Population trends in Baltic passerine migrants, elucidated by a combination of ringing data and point- and summer-count indices

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(Med et dansk resumé: Ændringer i bestandsstørrelserne af trækkende spurvefugle i Østersøområdet, belyst gennem ringmærkning på Christiansø og punkt- og sommertællinger i Danmark, Sverige og Finland)

Introduction

The small Danish island Christiansø, near Bornholm in the Baltic Sea (Fig. 1), is visited by large numbers of passerine migrants during both spring and autumn. From 1976 to 1997, the *Danish National Forest and Nature Agency* operated a bird ringing station on the island with the purpose of using ringing figures as a way of monitoring the Baltic populations of migrant passerines (Rabøl 1999). The results were summarised in yearly, comprehensive reports (Lyngs & Faldborg 1984, Lyngs et al. 1990).

An analysis of five passerine migrants implied that the numbers of migrants ringed on Christiansø reliably reflected the true size of the populations passing through the area, when corrected for trapping effort (Rabøl & Lyngs 1988). In this paper, we present an analysis of 29 ringed migrant passerine species from 1976 through 1996. The aims are to describe the time-trends in these species and to test whether the species' populations were unchanged, increasing or declining during the period considered, and whether there are common time-trends over all species or suites of species within defined migratory categories. These topics have received much attention (e.g., Berthold et al,. 1986, 1993, Askins et al. 1990, Baillie et al. 1992, Böhning-Gaese 1992, Terborgh 1992, Greenwood et al. 1993, 1995, Rappole & McDonald 1994, Kirk et al. 1997) owing to public concern that populations of migratory bird species decline and bird communities deteriorate.

Population indices based on caught birds during their spring and autumn migration close to the breeding ground provide information on population sizes for two fixed points of the species' yearly life-cycle: one immediately before breeding, and one immediately after leaving the breeding or post-fledgling areas (Fig. 2). If an unbiased index of the population size is known in these stages, it provides great potential to detect in which stage(s) density-dependent regulation of migrating passerines might occur (breeding grounds or winter quarter). Thus, despite the limitations of population indices based on migratory ringing and counts, they are valuable means of gathering new information on population sizes and changes not otherwise available from traditional point counts or

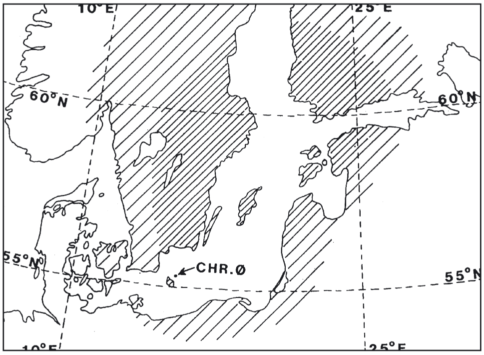

Fig. 1. The major breeding grounds of the migrants passing Christiansø (CHR.Ø) in the Baltic Sea. Degrees of shading indicate generalised densities in the origins of birds caught on Christiansø.
De vigtigste yngleområder for de trækfugle, der raster på Christiansø.

breeding-ground surveys. We hope that the results presented in this paper may inspire others to continue to explore the enormous amounts of migratory data gathered for decades, especially in Europe and North America. However, if migratory data are to be relied on in analyses of population changes and its potential causes, standardised catches of birds on migration must provide reliable indices of the sizes of the populations passing the field station, and the birds in the autumn and spring indices must belong to the same breeding areas. Both aspects are evaluated and discussed in this paper.

Materials and methods

Species involved and migratory categories

The 29 most numerous and regular migrant passerine species ringed on Christiansø (Fig. 1) were divided into three major, migratory categories: short- and medium-distance migrants (9 species), long-distance migrants to sub-Saharan Africa (18), and long-distance migrants to India (2) (Zink 1973, 1975, 1981, 1985, Zink & Barlein 1995, J.J. Madsen 1994, 1995, pers. comm.).

The short- and medium-distance migrants include Wren *Troglodytes troglodytes*, Blackbird *Turdus merula*, and Goldcrest *Regulus regulus* that winter in Germany, Benelux, the British Isles, and France, and Dunnock *Prunella modularis*, Robin *Erithacus rubecula*, Song Thrush *Turdus philomelos*, Redwing *Turdus iliacus*, Chiffchaff *Phylloscopus collybita*, and Reed Bunting *Emberiza schoeniclus* that mainly winter in the southwestern Mediterranean region from southern France to Morocco and Algeria, with the Redwing wintering somewhat more easterly.

The long-distance migrants to sub-Saharan Africa comprise three different groups. 1) the "southwestern migrants" include Redstart *Phoenicurus phoenicurus*, Whinchat *Saxicola rubetra*, Grasshopper Warbler *Locustella naevia*, Reed Warbler *Acrocephalus scirpaceus*, Whitethroat *Sylvia communis*, and Pied Flycatcher *Ficedula hypoleuca*. All have autumn migratory routes that mainly pass west of Italy and winter quarters in western, tropical Africa. In the spring, migration routes are more directly towards the breeding grounds. 2) The "southern migrants" include Tree Pipit *Anthus trivialis*, Sedge Warbler *Acrocephalus schoenobaenus*, Icterine Warbler *Hippolais icterina*, Garden Warbler *Sylvia borin*, Wood Warbler *Phylloscopus sibilatrix*, and Spotted Flycatcher *Muscicapa striata*. All have autumn migratory routes that pass over the central and western Mediterranean Sea to winter quarters in central and southern tropical Africa. 3) The "southeastern migrants" include Thrush Nightingale *Luscinia luscinia*, Marsh Warbler *Acrocephalus palustris*, Lesser Whitethroat *Sylvia curruca*, Blackcap *Sylvia atricapilla*, Willow Warbler *Phylloscopus trochilus*, and Red-backed Shrike *Lanius collurio*. All have autumn migratory routes over Balkan towards Egypt, and they winter in eastern tropical Africa; in spring, they may migrate by a more eastern route over the eastern Mediterranean.

The group of long-distance migrants to India includes Red-breasted Flycatcher *Ficedula parva* and Scarlet Rosefinch *Carpodacus erythrinus*. Migrants trapped on Christiansø have probably overshot their breeding areas in the eastern Baltic in spring or, in autumn, are on reverse migration from that region.

The population indices

Analyses were based on comparisons of the numbers of ringed birds of the 29 migrant species that were captured on Christiansø and ringed from 15 March to 15 June and from 1 August to 15 November in the years 1976-1996. The daily numbers of ringed birds of each species were corrected for trapping effort (i.e., net-metre-hours) and summed to RS for spring and RA for autumn. Indices were calculated corresponding to the average numbers caught in 60 metres of net during the first five morning hours. All ringed birds were – when possible – aged and sexed (for further details, see Rabøl & Lyngs 1988). RS and RA are supposed to track the (unknown) population densities in a significant positive way, i.e., they were considered reliable indices of the "Baltic" population densities spring and autumn. Through ringing recoveries, we know the breeding areas, migratory routes and wintering areas of most species passing Christiansø each spring and autumn reasonably well (Fig. 1, based on data in Lyngs et al. 1990, J. J. Madsen pers. comm.).

We compared RS and RA with the Danish (DK) and Swedish (SW) point counts and the Finnish (SF) point/summer-count indices for the period 1976-1993, where we have data available for *all* five indices (data obtained from Jacobsen 1994, Svensson 1994, R.A. Väisänen in litt.). Traditionally, point- and summer-count indices are supposed to track the breeding populations of the species and countries in consideration. Thus, we should expect positive and mostly significant correlations between these three indices if the migratory routes and wintering areas are more or less identical, and if the summer weather in the different regions in a given year is about the same, assuming a correlation between summer weather and breeding success and survival of fledglings.

In general, we should also expect an overall positive correlation between the point- and summer-count indices and RA and especially RS. However, and especially at single species level, the influence of weather on the numbers of birds descending to Christiansø may significantly differ between years. Furthermore, the age distributions of caught migrants in both spring and autumn do not truly mirror those of the passing populations (Fig. 2) or – more importantly – the age distribution of birds detected in point and summer counts, which are probably biased towards (breeding and non-breeding) singing males (see, e.g., V. Madsen 1994). Summer/point counts and ringing of migrants also yield different age distributions because of the different seasons in which they take place. Thus, the migration and breeding season indices track somewhat different parts of the same population (Fig. 2). Nevertheless, the overlap and coupling should be high between the age categories recorded with RS and RA and the point- and summer-count indices.

Hence, correlations for individual species are unlikely to be very close within and between RS and RA and the three point- and summer-count indices. Neither can significant correlations be expected between different indices of a population otherwise considered stable. Significant positive correlations between the indices should only be expected in populations with significant time-trends such as declines, increases, cycles, or modal developments.

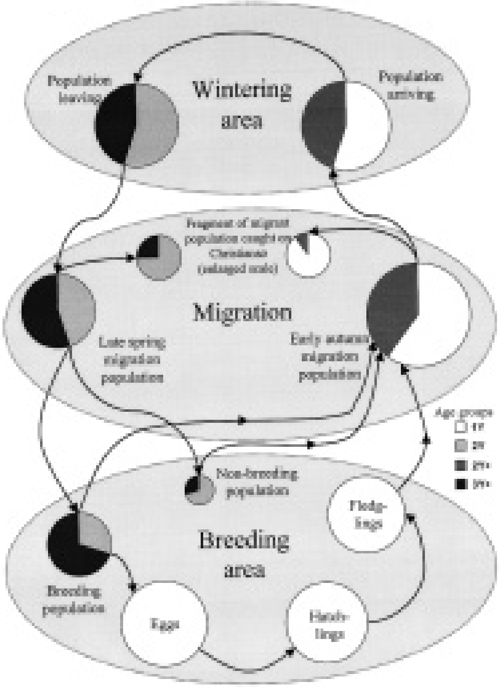

Fig. 2. Schematic illustration of the annual life cycle of a migrant bird population. The area of each circle is proportional to the assumed density, and the proportions of young (1Y, 2Y) and old birds (2Y+, 3Y+) are indicated.
Den årlige livscyklus for en trækfuglebestand. Jf. Fig.14 og omtalen heraf i Rabøl (1999).

Statistics

The Spearman rank correlation coefficient (r_s) is used to test all correlations. When conducting multiple tests, appropriate probability values must be adjusted for the number of simultaneous tests to a) control the probability of incorrectly rejecting one or more true null hypotheses (component $H_{0,i}$) and b) simultaneously maintain substantial power in detecting one or more component false $H_{0,i}$ (Rice 1989). Thus, for tables with multiple correlation tests, we followed Greenwood & Baillie (1991) and incorporated the sequential Bonferroni procedure (Rice 1989, based on Holm 1979)

to adjust the level of significance. Basically, this is an a posteriori test that evaluates the significance of each of the individual tested time-trends within a table. For significant time-trends, the annual percentage rates of changes are calculated as 100 (antilog_{10} (regression slope) – 1), which has been suggested as being more intuitively appealing and transparent than correlation coefficients (Marchant 1992). One-sample t-tests are used to test if the mean correlation coefficient (r_s) in a sample of correlation coefficients deviates significantly from zero, i.e., whether the sign of the mean correlation coefficient is noteworthy. All calculations here were conducted using untransformed correlation coefficients (r_s) (no significant differences could be distinguished for samples tested with arcsine transformation). All statistical tests are two-tailed.

