

# Effects of changes in tropical environments on the North European avifauna

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Svensson, S. E. 1985: *Effects of changes in tropical environments on the North European avifauna*. — *Ornis Fennica* 62:56–63.

The primary winter habitats of North European tropical migrants are the grass steppes and savannas between the Sahara and the rain forest belt, East Africa and the dry areas south of the equatorial rain forests. The favoured explanation for the lack of Palaearctic migrants in the equatorial rain belt is competition from the African birds. In the very seasonal dry belts, the African birds cannot build up populations dense enough to compete with the tropical migrants, which arrive just after the rains, when the feeding conditions suddenly become extremely good. When looking for factors in the tropics that may affect the number of birds in North Europe, we must consequently concentrate on events in the dry belts of Africa. There are two main agents causing habitat changes: the climate and man. Man causes long-term changes by fires, cutting the forest, irrigation, drainage of wetlands, farming and grazing of cattle. On a shorter time scale, the most important factor is the amount and distribution of rainfall, especially the pronounced drought periods. In summary, the evidence for a connection between the rainfall in Africa and the number of birds in North Europe is very inconclusive. There are a number of positive correlations, but they must be interpreted with the utmost care, since there is little evidence of a causal relation. For many species it seems as likely that the population changes are caused by events in the breeding areas, both alteration of habitats and climatic factors.

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## Introduction

Recently Alerstam & Högstedt (1982) opened a broad discussion on the differential dependence of bird species on what they called breeding and survival habitats. They suggested that for many species the survival habitats, i.e. the non-breeding habitats, are more important than the breeding habitats in determining total population size (and a number of adaptive traits). In a sense this is a rephrasing of Liebig's classical principle of the minimum: that particular essential resource that is available in the smallest amount determines population size and acts most strongly as a selective force. Alerstam & Högstedt identified the majority of small terrestrial Holarctic passerines as being B-species, i.e. having surplus of breeding resources, but restricted survival resources during the non-breeding season. If this conjecture is correct the fluctuations that we observe in the population size of tropical migrants should primarily reflect the quality and size of their winter habitats.

One particular case may have helped to increase the interest of ornithologists in the factors acting on our breeding birds in their tropical habitats. Between 1968 and 1969 the British Whitethroat *Sylvia communis* population declined drastically (Winstanley et al. 1974). A period of drought in the Sahel region south of the Sahara had caused a deterioration of the wintering habitats of the Whitethroat, and also of some other species that had declined (e.g. Berthold 1974, 1976a, b). The number of Whitethroats

trapped in the autumn at Ottenby could be positively correlated with the water level of Lake Chad (Hjort & Lindholm 1978).

In this paper I will discuss only land birds, mostly small passerines, but several shore birds and waterfowl also travel to tropical Africa. Very few North European species winter in tropical areas other than the African ones.

## Distribution of North European birds in Africa

The pattern of distribution of North European bird species in tropical Africa is complicated. It has become apparent that during their six to seven months' stay in Africa many species move from one part of Africa to another. These movements can be extensive and involve migrations from, for example, Ethiopia and the Sudan to Rhodesia and Moçambique. This has recently been observed in the Marsh Warbler *Acrocephalus palustris*, the Whitethroat and the Thrush Nightingale *Luscinia luscinia* (Pearson & Backhurst 1976, Backhurst & Pearson 1981). Morel (1973) reported similar migration in West Africa. These movements within Africa seem largely to be governed by the food conditions, which in turn are affected by the rains. A complicating factor is also that different breeding populations winter in different parts of Africa. This is true even for populations that breed very close to each other. A classical example is the West and East European populations of the White Wagtail *Motacilla alba*. Another

example is one of our most common birds, the Willow Warbler *Phylloscopus trochilus* (Hedenström & Pettersson 1984).

In 1966 Moreau listed the number of Eurasian species so far recorded in a number of fairly well-surveyed parts of Africa. Curry-Lindahl (1981) updated the list for the year 1977. He also added one region: Eastern Zaire, Rwanda and Burundi. Thus in 1977 the following number of Eurasian bird species had been observed:

West Africa	175 species
The Sudan	198 species
Eastern Zaire, Rwanda & Burundi	127 species
Kenya	147 species
Rhodesia	75 species
Cape Province	58 species

The list shows that the number of species declines from north to south, being highest between the southern border of the Sahara and about 10°N. Further, it is higher in Kenya than in the central parts of Equatorial Africa.

