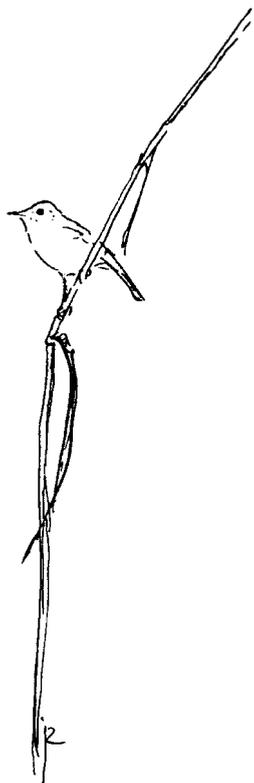


DUTCH SEDGE WARBLERS *ACROCEPHALUS SCHOENOBAENUS* AND WEST-AFRICAN RAINFALL: EMPIRICAL DATA AND SIMULATION MODELLING SHOW LOW POPULATION RESILIENCE IN FRAGMENTED MARSHLANDS

RUUD FOPPEN¹, CAJO J.F. TER BRAAK², JANA VERBOOM¹ & RIEN REIJNEN¹



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Sedge Warbler populations in The Netherlands have declined dramatically over the last 25 years, especially between 1973-75 and 1982-85. Population declines correlate with yearly rainfall in the western part of the Sahel-Soudan zone, the most probable wintering area of West-European birds (after removing effects of autocorrelation, $r_s = 0.58$). However, populations in relatively unfragmented landscape showed a clear recovery after 1984, while those in heavily fragmented landscapes showed no recovery. A spatially explicit population simulation model was used to test the general hypothesis that bird populations in fragmented landscapes show stronger declines and less resilience than populations unfragmented habitats in response to a catastrophe such as winter drought. The simulations demonstrated that in fragmented landscapes (less than 1% marshland), the relative decrease in numbers was 50% higher than in less fragmented habitats (more than 1% marshland). Furthermore, after a decrease, the recovery to initial numbers in landscapes with less than 1% marshland would take about five times longer than in areas with more than 15% suitable habitat. We tentatively conclude that Sedge Warblers breeding in fragmented marshland habitats are more vulnerable to drought events in West-Africa than those in unfragmented habitats.

Key words: *Acrocephalus schoenobaenus* - habitat fragmentation - metapopulations - spatially explicit population dynamic modelling - reedbeds - Sahelian droughts

¹Institute for Forestry and Nature Research (IBN-DLO), P. O. Box 23, 6700 AA Wageningen, The Netherlands; ²Centre for Biometry, CPRO-DLO, P. O. Box 100, 6700 AC Wageningen, The Netherlands; E-mail: r.p.b.foppen@ibn.dlo.nl.

INTRODUCTION

The Sedge Warbler *Acrocephalus schoenobaenus*, a widespread trans-Saharan migrant, has suffered long-lasting and dramatic declines in large parts of its European breeding range. Populations numbers in the United Kingdom (Marchant *et al.* 1990), Belgium (Lippens & Wille 1972), Germany (Glutz von Blotzheim & Bauer 1987) and The Netherlands (Teixeira 1979; SOVON 1987) showed declines of well over 50% during the period 1970-1985. In most areas the major declines

began in the early 1970s (Marchant *et al.* 1990; Teixeira 1979; Glutz von Blotzheim & Bauer 1987). In the same period the Whitethroat *Sylvia communis* population in western Europe also crashed. For this species, the decline coincided with reduced rainfall in their wintering quarters in Africa (e.g., Berthold 1974; Witstanley *et al.* 1974). For the Sedge Warbler this correlation has also been demonstrated in the British population; Sahelian rainfall was correlated with mortality (Peach *et al.* 1991). This paper presents empirical data that confirm the relationship between Sahe-

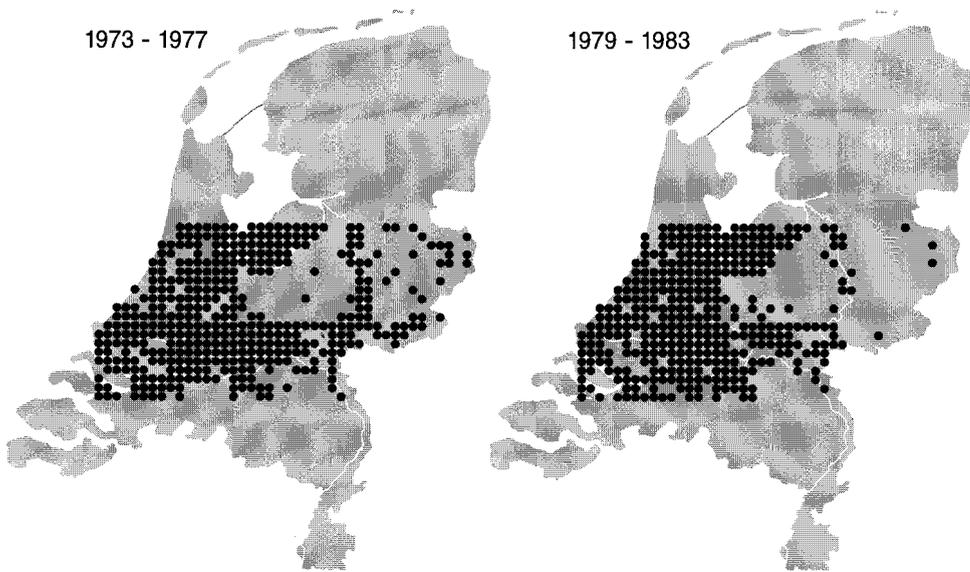


Fig. 1. Change in distribution of the Sedge Warbler in the central part of The Netherlands between 1973-77 and 1979-83. Distributions are on 5x5 km grid basis, based on data in Teixeira (1979) and SOVON (1987). A black dot in a grid means that breeding was reported during the study period.

lian rainfall and population indices of Dutch Sedge Warblers.