Results

For each of the 29 species in the period 1976-1993, the comparable correlation coefficients between the indices of RS, RA, DK, SW and SF and year (1976-1993) are given in Table 1, whereas the correlation coefficients between the indices for each species are listed in Table 2 (untransformed indices) and Table 3 (yearly changes, i.e., log P_{i+1}/P_i transformed, following suggestions by Greenwood & Baillie 1991). For the prolonged period 1976-1996, the correlation coefficients of the two Christiansø indices, RS and RA, and their inter-seasonal and cross-seasonal correlation coefficients are listed in Table 4. Figs 3-7 show bivariate plots of the individual time-trends grouped by migratory categories.

Species and species groups

Short- and medium-distance migrants (Fig. 3)

When considering the Bonferroni test figures only (i.e., correction of significance level for multiple tests), none of the nine species shows any significant increase or decrease in RS or RA in the period 1976-1993 (Table 1) or in the prolonged period of 1976-1996 (Table 4), and also the "inter-seasonal" and "cross-seasonal" correlation coefficients between RS and RA remain insignificant (Table 4). However, in the correlations between RS, RA, DK, SW, and SF for the period 1976-1993 a few positive (Wren in DK/SW, Goldcrest in RS/SF and SW/SF) and negative (Chiffchaff in DK/SF) correlations still remain significant after correction for multiple testing. Significant, positive time-trends are found in four of the Danish indices (Wren, Robin, Blackbird, Chiffchaff), in one of the Finnish indices (Dunnock), and in one Swedish index (Goldcrest). In contrast, there are only two species with negative time-trends (Dunnock in DK and Chiffchaff in SF), and both show significant, inverse time-trends in DK and SF. No overall trend of decrease or increase was found for this migratory category in the years 1976-1993 (mean of 42 correlation coefficients = -0.04, P>0.05, one-sample t-test, Table 1), although the trends are significant within RA and SW (mean = -0.18 and 0.29, respectively, both P<0.05, one-sample t-test, Table 1), but in opposite directions, and it disappeared for RA in the prolonged time-series from 1976 through 1996 (mean = -0.10, P>0.05, one-sample t-test, Table 4).

Table 1. Spearman rank correlation coefficients (1976-1993, n=18) between year and five population indices: Christiansø spring migrants (RS), Christiansø autumn migrants (RA), Danish point counts (DK), Swedish point counts (SW), and Finnish point/summer counts (SF). For DK, SW and SF, only species also represented by RS- and RA-indices are included. The SF indices start in 1979 (i.e., n=15). If a species index starts later than 1976 (or 1979 for SF), the number of years covered is denoted as a superscript. Significance levels are: * P<0.05, ** P<0.01, and *** P<0.001 (two-tailed), parentheses indicate insignificance (P>0.05) when adjusting for multiple testing with the sequential Bonferroni procedure at the table-wide level, i.e., each column (e.g., RS) handled separately.
Korrelationskoefficienter mellem årstal og årlige index-værdier: korrigerede indexer baseret på ringmærkningen på Christiansø forår (RS) og efterår (RA) i perioden 1976-1993, samt danske (DK), svenske (SW) og finske (SF) punkt- og sommertællings-indexer i samme periode. Signifikans er angivet med stjerner, men hvor disse står i parentes forsvinder signifikansen, når der korrigeres under hensyn til datasættet i sin helhed (og arten altså ikke betragtes isoleret).

	RS	RA	DK	SW	SF
Short- and medium-distance migrants					
Troglodytes troglodytes	-0.17	-0.10	0.69**	0.54(*)	0.86(**)^{7}
Prunella modularis	-0.30	-0.38	-0.95***	0.01	0.76**
Erithacus rubecula	0.14	-0.26	0.69**	0.30	-0.53(*)
Turdus merula	-0.18	0.16	0.73**	0.28	-0.27
Turdus philomelos	0.01	-0.33	0.35	-0.18	0.24
Turdus iliacus	-0.23	-0.16		0.51(*)	-0.61(*)
Phylloscopus collybita	0.58(*)	-0.48(*)	0.85***		-0.84***
Regulus regulus	-0.08	0.12	-0.03	0.63**	-0.04
Emberiza schoeniclus	-0.47(*)	-0.21	-0.06^{14}	0.24	
Long-distance migrants					
Anthus trivialis[b]	0.19	-0.23	0.75***	-0.21	-0.82***
Luscinia luscinia[c]	0.03	-0.25	-0.30	-0.27	0.29^{10}
Phoenicurus phoenicurus[a]	-0.56(*)	-0.49(*)	-0.01^{14}	0.21	-0.23^{13}
Saxicola rubetra[a]	-0.40	0.07		-0.58(*)	-0.75(**)^{12}
Locustella naevia[a]	-0.37	0.16			
Acrocephalus schoenobaenus[b]	-0.60(**)	-0.51(*)			-0.24^{13}
Acrocephalus palustris[c]	-0.22	0.38	-0.88***^{14}		
Acrocephalus scirpaceus[a]	-0.58(*)	-0.56(*)	-0.22^{14}	0.94***	-0.07^{7}
Hippolais icterina[b]	-0.52(*)	-0.34	-0.66**	0.37	0.04^{9}
Sylvia curruca[c]	-0.02	0.16	-0.68**	-0.23	-0.34
Sylvia communis[a]	-0.25	0.32	-0.43	0.70**	0.90***
Sylvia borin[b]	-0.55(*)	-0.54(*)	0.14	0.56(*)	-0.08
Sylvia atricapilla[c]	-0.18	-0.54(*)	0.97***	0.88***	0.56^{10}
Phylloscopus sibilatrix[b]	0.43	0.02	-0.11	0.71**	0.79***
Phylloscopus trochilus[c]	0.25	0.27	-0.20	0.81***	0.62(*)
Muscicapa striata[b]	-0.14	-0.07		-0.19	-0.04
Ficedula parva[d]	0.03	0.17			
Ficedula hypoleuca[a]	-0.50(*)	-0.23	-0.59(*)^{14}	0.85***	0.40
Lanius collurio[c]	-0.55(*)	-0.47		-0.84***	-0.44^{10}
Carpodacus erythrinus[d]	0.26	0.04			0.04

[a] Southwestern migrants to sub-Saharan Africa
[b] Southern migrants to sub-Saharan Africa
[c] Southeastern migrants to sub-Saharan Africa
[d] Long-distance migrants to India

The **Wren** shows a decline in both RS and RA until 1985 following the first of three consecutive hard winters, after which the indices increase. The high RS and RA in 1996 are noteworthy, following the rather hard winter of 1995/96 (with much snow in Denmark) and below average breeding populations in Denmark in 1996 (the index for DK was almost halved from 1995 to 1996). The large positive percentage rates of change for DK (6.2% per year), with similar tendencies in SW and SF, are due to marked increases following the last hard winter in 1987 (Table 2), and the correlation between DK and SW is significant (Tables 2 and 3). The **Dunnock** shows no clear time-trends in RS or RA, and the fluctuations in these two indices are not coupled (Tables 1 and 4). The very heavy decline in DK (-7.3% per year), the contrasting significant increase in SF (2.6% per year), and the tendency for a negative correlation in RA/SF and DK/SF are notable (Tables 1 and 2). The hard winter of 1985 seems to have had a depressing effect on RS and RA. The low SW-values in 1985-1988 are probably also caused by increased winter mortality. The **Robin** shows no time-trends in RS or RA, but DK increases significantly (3.0% per year) (Tables 1 and 4). No couplings exist between any of the indices (Tables 2 and 3). The very low RA in 1983 is owing to steady, westerly winds and passages of cyclones in the main migratory period. This also occurred in species like Song Thrush, Chiffchaff, and Goldcrest. The low 1983-value of RS (Robin only) also suggests a low initial population size as influential on RA 1983. The **Blackbird** shows no time-trends in RS or RA,

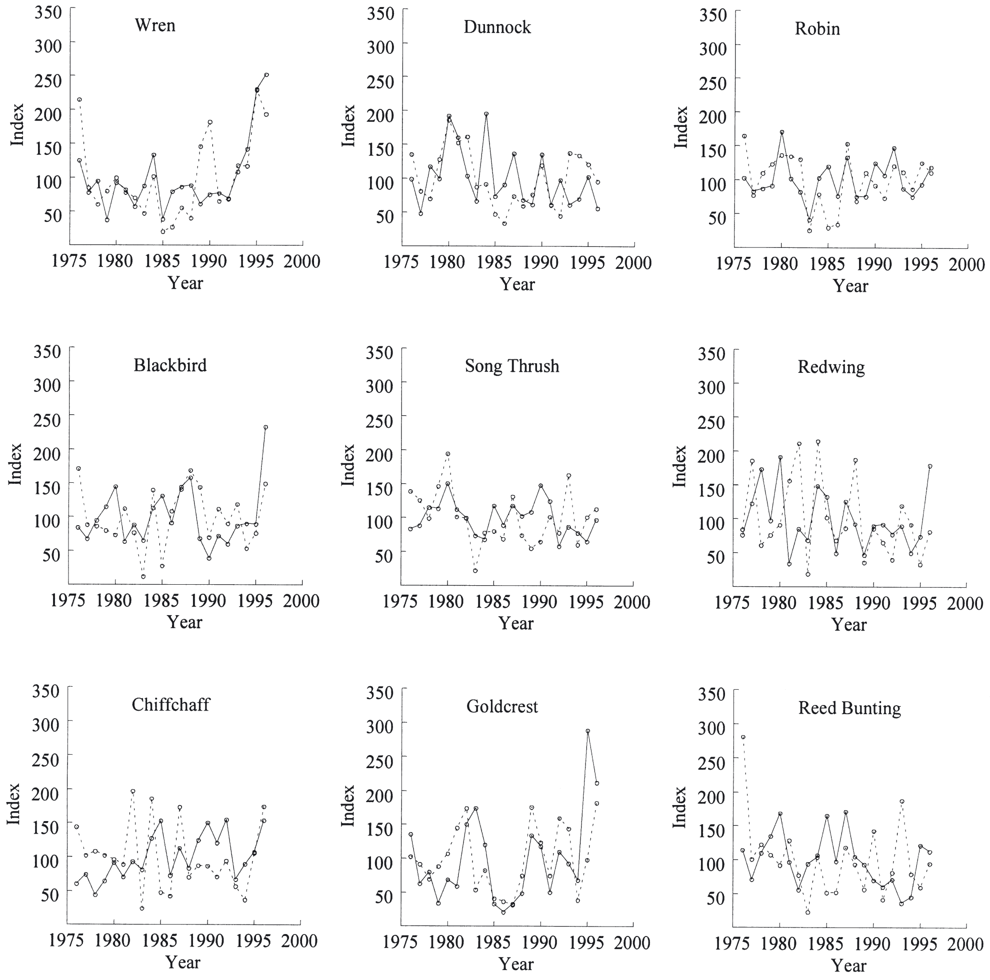

Fig. 3. Time-trends of RS (solid line) and RA (dashed line) in 9 short- and medium-distance migrants, caught on Christiansø 1976-1996. All indices are standardised to a mean of 100.
Index-værdierne RS (fuldt optrukket) og RA (stiplet) for de 9 kort- og mellemdistancetrækkere. Indexerne er standardiserede, så middelværdien er 100 (de sande index-værdier kan skønnes ud fra RA/RS i Tabel 6).

