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Long-term population declines in Danish trans-Saharan migrant birds

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Capsule Long-distance migrant birds show less favourable trends than sedentary/short-distance species.
Aims To use breeding bird surveys to contrast population trends amongst common species according to their migration pattern.
Methods Changes in abundance of 62 Danish breeding sedentary, short-distance (Europe/North Africa) or long-distance (trans-Saharan) migrants were described by fitting log linear regression models to point-count census data gathered during 1976–2005.
Results Trans-Saharan migrants declined by 1.3% per annum during this period, while short-distance migrants and sedentary species increased by 1.4% and 1.0% per annum, respectively. There were no significant decadal declines amongst species using different summer breeding habitats, except for wetlands, and there was no consistent variation in trends associated with wintering regions or habitats or diet.
Conclusions More information is urgently needed on diet, feeding ecology, habitat requirements, winter distribution and intra-African movements of the commoner European summer visitors to identify causes of the declines and highlight when in the annual cycle detrimental effects occur. Studies linking individuals on their breeding, staging and wintering grounds are especially needed. Danish trends resemble those from elsewhere in Europe, confirming that restoration to favourable conservation status requires inter-continental action to meet European and global targets to reduce or halt biodiversity loss.

European Union states are required to maintain naturally occurring wild bird populations (Directive 79/409/EEC, hereafter the Birds Directive) and reduce or halt biodiversity loss by 2010 (following the Gothenburg Summit 2001). Effective conservation of long-distance migratory birds poses a particular challenge, because throughout the annual cycle they exploit geographically discrete 'survival habitats', 'breeding habitats' (*sensu* Alerstam & Högstedt 1982) and critical refuelling sites along migratory corridors between ultimate destinations. Hence, factors affecting survival and reproductive output may operate throughout the annual cycle, affecting overall population size in any given country (including so-called carry-over effects, Norris 2005), but not necessarily subject to political or nature conservation influence by that state.

The EU Birds Directive and the African Eurasian Waterbird Agreement (AEWA) recognize that shared natural resources, especially where human exploitation (such as hunting) potentially affects survival rates, require a common approach to effective conservation management. Many terrestrial birds undertake trans-continental migrations, especially between African wintering areas and European nesting grounds, and evidence is mounting that species with contrasting migration strategies show different population trends (Berthold *et al.* 1998, Sanderson *et al.* 2006).

To meet obligations relating to migratory bird conservation and biodiversity loss, it is essential to identify declining species and the causes of declines to confirm the root problem and target effective management actions. Macro-environmental factors operating in Africa are known to affect the population dynamics of migratory passerines breeding in Europe. For example, rainfall (perhaps as a proxy for food availability) in the Sahel in west Africa has been linked to population change in several western European passer-

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*Correspondence author. Email: tfo@dmu.dk ine species, especially during the droughts of the 1980s (Peach *et al.* 1991, Baillie & Peach 1992, Bryant & Jones 1995, Cowley & Siriwardena 2005). The Sahel is particularly important for staging inter-continental migrants crossing the Sahara to and from European breeding areas, some of which continue on into other parts of Africa (Jones *et al.* 1996). Although rainfall has increased in the western Sahel since the 1990s, this has not attained the levels reached prior to the 1980s (Nicholson *et al.* 2000, Grist & Nicholson 2001, Foley *et al.* 2003). Intensified agricultural use and wood gathering are thought to have contributed to wide-scale desertification and habitat degradation over the last three decades (Jones 1985, Morel & Morel 1992, Thiollay 2006), with natural habitat loss exceeding 60% across the region (Leisinger & Schmidt 1995).

Despite good reasons for suspecting that habitat change in sub-Saharan Africa has contributed to passerine migrant population change, the possibility remains that declines result from factors on the breeding grounds. Climate change may also enable short-distance migrants to return earlier to breeding grounds (Forchhammer *et al.* 2002) and shift wintering areas northwards (Lemoine & Böhning-Gaese 2003, Bearhop *et al.* 2005). This potentially gives short-distance migrants and sedentary species a competitive advantage over long-distance migrants, whose spring migration phenology is more influenced by conditions on the winter quarters (Gordo *et al.* 2005). It is therefore essential that we gather more evidence to test the hypothesis that trans-Saharan migrants are showing consistent differences in population trends compared to shorter-distance migrants and more sedentary populations, and that we attempt to understand dietary, habitat and geographical patterns that may help explain the changes in abundance.

In this paper, we use 30 years of common bird monitoring data from point counts from within a restricted area of the western European breeding grounds (Denmark) to compare long-term (1976–2005) and shorter term (1996–2005) changes in abundance of 62 species of contrasting ecology, migration patterns, diet and habitat use. Denmark has not witnessed the same level of declines in abundance of common (but largely resident) terrestrial birds witnessed elsewhere in western Europe, especially those associated with farmland (Fox 2004). In particular, we test whether changes are coincident in time since the 1970s amongst trans-Saharan African migrants compared to those showing other migrant categories, and attempt to detect any consistent patterns to account for changes associated with common breeding or wintering habitats, diet, or wintering region.

MATERIALS AND METHODS

Point-count data for 62 breeding passerines were derived from the Common Birds Census in Denmark 1976–2005 (Heldbjerg 2005, 2007) and used to construct population trends in abundance for 62 breeding passerines in Denmark. We make no attempt to account for differential detection probabilities inherent in such point counts (Williams *et al.* 2002), but make the presumption that factors such as weather, habitat, time and observer effects are unlikely to generate systematic patterns of change in abundance of individual species across different migration categories. Numbers of censused point-count routes increased from less than 100 in the first few years to more than 300 in the last two decades (Heldbjerg 2005). Because of this difference in effort, annual abundance indices were generated for 46 species during 1976–2005 (starting with the index set to 100); 16 other species were included from only 1986 to 2005 because of poor coverage in earlier years (Heldbjerg 2005).

Trends were calculated by fitting a log linear regression model to point-count data with Poisson error terms using the software TRends and Indices for Monitoring data (TRIM, Pannekoek & van Strien 2001), where the count at a given site in a given year is assumed to be the result of an interaction between a site and a year effect. The program also estimates the dispersion factor, correcting for overdispersion where this occurs, and takes account of serial correlation between counts at the same site in different years. Standard errors for the indices are generated based on the assumption that the variance is proportional to the mean, and on a pattern of serial correlation which declines exponentially with time between counts (Pannekoek & van Strien 2001).

To test for significant change in relative abundance, we fitted regression models to the long-term trends for each migration category using the Linear Trend model in TRIM, with a break point set in 1996. The trends for 1996–2005 were also computed in order to show recent trends and compare the short-term (decadal) trends with long-term (three-decade) trends. Whilst we acknowledge that fitting of linear trends over longer (30-year) periods may smooth much variation, we are here interested in comparing general patterns in the long-term trajectories of migratory bird species. For this reason, we leave more complex modelling and interpretation for a future analysis and concentrate here on comparisons between different migration patterns.

Fitting of a linear trend to long-term changes in species abundance risks obscuring more detailed patterns or stepped phase changes within the time frame. We are here also interested in undertaking comparisons between species to gain insight about temporal patterns of change in abundance that are common to species sharing similar migration strategies, wintering habitats or winter quarters. We therefore compared the mean index values derived from each of the three decades 1976–85 (D1), 1986–95 (D2) and 1996–2005 (D3) for each species. In this way, we derive information about the mean population level in each decade and rate of change between decades in each of the populations. Although ultimately arbitrary, we considered that decades were of sufficient duration to obscure short-term perturbations in abundance, but long enough to provide valid comparisons over longer time periods, potentially obscured by the linear modelling. Tests for significant differences between the index values in each of the time periods were undertaken using a one-way ANOVA; *a posteriori* multiple comparisons were made by the Holm–Sidak method or Student *t*-tests, performed in SigmaStat 3.11 (SigmaStat 2004) or SAS 9.13 (SAS 2007).

