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25-Year Study of the Population Development of Central European Songbirds: A General Decline, Most Evident in Long-Distance Migrants

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During the past century a decline has been noted in European bird populations, both in large species [1] and possibly also in songbirds [2]. Today the "Red List" (of endangered species) includes about 50% of the avifauna in most Central European countries; about 30% of species are declining to an extent that threatens their continued existence in Central Europe. These include songbirds, mainly open-country species that are easy to monitor. Trends in the numbers of many unobtrusive songbird species, however, have remained largely unclear [3]. To assess their population changes our institute began a census program in 1972 with the help of hundreds of amateur ornithologists [4]. A trapping station in this project in southern Germany has provided data on 35 species over 25 years – the first dataset based on strictly standardized methods over such a long period. During this entire period the number of trapped birds has fallen slowly but continuously, by an average of about 1% per year. The decrease is greatest for long-distance migrants, and it heralds profound changes in the Central European avifauna.

Populations of large birds such as eagles and storks can be determined accurately, and most of the European breeding pairs are monitored. For species that are more common or are harder to observe, such as crows and owls, only rough estimates are possible [3]. Serious problems are encountered in songbirds. Abundant, widely distributed, and unobtrusive species cannot be counted completely or directly; regional estimates must be based on indirect procedures such as recording territorial song. Such estimates are often biased by varying, nonquantifiable "observer quality" [5]. Therefore only a few countries have established sufficiently reliable programs for monitoring songbirds during the breeding period [6, 7].

In 1968 we began testing standardized trapping procedures for monitoring songbird populations in order to reduce differences among observers by a more objective method. The results were positive [8], and in 1972 we therefore initiated the "Mettnau-Reit-Illmitz" program (based on three stations, Mettnau in southern Germany, Reit in northern Germany, and Illmitz in Austria. This program was later extended, and temporarily grew into an ESF network encompassing Europe and Africa [9]). The Mettnau station has operated since the outset, and we report here on the results of a full quarter of a century of songbird population monitoring.

The samples are obtained by trapping passage migrants during the autumn migration while staging at rest sites. A suitable study area must (a) be characterized by largely unchanging vegetation, (b) include different habitats so that birds with different ecological requirements can rest there, and (c) be a protected area of guaranteed long-term existence. The Mettnau peninsula, with a 50-year-old bird sanctuary, is ideal for the purpose [10]. The 35 songbird species selected for monitoring include regularly staging long-, intermediate-, and short-distance migrants (Table 1).

The birds are trapped in nylon nets normally used to catch birds for ringing; 2 m high and 7 m long, they are set up between wooden bars on poles. A wall is formed by 52 nets extending through 8 different habitats (from a brush zone through forested and wet regions). The annual trapping period is June 30–November 6 and includes the entire autumn migratory period of songbirds in Central Europe. The nets are checked hourly from dawn until soon after dusk; trapped birds are ringed (to prevent double counting), subjected to biometric tests and then released. The monitoring conditions (annual setting up of the nets, collecting the birds, data collection, etc.) are standardized as far as possible [10]. Most of the investigated birds come from Central Europe, although some have traveled from northern, eastern, and western Europe, and a small proportion are local breeding birds. These origins are known from recoveries of ringed individuals [11] and from biometric data on population differentiation [10].

Test studies have confirmed that standardized trapping procedures effectively give reliable estimates of songbird populations. Safriel and Lavee (1991) showed that the number of palaearctic songbird migrants trapped in Sinai is correlated positively with estimates of their European premigratory population sizes [12]. Dunn et al. (1997) demonstrated that trends in the annual capture indices of songbirds trapped during autumn migration in Michigan are correlated positively with trends in breeding bird survey data from their breeding grounds and conclude that "intensive standardized netting can be a useful population monitoring tool" [13]. We have consistently found that trends in trapping data reliably reflect those from other sources such as single-species population studies and countrywide population estimates for Red Lists, etc. [4]. Thus data from 147,661 individuals that were caught at Mettnau between 1972 and 1996 reflect the population development of 35 Central European songbird species, as follows.