Whinchat. Photo: Erik Thomsen.

Bynkefuglen er fanget i meget varierende antal på Christiansø, men nogen langtidstendens har ikke kunnet påvises.

but DK increases significantly (2.3% per year) (Table 1). Only parts of the populations in Sweden and particularly in Denmark are migratory. Thus, the tendency for negative correlations between RS and SW and the one positive correlation between RA and DK are interesting and may reflect different proportions of migratory versus residential birds in the two populations. Worth noting is a significant increase in DK since 1985 (three hard winters followed by six mild ones). As in the case of the Wren, the high RS of 1996 – following a hard winter – is outstanding. The **Song Thrush** shows much the same pattern as the Robin. RA of the two species is significantly positively correlated, and RS almost so. The **Redwing** shows neither time-trend coupling between indices nor tendencies to follow other species. The **Chiffchaff** is the only of the 29 species that shows opposite tendencies among RS and RA, at least until 1993 (Table 1). Thus, whereas RS increased by 4.2% per year, RA decreased by 2.8% per year, though neither trend is significant (Table 1). The significant, positive time-trend in DK (5.4% per year), which is negatively correlated with SF (Table 2), the significant, negative time-trend in SF (-6.0% per year), the tendency for parallel, negative time-trends in RA and SF and positive time-trends in RS and DK, all also support the suspicion that two rather different populations pass over Christiansø in spring and autumn (see Helbig et al. 1996 for species limits in the Chiffchaff complex). Migrants in the spring probably originate in the Baltic and southern parts of Scandinavia and winter in southwestern Europe and northwestern Africa, whereas birds in the autumn probably originate in northern Scandinavia and winter in the eastern Mediterranean and East Africa (i.e., have status of partially long-distance migrants). The latter could explain the small numbers caught on Christiansø in the autumn in westerly winds, in contrast to easterly winds. The **Goldcrest** shows much fluctuation, but no time-trends in RS and RA or DK and SF, whereas SW is distinguished by a significant increase (5.4% per year) (Table 1) and a positive correlation with SF (Table 3). RS and RA tend to intercorrelate positively and also to correlate with SW and SF (Tables 2 and 4). Noticeable, in all indices the species peaks in 1983 and 1990. The fluctuations are perhaps not only caused by hard winters, but may also reflect (more or less delayed) responses to insect prey abundance in coniferous forests (M. Münster-Swendsen, pers. comm.). The **Reed Bunting** shows no time-trends or couplings between indices, except for a tendency for a negative correlation between RS and SW (Table 2).

Long-distance migrants to sub-Saharan Africa – southwestern migrants (Fig. 4)

As in the previous category of migrants, all individual, significant time-trends both in RS or RA (Table 1) and in the "inter-seasonal" and "cross-seasonal" correlation coefficients between RA and RS (Table 4) disappear when applying the sequential Bonferroni procedure. Of the correlations between the five indices, only the positive correlation for Whitethroat in SW/SF remains significant (Tables 2 and 3). Significant positive time-trends remain in three Swedish indices (Reed Warbler, Whitethroat, Pied Flycatcher) and in one Finnish index (Whitethroat); conversely, no significant negative time-trends exist in any of the indices. No general trend of decrease or increase is apparent (mean of 26 correlation coefficients = -0.09, P>0.05, one-sample t-test, Table 1). Within the indices, only RS shows a significant trend, which is negative (mean -0.44, P<0.001, one-sample t-

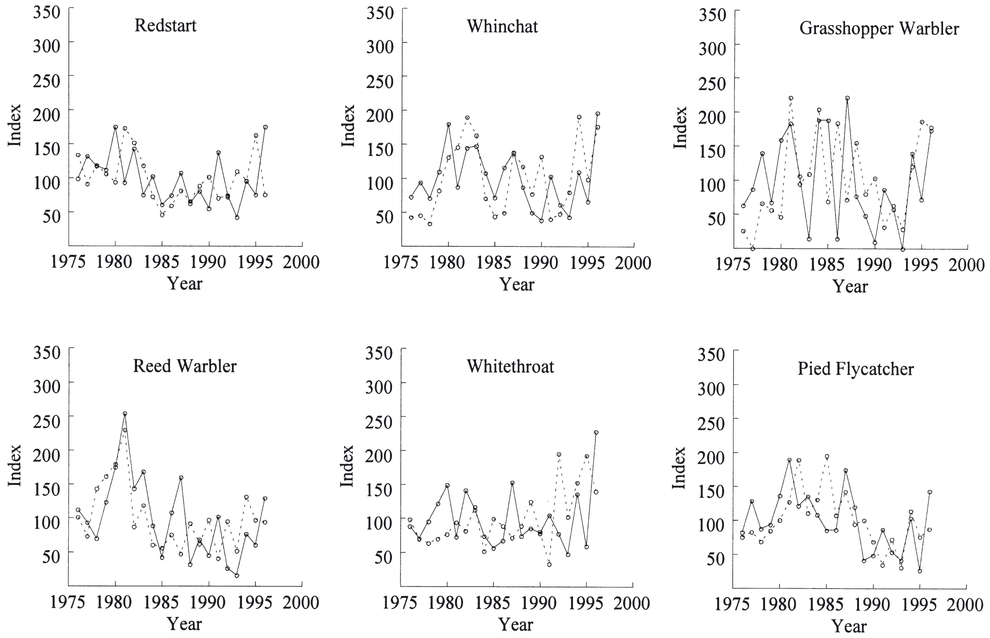

Fig. 4. Time-trends of RS (solid line) and RA (dashed line) in 6 long-distance, southwestern migrants to sub-Saharan Africa, caught on Christiansø 1976-1996. All indices are standardised to a mean of 100.
Som Fig.3, for de 6 sydvest-trækkende langdistancetrækkere til Afrika.

test, Table 1); this is found also when including the years 1993-1996 (mean -0.25, P< 0.01, one-sample t-test, Table 4).

The **Redstart** shows an initial decrease in the indices (except SF) until 1985, followed by an increase. Tendencies for negative correlations exist in time-trends of RS and RA for the years 1976-1993 (Table 1), but disappear when 1994-1996 are included (Table 4). Tendencies for positive couplings exist between RA and RS the following year (Table 4), RA/DK (Table 2), and between RS/DK and RS/SW (Table 3). The **Whinchat** follows a sinusoidal curve also found in other long-distance migrants and shows no significant time-trends in RS and RA or between indices (Tables 1-4). However, tendencies exist for significant, negative time-trends in SF and SW (Table 1). The **Grasshopper Warbler** also shows the sinusoidal variation common among long-distance migrants and no time-trends in or between RS and RA (Tables 1 and 4). No data are available for the other indices. The **Reed Warbler** shows tendencies for significant declines in RS and RA (Tables 1 and 4): initial increases from 1976 to 1981 are followed by much longer and stronger declines. The two indices also tend to inter-correlate (Table 4). A strongly significant increase is observed in SW (4.0% per year) (Table 1). The **Whitethroat** shows a tendency for a positive time-trend in RA but not in RS (Table 4). Populations in both SW (3.0% per year) and SF (4.5% per year) increase significantly, and are positively correlated (Table 2). The tendency for a negative correlation between RS and SW should be noted (Tables 2 and 3). The **Pied Flycatcher** shows the sinusoidal curve of most long-distance migrants (Table 4). A tendency for a general decrease in RS (Table 1) diminishes over the last couple of years (Table 4). RS and RA tend to be inter-correlated (Table 4). The significant increase is notable in SW (3.5% per year) compared with the tendency of a decrease in DK (Table 1).

Long-distance migrants to sub-Saharan Africa – southern migrants (Fig. 5)

The only correlation involving RS or RA that remains significant after applying the Bonferroni procedure is RS/DK for Icterine Warbler (Tables 1-4). Other significant correlations are the opposing positive (DK) and negative (SF) time-trends in Tree Pipit, the positive correlation between SW and SF in the same species, the negative time-trend for Icterine Warbler in DK, and the positive time-trends for Wood Warbler in SW and SF (Tables 1-3). Again, no overall trend of decrease or increase is found for the years 1976-1993 (Table 1, mean of 27 correlation coefficients = -0.07, P>0.05, one-sample t-test). Within the indices, only RA shows a significant trend, which is negative (Table 1, mean -0.28, P<0.05, one-sample t-test, Table 1), but it disappears when figures for 1994-1996 are included (mean -0.12, P>0.05, one-sample t-test, Table 4).

The **Tree Pipit** shows no general time-trend in RS or RA (Tables 1 and 4). The positive time-trend of DK (6.2% per year) is in contrast to a significant decrease in SF (-3.6% per year) (Table 1), and SF is positively correlated with SW (Tables 2 and 3). The tendency for positive correlation between RS and DK should also be noted (Table 2, but see also Table 3). The **Sedge Warbler** tends to decline in both RS and RA until 1993, but then increases rather dramatically, particularly in RA (Tables 1 and 4). The **Icterine Warbler** peaks in 1982-1984 in RS, RA, DK, and SW. The decline hereafter is more prominent than the initial increase, especially in DK, which shows an overall, significant decline (-3.6% per year), and in RS, which shows a similar tendency (Tables 1 and 4). RS and RA tends to be inter-correlated (Table 4), and to be positively correlated with DK (Table 2). The general pattern resembles that of the Reed Warbler. The **Garden Warbler** shows a marked decrease in both RS and RA until the early 1990s (compare Tables 1 and 4). The general tendency in SW is increasing (Table 1). No indications exist of inter-correlation among indices (Tables 2 and 3). The **Wood Warbler** shows no clear time-trend in RS or RA which both fluctuate much, with a suggestion of a 3-5 year cycle in RS (Tables 1 and 4). Both SW and SF show a significant increase (3.3% and 2.8% per year, respectively). No significant correlations exist among indices (Tables 2 and 3). In **Spotted Flycatcher** no significant correlations are found in any of the indices or between indices (Tables 1-4); yet, it is noticeable that the two peak years of RS, 1986 and 1987, both have very low RA-values.

Long-distance migrants to sub-Saharan Africa – southeastern migrants (Fig. 6)

Significant correlations, also after using the Bonferroni procedure, are negative time-trends in Marsh Warbler (DK), Lesser Whitethroat (DK), and Red-backed Shrike (SW), and positive trends in Blackcap (DK and SW) and Willow Warbler (SW) (Table 1). Some of the positive correlations between the five indices also remain significant: in Blackcap and Lesser Whitethroat between DK and SW, and in Willow Warbler between SW and SF (Tables 2 and 3). None of the correlations involving RS and RA remains significant. As for the other groups of migrants, no overall trends of decrease or increase are apparent (mean of 27 correlation coefficients = -0.04, P>0.05, one-sample t-test, Table 1). No trends were found within individual indices, either.