Each common Danish breeding species was categorized according to its known winter quarters: long-distance migrants wintering in Africa south of Sahel (trans-Saharan migrants), short- and medium-distance migrants wintering in Europe and North Africa (north of Sahel, here termed European migrants) and sedentary species wintering in or close to Denmark. Blackcap (see Table 1 for scientific names) is considered as being a European migrant even though there is a migratory divide through Denmark with a minor part of the eastern Danish breeding birds following an eastern route to Africa (Bønlykke *et al.* 2006).

We combined the individual species' annual TRIM index values to calculate annual geometric mean multi-species indices (hereafter 'composite index') for each of the three migratory categories to generate time series following the methods (including the generation of standard errors) of Gregory *et al.* (2005). Although potentially simplistic, we adopted this procedure to give equal weight to each species index in the indicator as a proxy for change in the migrant communities, rather than directly using or individually weighing their abundances. The use of the geometric mean (rather than the arithmetic one) equates an index change from 200 to 100 to that from 100 to 50.

As well as calculating trends for individual species (Heldbjerg 2005) and generating multi-species indices from their annual values, TRIM was also used here to generate trends for species sharing migration strategies. For these calculations, TRIM was run on combined abundance data from all species within each of the three migration categories to generate a multi-species trend (hereafter 'migration group index') to contrast trends between migration categories.

Declines amongst trans-Saharan migrants could be due to specific factors acting upon populations on the breeding grounds, for example, because they also share common breeding habitat. For this reason, we also analysed changes in abundance with regard to breeding habitat, defined for each species following Tucker & Evans (1997) and grouped according to (1) forest, (2) farmland, (3) wetland, (4) others; the last group consists of species with a preference for any other habitat or one which is common in more than one habitat type (Table 1). We compared mean decadal indices statistically for each of the species groupings following Sanderson *et al.* (2006), presenting an assessment of the variance within each group to visualize the differences and changes over time, rather than undertaking more sophisticated multivariate modelling.

Using the same approach, we also classified each species according to dominance in diet of foods on the breeding areas (insectivores, omnivores and seed-eaters) after Cramp (1977–94). We also looked for differences in patterns of change in species abundance according to wintering habitat of the trans-Saharan migrants, based on the assumption that dry savannah and scrub areas have been subjected to the greatest habitat degradation and loss. We classified each species using information from Cramp (1977–94), grouped after Sanderson *et al.* (2006) into the following habitat types: (1) forest or wooded savannah, (2) wet grassland or wetland, (3) dry savannah, grassland or other dry open habitats, (4) freshwater or coastal, (5) all terrestrial habitat (Table 2). Finally, we looked for differences between regions of Africa (simply divided into east, central, west and south) for contrasting trends in species based on information from, and the regional classification used by, Cramp (1977–94).

RESULTS

Long-term trends amongst species

Thirty-four out of 46 (74%) passerine species breeding in Denmark showed a significant trend over the period

Table 1. Long-term and short-term trends in abundance for 62 passerine breeding birds in Denmark based on fitted log linear models to point-count data described in the text.

Species	Total number	1976–2005 (%/year)	1986–2005 (%/year)	1996–2005 (%/year)	Migratory strategy	Breeding habitat
Skylark *Alauda arvensis*	141 872	–1.5		–4.96*	European	Farmland
Sand Martin *Riparia riparia*	23 397	–5.07*		–5.91*	Trans-Saharan	Wetland
Barn Swallow *Hirundo rustica*	90 773	–1.04		–0.9*	Trans-Saharan	Farmland
House Martin *Delichon urbicum*	42 371	1.3		1.36	Trans-Saharan	Farmland
Tree Pipit *Anthus trivialis*	18 374	–1.13*		0.3	Trans-Saharan	Forest
Meadow Pipit *Anthus pratensis*	5270		–2.31*	–3.29*	European	Farmland
Yellow Wagtail *Motacilla flava*	1426		–6.46*	–11.18*	Trans-Saharan	Farmland
Pied Wagtail *Motacilla alba*	12 492	3.02		0.68	European	Farmland
Wren *Troglodytes troglodytes*	48 836	2.62*		1.59*	European	Other
Dunnock *Prunella modularis*	10 323	–2.9*		0.83	European	Other
Robin *Erithacus rubecula*	25 501	0.37		–2.03*	European	Forest
Thrush Nightingale *Luscinia luscinia*	19 375	–1.42*		–1.6*	Trans-Saharan	Wetland
Common Redstart *Phoenicurus phoenicurus*	4276	1.55*		2.64*	Trans-Saharan	Forest
Whinchat *Saxicola rubetra*	3518	–4.25		–7.48*	Trans-Saharan	Farmland
Blackbird *Turdus merula*	178 323	1.26*		–0.26	Sedentary	Other
Fieldfare *Turdus pilaris*	4391		–3.2*	–11.5*	Sedentary	Farmland
Song Thrush *Turdus philomelos*	29 995	–0.44*		4.04*	European	Other
Mistle Thrush *Turdus viscivorus*	2418		–1.71*	–3.67*	European	Forest
Grasshopper Warbler *Locustella naevia*	924		–5.45*	–12.34*	Trans-Saharan	Wetland
Sedge Warbler *Acrocephalus schoenobaenus*	1870		–0.62	–1.81	Trans-Saharan	Wetland
Marsh Warbler *Acrocephalus palustris*	7400	0.91*		2.46*	Trans-Saharan	Wetland
Reed Warbler *Acrocephalus scirpaceus*	13 357	–1.03*		–1.71*	Trans-Saharan	Wetland
Icterine Warbler *Hippolais icterina*	8318	–4.2		0.89	Trans-Saharan	Farmland
Lesser Whitethroat *Sylvia curruca*	9083	–2.63*		2.08*	Trans-Saharan	Other
Common Whitethroat *Sylvia communis*	52 008	0.34		1.79*	Trans-Saharan	Farmland
Garden Warbler *Sylvia borin*	32 100	–1.35*		–1.54*	Trans-Saharan	Forest
Blackcap *Sylvia atricapilla*	42 233	2.76*		3.42*	European	Other
Wood Warbler *Phylloscopus sibilatrix*	4864	–3.62*		–9.18*	Trans-Saharan	Forest
Common Chiffchaff *Phylloscopus collybita*	27 341	5.72*		1.41*	European	Forest
Willow Warbler *Phylloscopus trochilus*	77 588	–2.94*		–4.24*	Trans-Saharan	Forest
Goldcrest *Regulus regulus*	12 976	–1.09*		0.94	Sedentary	Forest
Spotted Flycatcher *Muscicapa striata*	1561		0.31	–1.97	Trans-Saharan	Forest

continued

1976–2005 and an additional nine out of 16 (56%) during 1986–2005 (Table 1). During these two periods, 63% of all 62 species showed significant declines (Table 1). During 1996–2005, 37 out of 62 species showed significant trends, of which 24 (65%) were declining.