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Table 1. Data on the species studied in three groups (L, long-distance migrants; M, medium-distance; S, short-distance migrants), in each case arranged from the most negative to the most positive correlation coefficients bottom

Species		Type	Total numbers	Annual mean	±SD	*r*	*P*
Phylloscopus trochilus	Willow Warbler	L	8066	336.1	114.39	−0.819	***
Phoenicurus phoenicurus	Common Redstart	L	1005	41.9	21.71	−0.786	***
Locustella naevia	Grasshopper Warbler	L	1166	48.6	23.60	−0.737	***
Sylvia curruca	Lesser Whitethroat	L	2391	99.6	61.56	−0.714	***
Jynx torquilla	Wryneck	L	158	6.6	4.75	−0.711	***
Acrocephalus paludicola	Aquatic Warbler	L	49	2.0	2.37	−0.684	***
Acrocephalus palustris	Marsh Warbler	L	1576	65.7	34.64	−0.682	***
Muscicapa striata	Spotted Flycatcher	L	867	36.1	19.84	−0.625	**
Phylloscopus sibilatrix	Wood Warbler	L	75	3.1	2.83	−0.618	**
Saxicola rubetra	Whinchat	L	300	12.5	4.93	−0.598	**
Acrocephalus arundinaceus	Great Reed Warbler	L	380	15.8	9.31	−0.566	**
Locustella luscinioides	Savi's Warbler	L	151	6.6	5.98	−0.489	*
Hippolais icterina	Icterine Warbler	L	610	25.4	13.26	−0.422	*
Sylvia borin	Garden Warbler	L	10607	442.0	132.41	−0.406	*
Luscinia svecica	Bluethroat	L	204	8.5	4.75	−0.351	
Sylvia communis	Whitethroat	L	496	20.7	8.42	−0.348	
Acroceph. schoenobaenus	Sedge Warbler	L	1576	65.7	28.90	−0.293	
Lanius collurio	Red-backed Shrike	L	183	7.6	3.51	−0.190	
Ficedula hypoleuca	Pied Flycatcher	L	776	32.3	16.54	−0.139	
Acrocephalus scirpaceus	Reed Warbler	L	45257	1885.7	297.88	−0.099	
Luscinia megarhynchos	Nightingale	L	228	9.5	4.86	0.029	
Carduelis carduelis	Goldfinch	M	513	21.4	14.06	−0.490	*
Emberiza schoeniclus	Reed Bunting	M	8759	365.0	154.26	−0.411	*
Regulus ignicapillus	Firecrest	M	184	8.8	6.06	−0.217	
Phylloscopus collybita	Chiffchaff	M	20012	833.8	279.67	−0.168	
Turdus philomelos	Song Thrush	M	1840	76.7	22.82	−0.160	
Erithacus rubecula	Robin	M	10902	454.3	96.46	0.038	
Prunella modularis	Dunnock	M	1472	61.3	18.79	0.082	
Phoenicurus ochruros	Black Redstart	M	568	23.7	9.39	0.155	
Sylvia atricapilla	Blackcap	M	15627	651.1	208.50	0.327	
Parus caeruleus	Blue Tit	S	6094	253.9	103.76	−0.487	*
Pyrrhula pyrrhula	Bullfinch	S	1016	46.2	36.31	−0.471	*
Troglodytes troglodytes	Wren	S	1421	59.2	23.36	−0.340	
Turdus merula	Blackbird	S	2683	116.7	35.76	−0.180	
Regulus regulus	Goldcrest	S	449	21.4	13.96	0.388	
Total			147661	6165.5			

* $P<0.001$, ** $P<0.01$, *** $P<0.05$, SPCC

The statistical treatment of bird-trapping counts has been discussed at length [4, 13], and on the basis of these considerations we subjected our data to a detailed regression analysis. The annual trapping totals were log-transformed to improve statistical normality and change multiplicative effects of environmental conditions to additive ones; the variable was log $(n+1)$ to allow log transformation of zeros. The null values for 1987 are due to a flood of the trapping area. Trends were calculated as the slope of the log-transformed annual trapping figures for species (Table 1), annual trapping totals (Fig. 1), and groups of birds as means of the slopes for individual species (below). We further used Spearman's correlation coefficients (SPCC) for individual species and annual trapping totals, covariance analysis (ANCOVA), and the test for equality of slopes of regression lines (test of parallelism [14]) for various regression lines. Mean values were tested by the Mann-Whitney *U* test.