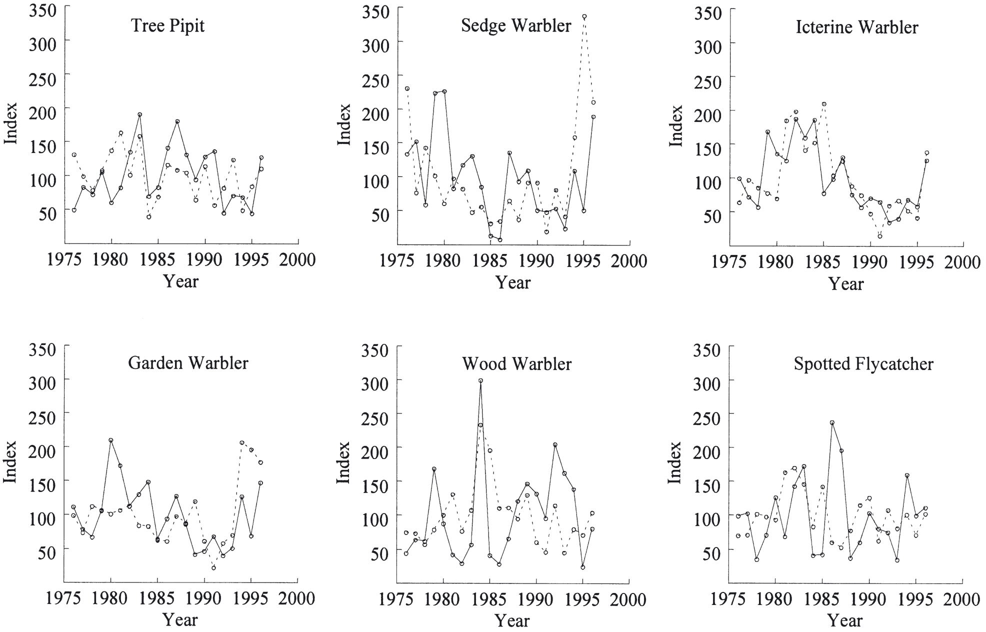

Fig. 5. Time-trends of RS (solid line) and RA (dashed line) in 6 long-distance, southern migrants to sub-Saharan Africa, caught on Christiansø 1976-1996. All indices are standardised to a mean of 100.
Som Fig.3, for de 6 syd-trækkende langdistancetrækkere til Afrika.

The **Thrush Nightingale** shows the sinusoidal curve found in many other long-distance migrants, for both RS and RA. There is a positive correlation between DK and SW (Table 3), and a tendency for a positive correlation between RS and DK (Table 3). The **Marsh Warbler** shows an increase in RS until 1989 and then declines, whereas RA increases until 1993 before declining. The species has declined significantly (-4.3% per year) in Denmark (Table 1), and DK and RS tend to be positively correlated (Table 2). The **Lesser Whitethroat** shows a high peak in RA for 1995 and in RS for 1996, but excluding these values there is no trend in RS or RA, and no mutual correlation, whereas DK decreases significantly (-3.6% per year). There is a positive coupling between DK and SW and a tendency for a negative correlation between RS and SF (Tables 1-4). The **Blackcap** shows no time-trend in RS or RA, and the two indices are not correlated, whereas the species increases significantly and almost monotonically in DK and SW (4.5% and 5.0% per year, respectively), which is also reflected in a positive correlation between DK and SW (Tables 1 and 2). In contrast, the correlation between RA and DK tends to be negative (Table 2). The **Willow Warbler** shows no clear time-trends in RS and RA. Noticeable correlations are the positive time-trend in SW (1.9% per year) with a similar tendency in SF (Table 1), the positive correlation between these two indices (Table 2), and a tendency for a positive coupling between RS and SW (Table 2). The **Red-backed Shrike** shows much fluctuation in both RS and RA, but the declines nevertheless approach significance (Tables 1 and 4). One should note that the lowest RS-value (0.9), in 1985, was followed by the highest RA-value (69.2), indicating a high variation in the numbers passing Christiansø in this species. The species declined significantly in SW (-7.1% per year) (Table 1).

Long-distance migrants to India (Fig. 7)

This group of migrants is too small to test for general tendencies; none of the few correlations within and between indices remain significant when applying the Bonferroni procedure.

The **Red-breasted Flycatcher** shows a tendency for positive coupling between RS and RA (Table 4). This is the only interesting correlation for a species without indices from DK, SW, and SF. The **Scarlet Rosefinch,** somewhat surprisingly, shows no increase despite having become established as a breeding bird in Denmark during the period considered. Looking further back, however, the species has indeed increased on Christiansø, from one or two observations each year (spring) in 1965-1970 to six ringed birds in the spring of 1973, and to much higher levels from 1976 onwards. The tendency of a negative correlation between RA and SF (Table 3) is strange and may be spurious.

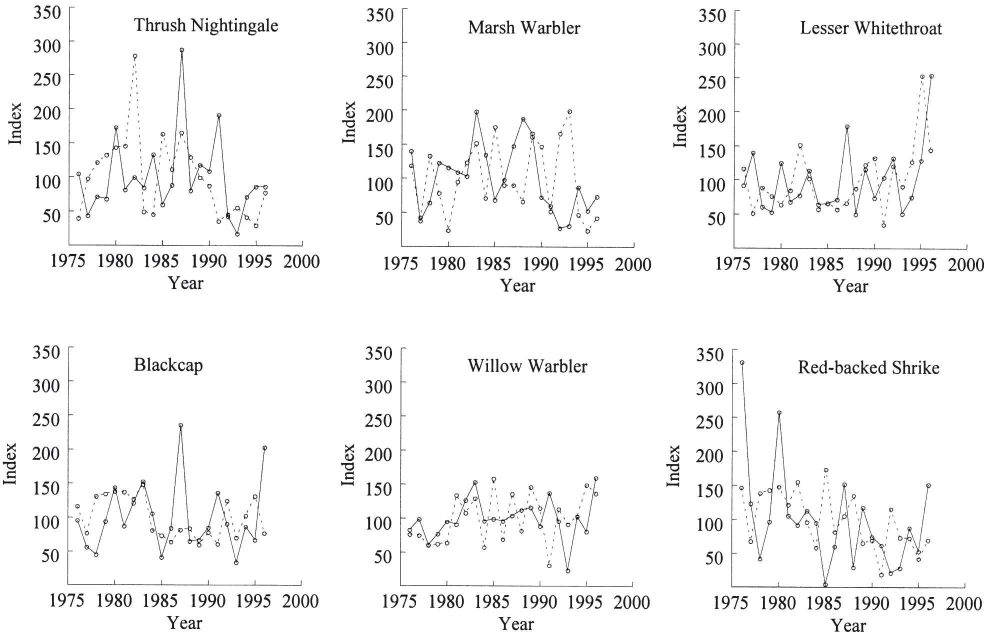

Fig. 6. Time-trends of RS (solid line) and RA (dashed line) in 6 long-distance, southeastern migrants to sub-Saharan Africa, caught on Christiansø, 1976-1996. All indices are standardised around a mean of 100.
Som Fig.3, men nu de 6 sydøst-trækkende lang-distance trækkere til Afrika.

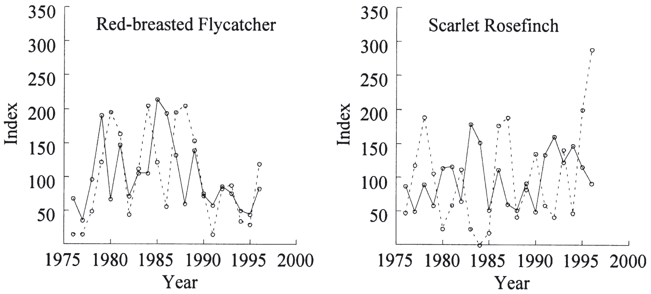

Fig. 7. Time-trends of RS (solid line) and RA (dashed line) in 2 long-distance migrants to India, caught on Christiansø 1976-1996. All indices are standardised to a mean of 100.
Som Fig.3, for de 2 langdistancetrækkere til Indien

General time-trends

When considering the period 1976-1993, the time-trends of RS and RA tend to be negative (20 species in spring and 18 species in autumn), but none of them remains significant when correcting for multiple testing (Table 1). Yet, mean correlation coefficients are significantly different from 0 for both RS (-0.17, $P<0.01$) and RA (-0.15, $P<0.05$, one-sample t-test). However, if data are included for three more years, extending the period to cover 1976-1996, the tendencies towards significant declines disappear for most species and the overall trends become insignificant for both RS (mean -0.08, $P>0.05$) and RA (mean -0.05, $P>0.05$), although the ratio of negative signs remains almost unchanged (Table 4). For the 20 long-distance migrants alone, RS – but not RA – just remains significant (mean -0.12, $P<0.05$ and mean -0.05, $P>0.05$, respectively).

For the period 1976-1993, most Danish and Finnish time-trends are also negative (Table 1), but among the significant ones there are more positive than negative (6 vs 4 and 3 vs 2, respectively), and no overall trend can be distinguished (mean 0.00, $P>0.05$ for DK, mean 0.01, $P>0.05$ for SF). SW differs in that 16 out of 23 correlations are positive (Table 1); seven are significantly positive and only one significantly negative, and the mean correlation coefficient (0.26) differs significantly from 0 ($P<0.02$).

Fig. 8 displays the pattern in overall time-trends if all annual RS- and RA-values are summed into one index for the 9 short- and medium-distance and the 20 long-distance migrants, respectively. In the long-distance migrants both RS and RA exhibit an initial increase, a longer decline, and a final increase. The fitted curves, based on distance-weighted least-squares smoothing, look much alike with maxima in 1981-1983 and minima in 1991-1993. However, the RS-curve is displaced by about 1½ year to the right compared with the RA-curve, causing the correlations between them to disappear ($r_S = 0.178$ between RS_i/RA_i, and 0.289 between RA_i/RS_{i+1}). In the short- and medium-distance migrants, the RS-curve shows some resemblance to the curve for the long-distance migrants, whereas the RA-curve is quite different, with a decline from 1976 to 1985 followed by an increase.

DK, SW, and SF are all chain indices and as such cannot be summed like RA and RS but are here presented as the means of the summed percentage index values for each species (Fig 9.). This makes the overall pattern of DK, SW, and SF comparable to those of RS and RA in Fig. 8. For the period in common (1976-1993), the overall hump-shaped pattern of the long-distance migrants in DK resembles the pattern found in RS and RA (compare Figs 8 and 9). In contrast, the overall trend of SW is a steady increase (Fig. 9). For short- and medium-distance migrants, the correspondance between DK and SW is slightly better (except during the first years), but while DK is similar to RA, SW looks more like RS.