Differences in long-term trends between migration categories

Using TRIM indices to generate migration group index trends during 1976–2005 amongst all species grouped by migration category, trans-Saharan migrants showed a significant negative trend (mean decline of 1.27% per annum, $P < 0.01$, $n = 21$) compared with significant positive trends amongst European migrants (1.38% per annum, $P < 0.01$, $n = 16$) and for sedentary species (0.95% per annum, $P < 0.01$, $n = 25$). The patterns of change in composite trends, based on individual species trajectories grouped by migration category, are shown in Fig. 1.

In the remaining results, presentation of indices is based only on migration group indices, by fitting TRIM indices to original abundance measures of all species grouped into a multi-species index. The rate of decline amongst trans-Saharan migrants was greatest in D3 (–2.37% per annum ± 0.76 se, $P < 0.05$), during which period European (–0.61% per annum ± 1.06 se, $P > 0.05$) and sedentary (0.19% per annum ± 0.73 se, $P > 0.05$) species showed no significant trends. There were significant but less marked declines during D1 and D2 combined for trans-Saharan migrants (–0.87% per annum ± 0.34 se, $P < 0.05$), when both European (1.91% per annum ± 0.54 se, $P < 0.05$) and sedentary

Table 1 continued.

Species	Total number	1976–2005 (%/year)	1986–2005 (%/year)	1996–2005 (%/year)	Migratory strategy	Breeding habitat
Pied Flycatcher *Ficedula hypoleuca*	2156	–2.82*		–8.93*	Trans-Saharan	Forest
Long-tailed Tit *Aegithalos caudatus*	1395		–1.34	–0.5	Sedentary	Wetland
Marsh Tit *Poecile palustris*	3392	–1.97*		–1.55	Sedentary	Forest
Crested Tit *Lophophanes cristatus*	1600		–2.35*	–2.08	Sedentary	Forest
Coal Tit *Periparus ater*	12 384	–1.49*		–6.41*	Sedentary	Forest
Blue Tit *Cyanistes caeruleus*	19 974	0.72*		–2.49*	Sedentary	Other
Great Tit *Parus major*	71 852	–0.95*		–0.61	Sedentary	Other
Nuthatch *Sitta europaea*	3798	2.07*		–0.07	Sedentary	Forest
Common Treecreeper *Certhia familiaris*	1724		1.96*	1.91	Sedentary	Forest
Red-backed Shrike *Lanius collurio*	1132		–1.85	1.84	Trans-Saharan	Farmland
Eurasian Jay *Garrulus glandarius*	9116	0.19		–0.84	Sedentary	Forest
Magpie *Pica pica*	30 210	0.67		0.94*	Sedentary	Farmland
Jackdaw *Corvus monedula*	44 176	–0.06		–0.72	Sedentary	Farmland
Rook *Corvus frugilegus*	93 616	1.56*		0.64	Sedentary	Farmland
Carrion/Hooded Crow *Corvus corone/cornix*	107 713	1.03*		0.41	Sedentary	Farmland
Raven *Corvus corax*	1607		9.29*	4.73*	Sedentary	Farmland
Starling *Sturnus vulgaris*	174 983	–1.79*		–2.34*	European	Farmland
House Sparrow *Passer domesticus*	57 193	–1.92*		–2.77*	Sedentary	Other
Tree Sparrow *Passer montanus*	33 368	2.5*		2.4*	Sedentary	Farmland
Chaffinch *Fringilla coelebs*	166 516	0.82*		0.03	European	Forest
Greenfinch *Carduelis chloris*	30 820	2.15*		–0.91	Sedentary	Other
Goldfinch *Carduelis carduelis*	3405		7.25*	–0.28	Sedentary	Farmland
Linnet *Carduelis cannabina*	22 526	–2.01*		–5.81*	European	Farmland
Redpoll *Carduelis cabaret*	2753		1.09	–7.75*	European	Forest
Common Crossbill *Loxia curvirostra*	4405		–1.97	–9.89*	European	Forest
Bullfinch *Pyrrhula pyrrhula*	3309	0.99		–6.02*	Sedentary	Forest
Hawfinch *Coccothraustes coccothraustes*	1628		–1.09	–2.69	Sedentary	Forest
Yellowhammer *Emberiza citrinella*	74 115	–2.26*		–3.23*	Sedentary	Farmland
Reed Bunting *Emberiza schoeniclus*	11 750	–1.15*		0.55	European	Wetland
Corn Bunting *Emberiza calandra*	7310	–2.71*		5.44*	Sedentary	Farmland

The mean annual percentage change in abundance index for the last 30, 20 and 10 years is shown for species for which these data are available. Asterisks indicate rates of change that attain statistical significance at $P < 0.05$ (with sample sizes showing number of bird encounters that contribute to index generation). Also shown are the classification of species according to migration category and breeding habitat following Sanderson *et al.* (2006).

(1.18% per annum ± 0.39 se, $P < 0.05$) species showed significant increases.

Population level changes between the last three decades

Decadal index values computed for each of the last three decades showed that 69% of trans-Saharan migrants showed decreasing abundance, compared with 33% and 28% for European migrants and sedentary species, respectively (Table 3). The patterns for the European migrants and sedentary species were very similar (Table 4). Largest declines among trans-Saharan migrants occurred between D2 and D3, whereas the largest increases among the European migrants and the sedentary species occurred between D1 and D2.

Short-term (decadal) versus long-term (three-decade) trends

Migration categories

During 1996–2005 (D3), more species showed significant declines (25) than were significantly increasing (12; Table 1). Of the 62 species considered here, 28 showed a significant long-term trend as well as a significant short-term trend. Only Blue Tit significantly increased over the long term but significantly decreased in the short term. Three species (Song Thrush, Lesser Whitethroat and Corn Bunting) showed significant declines over the last 30 years, but significantly increased in D3. Most species (24) maintained the same significant trend independent of the length of the time series. The mean annual change per year was significantly highly correlated between the long-term

Table 2. African wintering region and wintering habitat classification for all long-distance migrant passerines breeding in Denmark.

Species	Wintering region[a]	Winter habitat[b]
Sand Martin *Riparia riparia*	West Africa	All terrestrial
Barn Swallow *Hirundo rustica*	South Africa	All terrestrial
House Martin *Delichon urbicum*	South Africa	All terrestrial
Tree Pipit *Anthus trivialis*	Central Africa	Forest or wooded savannah
Yellow Wagtail *Motacilla flava*	West Africa	Dry open habitats
Thrush Nightingale *Luscinia luscinia*	East Africa	Forest or wooded savannah
Common Redstart *Phoenicurus phoenicurus*	West Africa	Forest or wooded savannah
Whinchat *Saxicola rubetra*	West Africa	Dry open habitats
Grashopper Warbler *Locustella naevia*	West Africa	Wet grassland or wetland
Sedge Warbler *Acrocephalus schoenobaenus*	West Africa	Wet grassland or wetland
Marsh Warbler *Acrocephalus palustris*	East Africa	Forest or wooded savannah
Reed Warbler *Acrocephalus scirpaceus*	West Africa	Dry open habitats
Icterine Warbler *Hippolais icterina*	South Africa	Forest or wooded savannah
Lesser Whitethroat *Sylvia curruca*	East Africa	Forest or wooded savannah
Common Whitethroat *Sylvia communis*	West Africa	Dry open habitats
Garden Warbler *Sylvia borin*	Central Africa	Forest or wooded savannah
Wood Warbler *Phylloscopus sibilatrix*	Central Africa	Forest or wooded savannah
Willow Warbler *Phylloscopus trochilus*	West Africa	Forest or wooded savannah
Spotted Flycatcher *Muscicapa striata*	Central Africa	Forest or wooded savannah
Pied Flycatcher *Ficedula hypoleuca*	West Africa	Forest or wooded savannah
Red-backed Shrike *Lanius collurio*	East Africa	Dry open habitats

[a]After Cramp *et al.* (1977–94). [b]After Sanderson *et al.* (2006)

trends and the short-term trends (Pearson correlation, $n = 28$, $r = 0.704$, $P < 0.0001$).