Although in general the Sedge Warbler population in The Netherlands is in decline, the decrease in numbers and distribution in marshland areas in the western part of the country appears to be smaller than in the generally drier landscapes in the eastern part (Teixeira 1978; SOVON 1987; Fig. 1). There are at least three possible explanations for this difference: migration direction, differential habitat quality changes, and a source-sink relationship on a national scale. Concerning migration direction, ringing recoveries on a European scale indicate that Sedge Warblers from eastern Europe choose a more eastern migratory route than western populations (Zink 1973). If this division in migration routes is also present in The Netherlands, this may imply different wintering quarters. Different wintering conditions could lead to different mortality rates. Concerning differential habitat quality changes, it may be that the quality of the marshlands in the eastern part of the country has deteriorated more quickly and to a

greater extent than in the west. Finally, concerning a source-sink relationship on a national scale, if marshlands in the western part of the country are of a better quality than those in the east, they could, in situations of Sahel-inflicted declines, 'draw' individuals from the eastern part in search for high quality territories. That would imply a smaller decrease in the habitats of the western part of the country because an immigration of individuals from eastern origin will buffer the effect, an example of source-sink systems (Fretwell 1972).

In this paper a further alternative explanation is explored: the habitat fragmentation hypothesis. Marshlands in the western part of The Netherlands are less fragmented than those in the eastern part of the country. We quantify and test differences in trends in Sedge Warblers between fragmented and non-fragmented marshlands. Habitat fragmentation can cause detrimental effects to bird populations because habitat units become too small. As a consequence, the probability of local populations going extinct by chance effects is en-

hanced. If these local extinctions are not counter-balanced by recolonisations, species may disappear over large ranges (Opdam *et al.* 1992; Verboom 1996). The crucial factor is dispersal (Opdam 1990). In viable networks of populations, habitat units are linked closely enough to ensure a sufficient dispersal flow (Hanski 1994). Catastrophes are particularly harmful for network populations (often called metapopulations). When a catastrophe causes high mortality, population numbers decline, but the dispersal flow will also decrease. This may cause a breakdown of the population network resulting in large-scale extinctions and a decreased population resilience.

To explore whether these effects might explain the observed difference in the decline of Sedge Warbler populations between the east and the west of The Netherlands a simulation study was conducted. A spatially explicit population

model was used to test the hypothesis that those parts of the Sedge Warbler population network in The Netherlands with a strong degree of fragmentation are more vulnerable to catastrophes and have a lower population resilience than parts with little or no fragmentation.

METHODS

Population indices

Quantitative mapping data for 180 areas with Sedge Warblers were selected from a large number of sources, the most important being the SO-VON databank. The areas are well distributed over The Netherlands, and were thus assumed to provide a good representation of marshlands (Fig. 2). Different census methods were used in different areas, including counts of singing males in ar-

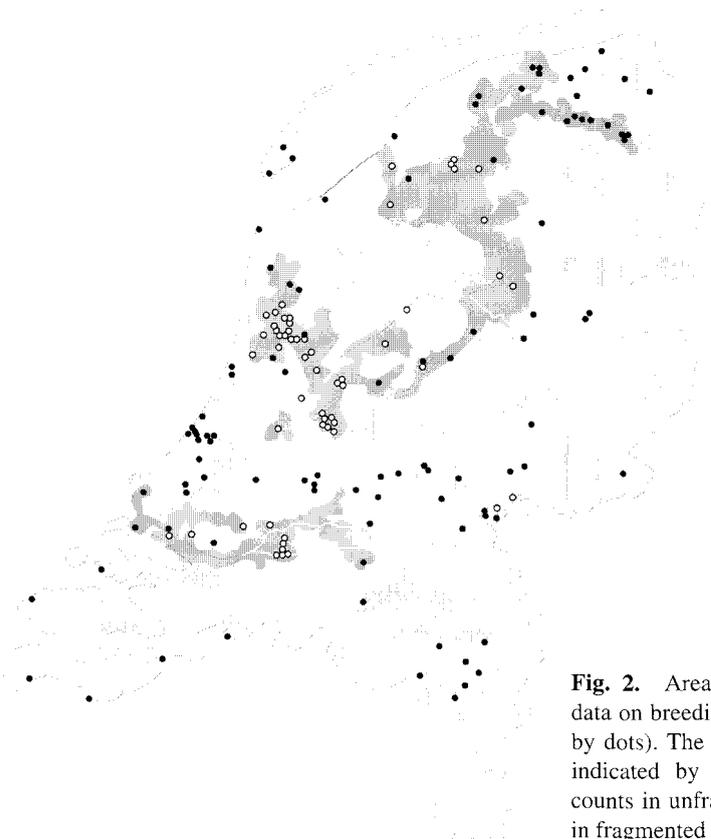


Fig. 2. Areas in The Netherlands for which count data on breeding Sedge Warblers were used (indicated by dots). The distribution of very large marshlands is indicated by grey shading. Open circles represent counts in unfragmented areas, filled circles are counts in fragmented marshlands.

eas, transects, and extensive territory mapping. For each time series, a check was made (e.g. by assessing descriptions of methods in the literature or asking the people responsible for the monitoring) as to whether counting effort and circumstances were relatively constant over the years. Only those areas with at least three annual censuses in a time span of at least five years in the period 1960-95 were selected. The number of missing data was about 70%. Only indices for years with more than 20 census areas (1966-94) were used in the analyses.

Time series data were divided into two sets: one in fragmented marshlands and one in unfragmented marshlands. To assess the degree of fragmentation of a marshland, a digitised map of marshlands in The Netherlands was analysed. Using ARC/INFO, the total area of marshland was calculated in a circle within a radius of 10 km from the central point of each marshland with census data. Count data were divided into two sets based on the frequency distribution of total area of habitat: a set with fragmented areas (FRAG) and a set with non-fragmented areas (CORE). In FRAG the percentage of habitat in the 10 km circle is approximately 0.01- 1% (mean 0.3%), in CORE the percentage of habitat is 1-30% (mean 5%). Only for those years with more than 60 areas (1984-94) were the data divided into a fragmented and non-fragmented set.