Correlations between indices

The mean "inter-seasonal" correlation coefficients within the two indices RS and RA are significantly different from zero (mean 0.13, $P<0.005$ for RS_i/RS_{i+1}, mean 0.21, $P<0.0001$ for RA_i/RA_{i+1}), as are the mean "cross-seasonal" correlation coefficients between RS and RA (mean 0.21, $P<0.0001$ for RS_i/RA_i, mean 0.14, $P<0.05$ for RA_i/RS_{i+1}, one-sample t-test) (Table 4). Furthermore, all of

Table 2. Spearman rank correlation coefficients between Christiansø spring migrants (RS), Christiansø autumn migrants (RA), Danish point counts (DK), Swedish point counts (SW), and Finnish point/summer counts (SF) based on untransformed indices (1976-1993, n=18). n is shown as a superscript when less than 18 (or 15 where SF is included). Significance levels are: * $P<0.05$, ** $P<0.01$, and *** $P<0.001$ (two-tailed). Parentheses indicate insignificance ($P>0.05$) when adjusting for multiple testing with the sequential Bonferroni procedure at the table-wide level, i.e., each column (e.g., RS/DK) handled separately.
Parvise korrelationskoefficienter mellem de fem indexer vist i Tabel 1 (undt. RS/RA).

	RS/DK	RS/SW	RS/SF	RA/DK	RA/SW	RA/SF	DK/SW	DK/SF	SW/SF
Short- and medium-distance migrants									
Troglodytes troglodytes	0.11	0.23	-0.32^{7}	0.24	0.45	0.29^{7}	0.88***	0.54^{7}	0.75^{7}
Prunella modularis	0.27	0.17	-0.47	0.41	0.50(*)	-0.72(**)	0.05	-0.82(***)	-0.46
Erithacus rubecula	-0.16	0.08	0.23	-0.24	0.13	0.09	0.41	-0.14	0.41
Turdus merula	-0.41	-0.63(**)	-0.32	0.41(**)	0.12	-0.34	0.62(**)	-0.24	0.34
Turdus philomelos	-0.31	0.13	-0.31	-0.30	0.26	-0.02	0.01	0.44	-0.04
Turdus iliacus		-0.15	0.09		-0.15	0.55(*)			-0.15
Phylloscopus collybita	0.46		-0.28	-0.36		0.20		-0.83***	
Regulus regulus	0.30	0.48(*)	0.78***	0.39	0.56(*)	0.48	0.43	0.38	0.57(*)
Emberiza schoeniclus	-0.03^{14}	-0.64(**)		0.10^{14}	0.03		0.45^{14}		
Long-distance migrants									
Anthus trivialis	0.50(*)	0.36	0.25	-0.26	0.16	0.40	0.18	-0.28	0.81***
Luscinia luscinia	0.39	0.19	0.36^{10}	0.31	0.26	0.20^{10}	0.56(*)	0.10^{10}	0.24^{10}
Phoenicurus phoenicurus	0.32^{14}	0.25	0.39^{13}	0.65(**)^{14}	0.34	0.25^{13}	0.51(*)^{14}	0.59(*)^{13}	0.13^{13}
Saxicola rubetra		0.13	0.52^{12}		-0.21	0.12^{12}			0.17^{12}
Acrocephalus schoenobaenus			0.39^{13}			0.53^{13}			
Acrocephalus palustris	0.54(*)^{14}			-0.31^{14}					
Acrocephalus scirpaceus	0.42^{14}	-0.42	-0.11^{7}	0.45^{14}	-0.49(*)	-0.07^{7}	-0.07^{14}	0.02^{7}	0.11^{7}
Hippolais icterina	0.76***	0.26	-0.19^{9}	0.63(**)	0.45	0.01^{9}	0.33	0.06^{9}	0.44^{9}
Sylvia curruca	0.01	-0.17	-0.29	-0.18	0.16	-0.12	0.52(*)	0.50(*)	0.56(*)
Sylvia communis	0.46	-0.47	-0.35	-0.03	0.47(*)	0.37	-0.21	-0.15	0.83***
Sylvia borin	0.43	-0.22	-0.25	0.20	-0.08	0.08	0.56(*)	-0.09	0.26
Sylvia atricapilla	-0.08	-0.13	-0.04^{10}	-0.54(*)	-0.36	-0.44^{10}	0.89***	0.53^{10}	0.50^{10}
Phylloscopus sibilatrix	-0.18	0.43	0.41	0.09	-0.29	-0.07	0.36	0.14	0.74(**)
Phylloscopus trochilus	0.37	0.53(*)	0.49	0.19	0.26	0.15	0.25	-0.15	0.83***
Muscicapa striata		0.06	0.21		0.18	-0.05			-0.07
Ficedula hypoleuca	0.65(**)^{14}	-0.34	-0.17	0.53(*)^{14}	-0.28	-0.31	-0.27^{14}	0.15^{14}	0.66(**)
Lanius collurio		0.40	0.02^{10}		0.52(*)	-0.18^{10}			-0.14^{10}
Carpodacus erythrinus			-0.38			-0.01			

Table 3. Spearman rank correlation coefficients between Christiansø spring migrants (RS), Christiansø autumn migrants (RA), Danish point counts (DK), Swedish point counts (SW), and Finnish point/summer counts (SF) based on the yearly changes in size of the indices, i.e., $\log(P_{i+1}/P_i)$ (1976-1993, n=17). n is shown as a superscript when less than 17 (or 14 where SF is included). Significance levels are: * $P<0.05$, ** $P<0.01$, and *** $P<0.001$ (two-tailed). Parentheses indicate insignificance ($P>0.05$) when adjusting for multiple testing with the sequential Bonferroni procedure at the table-wide level, i.e., each column (e.g., RS/DK) handled separately.

Samme som Tabel 2, men sammenligningen gælder her ændringerne i index-værdierne fra år til år, ikke index-værdierne selv.

	RS/DK	RS/SW	RS/SF	RA/DK	RA/SW	RA/SF	DK/SW	DK/SF	SW/SF
Short- and medium-distance migrants									
Troglodytes troglodytes	0.37	0.35	-0.64^{7}	0.05	0.20	-0.66^{7}	0.89***	-0.09^{7}	0.09^{7}
Prunella modularis	-0.04	-0.26	-0.38	0.06	-0.05	-0.61(*)	-0.02	-0.41	0.34
Erithacus rubecula	-0.39	0.00	0.06	0.05	0.29	-0.13	0.48(*)	0.36	0.23
Turdus merula	-0.33	-0.24	0.02	0.04	0.28	0.06	0.50(*)	0.01	0.43
Turdus philomelos	-0.07	0.19	0.07	-0.33	0.23	0.03	0.24	0.24	0.30
Turdus iliacus		0.09	0.06		-0.02	0.39			-0.09
Phylloscopus collybita	0.10		-0.35	0.32		-0.06		-0.16	
Regulus regulus	0.34	0.51(*)	0.42	0.12	0.25	0.23	0.61(**)	0.39	0.76**
Emberiza schoeniclus	-0.03^{14}	-0.36		-0.13^{14}	-0.16		0.34^{14}		
Long-distance migrants									
Anthus trivialis	-0.22	0.10	0.07	-0.28	-0.17	0.16	0.16	0.41	0.76**
Luscinia luscinia	0.51(*)	-0.01	0.13^{10}	-0.30	-0.35	0.05^{10}	0.68(**)	-0.20^{10}	-0.28^{10}
Phoenicurus phoenicurus	0.52(*)^{14}	0.57(*)	0.29^{13}	0.20^{14}	0.10	0.06^{13}	0.43^{14}	0.30^{13}	-0.14^{13}
Saxicola rubetra		0.20	0.04^{12}		0.47	-0.38^{12}			-0.29^{12}
Acrocephalus schoenobaenus			0.04^{13}			0.06^{13}			
Acrocephalus palustris	0.08^{14}			0.30^{14}					
Acrocephalus scirpaceus	0.38^{14}	0.17	0.54^{7}	-0.14^{14}	0.30	-0.31^{7}	0.27^{14}	0.54^{7}	0.60^{7}
Hippolais icterina	0.09	0.05	-0.19^{9}	-0.29	-0.02	-0.48^{9}	0.56(*)	-0.02^{9}	0.10^{9}
Sylvia curruca	0.14	-0.10	-0.56(*)	-0.26	-0.13	-0.19	0.73***	0.38	0.51
Sylvia communis	0.36	-0.48(*)	-0.32	0.30	0.43	0.35	0.08	0.06	0.73(*)
Sylvia borin	0.16	-0.01	-0.45	0.42	0.07	-0.01	0.39	-0.09	0.22
Sylvia atricapilla	0.04	-0.18	0.17^{10}	0.14	0.35	-0.33^{10}	0.36	0.02^{10}	0.05^{10}
Phylloscopus sibilatrix	-0.20	0.04	0.19	0.20	0.13	0.30	0.59(*)	0.07	0.26
Phylloscopus trochilus	0.42	0.48	0.36	-0.02	-0.22	0.06	0.55(*)	0.30	0.60(*)
Muscicapa striata		0.07	0.23		-0.03	-0.13			-0.07
Ficedula hypoleuca	0.27^{14}	0.37	0.50	0.42^{14}	-0.04	0.03	0.44^{14}	0.40^{14}	0.62(*)
Lanius collurio		-0.19	-0.02^{10}		0.30	-0.17^{10}			-0.53^{10}
Carpodacus erythrinus			0.28			-0.57(*)			

Table 4. Spearman rank correlation coeffients between Christiansø spring migrant indices (RS) and Christiansø autumn migrant indices (RA) and year (1976-1996, n=21), "the inter-seasonal" correlation coefficients of the two Christiansø indices (i.e., RS_i/RS_{i+1}, and RA_i/RA_{i+1}) from one year to the next (n=20), the "cross-seasonal" correlation coefficients, i.e., the correlation coefficients between RS and RA in the same calendar year (RS_i/RA_i, n=21) and between RA and RS in the following calendar year (RA_i/RS_{i+1}, n=20). Significance levels are: * P<0.05, and ** P<0.01 (two-tailed), parentheses indicate insignificance (P>0.05) when adjusting for multiple testing with the sequential Bonferroni procedure at the table-wide level, i.e., each column (e.g., RS/DK) handled separately.
Korrelationskoefficienter mellem RS henholdsvis RA og årstal, samt mellem RS for ét år og RS for det følgende år, tilsvarende for RA, mellem RS og RA for samme år, og mellem RA for ét år og RS for det følgende år. Perioden er her 1976-1996, hvorfor de to første søjler afviger fra de tilsvarende søjler i Tabel 1, der dækkede 1976-1993.