There was no significant difference between the mean of the percentage annual change for the three migration categories for the short-term trends ($F = 0.908$, df = 2, $P = 0.409$), although all showed negative tendencies (mean annual change value for the trans-Saharan migrants –2.640 ± 4.724 se, European migrants –1.699 ± 3.983, sedentary species –1.021 ± 3.466).

Calculating the mean percentage change amongst all trans-Saharan migrants from D1 to D2 and from D2 to D3 showed significant declines in both periods ($t_{15} = 2.53$, $P = 0.023$ and $t_{20} = 2.60$, $P = 0.017$, respectively, Fig. 2). This was not the case amongst European migrants or sedentary species ($0.56 > t > 1.15$, $P > 0.27$, Fig. 2).

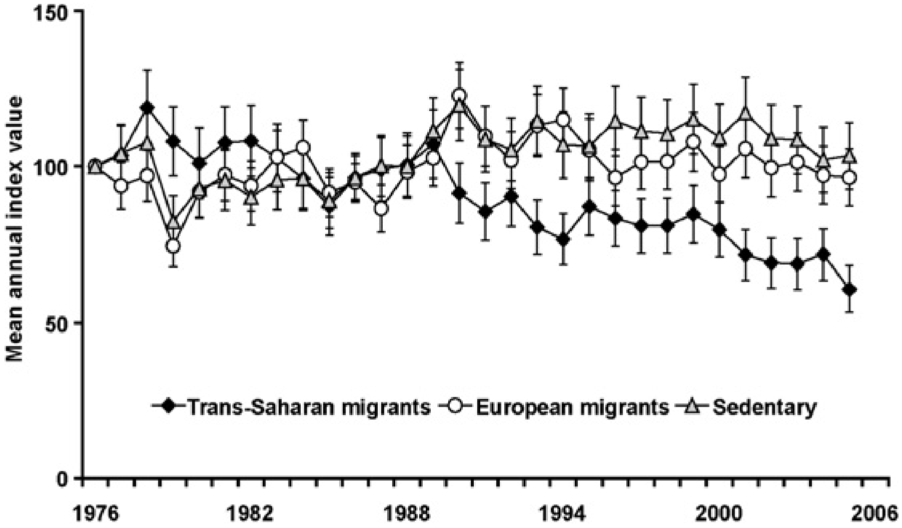

Figure 1. Result of log linear model fitting to Danish breeding bird point-count data, showing annual geometric mean of abundance indices (± se) for the period 1976–2005 for species grouped by their three discrete migration categories (see Table 1 for assignment of species to categories).

Breeding habitats, wintering regions and habitats and diet

Danish wetland breeding birds showed significant declines between D2 and D3 (t_7 = 2.44, P = 0.045), otherwise none of the changes between decades for breeding habitat categories differed significantly from zero change (t-tests P > 0.27, Fig. 2). None of the changes between decades differed significantly from zero change in any of the wintering areas, habitats or diet categories (Fig. 2, diet categories not illustrated), although those in west Africa came closest to differing significantly from zero change between D1 and D2 (t_6 = 2.00, P = 0.092) and D2 and D3 (t_9 = 2.12, P = 0.063).

DISCUSSION

International legislation requires signatory states to maintain migratory passerine populations, despite our rudimentary understanding of factors limiting and

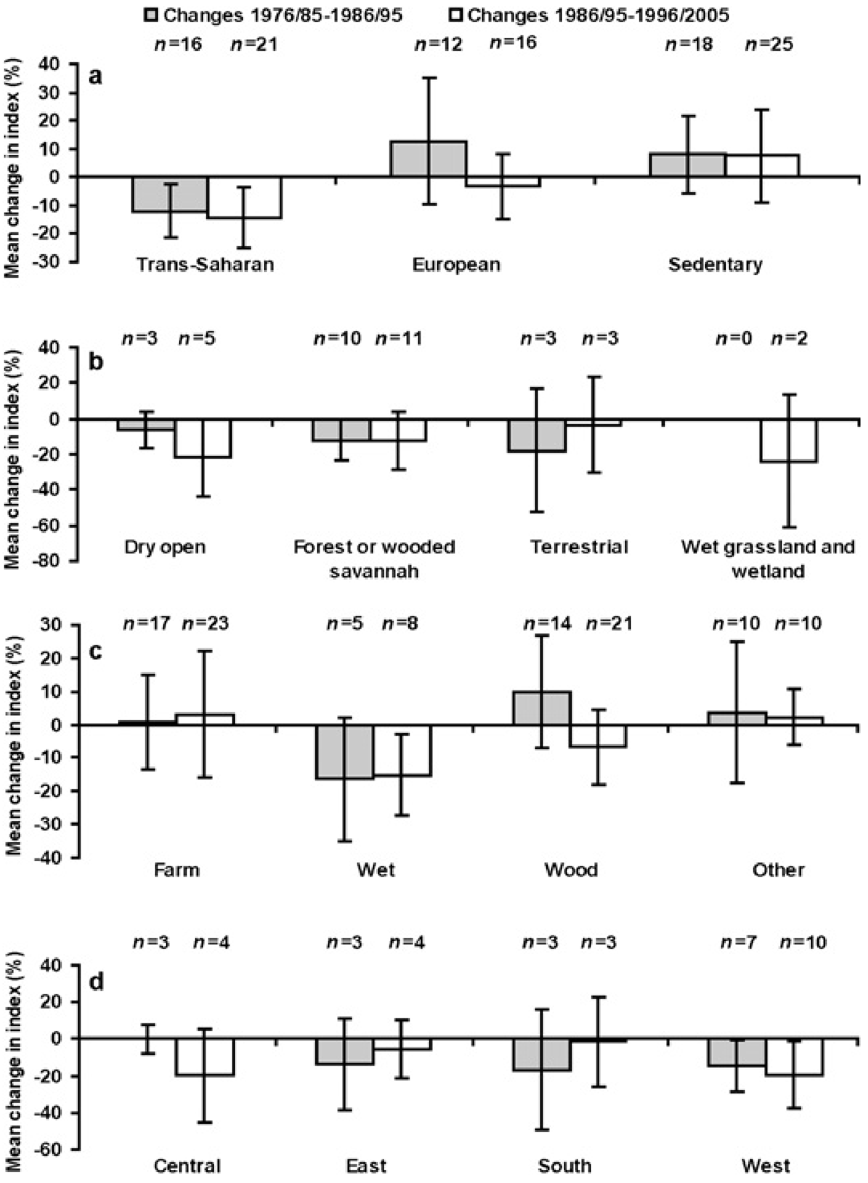

Figure 2. Histograms showing the mean percentage change in index values generated by log linear modelling of Danish breeding bird point-count data over the last three decades (±95% confidence intervals). All species are grouped according to their wintering grounds (a) and breeding habitat (c). Data are also presented for trans-Saharan migrants, grouped according to their winter habitat (b) or wintering area within Africa (d). See text for definitions of categories and data sources.