We obtained four main results: (a) The overall annual trapping figures, pooled for all species, decreased during the study period ($r=-0.4562$, SPCC$=-0.4565$, $P<0.02$; Fig. 1). (b) The greatest decline was found in long-distance migrants (Table 1; significant trends for 12 out of 21 species; medium- and short-distance migrants showed only 4 negative trends). Accordingly, *r* and SPCC were also highly significant for long-distance migrants (–0.6484 and –0.5991, $P<0.001$) but not significant for medium- plus short-distance migrants (–0.1713 and –0.1887). The slope of the regression lines for long-distance migrants differed significantly from that for medium- plus short-distance migrants ($F=4.33$, $P<0.04$; 1980 was treated as an outlier because of the extremely large trapping total). (c) The average decrease in numbers trapped was 0.82% per year for all species, 1.14% for long-distance migrants and 0.46% for medium- plus

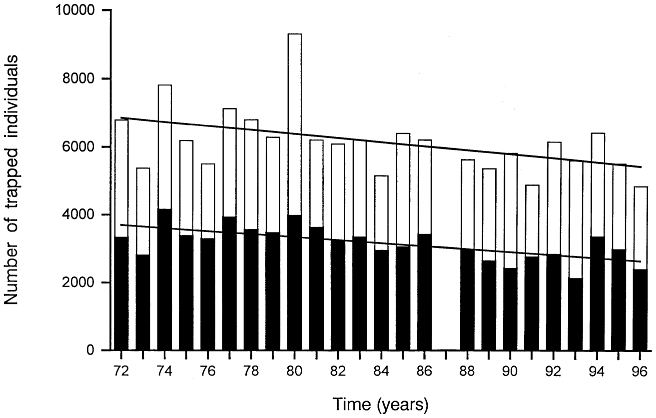

Fig. 1. The annual trapping counts for the species studied. *Black bars*, long-distance migrants; *white bars*, medium- plus short-distance migrants. *Regression lines: below*, for long-distance migrants; *above*, for trapping totals

short-distance migrants. (d) The average annual total of trapped individuals was 6639.2 ± 1074.13 in the first half of the study period (1972–1983) and fell to 5665.9 ± 547.62 in the second half, a decrease of 973 individuals or 15% ($P<0.02$, U). Long-distance migrants declined most from 3514 to 2831 individuals, i.e., by 683, or 19% ($P<0.001$); the values for medium- plus short-distance migrants were 3125 and 2836 (–289, or 9%).

A recent decline in long-distance migrants has also been described in other publications treating Central European songbirds [3, 15–17]. A decline in many species was shown by trapping stations that we operated until 1993 in northern Germany and Austria and by single-species studies conducted by our volunteer coworkers. In western and northern Europe the decline in songbirds presently appears to be less pronounced, which may be related to a better breeding-habitat quality [18, 19].

Resident birds can be affected only in one region: their all-year-round habitat. Migratory birds can decline in three regions: the breeding grounds, the winter quarters, and passage areas. The breeding grounds of many European birds have been progressively restricted or reduced in their habitat quality by human encroachment [20]. As a result, many resident species such as Capercaillie (*Tetrao urogallus*) or Common Partridge (*Perdix perdix*) have long been decreasing [3]. Migratory birds are similarly affected but are also known to be declining in their winter quarters and passage areas. Among these are ducks (e.g., garganey, *Anas querquedula*), birds of prey (e.g., honey buzzard, *Pernis apivorus*), and various songbirds (e.g., redstart, *Phoenicurus phoenicurus*). All of these have exhibited marked declines, whereas related lesser migratory species are less affected.