	RS	RA	RS_i/RS_{i+1}	RA_i/RA_{i+1}	RS_i/RA_i	RA_i/RS_{i+1}
Short- and medium-distance migrants						
Troglodytes troglodytes	0.26	0.25	0.10	0.37	0.45(*)	0.19
Prunella modularis	-0.34	-0.17	-0.16	0.47(*)	0.30	0.03
Erithacus rubecula	0.08	-0.15	0.02	0.43	-0.28	-0.28
Turdus merula	0.02	0.05	0.28	-0.09	0.18	-0.18
Turdus philomelos	-0.22	-0.27	0.29	0.12	0.25	-0.04
Turdus iliacus	-0.17	-0.22	-0.11	-0.27	0.28	-0.40
Phylloscopus collybita	0.58(**)	-0.26	0.26	-0.23	0.08	-0.27
Regulus regulus	0.20	0.14	0.37	0.27	0.59(**)	0.33
Emberiza schoeniclus	-0.30	-0.27	0.40	-0.16	0.08	-0.21
Long-distance migrants						
Anthus trivialis	-0.02	-0.27	0.25	-0.11	0.18	0.15
Luscinia luscinia	-0.01	-0.42	-0.02	0.48(*)	0.01	0.35
Phoenicurus phoenicurus	-0.31	-0.28	-0.02	0.40	0.14	0.62(**)
Saxicola rubetra	-0.18	0.30	0.11	0.40	0.47(*)	0.17
Locustella naevia	-0.16	0.34	-0.12	0.28	0.21	0.20
Acrocephalus schoenobaenus	-0.39	-0.00	0.18	0.30	0.38	0.40
Acrocephalus palustris	-0.33	-0.05	0.45(*)	0.03	-0.03	0.04
Acrocephalus scirpaceus	-0.46(*)	-0.33	0.39	0.18	0.35	0.58(**)
Hippolais icterina	-0.46(*)	-0.38	0.53(*)	0.63(**)	0.63(**)	0.56(*)
Sylvia curruca	0.20	0.43	-0.26	0.22	0.19	0.19
Sylvia communis	-0.06	0.56(**)	-0.27	0.17	-0.14	-0.11
Sylvia borin	-0.29	0.02	0.41	0.46(*)	0.37	0.34
Sylvia atricapilla	-0.02	-0.38	0.01	0.33	0.33	0.24
Phylloscopus sibilatrix	0.25	-0.04	0.22	0.18	0.04	-0.37
Phylloscopus trochilus	0.27	0.42	-0.06	-0.13	0.27	0.29
Muscicapa striata	0.06	-0.03	-0.11	0.19	-0.11	0.22
Ficedula parva	-0.18	-0.01	0.15	0.44	0.52(*)	0.30
Ficedula hypoleuca	-0.34	-0.17	0.18	0.53(*)	0.53(*)	0.11
Lanius collurio	-0.39	-0.55(*)	0.05	0.11	-0.01	0.43
Carpodacus erythrinus	0.34	0.26	0.22	0.20	-0.28	0.12

the seven "inter-seasonal" and nine "cross-seasonal" correlations that would have been significant without the Bonferroni correction of significance level are positive (Table 4). Similarly, most of the significant correlations, as well as the correlations turned insignificant as a result of the Bonferroni procedure, are positive (32 of 39 in Table 2, 18 of 22 in Table 3). This tendency is supported by the resulting mean correlations between the five indices. All means except one are positive, and several are significant (Table 5), indicating that, in general, the indices could describe the same populations.

Variation between years and the autumn/spring ratios

The coefficient of variation (CV) is significantly higher in RS and RA than in DK, SW, or SF (all P<0.001, Wilcoxon two-sample tests) (Table 6), whereas no differences were found between DK, SW and SF, or between RS and RA. However, if only considering the short- and medium-distance

Table 5. Mean Spearman rank correlation coefficient for each of the ten two-index comparisons between Christiansø spring migrants (RS), Christiansø autumn migrants (RA), Danish point counts (DK), Swedish point counts (SW), and Finnish point/summer counts (SF). The figures of the upper matrix are calculated as the average of the correlation coefficients for the species in common within each pair of indices, based on the untransformed index P_i (Table 2). The lower matrix shows the means of the correlation coefficients in Table 3, based on $\log(P_{i+1}/P_i)$. For comparability, in the case of RS/RA the years included are 1976-1993 (not 1976-1996). Significance levels are: * P<0.05, ** P<0.01, and *** P<0.001 (one-sample t-test).

Gennemsnitlige korrelationskoefficienter mellem diverse index-konstellationer, baseret på Tabel 2 (øverst) eller Tabel 3 (nederst).

P_i	RS	RA	DK	SW
RA	0.19^{***29}			
DK	0.23^{**21}	0.12^{21}		
SW	0.02^{23}	0.12^{23}	0.34^{***19}	
SF	0.04^{25}	0.06^{25}	0.04^{19}	0.35^{***22}

$\log(P_{i+1}/P_i)$	RS	RA	DK	SW
RA	0.09^{29}			
DK	0.12^{21}	0.04^{21}		
SW	0.06^{23}	0.10^{23}	0.44^{***19}	
SF	0.02^{25}	-0.09^{25}	0.13^{*19}	0.24^{**22}

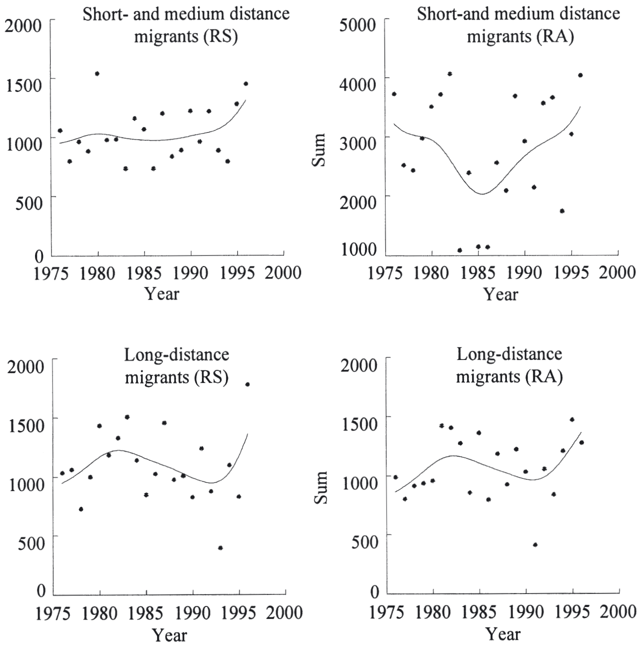

Fig. 8. Overall combined time-trends in the Christiansø spring-migrants (RS) and autumn-migrants (RA), 1976-1996, for 9 short- and medium-distance migrants and 20 long-distance migrants. The ordinate is the sum of all indices. Curves are fitted by distance-weighted least-squares smoothing.

De summerede index-værdier for 1) kort-og mellemdistancetrækkere (9 arter) og 2) langdistancetrækkere (20 arter), forår (RS) og efterår (RA) 1976-1996.

Table 6. Coefficients of variation (CV) for Christiansø spring migrants (RS), Christiansø autumn migrants (RA), Danish point counts (DK), Swedish point counts (SW), and Finnish point/summer counts (SF) 1976-1993. The SF indices start in 1979 (i.e., n=15). If a species index starts later than 1976 (or 1979 for SF), the number of years covered is denoted as a superscript. Means for RS and RA when including 1994-1996 are 48.9 and 49.5, respectively. The last column shows mean RA divided by mean RS (1976-1996), with mean RA in parentheses.
Variationskoefficienter (CV) for de fem indexer (1976-1993). Sidste søjle viser for 1976-1996 forholdet mellem gennemsnitlig RA og gennemsnitlig RS (samt i parentes den gennemsnitlige RA-værdi).

	RS	RA	DK	SW	SF	RA/RS
Short- and medium-distance migrants						
Troglodytes troglodytes	30.8	60.8	44.2	62.5	33.3^{7}	1.6 (45.1)
Prunella modularis	43.0	47.4	44.7	22.4	15.9	0.7 (55.3)
Erithacus rubecula	30.2	43.5	21.9	18.0	21.5	1.8 (950.9)
Turdus merula	36.0	43.2	15.9	14.4	22.6	0.9 (64.6)
Turdus philomelos	24.4	42.7	11.9	11.7	15.4	2.6 (278.6)
Turdus iliacus	42.7	58.4		17.0	14.6	1.3 (37.7)
Phylloscopus collybita	35.6	50.7	32.2		30.3	1.6 (44.9)
Regulus regulus	54.4	47.9	37.4	43.5	26.4	9.7 (1225.5)
Emberiza schoeniclus	38.5	59.5	9.7^{14}	14.9		1.9 (21.1)
Long-distance migrants						
Anthus trivialis	41.5	33.8	35.1	10.5	18.1	1.3 (20.5)
Luscinia luscinia	61.4	58.8	15.0	12.8	19.4^{10}	0.5 (5.4)
Phoenicurus phoenicurus	36.0	34.8	26.3^{14}	21.2	29.0^{13}	1.2 (88.2)
Saxicola rubetra	40.7	55.5		14.9	10.3^{12}	0.7 (6.8)
Locustella naevia	73.3	70.9				1.6 (3.2)
Acrocephalus schoenobaenus	65.7	66.5			22.2^{13}	1.8 (6.5)
Acrocephalus palustris	49.6	45.4	21.2^{14}			0.2 (2.4)
Acrocephalus scirpaceus	61.1	52.7	13.6^{14}	20.8	32.8^{7}	0.4 (13.0)
Hippolais icterina	48.3	52.9	30.4	29.4	24.7^{9}	0.3 (12.3)
Sylvia curruca	40.1	36.9	27.2	18.5	20.3	0.7 (58.4)
Sylvia communis	33.7	38.8	11.2	21.6	21.0	0.5 (14.6)
Sylvia borin	48.3	30.6	17.0	19.1	14.2	0.7 (82.5)
Sylvia atricapilla	50.5	32.1	23.8	26.6	12.8^{10}	1.5 (74.2)
Phylloscopus sibilatrix	70.1	48.3	26.7	24.4	16.0	2.8 (29.8)
Phylloscopus trochilus	29.1	37.5	11.2	12.4	15.9	0.8 (363.2)
Muscicapa striata	61.4	36.3		18.8	11.5	2.0 (54.0)
Ficedula parva	48.9	66.2				0.5 (4.3)
Ficedula hypoleuca	41.9	44.8	29.1^{14}	22.8	21.9	2.8 (143.0)
Lanius collurio	81.8	40.5		53.8	13.5^{10}	2.0 (41.5)
Carpodacus erythrinus	43.0	73.5			9.0	0.3 (1.4)
Mean	47.0	48.6	24.1	23.1	19.7	

migrants, CV is significantly higher in RA than in RS (P<0.02).

Given the same trapping probability in spring and autumn, the numbers of birds trapped and ringed at a station like Christiansø should be 2 or 3 times higher in autumn than in spring (Moritz l993). Strangely, the ratios of RA/RS are rarely that high and vary between 0.2 in the Marsh Warbler and 9.7 in the Goldcrest (Table 6). As a group, however, the short- and medium-distance migrants fit the prediction. The difference between these (mean 2.5) and long-distance migrants (mean 1.1) is statistically significant (Mann-Whitney U-test, P<0.05). However, if excluding the Goldcrest which numerically dominates the group of short- and medium-distance migrants, the pattern disappears (means 1.5 and 1.2, respectively; Mann-Whitney U-test, P<0.10).

Discussion

The time-trends

In our analyses of 29 passerine migrant species we found no overall, significant trends for individual migratory categories, neither in the migratory indices or the point- and summer-count indices from Sweden, Denmark, or Finland (Tables 1 and 4). A few trends were significant for indices of individual species, but often in opposite directions even within the migratory categories, and those of RS and RA disappeared when data from more recent years were included (compare Table 1 and Table 4). Although there was some tendency for more negative than positive time-trends in RS and RA, no species exhibited a significantly negative or positive trend in either season, and most of the significant trends in the other indices were positive (6 of 10 in DK, 7 of 8 in SW, 3 of 5 in SF) (Table 1). None of the species showed significant, negative tendencies in all three indices (breeding areas), which could have been caused by a common factor in, e.g., the wintering area. Actually, a significant, negative trend in one index was sometimes contrasted by a significant, positive trend in another index: Tree Pipit (SF vs DK), Dunnock (SF vs DK), Chiffchaff (SF vs DK). On the other hand, significant, positive trends often corresponded among indices: Whitethroat (SW and SF), Blackcap (DK and SW), Wood Warbler (SW and SF).

