqrt{2/n}}$$

After putting $m_1-m_2 = d$, a rearrangement gives

$$n = 2 (ts/d)^2.$$

When n is not too small t is approximately 2 for the 95% level of significance, and we use this value. We obtain

$$n = 8 (s/d)^2.$$

Here s is most easily expressed as the coefficient of variation and d as percentage difference between the two means.

For example, when the annual count is about 100 individuals a typical coefficient of variation is 10% in a

Tab. 6. The sample size (number of years with counts) that are required both before and after a sudden change in population level in order to determine that change with 95% probability, with different levels of residual variance in the counts and different levels of change. The variation is assumed to be the same before and after the change.

Coefficient of variation per cent	Per cent change in the mean count				
	5	10	25	50	100
5	8	2	1	1	1
10	32	8	2	1	1
25	200	50	8	2	1
50	800	200	32	8	2
100	3200	800	128	32	8

breeding census and 40% in a trapping count. If we assume that we would like to be able to determine with 95% probability a change in numbers of 25% we need at least $n = 8 (10/25)^2 = 2$ years both before and after the change in a breeding bird census and $n = 8 (40/25)^2 = 21$ years in a trapping count.

Tab. 6 gives some examples for selected levels of variation and change. We can see that if the change is greater than 25% and the coefficient of variation of the count is smaller than 25% we have a good chance of detecting the change very rapidly.

For eight selected species observed coefficients of

Tab. 7. The smallest change detectable and the smallest number of years required for detection of specified changes with the two sampling methods: the trapping count at bird stations and the censuses of breeding populations. Eight species were selected. The coefficients of variation from the trapping counts are the mean coefficients for the four bird station counts (Ottenby spring and autumn, Falsterbo spring and autumn). N is the average number of birds on which the C.V.-value is based. 95% significance was used in all calculations. T = Trapping count, C = Census of breeding birds.

Species	Trapping method		Census method		Smallest detectable change between two 5-year periods			Least no. of years required, both before and after, for detection of a change of					
	C.V. %	N	C.V. %	N				25%		50%		100%	
					T	C	T/C ratio	T	C	T	C	T	C
<i>Turdus philomelos</i>	53	136	12	98	67	15	4.5	36	2	9	1	3	1
<i>Phoenicurus phoenicurus</i>	29	193	15	13	37	19	1.9	11	3	3	1	1	1
<i>Erithacus rubecula</i>	54	1597	22	163	68	29	2.3	37	7	10	2	3	1
<i>Sylvia borin</i>	77	62	8	166	97	10	9.7	76	1	19	1	5	1
<i>Phylloscopus trochilus</i>	43	487	9	498	54	11	4.9	24	2	6	1	2	1
<i>Regulus regulus</i>	97	687	34	50	123	43	2.9	121	15	31	4	8	1
<i>Prunella modularis</i>	51	53	21	52	65	27	2.4	34	6	9	2	3	1
<i>Anthus trivialis</i>	55	57	5	132	70	6	11.7	39	1	10	1	3	1

Tab. 8. Comparison of the costs for the acquisition of data with different sampling methods. SBCC = Swedish breeding bird census, SWBC = Swedish winter bird census.

Method and programme	Amount of work, personnel	No. of man-days	No. of birds per year	No. of birds per man-day
<i>Trapping</i>				
MRI-programme	30.6.–6.11., 130 days, 3 × 3 pers.	1170	20.000	17
Ottenby ¹	15.4.–15.11., 210 days, 2 pers.	510	16.000	31
	1.7.–30.9., 90 days, 1 pers.			
Falsterbo ¹	1.4.–31.5., 1.7.–31.10., 180 days, 1 p.	300	13.000	44
	1.7.–31.8., 60 days, 2 pers.			
<i>Territory mapping²</i>				
Farmland, 2 terr./ha	3 min./ha, 8 visits + 1 day	9	240	27
Woodland, 5 terr./ha	6 min./ha, 10 visits + 1 day	11	300	27
Woodland, 12 terr./ha	12 min./ha, 10 visits + 1 day	11	360	33
<i>Point sampling</i>				
SBCC 1975	86 routes, 0.5 day each, 1 pers.	43	28.700	667
SWBC 1974/75 & 75/76	576 routes, 0.5 day each, 1 pers.	288	230.600	800
<i>Visible migration count</i>				
Ottenby 1947–56	1.6.–31.10., 1 person	150	282.700	1900
Falsterbo 1949–60	about 1.7.–15.11, 1 pers.	140	1.000.000	7000

1. The first line for Ottenby and Falsterbo refers to trapping of small passerines, the second to trapping of waders.

2. I have assumed 6 h of work per day and 1 h for travelling. The extra day is added for preparatory work. The figure for 'no. of birds per year' refers to a plot covered in 6 h.

variation have been used to calculate the smallest detectable change between two five year periods and the smallest number of years required for detecting changes of 25, 50 and 100%. The results are given in Tab. 7.

The smallest detectable change between two five year periods was found to be on the average for the eight species five times greater for the trapping than for the breeding census method, for most of the species 2–4 times greater. The smallest number of years required was also much greater with the trapping method than with the breeding census method.

4.4. Costs of data collection

To complete the analysis of the pros and cons in using the different methods for determining population level changes it now only remains to estimate the costs of collecting the data. These costs can be estimated very accurately since we know the number of observers required, the number of hours they work, and the number of birds they will count or catch. A summary is found in Tab. 8.

The following procedures were used in calculating the time cost estimates. For the MRI-programme I used the figures given by Berthold and Schlenker (1975). The estimate for Ottenby is based on the assumption that the Heligoland traps and the mistnets for trapping small passerines were operated 6 hours a day during 7 months, that the wader traps were operated during 3 months (July–September) on a whole day schedule (16 hours a day on the average). I have further assumed a personnel of 2 persons for the nets and wader traps in the morning hours and 1 person for the wader traps during the rest of the day. The estimate for Falsterbo is based on the data provided by Roos (1977).

The time costs for carrying out a territory mapping census were calculated in the following way for three different levels of density of birds: 1) a simple plot, for example a farmland plot with a bird density of 20 pairs per 10 ha, 2) an average woodland plot with a density of 50 territories per 10 ha, and 3) a difficult plot with a high density of 120 pairs per 10 ha. In each case I allowed one hour per visit for travelling from and to the plot. A man-day was assumed to consist of this hour and six hours of census work. An extra day was added to cover the costs of preparing the plot.

The estimates for the point sampling method are the precise data obtained in actual work (Svensson 1976, Källander and Svensson 1975, Källander et al. 1976, 1977) in the same region as the territory mapping censuses were made.

The data for visible migration counts were obtained from Edelstam (1972) for Ottenby and from Ulfstrand et al. (1974) for Falsterbo.

Averaging the figures for the three trapping programmes we find that about 31 birds were trapped per man-day. Doing the same for the three levels of bird

density using the mapping census we obtain a figure, 29 pairs, that is almost the same. We can conclude that it will take the same amount of time to trap a bird at a bird station as to map the territory of a male with the mapping technique. Thus the coefficients of variation and the calculations of the relations between alertness in trend detection are directly comparable in the two methods.

The point sampling method is much more efficient in terms of sample size collected per unit time. So far I know too little about the variability between years in this method to be able to evaluate its merits fully.

Counts of visible migration are very efficient in terms of sampling speed. However, since it seems impossible to obtain coefficients of variation better than about 50% even with very large samples, it does not help. The method remains of low efficiency for monitoring purposes.

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