Table 3. Mean decadal index value for 62 passerine breeding birds in Denmark based on fitted log linear models to point-count data described in the text.

Species	*F*	*P*	1976–85 (D1)	1986–95 (D2)	1996–2005 (D3)	D1 vs D2	D1 vs D3	D2 vs D3
Skylark *Alauda arvensis*	8.12	0.002	75.2 ± 13.2	68.6 ± 4.0	57.7 ± 9.8	No	Yes	Yes
Sand Martin *Riparia riparia*	10.24	<0.001	66.1 ± 37.6	31.7 ± 5.8	23.6 ± 6.6	Yes	Yes	No
Barn Swallow *Hirundo rustica*	3.31	0.052	81.8 ± 14.5	73.6 ± 10.7	69.0 ± 7.3			
House Martin *Delichon urbicum*	6.66	0.004	113.7 ± 19.5	122.9 ± 22.1	149.7 ± 26.7	No	Yes	Yes
Tree Pipit *Anthus trivialis*	4.12	0.027	124.5 ± 17.9	126.6 ± 34.6	100.3 ± 6.0	No	Yes	Yes
Meadow Pipit *Anthus pratensis*	11.15	0.004		102.7 ± 16.6	81.0 ± 12.1			Yes
Yellow Wagtail *Motacilla flava*	14.20	0.001		71.3 ± 26.5	37.3 ± 10.4			Yes
Pied Wagtail *Motacilla alba*	22.30	<0.001	132.0 ± 49.0	213.6 ± 23.2	220.7 ± 18.1	Yes	Yes	No
Wren *Troglodytes troglodytes*	6.01	0.007	88.3 ± 29.2	130.3 ± 37.7	136.0 ± 33.3	Yes	Yes	No
Dunnock *Prunella modularis*	37.80	<0.001	75.5 ± 14.9	43.2 ± 6.6	41.2 ± 5.2	Yes	Yes	No
Robin *Erithacus rubecula*	1.76	0.19	132.5 ± 25.3	150.2 ± 26.3	134.0 ± 17.5			
Thrush Nightingale *Luscinia luscinia*	11.64	<0.001	137.6 ± 23.0	130.8 ± 18.0	100.7 ± 11.8	No	Yes	Yes
Common Redstart *Phoenicurus phoenicurus*	24.33	<0.001	98.7 ± 19.4	96.8 ± 12.8	140.4 ± 14.3	No	Yes	Yes
Whinchat *Saxicola rubetra*	26.84	<0.001	111.8 ± 23.3	96.3 ± 23.4	48.9 ± 10.6	No	Yes	Yes
Blackbird *Turdus merula*	23.82	<0.001	91.0 ± 7.8	108.5 ± 11.7	118.0 ± 6.2	Yes	Yes	Yes
Fieldfare *Turdus pilaris*	4.60	0.046		231.9 ± 90.1	159.4 ± 57.4			Yes
Song Thrush *Turdus philomelos*	3.43	0.047	89.4 ± 13.0	77.1 ± 5.4	77.4 ± 15.2	No	No	No
Mistle Thrush *Turdus viscivorus*	15.90	<0.001		99.5 ± 17.2	75.4 ± 8.3			Yes
Grasshopper Warbler *Locustella naevia*	12.70	0.002		129.2 ± 36.4	73.9 ± 32.9			Yes
Sedge Warbler *Acrocephalus schoenobaenus*	0.25	0.624		175.2 ± 44.9	166.5 ± 32.5			No
Marsh Warbler *Acrocephalus palustris*	5.01	0.014	123. ± 14.9	125.4 ± 24.1	145.6 ± 11.3	No	Yes	Yes
Reed Warbler *Acrocephalus scirpaceus*	6.88	0.004	99.4 ± 14.7	90.3 ± 9.0	81.3 ± 7.6	No	Yes	No
Icterine Warbler *Hippolais icterina*	85.47	<0.001	120.3 ± 15.8	61.9 ± 15.4	49.1 ± 4.1	Yes	Yes	Yes
Lesser Whitethroat *Sylvia curruca*	36.99	<0.001	103.1 ± 19.0	62.8 ± 8.4	58.4 ± 7.9	Yes	Yes	No
Common Whitethroat *Sylvia communis*	1.77	0.19	106.2 ± 11.6	109.9 ± 10.2	114.7 ± 8.5			
Garden Warbler *Sylvia borin*	12.23	<0.001	131.6 ± 15.0	121.6 ± 18.4	99.8 ± 9.2	No	Yes	Yes
Blackcap *Sylvia atricapilla*	52.27	<0.001	118.5 ± 15.3	154.1 ± 15.8	202.7 ± 23.3	Yes	Yes	Yes
Wood Warbler *Phylloscopus sibilatrix*	16.05	<0.001	68.8 ± 15.5	72.8 ± 22.3	35.3 ± 7.3	No	Yes	Yes
Common Chiffchaff *Phylloscopus collybita*	52.90	<0.001	147.7 ± 29.9	287.4 ± 77.4	474.3 ± 91.4	Yes	Yes	Yes
Willow Warbler *Phylloscopus trochilus*	38.33	<0.001	93.9 ± 8.2	72.1 ± 11.7	54.3 ± 10.2	Yes	Yes	Yes
Goldcrest *Regulus regulus*	2.74	0.083	75.1 ± 16.4	66.3 ± 22.3	57.3 ± 10.1			

continued

regulating their abundance and distribution (Newton 1998). Northern hemisphere inter-continental migrants have declined in the New and Old Worlds (Robbins *et al.* 1989, Sanderson *et al.* 2006). The relative contributions of changes in non-breeding period survival rates (Baillie & Peach 1992, Rappole & McDonald 1994) compared with factors operating on the breeding grounds (especially those affecting reproductive success, Schmidt 2003) and interactions between the two (Norris *et al.* 2004) are likely to vary between species and have been widely debated (Holmes 2007).

Results presented here are the first to document, from a restricted area of the Palearctic breeding grounds (i.e. Denmark, where many land birds show more favourable conservation status than in neighbouring states), that African-wintering passerines have shown more sustained declines than have European migrant and sedentary species during 1976–2005. The greater propensity for declines amongst trans-Saharan migrants contrasts with more stable or increasing trends amongst sedentary or short-distance migrants, suggesting that limiting or regulating factors have more effect outside of the breeding period than do those operating in Denmark (with the possible exception of wetland breeding species). However, we should be aware that susceptibility to decline may be a consequence of some shared life-history trait characteristic of migrant taxa (which are drawn from varying taxonomic groups). Whilst it would seem worthwhile to control for phylogeny in such an analysis, we have chosen not to do so here because this database offers only four sets of kindred species pairs (after Sanderson *et al.* 2006) to compare

Table 3 continued.