Time series were combined to calculate a trend using a loglinear Poisson regression (Weinreich & Oude Voshaar 1992; Ter Braak *et al.* 1994; Thomas 1996; Goedhart & Ter Braak 1998). This is a special case of generalised linear modelling (GLM) (McGullagh & Nelder 1983), able to deal with incomplete data sets. First, a simple model was used that only took into account site and time:

$$\text{LOG (Expected count)} = \text{constant} + \text{LOG (site effect)} + \text{LOG (year effect)}$$

Then, fragmentation was added as a covariate with two levels. Counts followed a Poisson distribution. The *F*-test based on deviances was used to

test for overdispersion. The expected counts per year were calculated from the maximum likelihood method. Year effects were re-expressed as year indices for population size compared to a base year. Computations were carried out using the statistical program GENSTAT (GENSTAT 5 Committee 1987). Variation between year, and site, effects were tested (*F*-test) and three simple models were compared that describe the trend effects: a linear model in time, a quadratic model in time and a model with time effects for every year (Goedhart & Ter Braak 1998).

Rainfall indices

Western European Sedge Warblers probably winter in the sub-Saharan region of Africa (Glutz von Blotzheim & Bauer 1987; Cramp & Brooks 1992). Ringing recoveries of British Sedge Warblers in Africa show that important wintering areas are situated in the floodplains of the rivers Niger and Senegal (Peach *et al.* 1991). There are two recoveries in winter of Dutch birds in Africa, also from this region (data Dutch Ringing Centre, Heteren). However, it is not yet clear whether a part of the population also winters in more eastern parts (e.g. Sudan) the probable wintering area for populations from eastern Europe. Therefore, three sets of rainfall data in the sub-Saharan region covering the total area from west to east were analysed. These sets correspond with zones in sub-Saharan Africa with equal amounts of annual rainfall (after Nicholson 1985; see Fig 3.). Two data sets were provided by the Climatic Research Unit at the University of East Anglia. These consist of yearly standardised anomalies in relation to the mean rainfall in 1951-1980 (see Nicholson 1985; Peach *et al.* 1991): (1) data for west African countries in the Sudan-Guinea zone (e.g. Sierra Leone, Liberia, Ghana, Benin, Togo, Côte d'Ivoire) and (2) data for central Sudan situated in the eastern part of the Sahel-Sudan zone. For the western Sahel-Sudan zone (between 10°N - 18°N and 14°W - 14°E; Burkino-Faso, Mali, Niger and Senegal), we analysed rainfall data from almost 300 meteorological stations (Fig. 3). The data consisted of monthly totals of rainfall (range

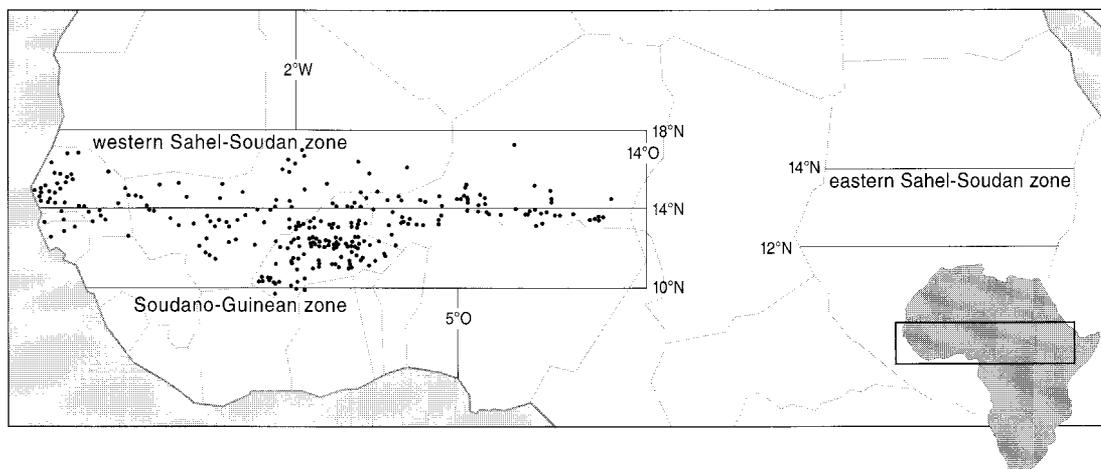


Fig. 3. Location of the sub-Saharan zones with rainfall. In the western Sahel-Soudan zone the dots indicate the weather stations for which rainfall data were analysed.

1900-94). The total amount of rainfall in the rainy season, May-October, was used for the calculation of the indices.

Rainfall indices were calculated using the same model as the bird population indices: a log-normal distribution for the total amount of rainfall in the selected period, a site (= meteorological station) and a year-effect. Population indices in year x were related to rainfall indices in year $x - 1$ (1965-93) because rainfall in the period May-October influences the population indices measured the following spring. Missing data exist, but their percentage was low in the selected period (15%).

A statistical problem in cross-correlating two timeseries is that of autocorrelation (Box & Jenkins 1976). In our data, the positive autocorrelation could be effectively removed by differencing the series (Box & Jenkins 1976), and the autocorrelations tended to be slightly negative. After differencing, a series $R(i)$ is replaced by the series of differences $R(i + 1) - R(i)$. Spearman Correlation Coefficients were calculated with and without differencing the series (Sokal & Rohlf 1981).

Simulation

The simulation was carried out with the METAPHOR model (Verboom 1996; Verboom & Ba-

veco 1998). METAPHOR is an individually based model that simulates the stochastic dynamics of a spatially structured population. A spatially structured population is a set of local populations connected through dispersal. The three most important model components are recruitment, mortality and dispersal. Recruitment and mortality determine the local population dynamics (i.e. of habitat units). Population dynamics are stochastic. There are two types of stochasticity. Demographic stochasticity is the variation between the fates of the individuals, environmental stochasticity is modelled by drawing annual mortality and recruitment ratio from specified distributions. The dispersal range defines the size of the habitat network - the set of habitat patches supporting a metapopulation or network population - for the Sedge Warbler (Opdam *et al.* 1992).