Alerstam (1982) made a more detailed study of the number of wintering Palaearctic species within 500-km squares for the whole of Africa south of the Sahara. He confined his comparison to 90 insect-feeding Eurasian species. Within a broad zone between the Saharan desert and the rain forest the average number of insectivorous species per 500-km square was around 25. An exception was the whole eastern part of that zone, including the Sudan, the western parts of Ethiopia and Kenya. Here the average number of species per square was 38. This contrasts strongly with the situation in the rain forest area along the coast from Sierra Leone to Cameroon and in the Congo Basin, where the average number of species was 12. South of the rain forest zone the number of species rose again, being 15 in the savanna zone of south Zaire and north Angola. In the western parts of the dry, mixed woodlands of south Angola and west Zambia it was a little higher again: 21 species. In the eastern part of that zone it was 31 species. The southern steppe grasslands had an average of 22 species, not very much lower than the western parts of the northern steppe grasslands. Further south there is a rapid decline in the number of Eurasian species.

The general pattern revealed here is different in different longitudinal sections of Africa. In West Africa the number of species increased from the Saharan border southwards and then declined again in the rain forests near the coast. Along a line from Tripoli to Cape Town there is a two-peak pattern: first an increase, then a decline and then an increase again. An eastern line from Egypt along the White Nile through Kenya south to Moçambique shows a third pattern: a rapid rise south of the Nubian desert, high numbers all the way south to Tanzania and a continuous decline through Zambia, Moçambique, Rhodesia and further south.

The Eurasian migrants do not exploit the rain forest zone, but remain north of it or go further

south. In East Africa, where no rain forest zone exists, high numbers prevail all the way to the south of the equator. The fact that birds from the Palaearctic areas avoid what we see as the most productive habitats and exploit dry or seasonal habitats has been called Moreau's paradox. Morel (1973) points out, however, that this paradox must be more apparent than real: the arid zones must be more productive than we have believed in order to support the great influx of Palaearctic birds.

Of the species that are fairly common and widespread in North Europe, only three seem to be more or less confined to the rain forest region: the Honey Buzzard *Pernis apivorus*, Wood Warbler *Phylloscopus sibilatrix* and Pied Flycatcher *Ficedula hypoleuca*. The Collared Flycatcher *F. albicollis*, which has a restricted distribution in North Europe, also belongs to this group.

### Climate and Man: the major forces responsible for habitat changes

There are two main forces acting on avian habitats in Africa. One is climate, more specifically the amount and temporal distribution of rain. It is generally assumed that the distribution of deserts, savannas and rain forests has been very different previously from what it is now. For example, fossil moving dunes now covered by rain forest show that deserts prevailed there earlier, occurring about five degrees further south than now. At other times steppes and savannas were distributed over large parts of the present Sahara and Lake Chad was almost 20 times larger and 60 m deeper than it is today.

It seems that great climatic fluctuations occurred during the last glaciation. Between about 20 000 and 15 000 years ago there was a distinctly drier period than now. This was followed by a wetter period 12 000 to 7 000 years ago (i.e. during the rapid end of the last ice age). Then came 5 000 years of alternating dry and wet periods, and finally at least 2 000 years with a fairly stable climate, with droughts and excessive rains of the same magnitude as during this century.

This picture has been challenged recently, however. When he analysed data from the Chad Basin, Durand (1982) did not find any support for drastic climatic changes over the last 50 000 years. He stated that "What is found are indications of variations generally similar to those that have been recorded since the beginning of scientific observations in the Basin".

The other force is human impact, which became a dominating factor comparatively recently, but is extremely important today. In some parts of Africa it is now difficult to tell what was the original vegetation. Cultivation, grazing and burning have transformed the face of the continent: vast areas of forest have been cut and are now savanna, steppe or farmland. Forests have been fragmented, a process that seems to be accelerating. In the drier zones desertification is a prominent phenomenon and the area of desert is believed to be increasing by thousands of square kilometres a year.