It is also obvious from Figs 3-9 that trends for individual species or migratory categories are not declining. For long-distance migrants in particular, this is a striking result in view of the general declines previously reported for several European populations (e.g., Berthold et al. 1986, Baillie et al. 1992, 1993, Böhning-Gaese 1992, Greenwood et al. 1993, 1995, Jacobsen 1994, 1998).

Real time-trends or trends in biases?

Several factors can affect a population index unidirectionally and generate spurious correlations.

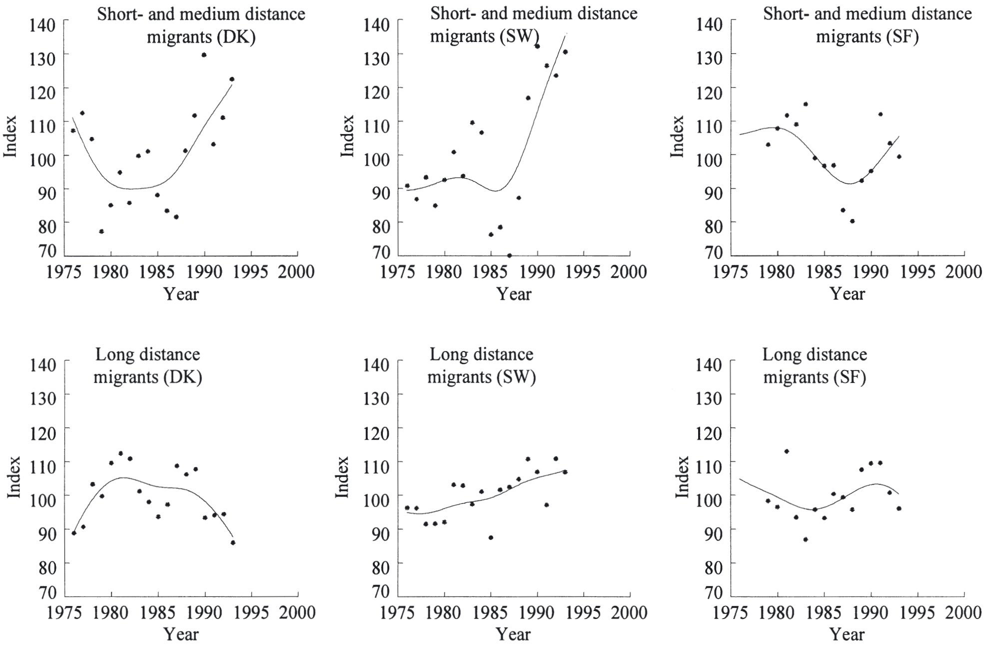

Fig. 9. Overall combined time-trends in the point-count indices from Denmark (DK) and Sweden (SW) and the point/summer-count indices from Finland (SF), 1976-1993, for short- and medium-distance (8 spp.) and long-distance migrants (13, 15, and 17 spp. for DK, SW, and SF, respectively). The ordinate shows means of the percentage index values for included species, i.e., all species contribute equally. Curves are fitted by distance-weighted least-squares smoothing.

Middelværdier over arter af index-værdier for 1) kort- og mellemdistancetrækkere (8 arter) og 2) langdistancetrækkere (13, 15 og 17 arter) for punkttællingerne i Danmark (DK), Sverige (SW) og Finland (SF), 1976-1993.

Red-backed Shrike. Photo: Poul Reib.

Rødrygget Tornskade er gået tilbage i Sverige, og fangsttallene på Christiansø har også været vigende, men med store årlige udsving.

Thus, some of the significant increases and decreases in the point- and summer-count indices may be statistically spurious, caused by autocorrelation in series of yearly non-independent indices. Another potential bias will result if different habitat types covered by, e.g., point-count routes, change with time disproportionally to the overall habitat changes in the breeding area monitored. The key assumption of censuses heavily relying on singing birds, that song rates are comparable regardless of habitat structure, is probably invalid, which may bias population density estimates significantly (McShea & Rappole 1997). Potential observer biases are manifold and can have a significant influence on analyses of population trends (Sauer et al. 1994, Kendall et al. 1996). Clearly, more simulations of all the procedures are needed to understand under which conditions spuriously significant time-trends may arise. Conceivably, some of the striking differences in time-trends between DK, SW, and SF (see above, Table 1) could be caused by such biases.

Vegetation and habitat structure at a migratory site or its surroundings may uni-directionally affect any indices based on migratory counts (e.g., Askins et al. 1990), also in cases where the real population sizes do not change. Thus, although efforts are made to keep habitat structure constant at the ringing station at Ottenby, Sweden (Pettersson 1993), the surroundings – the southern part of Öland – have become successively more bushy and woody over the years and may have attracted an increasing proportion of the passing migrants. On Christiansø, the habitat is kept relatively unchanged, being strictly preserved because of natural, historical, and architectural value, and as a tiny island the surroundings are simply water. Neither have different ringers or net types had any significant long-term influence on Christiansø, as only nets no. 1012 and 1013 from Heindl in Germany have been used, and they have been operated by relatively few, skilled ringers, following the same standardised routines since 1976.

Correlations between the indices

We found strong positive correlations among the indices of neighbouring countries, i.e., between DK and SW, and between SW and SF (see also Marchant 1992), whereas the correlations of the untransformed indices between DK and SF were smaller and not significant (Table 5). The generally good correlations within and between RA- and RS-indices, and between RS and RA for all the species combined, indicate that these indices track variations in real populations, and that in most species the same (or closely connected) migrant populations are involved in spring and autumn. On average, with one exception the overall correlations between the migration indices and the point-count indices, and the pairwise correlations between the three point-count indices, are positive (Table 5), suggesting that the indices describe the variations in the same populations.

Several comparisons have been made of breeding-season counts in different countries (e.g., Marchant 1992), of breeding and migration counts (e.g., Svensson et al. 1986, Rabøl & Lyngs 1988, Svensson 1993, Dunn & Hussell 1995, Dunn et al. 1997), and of migration counts within the same region (e.g., Busse et al. 1995, Tynjälä et al. 1995). Comparisons between breeding and migratory counts have generally resulted in low and insignificant correlations (e.g., Svensson 1993), although examples of significant, positive correlations are often highlighted (e.g., Hussell 1981, Lifjeld 1993) and sometimes generalised to typify the overall pattern of correlation. The procedure of comparison in such analyses has sometimes been a simple display of the time-trends in the same graph (as in our Figs 3-7), leaving the evaluation to the reader (e.g., Lifjeld 1993). When statistical comparisons and evaluations are applied, it often happens that "the computations [become] quite complex" (Hussell 1981: 94) and include multiple, and backward, stepwise regression procedures, transformations, and "corrections" of data biased by, e.g., weather (Hussell 1981). Such procedures tend to contain many (hidden) statistical and biological assumptions, making it uncertain whether the results are meaningful and comparable with indices calculated in very different ways. Basically, we face the question whether obtained results are dominated by methodological procedures and constraints, or whether they are biologically significant.

When the method of Hussell (1981) is applied to the indices in Table 5, only RS/RA and RS/DK were significant at the 5% level ($r = 0.394$, $n = 29$, and $r = 0.475$, $n = 21$, respectively), i.e., all significance among non-migratory indices disappeared. We prefer the more direct one-sample t-test when comparing overall tendencies like those in Table 5.

Regarding comparisons between migration counts within the same region, both Busse et al. (1995) and Tynjälä et al. (1995) found mostly low and insignificant correlations between numbers of ringed *Sylvia* warblers and Willow Warbler *Phylloscopus trochilus* at different stations in the Baltic region. However, low correlations are to be expected, especially in species without significant time-trends and for stations separated by hundreds of kilometres, because of the influence of weather (including wind-drift). The low correlations between the stations are therefore not an argument, per se, against the use of RS and RA as indices of population size.

The distances between the regions from where the indices were obtained probably influence the degree of correlation between the five indices in Table 5. The better overall correlation between DK and RS than between SW and RS may be caused by a the shorter distance, although the "centre of gravity" of the Swedish point-count routes (Lake Vättern) is only a little further from Christiansø than is the Danish "centre". The significant correlations between DK and SW and between SW and SF, and the general lack of correlation between DK and SF, all support the expectation that distance matters (Table 5).

Contrary to expectation, however, the Danish point-count indices from West (Jutland) and East Denmark correlate equally well to RS and SW (data from E.M. Jacobsen in litt.). We would also expect southwestern migrants from Finland to be better correlated to RS and particularly to RA than southeastern migrants from Finland, and the opposite for the Danish southwestern and southeastern migrants, respectively. Neither of these expectations are met (Tables 2 and 3).

Similar results were found when investigating the correlations of the four indices, RS, RA, SW and eastern Denmark (EDK) with data from a mapping-census investigation 1953-1992 in Fågelsångdalen (F) in Scania, Sweden (Enemar et al. 1994), 120 km WNW of Christiansø. In the 13 most numerous species from Fågelssångdalen also represented in the four other indices, the mean correlation coefficients were mostly low and insignificant (0.10 for F/RS, 0.16 for F/RA, 0.20 for F/SW, 0.27 for F/EDK). In only one species, Garden Warbler, F/RS and F/RA were both statistically significant ($P<0.05$).

Significance of lack of correlations

In our analyses, we found many non-significant correlations. These are to be expected for several reasons and do not, per se, contradict the above considerations. Thus, for stable populations, even small errors of estimation in compared indices will lead to a correlation coefficient close to zero. In general, high positive correlation values are mainly to be expected in species whose populations decrease or increase markedly (as the Red-backed Shrike), fluctuate strongly (Goldcrest), or exhibit humpback-shaped development curves (Icterine Warbler).

Low or no correlation between RS and RA may occur when the migrants in spring and autumn belong to different or only partly overlapping breeding populations (as discussed for Chiffchaff). Likewise, low or no correlation between indices based on migration counts (as RS and RA) and indices based on breeding-ground counts (DK, SW, SF) may occur if the indices track different or only partly overlapping sub-populations. Thus, a non-significant positive correlation, or even a negative correlation, between a migration index and a breeding-stage index does not necessarily invalidate the significance of the migration index. As discussed previously, neighbouring breeding-stage indices may also correlate badly (as DK and SW).

Use of migration indices and weather biases

Their merits notwithstanding, migratory data are often influenced by various biases which potentially may obscure true biological patterns, and also spuriously induce statistically significant test results. The main problem in using such data in calculating population indices is the potentially profound influence of weather on bird migration (e.g., Alerstam 1978, Richardson 1978) and on the numbers of birds trapped and ringed. Ideally, the numbers of migrants caught should be proportional to the numbers of birds passing the ringing site and, furthermore, the seasonal total should be proportional to the size of the migrant population. Both assumptions are problematic, and only approximate corrections are possible, even if local and regional weather conditions are monitored.