A METAPHOR Sedge Warbler model was developed in order to simulate a set of Sedge Warbler populations in a marshland network (see the Appendix for a global description of the model and parameter settings). The Sedge Warbler model uses specific input data for the underlying landscape pattern. At a European scale, the cluster of marshlands in the Dutch Delta is well separated from the clusters in neighbouring countries

(e.g. eastern parts of Germany; Moss *et al.* 1991). In the intermediate parts of western Europe, the density of marshland patches is very low. Thus a GIS database comprising a pattern of marshlands of only The Netherlands and some marshlands in Belgium and Germany close to the Dutch border was considered suitable as a habitat basis. The database comprised only marshlands larger than one ha. Although Sedge Warblers may occasionally occupy habitat patches smaller than one ha, the resulting habitat pattern was compared with distribution maps (Teixeira 1979; SOVON 1987) and appeared to be a reliable image of Sedge Warbler habitat in The Netherlands. With the habitat pattern in a GIS database each patch could be assigned a degree of fragmentation following the same routine as for the empirical data. Four classes were distinguished in the degree of fragmentation: mean habitat percentages of 0.1%, 1%, 3% and 15%.

To simulate the effect of drought conditions in West Africa, drought spells in the wintering quarters were assumed due to lead to an overall decrease in numbers of 50% (based on empirical data). This assumption and the data on the correlation between rainfall and mortality rates (Peach *et al.* 1991) were used to generate two mortality settings (normal and high mortality).

Two types of simulations were run. First, to determine whether isolated populations show a higher vulnerability to catastrophes, we manipulated mortality levels. A situation with high mortality was compared with a situation with normal mortality for both fragmented and unfragmented patches. Second, to assess the extent of a low population resilience under fragmented conditions, the recovery period in fragmented and unfragmented habitat units was calculated from simulated data. In the simulation model this was achieved by a shift from a period of years with high mortality rates to a period of years with normal mortality rates. The first type of simulation starts with all habitat units fully occupied (at carrying capacity). Because populations need some time to reach equilibrium, the first 50 years are not taken into account for the statistics. Overall

the period simulated is 150 years and is repeated 100 times. The second type of simulation also starts with all patches fully occupied and with the mortality conditions of the drought period. After equilibrium is reached (50 years), a shift is made to the mortality figures for normal years and recovery commences. The statistics begin with the first year after the shift in mortality figures. The model predicts an average number of individuals per habitat unit per year.

RESULTS

Population trend and rainfall indices

Site and time proved to be highly significant factors in the trend analysis (Table 1). The best model was that which allowed a separate effect per year because this year effect model was a significant improvement over the quadratic model ($P < 0.001$). The trend for the Sedge Warbler in The Netherlands in the period 1966-94 shows several periods with a moderate (e.g. 1973-75) and one with a strong decrease (1982-85; Fig. 4). After the strong decrease the population recovered, but failed to reach the starting level. The year of the minimum population in The Netherlands (1984) coincides very well with British data (Peach *et al.* 1991).

Long-term trends in the distinct sub-Saharan zones indicate that, particularly after 1965, yearly rainfall decreased (Fig. 4). Rainfall data for the period 1965-93 in the western Sahel-Sudan and Sudan-Guinea zone showed a declining trend until 1985 with decreases particularly around 1972 and 1983. After 1985 there was an apparent increasing rainfall trend. Although the trend in the eastern part of the Sahel-Sudan zone was similar it showed no increase after 1985, but there were large fluctuations. The correlations between population and rainfall indices after differencing the data are significant for the western Sahel-Sudan zone ($r_s = 0.58$, $P < 0.001$, $n = 26$; see Fig. 5) but not for the Sudan-Guinea ($r_s = 0.14$, $P > 0.05$, $n = 26$) and eastern Sahel-Sudan zones ($r_s = 0.15$, $P > 0.05$, $n = 26$). These findings suggest that the most

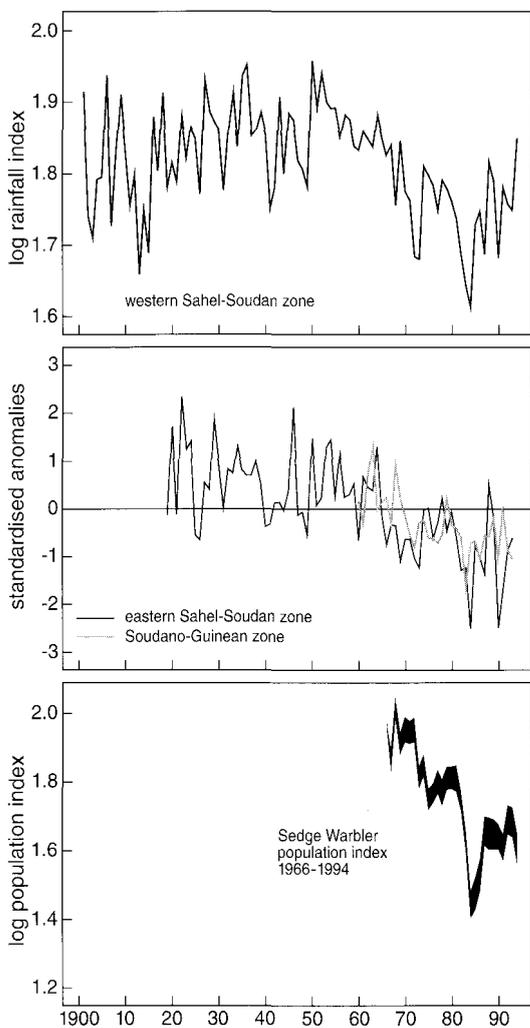


Fig. 4. Trends for rainfall in the sub-Saharan zone and the Sedge Warbler population in The Netherlands. (A) The long-term trend for rainfall in the western Sahel-Soudan zone based on GLM-indices. (B) The long-term trend for rainfall in the eastern Sahel-Soudan zone (1920-93) and in the Sudan-Guinea zone (1960-93) based on standardised anomalies (empirical data). (C) The trend for the Sedge Warbler population in The Netherlands in the period 1966-94. The trend indices are shown as logarithms of the calculated index; year 1966 was taken as the reference year (index = 100). 95% confidence intervals for the yearly trend indices are shown.