Since most of our tropical migrants winter in comparatively dry regions the process of desertification is of particular interest. It depends upon a combination of human impact and climatic factors. There is a continuous degradation of land by human activities: overgrazing, cutting of wood for domestic purposes, and burning. This long-term process is strongly modified by shorter-term climatic events, such as

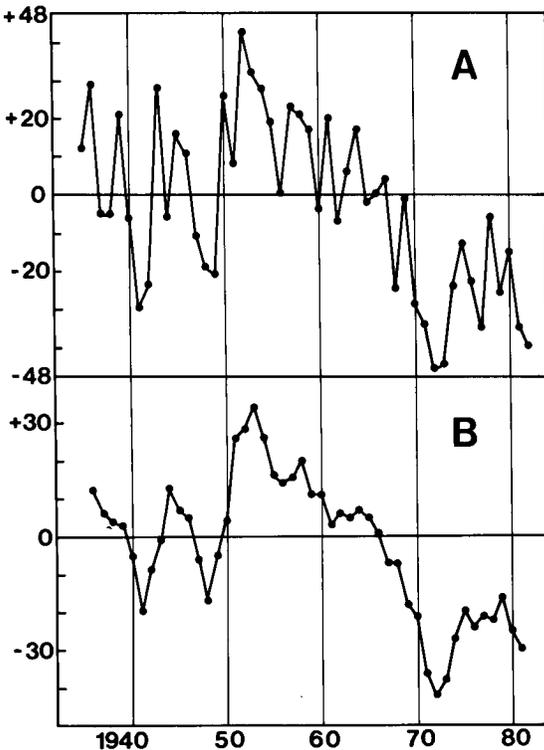


Fig. 1. Rainfall index for 24 stations in the Sahel region of Africa in 1935–1982. Upper diagram A: annual index. Lower diagram B: three-year running mean. Method of calculating the index described in the text.

the drought prevailing over large parts of Africa since about 1968. Such droughts have alternated with more humid periods as long as climatic records can be traced: droughts are even described in the Bible.

A period of excessive rainfall started in about 1950 in Africa and lasted to about 1965 (Fig. 1). It was followed by a period of insufficient rainfall, with particularly severe droughts in the early seventies, which is still continuing.

For my rainfall index I used the analyses of Courel (1983) (Figs. 1 and 2). These provide information on rainfall at 24 stations in the Sahel zone from Dakar in the west to Lake Chad in the east. For each year and station the amount of rain is given in five classes: 1) marked deficit (deficit 20 % or more compared with the average), 2) deficit, 3) normal, 4) excess, and 5) marked excess (20 % or more). To each station I gave points for each year, -2, -1, 0, +1 and 2, depending on the rainfall class. Then I added the points of all the stations for each year. This index is presented in Fig. 1. As there were 24 stations, the index can attain a maximum value of 48 (or a minimum of -48). This index was tested against the actual rainfall at the stations for which data were given for the years 1968–1980 (Courel 1983: table 4). The correlation between true rainfall and the index was +0.98.

#### Autumn migration at Ottenby and rainfall in the Sahel

Birds have been trapped for ringing at Ottenby Bird Observatory since 1946 (Hjort et al. 1981). From

1947 the autumn trapping period has lasted till at least the end of October. Thus the whole autumn migration of the tropical migrants is included. The spring trappings have begun later than the arrival of tropical migrants and have not been carried out with the same regularity in all years.

Over the long period of trappings at Ottenby there has been a number of changes in the trapping system: the number, kinds and location of permanent traps (mainly of the Heligoland type) have shifted several times, mist nets have been introduced and the habitat around the bird observatory has changed. The trapping profile and efficiency of different kinds of traps and nets are not very well known, but it has been demonstrated that the trapping figures are strongly affected by the location of traps in relation to different kinds of vegetation (Berthold 1976). In order to use the Ottenby trapping figures as a measure of the amount of birds resting in the garden, one must assume that the lack of standardization of the trapping work has not affected the number of birds trapped. This assumption does not seem unreasonable for the species that concern us here. The trapping area is small and isolated and I therefore believe that the majority of the birds present have been trapped. Other factors, such as the weather, are probably more important sources of error in using the Ottenby trapping figures as an index of population size.