Species	*F*	*P*	1976–85 (D1)	1986–95 (D2)	1996–2005 (D3)	D1 vs D2	D1 vs D3	D2 vs D3
Spotted Flycatcher *Muscicapa striata*	0.19	0.672		105.3 ± 23.0	117.2 ± 20.8			No
Pied Flycatcher *Ficedula hypoleuca*	14.71	<0.001	145.8 ± 33.6	141.5 ± 33.5	81.6 ± 19.7	No	Yes	Yes
Long-tailed Tit *Aegithalos caudatus*	3.92	0.063		110.2 ± 35.9	84.4 ± 20.1			No
Marsh Tit *Poecile palustris*	14.17	<0.001	79.3 ± 15.2	62.2 ± 8.7	53.4 ± 7.7	Yes	Yes	No
Crested Tit *Lophophanes cristatus*	7.55	0.013		70.2 ± 13.0	56.1 ± 9.7			Yes
Coal Tit *Periparus ater*	2.26	0.123	69.6 ± 19.8	62.9 ± 9.0	55.0 ± 15.2			
Blue Tit *Cyanistes caeruleus*	3.31	0.052	82.7 ± 15.4	88.3 ± 10.1	99.1 ± 16.9			
Great Tit *Parus major*	14.75	<0.001	105.9 ± 4.8	90.4 ± 9.8	88.3 ± 8.4	Yes	Yes	No
Nuthatch *Sitta europaea*	7.52	0.003	131.7 ± 34.2	205.0 ± 58.8	187.6 ± 35.2	Yes	Yes	No
Common Treecreeper *Certhia familiaris*	7.46	0.014		126.0 ± 20.3	152.7 ± 23.3			Yes
Red-backed Shrike *Lanius collurio*	0.29	0.596		68.2 ± 22.2	63.7 ± 14.7			No
Eurasian Jay *Garrulus glandarius*	3.01	0.066	106.1 ± 22.0	124.5 ± 16.3	109.2 ± 14.8			
Magpie *Pica pica*	8.36	0.001	116.8 ± 11.6	126.1 ± 10.8	134.7 ± 6.3	No	Yes	No
Jackdaw *Corvus monedula*	0.33	0.724	206.8 ± 56.0	207.5 ± 17.7	196.4 ± 10.0			
Rook *Corvus frugilegus*	19.92	<0.001	135.3 ± 19.4	161.1 ± 16.4	182.9 ± 14.5	Yes	Yes	Yes
Carrion/Hooded Crow *Corvus corone/cornix*	35.3	<0.001	121.2 ± 9.5	134.3 ± 6.9	150.4 ± 6.6	Yes	Yes	Yes
Raven *Corvus corax*	76.07	<0.001		177.4 ± 62.5	474.9 ± 88.0			Yes
Starling *Sturnus vulgaris*	17.54	<0.001	95.7 ± 15.9	80.1 ± 8.7	66.0 ± 6.9	Yes	Yes	Yes
House Sparrow *Passer domesticus*	11.13	<0.001	76.8 ± 18.4	65.9 ± 5.3	52.8 ± 4.6	Yes	Yes	Yes
Tree Sparrow *Passer montanus*	23.38	<0.001	106.9 ± 20.7	169.5 ± 26.1	175.0 ± 27.1	Yes	Yes	No
Chaffinch *Fringilla coelebs*	19.42	<0.001	117.8 ± 12.3	134.4 ± 3.6	137.7 ± 3.4	Yes	Yes	No
Greenfinch *Carduelis chloris*	43.90	<0.001	121.8 ± 22.5	191.8 ± 21.0	189.3 ± 11.3	Yes	Yes	No
Goldfinch *Carduelis carduelis*	28.60	<0.001		251.4 ± 109.7	503.5 ± 100.9			Yes
Linnet *Carduelis cannabina*	9.87	<0.001	64.9 ± 16.1	57.8 ± 8.1	43.4 ± 6.2	No	Yes	Yes
Redpoll *Carduelis cabaret*	0.15	0.705		113.8 ± 54.5	106.8 ± 19.4			No
Common Crossbill *Loxia curvirostra*	0.70	0.416		204.5 ± 183.7	149.9 ± 95.2			No
Bullfinch *Pyrrhula pyrrhula*	2.06	0.147	67.8 ± 25.8	88.5 ± 26.7	89.2 ± 27.8			
Hawfinch *Coccothraustes coccothraustes*	0.17	0.687		73.8 ± 21.2	77.8 ± 22.2			No
Yellowhammer *Emberiza citrinella*	41.44	<0.001	92.2 ± 5.4	80.9 ± 11.1	59.7 ± 6.7	Yes	Yes	Yes
Reed Bunting *Emberiza schoeniclus*	62.04	0.006	67.3 ± 17.2	55.8 ± 4.2	51.5 ± 3.2	Yes	Yes	No
Corn Bunting *Emberiza calandra*	11.85	<0.001	53.7 ± 23.9	24.4 ± 3.8	30.4 ± 4.1	Yes	Yes	No

The results of overall ANOVA tests comparing between decades are shown as *F*-ratio and *P* values, together with the results of Holm–Sidak multiple comparison tests between decades for each species (indicated as attaining statistically significant differences by 'Yes' or otherwise in the comparisons shown in the right-hand columns).

between migration categories, and all species pairs differed sufficiently in breeding habitat and ecology to complicate any such comparisons.

Danish survey results suggest no consistent differences between trends of species wintering in different parts of Africa, although seven out of ten west African species showed significant declines. Only two species increased significantly during 1976–2005: Common Redstart (which winters in west Africa) and Marsh Warbler (east Africa). Whitethroat (west Africa) and Lesser Whitethroat (east Africa) have also increased in abundance over the last ten years, although the Whitethroat has probably recovered from earlier depressed population levels caused by Sahel droughts (Peach *et al.* 1991).

Danish nesting passerines showed no consistent patterns in trends between different wintering habitats, although Sanderson *et al.* (2006), considering a broader range of European nesting species, found that declines were largely confined to passerine species wintering in dry open African habitats.

The Sahel region is important for wintering Palearctic migrants and staging birds ultimately wintering in west, central and southern Africa. This area is currently undergoing significant anthropogenic degradation that is likely to reduce its value in this regard (Wilson & Cresswell 2006). However, we have little information to conclude that this represents cause and effect (Cresswell *et al.* 2007). Despite the work of several authors (Moreau 1966, Jones 1985, Jones *et al.* 1996, Wilson & Cresswell 2006), until very recently there was lamentably little information on winter distributions and habitat requirements of Palearctic migrants in Africa (Walther & Rahbek 2002, Salewski & Jones 2006), and little understanding of the impact

Table 4. Comparisons of population change between the last three decades for 46 Danish passerine breeding bird species for which adequate data are available.

Migration category	Number of species	Population change	1976–85 vs 1996–2005 (%)	1976–85 vs 1986–95 (%)	1986–95 vs 1996–2005 (%)[a]
Trans-Saharan	16/21	Increasing	19	0	14
		Declining	69	25	48
		ns	13	75	38
European	12/16	Increasing	50	50	13
		Declining	33	17	25
		ns	17	33	63
Sedentary	18/25	Increasing	39	33	24
		Declining	28	28	16
		ns	33	39	60

Species are classified according to migration category on the basis of wintering areas. [a]Data based on comparisons of all 62 species.

of habitat loss and degradation on wintering Palearctic migrant populations (Baillie *et al.* 2006).

Some generalist feeding species show high site fidelity and may defend winter territories (e.g. Pied Flycatcher), while more specialist feeders appear to exhibit itinerancy (e.g. Willow Warbler, Salewski *et al.* 2002); such strategies may make species differentially susceptible to local habitat change or destruction. Itinerancy makes it difficult to pinpoint the most important limiting factors in the winter cycle. Even less is known about routes taken by common European-nesting passerines to ultimate wintering habitats, their refuelling strategies and critical staging habitats (with the exception of crossing the Sahara, Salewski & Schaub 2007). More information is needed about habitat selection and feeding ecology (e.g. for Whitethroat, Vickery *et al.* 1999) of common trans-Saharan migrant passerines. Ringing recoveries provide some descriptors of migration routes taken through Europe and the Mediterranean, but information on wintering areas and intra-seasonal movements within Africa is lacking (Bønlykke *et al.* 2006).