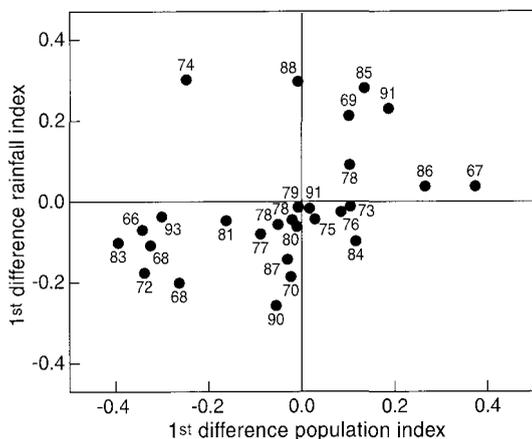


Fig. 5. A correlation plot of indices of rainfall in the western Sahel-Soudan zone and Sedge Warbler population (empirical data). For every data point the year is indicated.

important wintering regions of Dutch Sedge Warblers are probably located in the western Sahel-Soudan zone. Because this is in agreement with other evidence (e.g. the ringing data) this data set was used for further analysis.

Simulation data

The results of the simulations show a relationship between the degree of fragmentation and a decrease in occurrence or in numbers under a situation with increased mortality (Fig. 6). The decrease was calculated as the relative difference between the simulation results with high and normal mortality. A high degree of fragmentation (e.g. patches in a landscape with less than 1% habitat) is causing a high probability of local extinctions, resulting in an average decrease in numbers of more than 70%. In unfragmented patches (patches in a landscape with more than 15% habitat) numbers decreased by less than 50%.

Simulating the recovery phase after a prolonged period of unfavourable drought conditions and resulting low population numbers showed that patches in a fragmented landscape recover slower than patches in unfragmented landscapes (Fig. 7). The recovery in the most fragmented

Table 1. Summary of the generalised linear model results (*F*-test) for time series of the Sedge Warbler population in The Netherlands, using site and time as explanatory variables.

| Factor | <i>df</i> | deviance | mean deviance | deviance ratio | <i>P</i> = |
|----------------|-----------|-----------|---------------|----------------|------------|
| site | 165 | 71303.497 | 432.142 | 57.97 | < 0.001 |
| time effects | | | | | |
| + linear | 1 | 1512.318 | 1512.318 | 202.89 | < 0.001 |
| + quadratic | 1 | 65.928 | 65.928 | 8.84 | 0.003 |
| + year effects | 28 | 784.658 | 30.179 | 4.05 | < 0.001 |

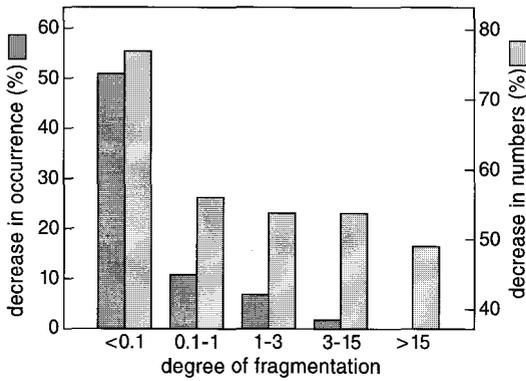


Fig. 6. Simulation data: the relationship between degree of fragmentation and decrease in occurrence (black bars) and numbers (white bars). Decrease is calculated as the difference relative to the 'normal' situation and is expressed as a percentage. Degree of fragmentation is expressed in % of suitable habitat in a landscape.

patches was lower in the exponential increase phase than in unfragmented patches. It took a fragmented patch 2 - 7.5 times as long as an unfragmented patch to increase from 50% to 95% of the expected numbers.

Empirical data: difference between fragmented and unfragmented landscapes

The population indices of Sedge Warblers in the Netherlands show a minimum in 1985 and a recovery in the years immediately after. Splitting the data into a set with unfragmented (CORE) and

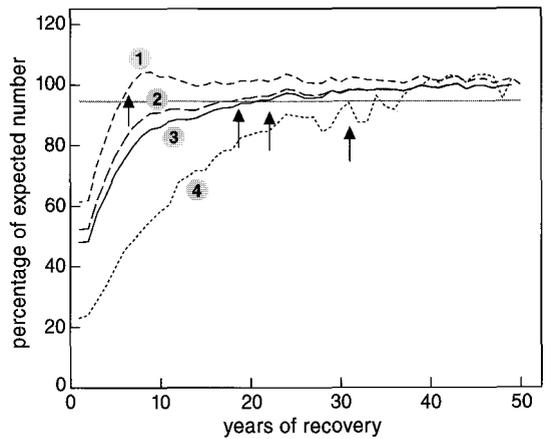


Fig. 7. Recovery phase for patches with different degrees of fragmentation (simulation data). Year 1 is the first year of recovery. Recovery is shown per year as mean percentage of population size under 'normal' conditions. Numbers refer to patches with an equal degree of fragmentation: 1 = 15% habitat, 2 = 3% habitat, 3 = 1% habitat, and 4 = 0.1% habitat. The arrows indicate the years when the population returned to 95% of its initial size.

fragmented (FRAG) patches reveals an interesting difference. The trend for FRAG patches shows a short period of recovery after 1985, but on the whole it is not an upward trend. The trend for CORE patches is upward after 1985 (Fig. 8). The difference between the two trends is statistically significant (GLM-Poisson regression, trend FRAG = -0.02, trend CORE = 0.08, *F* = 15.45, *df* = 1, *P* < 0.01). Correspondingly, the correlation