A more serious objection that can be made to the autumn trapping figures is that they show primarily the annual production of young rather than the size of the population that will return to breed, because the majority of the birds trapped, often up to 90 %, are yearlings (Pettersson 1984). This introduces considerable variation when the breeding numbers are to be compared with the conditions during the previous winter. The problem can be circumvented by using numbers averaged over several years. It seems reasonable to assume that the average production of young per pair does not change over longer periods of time. Consequently, autumn figures will also reflect changes in population size.

I have used the Ottenby autumn data in two different ways. In one analysis I selected two ten-year periods, one with excessive rainfall (1958–1967) and one with a deficit of rain (1971–1980) in the Sahel zone. The change in the numbers trapped at Ottenby during these two periods is given in Fig. 2 for 22 species.

The change is significant for nine species. Five of them (Ap, Ai, Ls, Sn, At; see Fig. 2 for species key) increased in numbers and four species (Su, Ms, Pp, Fp) declined. No species was less than half as common during the second period as during the first, but three species (Marsh Warbler, Reed Warbler *Acrocephalus scirpaceus* and Bluethroat *Luscinia svecica*) more than doubled their numbers. There is a negative linear relationship between the abundance of the species and the magnitude of the

change. Moreau suggested that the fragmentation of habitats in Africa may improve the situation for Palaearctic migrants in general, but the data from Ottenby seem to indicate that it improves the situation only for the less common species and that the dominant Palaearctic visitors suffer from the disappearance of their habitats. It is not possible to draw any final conclusions since it is not yet known whether we should look for the underlying causes in Africa or in the European breeding grounds. It may be that the common species are common because they depend on habitats of extensive distribution, which are strongly affected by a deficit of rain, whereas the less common species depend on special habitats, which do not suffer so much from drought.

The species can be grouped into three categories according to their winter areas (habitat selection from Curry-Lindahl 1981): 1) species that winter almost exclusively in the Sahel region (Ls, Sr, Oo, Pc, Su, So, Pp), 2) species that winter partly in the Sahel region but also in other areas or habitats (Ah, Sa, Lc), and 3) species that winter mainly outside the Sahel region. Among the Sahel species, four show an increase and three show a decline. Among the three partly Sahel species, all show a small but insignificant increase. Among the other species, six show an increase and six a decline. Thus there seems to be no indication that the Sahel species differ from the other species in terms of the direction of change.

Although it seems unlikely that the number of birds trapped at Ottenby in the autumn should correlate with the annual rainfall in the Sahel region, the results obtained by, for example, Hjort & Lindholm (1978) for the Whitethroat makes it worthwhile to perform the calculation. I calculated the correlation coefficients for the Ottenby autumn trapping totals in the two 15-year periods 1951–1965 and 1966–1980 and the Sahel rainfall in the periods 1950–1964 and

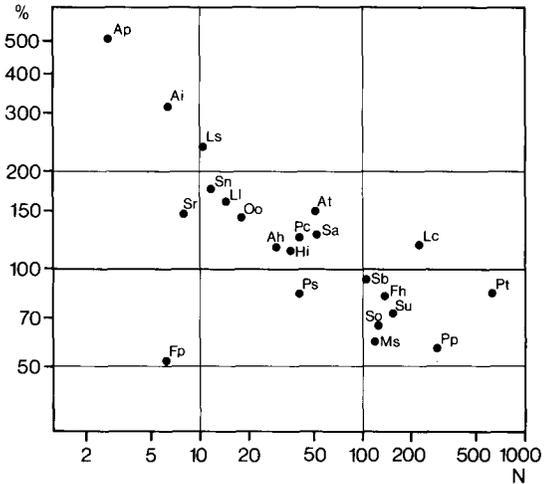


Fig. 2. Change in numbers trapped at Ottenby between the periods 1958–67 and 1971–80. N(x-axis) = mean number of birds trapped per year during all 20 years. % (y-axis) = number during the second period in percent of the number during the first period. Species: Ah = *Acrocephalus schoenobaenus*, Ai = *A. scirpaceus*, Ap = *A. palustris*, At = *Anthus trivialis*, Fh = *Ficedula hypoleuca*, Fp = *F. parva*, Hi = *Hippolais icterina*, Lc = *Lanius collurio*, Ll = *Luscinia luscinia*, Ls = *L. svecica*, Ms = *Muscicapa striata*, Oo = *Oenanthe oenanthe*, Pp = *Phoenicurus phoenicurus*, Pc = *Phylloscopus collybita*, Ps = *Ph. sibilatrix*, Pt = *Ph. trochilus*, Sa = *Sylvia atricapilla*, Sb = *S. borin*, Sn = *S. nisoria*, So = *S. communis*, Su = *S. curruca*, Sr = *Saxicola rubetra*.