One such approach, aiming at reducing the influence of weather on migration data by use of various regression procedures, was developed by Hussell (Hussell 1981, Hussell et al. 1992). However, this procedure requires good-quality weather data that may not be locally available, and it is impossible to verify that corrected results are better (i.e., biologically more meaningful) than the raw data. In addition, it is unclear to which extent weather and migration data fulfil basic assumptions behind regression procedures. Even if one succeeds in reducing the variation caused by weather (a component of the coefficient of variation, CV), the statistical and biological significance of this reduction remains to be documented. The CVs in Hussell's weather-corrected migration indices (Figs 1 and 2 in Hussell et al. 1992), are on average significantly higher than our raw, uncorrected RS- and RA-indices. For six randomly selected series each of 18 years from Hussell et al. (1992), we thus calculated a mean CV of 55 (compare with our Table 6). Possibly the CVs of Hussell would have been even higher without the corrections and back-transformations. Yet, we can hardly conclude that just because our RS and RA have smaller CVs, they are less biased by weather. Reducing the CV is not a sufficient, but only a necessary step towards a better index.

Weather-corrected values of RS and RA could be obtained following the methodological pathway indicated by Hussell (1981, Hussell et al. 1992). However, more simple and practical approaches may turn out to be both statistically and biologically more appropriate, even if empirically derived. For example, one simple correction would be to omit from the calculation of yearly indices those days in which the general weather situation (or certain weather factors) forecast a very low rate of immigration (RS and RA then have to be expressed as the means of the days considered). Likewise, the influence of unusually high daily numbers could be dampened by transformation, using a function like, e.g., $n^{0.9}$ (logarithmic transformation, like log (n + 1), tends to result in too excessive a dampening, see Rabøl & Lyngs 1988). In the case of RS and RA, a criterion for improvement could be that, after correction, they correlate significantly better with each other and with the point-count indices – not necessarily in all species, but on the average.

Concluding remarks

The conclusions of the present study contradict several previous reports of widespread declines in European songbird populations. In addition to differences in methodology and the geographical area covered, the conflicting results may partly be traced to the different time periods of the studies. Our ringing data for 1976-1993 (RS and RA) correlated negatively with year when averaged over species, but the correlation disappeared when the three years 1994-1996 were included; only RS for the long-distance migrants alone barely remained significant. Periods of decline are also apparent in the graphs for several long-distance migrants in Figs 4-7, especially during the 1980s. However, such periods are offset by periods of increase and no overall significant decline is detected in any of the 29 species whether measured in the period 1976-1993 or 1976-1996.

So, are a majority of our songbird species really declining at present? There seems to be solid

Sedge Warbler. Photo: Johanna M. Hartmann.

Willow Warbler. Photo: Lone Eg Nissen.

To sangere med meget forskellige mønstre i fangsterne på Christiansø gennem årene. Løvsanger (t.h.) har optrådt stabilt uden op- eller nedadgående tendenser. Sivsangeren (t.v.) lå på et meget lavt niveau gennem firserne, men efter 1993 er tallene steget dramatisk, især om efteråret.

evidence that populations of species depending on man-made agricultural landscapes have decreased in Europe during the last decades as agricultural land-use changed (Fuller et al. 1995, Siriwardena et al. 1998). Also, the significant, human-inflicted changes in the atmospheric concentration of carbon dioxide and in the global nitrogen cycle (Vitousek 1994) may have significant long-term effects on the species composition and the densities of bird communities. Nevertheless, such effects of global climatic change have yet to be demonstrated unambiguously at the community level (but see Hughes 2000). On the other hand, it seems clear that the profound changes incurred by agriculture and felling of primary forests (e.g., Vitousek 1994, Newton 1995) have had a negative influence on many local bird species. But, is there any substantial, scientific evidence that the environmental conditions on breeding grounds, migratory routes, or wintering areas have changed so much within the last 20-30 years that there is a *general* decline in European songbird populations? For the Baltic populations, the time-trends in RS and RA, and in DK, SW, and SF, clearly do not support such a scenario.

Summary

Large numbers of migrant passerines were ringed during spring and autumn on the small Danish island of Christiansø in the Baltic Sea. For the period 1976-1996 we investigated the population trends using catches (corrected for trapping effort) of 29 species as population indices. Populations of most species remained stable; only three species showed a tendency to decline in spring or autumn, and two species to increase. Seen at a finer time scale, numbers of most species increased during the first 6-9 years, decreased during the following 10-12 years, and then increased again. The spring and autumn indices of migrants on Christiansø appear to reflect the variations in the populations involved, although they correlate rather poorly with the point- or summer-count indices from Sweden, Denmark, or Finland. A major cause of the poor correlation probably is that point-count indices mainly track the singing, territorial males, whereas ringing of migrants monitors both sexes and all age-classes, with some over-representation of the young population segments.

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Resumé

Ændringer i bestandsstørrelserne af trækkende spurvefugle i Østersøområdet belyst gennem ringmærkning på Christiansø og punkt- og sommertællinger i Danmark, Sverige og Finland

I perioden 1976-1997 fungerede Christiansø som ringmærkningsstation med det overordnede formål at monitere de rastende trækfuglebestande (Rabøl & Lyngs 1988, Rabøl 1999). I denne artikel præsenterer vi variationerne i mærkningstallene forår og efterår gennem de 18 år fra l976 til 1993 og sammenligner dem med punkttællingsindexer (som formodes at afspejle ynglebestandenes størrelser) for Danmark, Sverige og Finland. Vi sammenligner også forårs- og efterårstallene fra Christiansø med hinanden for at se, om de svinger i takt, hvad der vil være indikation på, at de trækfugle, der raster på øen forår og efterår, kommer fra samme bestand. Endelig ser vi også på tidsudviklingen i forårs- og efterårsringtallene helt frem til 1996 for at se, om bestandene går op eller ned. Da stationen startede i 1976 var det med en vis forventning om bestandsnedgange både på kortere og længere sigt, baseret i antagelser om en eskalerende regional/global landskabsforarmning og forurening. I denne artikel kan vi så bringe det gode budskab, at sådanne nedgange ikke er sket, eller i hvert fald ikke er generelle.

Vi har set på de 29 mest almindelige og regelmæssige arter, der fanges på Christiansø. Der er ringmærket dagligt i perioderne 15. marts – 15. juni og 1. august – 15. november, og der er korrigeret for den daglige fangstindsats således, at det daglige, korrigerede ringtal svarer til fangsten i 60 meter net i de første 5 timer efter solopgang. De daglige, korrigerede ringtal er derefter summeret for hele forårsperioden (RS) og for hele efterårsperioden (RA). RS og RA antages at variere i takt med det antal trækfugle af den pågældende art, der passerer øen i den pågældende sæson.

De 29 arter kan deles i nogle hovedgrupper: 1) 9 kort- og mellemdistancetrækkere, der overvintrer i Vesteuropa eller det vestlige Middelhavsområde, 2) 18 langdistancetrækkere, der overvintrer i tropisk Afrika syd for Sahara, og 3) 2 langdistancetrækkere, der overvintrer i Indien. Afrika-trækkerne kan igen deles i tre lige store undergrupper: SV-, S- og SØ-trækkerne.

På Fig. 3-8 har vi vist variationerne fra år til år i RS og RA, dels for de enkelte arter og dels for hovedgrupperne. Fig. 9 viser variationerne i de danske, svenske og finske punkt- og sommertællingsindexer for de samme arter, der indgår i RS og RA. Som det fremgår af Tabel 2-5 er der som oftest positive og ind imellem særdeles signifikante korrelationer mellem diverse indexer (især mellem punkttællingerne i Danmark og Sverige, og Sverige og Finland). Konklusionen af disse sammenligner er, at indexerne svinger rimeligt i takt med de sande bestandsstørrelser.

Det er op til læseren at gå på jagt i tabeller og figurer efter det index eller den eller de arter, der har hans/hendes interesse. Med kendskab til de her publicerede resultater beskrev Rabøl (1999) på dansk i mere generelle vendinger selve moniteringen på Christiansø samt den overordnede sammenhæng med, og udviklingen i de danske, svenske og finske punkttællinger, og vedr. de spørgsmål kan henvises til denne tekst.

Hvis vi ved hjælp af en såkaldt Bonferroni-procedure tager hensyn til den tilfældige variation i hele gruppen af 29 korrelationskoefficienter mellem RS og tiden eller mellem RA og tiden (1976-1996), så er der ingen af arterne gået statistisk signifikant frem eller tilbage over de 21 år. De tre nedgange og to opgange (markeret med stjerner i Tabel 4) er altså kun signifikante, hvis de betragtes løsrevet fra hvordan alle de andre arter opfører sig.

En tredje måde – der forekommer relevant, når spørgsmålet er om arterne generelt går tilbage – er at teste en gruppe af arter under ét og se, om middelværdien statistisk afviger fra nul (= ingen ændring). RS for de alle 29 arter 1976-1996 giver som gennemsnitlig korrelationskoefficient (Fig.4) -0.082, hvad der ikke signalerer en generel nedgang (dette ville kræve en middelværdi på -0.103). Ser vi på gruppen af 20 langdistance trækkere er middelværdien (-0.124) dog signifikant på 5% niveauet (grænsen går ved -0.118). RA viser ingen tydelige tendenser til generel nedgang (middelværdien er -0.051, hvor grænsen er -0.110).

Hvilke tendenser, man får, afhænger meget af den betragtede periode. Rabøl & Lyngs (1988) fandt således opgange for de fleste arter i de første 9 år, men for 18-års perioden 1976-1993 (Tabel 1) fås signifikante nedgange i såvel RS som RA. Middelværdierne kan beregnes til henholdsvis -0.171 og -0.148, og fire arter (Rødstjert, Sivsanger, Rørsanger og Havesanger) går, isoleret betragtet, signifikant tilbage både forår og efterår. Men i den lidt længere periode fra 1976 til 1996 sker der altså ingen dramatiske eller vedvarende nedgange i de trækfuglebestande, der raster på Christiansø.

Som det fremgår af sidste kolonne i Tabel 6 og Fig. 8 er indextallene ret ens forår og efterår, selv om vi burde forvente ca dobbelt så store indextal om efteråret. Efterårsbestanden er jo meget større end forårsbestanden. Årsagen er, at andelen af ungfugle i efterårsfangsterne på Christiansø er ca 90% for mange arter (f.eks. Broget Fluesnapper). Hvorfor så få gamle fugle går ned på øen om efteråret er så en anden historie.

Det er også klart, at nogle af de meget store forskelle (Fig. 3-8) i RS eller RA fra et år til et andet – eller fra RS til RA samme år, eller fra RA til RS næste år – må skyldes vejrets indflydelse på tiltrækket. Vi ved, at tåge, kraftig vind eller klart højtryksvejr resulterer i et meget ringe tiltræk af af fugle. Hvis sådanne vejrtyper dominerer i en given sæson, resulterer det i lave indexværdier. På længere sigt håber vi at blive i stand til at korrigere indexerne for vejrbetingede udsving, så de kommer til at svinge bedre i takt med de sande bestandsstørrelser.

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