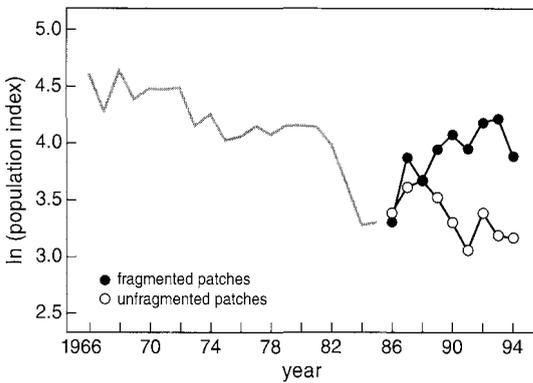


Fig. 8. Population indices for Sedge Warbler populations in fragmented and unfragmented patches in the period 1985-94.

between rainfall index and population index in the period 1985-94 is significant for CORE ($r_s = 0.64$, $P < 0.05$, $n = 10$), but not significant for FRAG ($r_s = 0.24$, $P > 0.05$, $n = 10$).

DISCUSSION

Is West African drought affecting the Dutch population?

Sedge Warblers in The Netherlands are clearly affected by drought conditions in Africa. The decrease in population size since the early 1970s as suggested by publications on mapping data in The Netherlands (Teixeira 1979; SOVON 1987) shows one remarkable period of severe decline (1982-85) and one period of moderate decline (1973-75). Both periods are characterised by drought in the wet season in West Africa. In this respect the Dutch populations are no different from British populations (Peach *et al.* 1991). Although the problem of autocorrelation exists, even after differencing the data the correlation remains significant and thus the relationship seems strong. Other Palearctic migrants for which population declines have been associated with drought in their African winter quarters are: Purple Heron *Ardea purpurea* (Den Held 1981; Cavé 1983), White Stork *Ciconia ciconia* (Kanyamibwa *et al.* 1990), Sand

Martin *Riparia riparia* (Szep 1995a,b), and Whitethroat *Sylvia communis* (Berthold 1974; Witstanley *et al.* 1974). Similar declines have been suggested for a number of other passerines breeding in The Netherlands (Wammes *et al.* 1983; Foppen & Reijnen 1996).

The causal mechanisms of the effect of drought in the Sahel zone of West-Africa on population dynamics remain unclear. Peach *et al.* (1991) showed that mortality rates of wintering Sedge Warblers increased in years with poor rainfall. Observations suggest that Sedge Warblers use freshwater fringing vegetation with papyrus and other emergent macrophytes during winter and that drought affects the area and/or quality of these habitats (Mullié & Brouwer 1994; Peach *et al.*, 1991). This suggests a reduction of carrying capacity and hence a density dependent mortality of Sedge Warblers.

Dispersal in fragmented landscapes: a problem for Sedge Warblers?

The simulation data show that populations in fragmented habitat situations have lower numbers and also a slower recovery after a decrease. In the model it is assumed that dispersal in fragmented habitat situations is not efficient and does not allow sufficient recolonisations. The possible mechanistic explanations for this assumption are: a higher dispersal mortality, unpaired individuals, and hampered territory shifts. As to a higher dispersal mortality, birds in fragmented landscapes might experience a greater mortality because they have to disperse through more inhospitable landscapes. Even for migrants this seems reasonable because natal dispersal may take place in the post-fledging period (for Sedge Warblers, see Catchpole 1972). For unpaired individuals, in small fragmented patches there is a larger chance of an unbalanced sex-ratio. This would cause a less optimal recruitment; some individuals remain unpaired (Allee 1938). In hampered territory shifts, juveniles may settle in a low quality territory instead of dispersing until they find a patch of a higher quality. In a fragmented landscape high quality patches may remain undiscovered

and thus empty (Verboom *et al.* 1991).

But are these assumptions supported by field data? Little data on dispersal behaviour of the Sedge Warbler are available. An analysis of ringing data revealed a median natal dispersal distance of 6.1 km and a mean of 40 km (Paradis *et al.* 1998). In the Dutch context this implies that no marshlands are entirely isolated and individuals can change sites, but that many marshlands will only exchange very low numbers of individuals. Effects of increased dispersal mortality or hampered territory shifts have not yet been documented.

Are the modelling data supported by the field data?

The simulation data suggest that the decrease in numbers, caused by a series of drought years in the winter quarters, is larger in fragmented populations. Unfortunately this could not be tested because only for the period after the decrease (1984-94) are field data available. However, a preliminary analysis clearly showed that numbers in fragmented landscapes showed a larger decrease than in unfragmented landscapes (Foppen 1994). Furthermore many local populations in the heavily fragmented marshland landscape in the east of The Netherlands went extinct (Fig. 1). The second prediction of the model, that resilience in fragmented landscapes is lower than in continuous, or less fragmented landscape, is supported by the finding that for populations in fragmented landscapes there is an absence of population recovery in the eight years after the onset of a period with more rainfall in West-Africa (1985-94), while populations in unfragmented landscapes seem to be able to recover rather fast (Fig. 8).

In the simulation, numbers of Sedge Warblers in fragmented patches increased moderately, while empirical data showed no recovery. There are at least four possible explanations for this difference. Firstly, a difference between actual rainfall pattern and simulated rainfall pattern. Because the reasons for the correlations between rainfall and mortality are not understood, we used a simplified approach of splitting the years into

normal or drought years, resulting in averaged mortality rates (with associated errors). It is not surprising, therefore, that the real recovery differs from the simulated one. Secondly, our simulations explored the rainfall effects by assuming a sudden shift in rainfall indices from drought to normal years. Actual rainfall data show a clearly upward trend but do fluctuate; in general the situation after 1984 improved, but even then drought years occurred and these may have suppressed recovery. Thirdly, other factors, not involved in the simulation, might have affected the recovery. Finally, the assumptions of the simulation model might be wrong.