1965–1979. The reason for dividing the 30-year period into two halves was that the first half roughly coincides with the excessive rainfall and the second half with the period of drought.

The results are given in Fig. 3. The correlation coefficients for the first period were almost all nega-

Table 1. Population indices of some tropical migrants in three different periods in South Finland (Järvinen & Väisänen 1978) and at Ottenby Bird Observatory (Hjort et al. 1981). The +, -, and = signs between the index values indicate whether the change falls above, within or below the limits given by Järvinen & Väisänen (1979): if the index was between 80 and 125 in comparison with 100, the change is probably not significant.

Species	South Finland			Ottenby	
	1936–49	1952–63	1973–77	1952–63	1973–77
Sahel rain index	+5	+24	-30	+24	-30
<i>Cuculus canorus</i>	110	= 130	- 100		
<i>Jynx torquilla</i>	15	+ 70	+ 100	Small sample	
<i>Ph. phoenicurus</i>	165	= 170	— 100	Small sample	100
<i>Hippolais icterina</i>	15	+ 30	+ 100	94	= 100
<i>Sylvia atricapilla</i>	15	+ 30	+ 100	67	+ 100
<i>Sylvia borin</i>	75	= 65	+ 100	114	= 100
<i>Phylloscopus trochilus</i>	95	- 60	+ 100	79	= 100
<i>Ph. collybita</i>	100	= 90	= 100	57	+ 100
<i>Ph. sibilatrix</i>	20	= 45	+ 100	119	= 100
<i>Muscicapa striata</i>	90	= 85	= 100	184	- 100
<i>Ficedula hypoleuca</i>	105	= 95	= 100	109	- 100
<i>Anthus trivialis</i>	65	= 60	+ 100	51	+ 100
<i>Lanius collurio</i>	15	+ 30	+ 100	82	= 100



and the Redstart). When assigning the species to the categories of increase or decline, I used the limits given by Järvinen & Väisänen (1977): an index of 80–125 compared with 100 should be considered no change. Thus the Finnish line transect material gives no evidence that differences in rainfall in the Sahel exert a general effect on the numbers of breeding birds.

If we compare the autumn figures from Ottenby (Table 1) with the Finnish breeding numbers, we find that the agreement between them is rather weak. There is one species that has decreased considerably in both, the Redstart, and there are three species that have increased in both, the Tree Pipit *Anthus trivialis*, Willow Warbler and Blackcap *Sylvia atricapilla*. One species showed little change in both, the Pied Flycatcher. The other six species showed little change in one of the counts but a large change in the other. For at least the Tree Pipit, Pied Flycatcher and Redstart there is a sufficient number of recoveries to show that substantial numbers of Finnish birds pass Ottenby (J. Pettersson, pers. comm., see also Järvinen & Väisänen 1979).

#### Breeding population size in South Sweden and drought in the Sahel

Apart from the counts at the bird stations, reliable data are lacking on the long-term trends of the bird populations in Sweden. Standardized counts of breeding birds have been performed only since 1970 (my own data). I have tested the possible correlation between the annual breeding population index (Fig. 4) and the rainfall index of the Sahel for nine tropical migrants for which sufficient counts exist. There are seven positive and two negative correlation coefficients (Table 2). Only one, that for the Spotted Flycatcher *Muscicapa striata* ( $r = 0.72$ ), is significantly different from zero at the 5% level. One significant coefficient out of nine can hardly support the assumption of a general dependence on Sahel rainfall, even if the dominance of positive correlations leaves it as a possibility.