We must be prudent in concluding that declines in long-distance migrant passerines since the 1970s are due to factors operating in Africa. Divergent population trends could occur if resident and migrant groups respond differently to similar stressors on the breeding grounds. In North America, it has been hypothesized that differences between migrant and resident population trends reflect differing susceptibilities to nest predation, migrants being smaller and nesting closer to the ground. Afro-Palearctic migrants are both smaller and lay fewer clutches than their sedentary counterparts (Monkkonen 1992), but it seems unlikely that these traits make them more vulnerable to predation.

Alternatively, decreases among long-distance migrants could relate to climate change. Avian migration correlates with spring temperatures and the North Atlantic Oscillation in western Europe (Forchhammer *et al.* 2002). Many European migratory species have advanced their arrival dates (Jonzén *et al.* 2006, Stervander *et al.* 2005, Tøttrup *et al.* 2006). Birds wintering furthest north are the earliest to migrate (Rubolini *et al.* 2005). However, Tøttrup *et al.* (2006) found no differences in changes of arrival dates at the breeding grounds between species wintering in different regions of Africa, and any impact of climate change on long-distance migrants are likely to be complex (Sanderson *et al.* 2006). Nevertheless, for some species, climate-change-induced modifications to the food supply at breeding grounds have caused a mismatch with timing of breeding, which is constrained by arrival to nesting areas and hence laying date (e.g. Pied Flycatcher, Both *et al.* 2006).

In strongly seasonal habitats, warming may advance food availability relative to an inflexible migration template, but also shorten the period of maximum prey abundance (e.g. Lepidopteran larvae pupate more rapidly in elevated temperatures, Buse *et al.* 1999). For this reason, we expect long-distance migrants (and those exploiting most markedly seasonal habitats) to be under greater potential threat from climate change at their nesting areas (Winkler *et al.* 2002). Long-distance migrant species arriving later to breeding areas are likely to be worse affected than those arriving earlier, because they experience a shorter season and have even less flexibility to adjust migration schedules. Competition from resident and short-distance migrants may intensify because of their enhanced overwinter survival and extended breeding seasons relative to later-arriving long-distance migrants, with which they must compete for resources. However, we found no correlation between the short-term and long-term trends with mean arrival dates of the different trans-Saharan migrants (based on data from Tøttrup et al. 2006). Neither was there any correlation between mean arrival dates and the rate of change in arrival dates of different species. There is thus no evidence to suggest that late-arriving species are less flexible in their response to global change (unpubl. data).

Knowledge that trans-Saharan migrants are in decline should direct research to annual demographic measures, non-breeding autecology, migration routes, precise staging and wintering habitats, diets and distributions. Attention should be given to those European migrants showing least favourable conservation status (i.e. greatest contraction of range and/or decreases in number over the longest periods) to determine when in the annual cycle regulatory or limiting factors are operating to cause declines. Species of sufficient abundance or accessibility and those comparatively well studied should be priorities for investigation (e.g. Yellow Wagtail, Grasshopper Warbler and Pied Flycatcher). Many such data exist already.

Constant Effort Ringing sites established in many parts of Europe could potentially provide annual measures of adult survival and relative reproductive output to model demographic trends between breeding seasons. Existing ringing data sets could also support survival analyses to establish within- and between-breeding-season survival of long-distance migrants. Most value would be derived from studies linking marked individuals on their breeding, staging and wintering areas (as successfully achieved in America by Holmes 2007). Such work should be coordinated throughout the flyway with local community involvement, as exemplified by the activities of the Leventis Ornithological Research Institute (2008) in Jos, Nigeria, to maximize research and conservation gain.

Common bird census data from other northern European states confirm similar declines amongst inter-continental migrants, e.g. in Sweden (Lindström & Svensson 2006), Norway (Husby *et al.* 2006), Finland (Väisänen 2005) and the UK (Gregory *et al.* 2002, Pan-European Common Bird Monitoring 2006, Sanderson *et al.* 2006). The issue should be tackled on an inter-continental scale, to meet targets to reduce or halt the loss of biodiversity in Europe and globally. Given these consistent declines and the difficulties presently posed to the statutory agencies responsible for restoring such long-distance migratory passerines to favourable conservation status, it is essential that we first identify and confirm which species are in decline, establish commonalities between declining taxa, and agree priorities for research and actions to understand the global causes of declines.

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REFERENCES

Alerstam, T. & Högstedt, G. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. *Ornis Scand.* **1:** 25–37.

Baillie, S.F. & Peach, W.J. 1992. Population limitation in Palearctic-migrant passerines. *Ibis* **131**(suppl.)**:** 120–132.

Baillie, S.R., Marchant, J.H., Crick, H.Q.P., Noble, D.G., Balmer, D.E., Coombes, R.H., Downie, I.S., Freeman, S.N., Joys, A.C., Leech, D.I., Raven, M.J., Robinson, R.A. & Thewlis, R.M. 2006. *Breeding Birds in the Wider Countryside: Their Conservation Status 2005.* BTO Research Report No. 435. BTO, Thetford.

Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen, G., Berthold, P. & Farnsworth, K. 2005. Assortative mating as a mechanism for the rapid evolution of a migratory divide. *Science* **310:** 502–504.

Berthold, B., Fiedler, W., Schlenker, R. & Querner, U. 1998. 25-Year study of the population development of central european songbirds: a general decline, most evident in long-distance migrants. *Naturwissenschaften* **85:** 350–353.

Bønlykke, J., Madsen. J.J., Thorup, K., Pedersen, K.T., Bjerrum, M. & Rahbek, C. 2006. *Dansk Trækfugleatlas.* Rhodos, Humlebæk.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441:** 81–83.

Bryant, D.M. & Jones, G. 1995. Morphological changes in a population of Sand Martins *Riparia riparia* associated with fluctuations in population size. *Bird Study* **42:** 57–65.

Buse, A., Dury, S.J., Woodburn, R.J.W., Perrins, C.M. & Good, J.E.G. 1999. Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Funct. Ecol.* **13**(suppl.)**:** 74–82.

Cowley, E. & Siriwardena, G.M. 2005. Long-term variation in survival rates of Sand Martins *Riparia riparia:* dependence on breeding and wintering ground weather, age and sex, and their population consequences. *Bird Study* **52:** 237–251.

Cramp, S. (ed.) 1977–94. *The Birds of The Western Palearctic*. Oxford University Press, Oxford.

Cresswell, W., Wilson, J.M., Vickery, J., Jones, P. & Holt, S. 2007. Changes in densities of Sahelian bird species in response to recent habitat degradation. *Ostrich* **78:** 247–253.

Foley, J.A., Coe, M.T., Scheffer, M. & Wang, G.L. 2003. Regime Shifts in the Sahara and Sahel: Interactions between Ecological and Climatic Systems in Northern Africa. *Ecosystems* **6:** 524–539.

Forchhammer, M.C., Post, E. & Stenseth, N.C. 2002. North Atlantic Oscillation timing of long- and short-distance migration. *J. Anim. Ecol.* **71:** 1002–1014.

Fox, A.D. 2004. Has Danish agriculture maintained farmland bird populations? *J. Appl. Ecol.* **41:** 427–439.