Lack of evidence for alternative explanations

Three alternatives already mentioned in the introduction will be discussed: the difference arises from a difference in wintering areas between the regional populations in The Netherlands, or the difference is caused by a different change in habitat quality between regions in The Netherlands, or in The Netherlands a source-sink system exists between the western and the eastern regions.

Because most of the fragmented marshlands are situated in the eastern part of the Netherlands the eastern population might have different winter quarters and thus experience other rainfall conditions. This was reported as the reason for the difference in population trends between western and eastern European White Storks (Kanyambwa *et al.* 1993). Survival of White Storks in western Europe correlated well with rainfall in western African wintering area, but for eastern European Storks there was no correlation with rainfall in their wintering areas. Furthermore rainfall in east Africa decreased less than in west Africa (Kanyambwa *et al.* 1993). The 'Zugscheide' they reported for the White Stork was also present in the Netherlands, cutting the country in a south-western and north-eastern part. For the Sedge Warbler however, this hypothesis is unlikely for two reasons: Firstly, an analysis of Sedge Warbler recoveries ringed in The Netherlands showed no significant geographically correlated differences in mi-

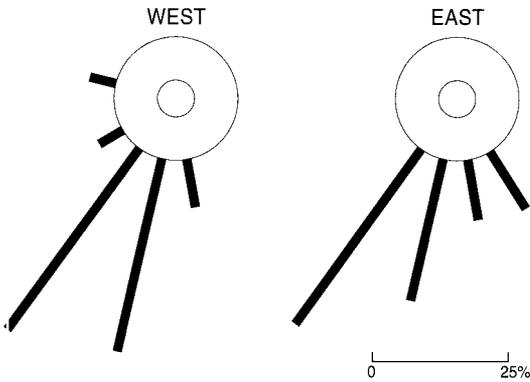


Fig. 9. Comparison between the migration directions of Sedge Warblers from the eastern ($n = 15$) and western ($n = 19$) parts of The Netherlands. Birds ringed in the period May-July and recovered at distances more than 100 kilometres away in the same year are shown.

gration direction. A selection was made of ringing recoveries consisting of birds ringed in the breeding season in the Netherlands (May-July) and recovered at distances larger than 100 km in the next autumn (data: Dutch Ringing Centre, NIOO). The group was split in two according to the longitude of the ringing area (boundary $5^{\circ}24'E$; see Fig. 9). Although there is a difference in the expected direction (western birds on aver-

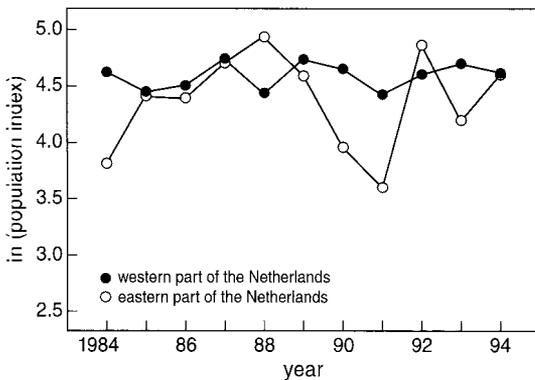


Fig. 10. Comparison of population trend data for Sedge Warbler populations in fragmented areas in the western and the eastern half of The Netherlands in the period 1984-94.

age (\pm SE) 8 degrees more to the west), this difference was not significant (west: $203 \pm 6.2^{\circ}$, $n = 15$, east $195 \pm 3.5^{\circ}$, $n = 18$, t -test, $P > 0.10$) and secondly, fragmented areas in the western half of The Netherlands showed no recovery after the 1984-85 decrease. The data set with fragmented areas was split into that from the western part and the eastern part of The Netherlands. Indices were calculated for the period 1983-94. In neither set of data did the indices show any change (Fig.10).

However, the difference can also be explained by the effect of habitat quality (explanation 2). Since the time when the first decreases in numbers were observed (1968-70), gradual changes in habitat quality in the breeding areas might have occurred. Assuming regional differences in this deterioration, this could have been the cause for the lack of resilience in some regions in The Netherlands. For example, Peach *et al.* (1991) hypothesise that increased drainage for agricultural purposes has led to major losses in British wetlands preventing populations to return to pre-drought levels. The same might apply for certain parts of The Netherlands. The sites in the western part of The Netherlands are situated in regions with peat or sea clay soils. The sites in the eastern part are partly situated in regions with sandy soils of Pleistocene origin. These areas seem more vulnerable to eutrophication and ground water reduction (Garritsen *et al.* 1989), which probably is an important cause for the reduction in area and in quality of reed marshland (Graveland 1996). However, the Sedge Warbler is typically a species of the drier parts of a reedland and does not seem to be particularly vulnerable in this respect (e.g. Catchpole 1972). We suspect that such effects will be small and cannot fully account for the observed difference.

The third hypothesis, a source-sink system on a national scale, assumes a large dispersal capacity of Sedge Warblers. For a source-sink system to function, the fluxes of individuals from sink to source (in this case) have to be quite substantial. This will only be the case when dispersal chances remain high, even at distances of many tens of kilometres. There are no indications that the

Sedge Warbler exhibits this kind of dispersal (Paradis *et al.* 1998). A mechanism is also lacking: how do Sedge Warblers in the eastern part of The Netherlands 'know' that territories are available in optimal habitat some 100 kilometres away? Examples of shifts in territory from sink to source habitat are known only for local situations (e.g. Krebs 1971). Furthermore there was no recovery of populations in fragmented, small patches in the western part of the country. These areas are close to the source and probably exhibit an identical habitat quality, so they would be expected to recover much sooner than the small patches in the east. However, the empirical data show that there was no recovery after the large crashes.