#### The problem of distinguishing between effects caused by changes in the breeding area and in the wintering area

In this paper I have concentrated upon the Sahel rainfall as a possible explanation for variations in the number of certain tropical migrants of North Europe. Certain correlations have been found, but generally the picture remains ambiguous. Even in the cases where a correlation was found, this is not definite proof of a causal relation. The possibility must first be excluded that the population fluctuations are caused by the conditions during the breeding period. This is important because there are large-

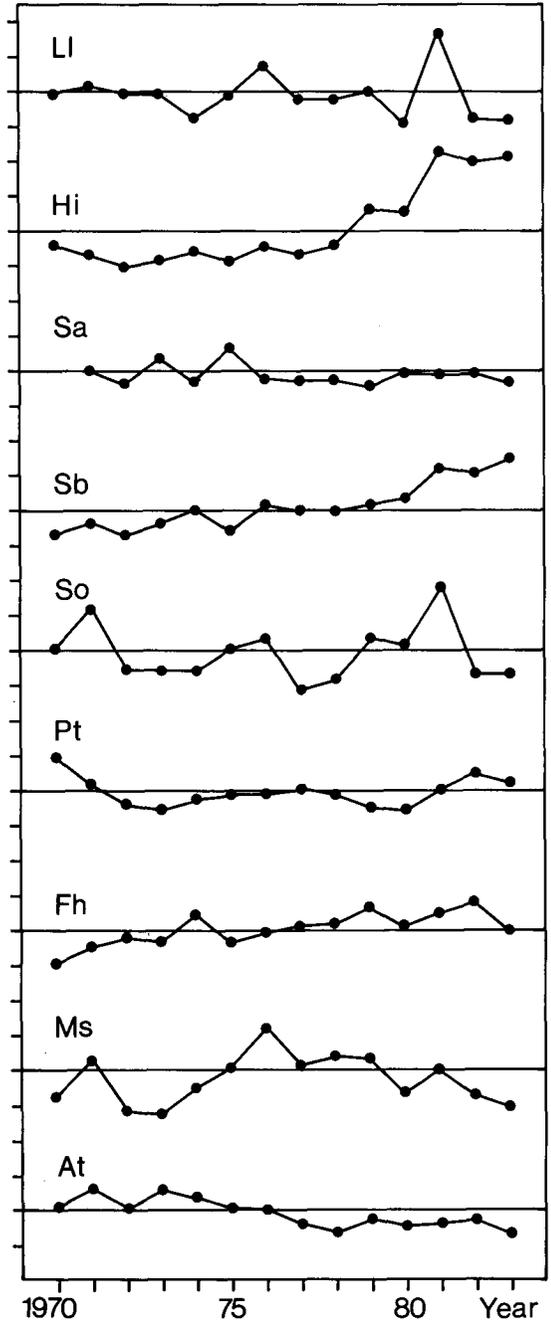


Fig. 4. Changes in population size of nine tropical migrants in the southern third of Sweden according to the Swedish Breeding Bird Census, 1970–1983. The vertical axis gives index values, with 20 units between each mark. Species as in Fig. 2.

scale correlations between the weather systems of the tropical and temperate regions.

I have not yet made any analysis of possible corre-

Table 2. Correlation between population index for South Sweden (1971–1982) and rainfall index for the Sahel region in the preceding year (1970–1981). Rain falls mainly during the three summer months: June, July and August. (Critical  $r$  at the 5 % significance level is 0.58).

Species	$r$
<i>Muscicapa striata</i>	+0.72
<i>Sylvia communis</i>	+0.54
<i>Luscinia luscinia</i>	+0.51
<i>Hippolais icterina</i>	+0.37
<i>Sylvia borin</i>	+0.35
<i>Ficedula hypoleuca</i>	+0.25
<i>Phylloscopus trochilus</i>	+0.09
<i>Sylvia atricapilla</i>	-0.30
<i>Anthus trivialis</i>	-0.50
Mean of all species	+0.23

lations between the number of birds and the weather during the breeding season in temperate Europe. But one example may serve to show that great caution must be exercised: I have calculated the correlation coefficient for the number of Yellowhammers *Emberiza citrinella* ringed at Ottenby and the Sahel rainfall in the previous year. For the period 1955–1980 I obtained a correlation coefficient of  $-0.62$ , significant at the 1 % level. Since no Yellowhammers cross the Sahara in the winter, the African rains cannot have any direct effect. This species showed deviant behaviour compared with other short-distance migrants in the analysis by Lindholm et al. (1983). In a principal component analysis of the Ottenby data, tropical and intra-European migrants fell into two groups, but neither contained the Yellowhammer.