With respect to the possible causes, a number of species have suffered severely from the Sahel drought and others from hunting, biocides, and habitat destruction; details are largely unknown [21, 3]. Thus it is not surprising that, as our study has shown, long-distance migrants are especially vulnerable. They may also be affected increasingly by another factor: the recent climatic warming. At higher latitudes milder autumns and winters and earlier springs reduce the normally high winter mortality of resident birds, the proportion of residents in partially migratory populations rises, short-distance migrants travel less far, migrants return sooner to the breeding grounds, and breeding begins earlier, which favors reproduction and population growth [22, 23]. Residents, partial migrants, and short-distance migrants are evidently at an advantage in this regard because they can adapt more rapidly to recent changes in their breeding areas than can birds that winter in Africa for up to half a year [24]. This may increase competition and lead to a progressive loss of breeding sites for the long-distance migrants, which arrive at the breeding grounds last [25, 26], and may result in a gradual restructuring of the European avifauna in favor of the permanent residents, partial and short-distance migrants, to the detriment of the long-distance migrants. Such a restructuring may well be underway [27, 28]. This may in part explain the population declines described here [28] and deserves close attention and analysis. Its consequences should also be carefully taken into account when plans are made for bird conservation in the future.

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Evidence for Loosening of a Protein mechanism

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Concomitant with the salting-out effect, according to which salts can be arranged in the Hofmeister series [1], there is a stabilizing effect, evidence for which has come primarily from observed increases in melting temperature T_m with salt concentration [1, 2]. Here we ask whether stabilization and destabilization can be manifested in ways more directly related to protein mechanism than the parameter T_m. For this purpose, we selected bacteriorhodopsin (bR), whose operation can be followed through a richly detailed set of spectroscopic changes [3]. Major conformational changes accompany bR functional activity [4], especially during the later part of the photocycle (i.e. t>1 ms). Hence photocycle kinetics should be affected if conformational destabilization occurs.

Existing evidence on the effect of conformational destabilization on enzyme operation is mixed. At room temperature (T_R), D-glyceraldehyde-3-phosphate dehydrogenase from the thermophilic eubacterium *Thermotoga maritima* acts much more slowly than its non-thermophilic relatives. The thermophilic enzyme has a higher melting temperature T_m, and thus the difference T_m–T_R is much greater and the enzyme is presumably more rigid. The action can be speeded up by low (sub-molar) concentrations of the chaotrope (a salting-in salt which destabilizes the native conformation [1]) guanidium chloride [5], which lowers T_m and hence presumably loosens the structure. A parallel example is the stimulation of NADP-glyceraldehyde-3-phosphate dehydrogenase by chaotropes [6]. Numerous contrary cases can be found, however. Kosmotropes (salting-out salts which stabilize the native conformation [1]) often enhance enzyme activity according to the Hofmeister series [7, 8], and chaotropes decrease the oxygen affinity of haemoglobin [9]. More or less complex enzyme reactions may not be the best vehicle for examining the effect of indifferent (i.e. not involved as reactant) salts on working speed: salts can intervene in too many ways for the unambiguous interpretation of an experimental result.

bR transduces luminous energy into chemical energy in *Halobacterium salinarium* and is the simplest proton pump known in biological systems. It is one of the best-characterized membrane proteins; its three-dimensional structure is known to 2.5-Å resolution [10], while its functional properties have been extensively studied by spectroscopic [3], photoelectric [11, 12] and molecular-genetic [13] methods. Upon illumination by visible light, bR pumps protons across the cell membrane, building up an electrochemical potential across it and, like visual rhodopsins, undergoes major conformational changes [4]. This so-called photocycle has been investigated over a wide range of environmental parameters, and kinetically characterized with extremely high precision [3, 11, 12].

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