Although the Dutch population of the Sedge Warbler is not threatened, its future in many parts of The Netherlands seems grim. Increases in the frequencies of droughts in the Sahel could eventually lead to a total disappearance of the species from some regions. An interesting issue is whether and how global climate change will influence rainfall in the Sahel. This might be examined using climate models that predict yearly rainfall as an input to metapopulation models, to explore the effect on survival of birds such as Sedge Warblers wintering in West-Africa.

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SAMENVATTING

In dit artikel wordt aannemelijk gemaakt dat de aantalsontwikkeling van de Rietzanger *Acrocephalus schoenobaenus* in Nederland samenhangt met de regenval in de Sahelzone. Bovendien is nagegaan of regio's waarin de habitat van de soort sterk versnipperd en gering van oppervlakte is, meer te lijden hebben van droogte catastrophes dan regio's met grote en weinig versnipperde moerassen. Sinds het begin van de jaren zeventig is de Rietzanger in Nederland sterk achteruitgegaan. Door voor een groot aantal gebieden tijdreeksen te achterhalen konden voor de periode 1965-94 indexcijfers berekend worden voor de populatiegrootte. Hieruit is gebleken dat er een periode is geweest met een matige terugval in aantallen (1973-75) en een periode met een sterke terugval (1982-85). Nadien is er een gering herstel opgetreden. De periode van terugval komt overeen met een periode met een geringe neerslag in de Sahel. Er bestaat een sterke correlatie tussen beide trends. De achteruitgang is in bepaalde regio's veel sterker dan in andere. Wat opvalt is dat in de meest getroffen regio's de habitat van de rietzanger sterk versnipperd is en het percentage geschikt habitat erg laag. Voorbeelden zijn met name te vinden in het oosten en zuiden van het land. Met behulp van een ruimtelijk gestructureerd populatiemodel kan voorspeld worden dat populaties op plekken in een landschap met een zeer laag aandeel geschikt habitat (< 1%) ongeveer 50% meer achteruitgaan dan populaties in een minder versnipperd landschap. Bovendien duurt het herstel na een zware klap veel langer, bijvoorbeeld in landschappen met minder dan 1% geschikt habitat vijfmaal langer dan in landschappen die minder versnipperd zijn (> 15% geschikt habitat). De oorzaak voor dit 'versnipperingseffect' is gelegen in het feit dat door catastrophes metapopulatiën (dat wil zeggen subpopulaties die met elkaar samenhangen door onderlinge dispersiestromen) uiteenvallen en dat de balans die er in een gezonde metapopulatie bestaat tussen toevallige uitsterfprocessen en koloniaties verstoord is. Indien de set gegevens opgedeeld wordt in versnipperde gebieden en niet-versnipperde gebieden, blijkt deze hypothese ondersteund te worden. In versnipperde gebieden treedt geen herstel op na de crash van 1982-85, in niet-versnipperde gebieden is er tot 1994 een duidelijk herstel te zien. Er zijn geen aanwijzingen, dat populaties uit het meer versnipperde oosten en zuiden van het land ergens anders overwinteren dan de populaties uit het westen. Bovendien vertonen gebieden in het westen van het land die

versnipperd zijn, ook een geringer herstelvermogen. Ook de alternatieven, dat habitatkwaliteit een rol speelt bij het totstandkomen van het verschil of dat er een bron-put relatie is op nationaal schaalniveau, lijken niet erg waarschijnlijk. Mogelijk dat er wel een aantal factoren samenspeelt. Concluderend kan worden gesteld dat de 'fragmentatie-hypothese' een mogelijke verklaring is voor het verdwijnen van Rietzangerpopulaties in Oost-Nederland en dat, in het algemeen gesproken, versnipperde populaties meer effecten zullen ondervinden van grootschalige catastrophes.

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APPENDIX

METAPHOR-Sedge Warbler model

Our simulation assumed a maximum number of 5 territories per ha. This is higher than densities in the field because numbers are normally below carrying capacity and because net suitable reed areas (determined as the area of reedland that was not mowed or burned) were used instead of using total marshland area as in most density figures from field data. The carrying capacity of a patch in the model is a linear function of patch area, truncated to discrete numbers.

Adult mortality is based on iterative simulation runs with a large patch of optimal habitat, assuming a stable and viable population. Mortality in this population is balanced by recruitment. The resulting figures (around 0.45 for populations close to carrying capacity) are close to the highest value for British Sedge Warblers in the period 1969-83 (Peach *et al.* 1991). However, most of the years in this period showed a lower than average rainfall and thus a decreased survival. So, assuming 'normal' wintering conditions the data are consistent. For the mortality levels under drought years we decided to use the mortality levels in the data of Peach *et al.* (1991) in years with rainfall below average (around 75%).

Recruitment figures were based on literature reports of mean annual production per breeding pair (Bibby 1978; Catchpole 1972). No data exist for first winter mortality. Therefore we used data for other small songbirds. For Reed Warblers a mortality of 0.76 was calculated from ringing data (Long 1975) which falls well within the range of 0.70-0.80 assumed for small songbirds (Von Haartman 1971; Reijnen & Foppen 1994).

In a metapopulation, local populations are connected through dispersal. In METAPHOR, within-patch dynamics and between-patch dynamics (dispersal) are iterated on a yearly basis: dispersal takes place after mortality and reproduction. First, a fixed fraction of the present individuals is chosen leaving the patch, creating a dispersal pool. This dispersal pool is supplemented with the number of individuals above carrying capacity. A relation file, describing the probabilities that individuals change to surrounding sites, is used to determine the exact number of immigrants for every

patch in the simulation. The relation file is mainly based upon the maximal dispersal distance, the inter-patch distances and the size of the receiving patch. Few data exist for Sedge Warblers. Most individuals do not disperse further than a few kilometres (breeding dispersal median 1.1 km, natal dispersal median 6.0 km, Paradis *et al.* 1998), although the maximum can be much further. In METAPHOR the parameters determining the relation file are calibrated on a median dispersal of a few kilometres. The maximum dispersal is truncated at 30 kilometres.