Though no clear causal connection could be demonstrated between the rainfall in Africa and the numbers of tropical migrants breeding in North Europe, the possibility of such a connection cannot be excluded. It may be that the African winter resources do not limit population size and it is also possible that the droughts simply mean that the dry regions shift geographically but remain large enough. In the case of the Sahel area, however, this would force the birds to fly a longer distance over the Sahara before reaching their winter quarters, which could increase mortality.

The fact that the droughts may last for several years suggests the operation of some positive feedback mechanism: a rainy year begets another rainy year, and the reverse. It is interesting to speculate whether alternating dry and rainy periods are governed by general atmospheric patterns that have little to do with the local conditions in Africa or whether those conditions can be an important factor, e.g. desertification itself affects rainfall. Generally, the amount of rain depends on the thermodynamic characters of the African monsoon, and these characters in turn depend on the properties acquired by the air masses during their transit of the Atlantic ocean.

Even in our latitudes local cloud formation and rain are clearly connected with properties of the land surface. This is much more so over the dry regions of the world, where the surface properties differ greatly, depending on the amount of vegetation. Satellite monitoring of the Earth's surface permits regular surveys of vast areas of the continents (e.g. Courel 1983, Courel & Habib 1983, Courel et al. 1984). Measurements of the albedo have been carried out and have been analysed in terms of vegetation cover. It has been concluded that a decrease of the albedo does not occur before but shortly after an increase in the rainfall and that the changes observed in the albedo are not sufficient to regulate atmospheric circulation on more than a local scale. The positive feed-back hypothesis is therefore unlikely to be correct. This means that the albedo maximum observed during the very dry years of 1972–1973 presumably did not initiate any irreversible process of desertification. Instead, it is probable that it is the properties acquired by the monsoon before it arrives in Africa that will determine the future rainfall over the Sahara and the Sahel region.

*Acknowledgements.* I am grateful to Thomas Alerstam, Christian Hjort and Jan Pettersson, who read the manuscript and suggested several improvements. This paper is Contribution no. 103 from Ottenby Bird Observatory. The study was financed by the Swedish Nature Conservancy through PMK grants.

### Selostus: Tropiikin ympäristömuutosten vaikutuksista Pohjois-Euroopan linnustoon

Pohjolan pitkämatkaisten muuttolintujen tärkeimmät talvehtimisalueet sijaitsevat Afrikassa Saharan eteläpuolen savanneilla aavikko- ja sademetsäalueiden välissä. Pohjoisten muuttolintujen puuttuminen sademetsistä selitetään yleensä niiden heikolla asemalla kilpailussa afrikkalaisten lintulajien kanssa. Vuodenajoittain vaihtelevammilla kuivemmillä vyöhykkeillä kilpailu on vähäisempää. Etsittäessä Pohjolan lintukantoihin mahdollisesti vaikuttavia tekijöitä tropiikista on siten keskityttävä Afrikan kuivien vyöhykkeiden tapahtumiin.

Ilmasto ja ihminen ovat tärkeimmät ympäristömuutoksia aiheuttavat tekijät. Ihmisen aiheuttamat ympäristön pitkäaikaismuutokset johtuvat mm. metsien hakkuusta ja poltosta, kosteikkojen kuivatuksesta, maanviljelyksestä ja laidunnuksesta. Lyhyemmällä aikavälillä tärkein tekijä on saateen määrä eri alueilla ja erityisesti huomattavat kuivat kaudet (kuva 1). Ottenbyssä rengastettujen lintujen määrässä on tapahtunut merkitseviä muutoksia (kuva 2), mutta ne eivät näytä olevan kovinkaan samansuuntaisia Sahelin sademäärissä (kuva 3) tai Suomen (taulukko 1) tai Ruotsin (kuva 4, taulukko 2) pesimälinnustossa todettujen muutosten kanssa. Kaiken kaikkiaan viitteet Afrikan sateiden ja Pohjois-Euroopan lintukantojen muutosten välisistä yhteyksistä ovat melko epämääräisiä. Monessa tapauksessa näyttää todennäköiseltä, että yhtä hyvin pesimäalueen ympäristömuutokset ja ilmasto-olot voivat olla kannanmuutosten syinä.

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Received September 1984