Gordo, O., Brotons, L., Ferrer, X. & Comas, P. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biol.* **11:** 12–21.

Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Procter, D., Gibbons, D.W. & Galbraith, C.A. 2002. The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002–2007. *Br. Birds* **95:** 410–448.

Gregory, R.D., van Strien, A., Vorisek, P., Gmelig Meyling, A.W., Noble, D.G., Foppen, R.P.B. & Gibbons, D.W. 2005. Developing indicators for European birds. *Phil. Trans. R. Soc. Lond., Ser. B* **360:** 269–388.

Grist, J.P. & Nicholson, S.E. 2001. A study of the dynamic factors influencing the rainfall variability in the West African Sahel. *J. Clim.* **14:** 1337–1359.

Heldbjerg, H. 2005. [Population changes of common birds in Denmark, 1975–2004.] *Dansk Orn. Foren. Tidsskr.* **99:** 182–195 (in Danish with English summary).

Heldbjerg, H. 2007. [*Monitoring Population Changes of Common Birds in Denmark 1975–2005*.] DOF BirdLife Denmark, Copenhagen (in Danish with English summary).

Holmes, R.T. 2007. Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. *Ibis* **149**(suppl.2)**:** 2–13.

Husby, M., Stueflotten, S. & Husby, A. 2006. *Norsk Hekkefugltaksering Årsrapport for 2005*. Norwegian Ornithological Society Report 6-2006. NOS, Trondheim.

Jones, P. 1985. The migration strategies of Palearctic passerines in West Africa. In MacDonald, A. & Goriup, P. (eds) *Migratory Birds: Problems and Prospects in Africa*: 9–17. ICBP, Cambridge.

Jones, P., Vickery, J., Holt, S. & Cresswell, W. 1996. A preliminary assessment of some factors influencing the density and distribution of Palearctic passerine migrants wintering in the Sahel zone of West Africa. *Bird Study* **43:** 73–84.

Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J.E., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R. & Stenseth, N.C. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. *Science* **132:** 1959–1961.

Leisinger, K.M. & Schmitt, K. 1995. *Survival in the Sahel: An Ecological and Developmental Challenge*. International Service for National Agricultural Research, The Hague.

Lemoine, N. & Böhning-Gaese, K. 2003. Potential impact of global climate change on species richness of long-distance migrants. *Conserv. Biol.* **17:** *577–586.*

Leventis Ornithological Research Institute 2008. Website address: http://www.aplori.org/default.htm (accessed 2 April 2008).

Lindström, Å. & Svensson, S. 2006. *[Monitoring Population Changes of Birds in Sweden. Annual report 2005.*] Department of Ecology, Lund University, Lund (in Swedish).

Monkkonen, M. 1992. Life history traits of Palaearctic and Nearctic migrant passerines. *Ornis Fenn.* **69:** 161–172.

Moreau, R.E. 1966. *The Bird Faunas of Africa and its Islands*. Academic Press, New York.

Morel, G.J. & Morel, M.-Y. 1992. Habitat use by Palaearctic migrant passerine birds in West Africa. *Ibis* **134:** 83–88.

Newton, I. 1998. *Population Limitation in Birds*. Academic Press, London.

Nicholson, S.E., Some, B. & Kone, B. 2000. An analysis of recent rainfall conditions in West Africa, including the rainy seasons of the 1997 El Niño and the 1998 La Niña years. *J. Clim.* **13:** 2628–2640.

Norris, D.R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos* **109:** 178–186.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliff, L.M. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds of a migratory bird. *Proc. R. Soc. Lond., Ser. B* **271:** 59–64.

Pan-European Common Bird Monitoring 2006. *The State of Europe's Common Birds 2005*. CSO/RSPB, Prague.

Pannekoek, J. & van Strien, A. 2001. *TRIM 3.0 for Windows (Trends & Indices for Monitoring data)*. Statistics Netherlands, Voorburg.

Peach, W., Baillie, S. & Underhill, L. 1991. Survival of British sedge warblers *Acrocephalus schoenobaenus* in relation to west African rainfall. *Ibis* **133:** 303–305.

Rappole, J.H. & McDonald, M.V. 1994. Cause and effect in population declines of migratory birds. *Auk* **111:** 652–660.

Robbins, C.S., Sauer, J.R, Greenberg, R.S. & Droege, S. 1989. Population declines in North American birds that migrate to the tropics. *Proc. Nat. Acad. Sci.* **86:** 7658–7662.

Rubolini, D., Spina, F. & Saino, N. 2005. Correlates of timing of spring migration in birds: a comparative study of trans-Saharan migrants. *Biol. J. Linn. Soc.* **85:** 199–210.

Salewski, V. & Jones, P. 2006. Palearctic passerines in Afrotropical environments: a review. *J. Orn.* **147:** 192–201.

Salewski, V. & Schaub, M. 2007. Stopover duration of Palearctic passerine migrants in the western Sahara – independent of fat stores? *Ibis* **149:** 223–229.

Salewski, V., Bairlein, F. & Leisler, B. 2002. Different wintering strategies of two Palearctic migrants in West Africa – a consequence of foraging strategies? *Ibis* **144:** 85–93.

Sanderson, F.J., Donald, P.J., Pain, D.J., Burfield, I.J. & van Bommel F.P.J. 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biol. Conserv.* **131:** 93–105.

SAS 2007. *SAS 9.13*. SAS Institute, Cary, North Carolina.

Schmidt, K.A. 2003. Nest predation and population declines in Illinois songbirds: a case for mesopredator effects. *Conserv. Biol.* **17:** 1141–1150.

SigmaStat 2004. *SigmaStat for Windows Version 3.11*. Systat Software, Inc., Richmond, California.

Stervander, M., Lindström, Å., Jonzén, N. & Andersson, A. 2005. Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. *J. Avian Biol.* **36:** 210–221.

Thiollay, J.-M. 2006. Severe decline of large birds in the Northern Sahel of West Africa: a long-term assessment. *Bird Conserv. Int.* **16:** 353–365.

Tøttrup, A.P., Thorup, K. & Rahbek, C. 2006. Patterns of change in timing of spring migration in North European songbird populations. *J. Avian Biol.* **37:** 84–92.

Tucker, G.M. & Evans, M.I. 1997. *Habitats for Birds in Europe: A Conservation Strategy for the wider Environment*. BirdLife International, Cambridge.

Väisänen, R.A. 2005. [Monitoring population changes of 84 land bird species breeding in Finland in 1983–2004.] *Linnut-vuosikirja* **2005:** 105–119 (in Finnish).

Vickery, J., Rowcliffe, J., Cresswell, W., Jones, P. & Holt S. 1999. Habitat selection by Whitethroats *Sylvia communis* during spring passage in the Sahel zone of northern Nigeria. *Bird Study* **46:** 348–355.

Walther, B.A. & Rahbek, C. 2002. Where do Palearctic migratory birds overwinter in Africa? *Dansk Orn. Foren. Tidsskr.* **96:** 4–8.

Williams, B., Nichols, J. & Conroy, M. 2002. *Analysis and Management of Animal Populations*. Academic Press, London.

Wilson, J.M & Cresswell, W. 2006. How robust are Palearctic migrants to habitat loss and degradation in the Sahel? *Ibis* **148:** 789–800.

Winkler, D.W., Dunn, P.O. & McCulloch, C.E. 2002. Predicting the effects of climate change on avian life-histories. *Proc. Nat. Acad. Sci.* **99:** 13595–13599.

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