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Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*

MICHAEL SCHAUB*†, WOJCIECH KANIA‡ and ULRICH KÖPPEN§

**Schweizerische Vogelwarte, CH-6204 Sempach, Switzerland; †Conservation Biology – Zoological Institute, Universität Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland; ‡Institute for Ornithology, Polish Academy of Sciences, PL-80–680 Gdańsk 40, Poland; and §Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern, Beringungszentrale Hiddensee, Badenstr. 18, D-18439 Stralsund, Germany*

Summary

1. The environmental conditions that migratory birds experience during their stay at different locations throughout the year can have significant impact on the variation of annual survival rates. Because migrants often crowd during non-breeding, environmental conditions can affect survival rates of individuals originating from different breeding populations, thus also provoking spatial synchronisation of annual survival rates. The identification of critical environmental factors affecting survival is therefore crucial for understanding large-scale population dynamics of migrants.

2. We studied temporal and spatial variation of survival rates of migratory white stork *Ciconia ciconia* from eastern Germany and Poland and examine factors associated with this variation. We used resighting and dead-recovery data from more than 30 000 individuals sampled over 19 years to estimate survival.

3. Survival rates of juvenile and adult white storks originating from the two countries varied in parallel over time. Thus, variation in survival was caused by environmental variation to which individuals of both age classes from both countries were similarly sensitive. Variation in the primary production (as reflected by the normalized difference vegetation index) at one staging area in the eastern Sahel that is visited from October to November contributed up to 88% to the temporal variation in survival. Annual survival was reduced when primary production in the Sahel was low.

4. As the population growth rate of white storks is very sensitive to changes in survival, variation in primary production in the Sahelian staging area contributed significantly to population changes and is likely to be an important reason for population synchrony.

5. This study demonstrates that dynamics of migratory bird populations inhabiting large breeding areas can result from environmental variation encountered at a staging area that is visited for only a short period of time.

Key-words: Africa, migration, NDVI, stopover, variance decomposition.

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Introduction

Migratory animals spend different periods of their annual cycle in widely separated and ecologically different locations. Environmental conditions or density-dependent effects experienced by the individuals at these locations potentially have an impact on the vital rates, and finally on population dynamics. The identification of the limiting factors of populations of migrants is challenging, because the spatio-temporal course of their migrations as well as the impact of these different environments on the vital rates must be known (Webster *et al*. 2002; Newton 2004).

Annual survival of migratory birds is the product of seasonal survival rates, i.e. of survival during breeding, migration and wintering. The seasonal survival rates that are the most variable over time contribute most to the temporal variation of annual survival, and thus

Correspondence: Michael Schaub, Schweizerische Vogelwarte, CH-6204 Sempach, Switzerland.
E-mail: michael.schaub@vogelwarte.ch

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potentially to variation of population size. The identification of factors that have the strongest impact on the temporal variation of annual survival is therefore crucial to understand population dynamics in migrants. Moreover, as migratory birds often crowd on migratory pathways at staging or wintering areas (Newton 1995), many individuals from different breeding populations are exposed to the same environment. If the temporal variation of seasonal survival at such sites is significant, this can be the reason for spatially synchronized annual survival rates. Spatial synchronization of survival rates result in reduced persistence of metapopulations (Palmqvist & Lundberg 1998), yet empirical demonstration of spatial synchronization of survival rates in migratory birds is lacking.

In this paper, we study the temporal and spatial variation of annual survival rates of white storks *Ciconia ciconia* (Linnaeus) inhabiting a large breeding area. The white stork populations in Europe are separated according to the main wintering area into the western populations migrating to western Africa and the eastern populations migrating to eastern and southern Africa. White storks from western European populations spent the whole winter in areas influenced by northern tropical rainfall regime (western African Sahel) without the possibility to move to other areas when unfavourable environmental conditions such as drought occur. Annual survival rates of individuals breeding in different western European countries increase with increasing amount of rainfall in the Sahelian wintering area (Kanyamibwa *et al.* 1990; Kanyamibwa, Bairlein & Schierer 1993; Barbraud, Barbraud & Barbraud 1999) and the occurrence of droughts in the Sahel is supposed to be a major factor affecting dynamics of the western populations (Dallinga & Schoenmakers 1987; Bairlein 1991). By contrast, survival rates of individuals from eastern European populations which migrate to south-eastern Africa are not well studied (Kanyamibwa *et al.* 1993). It is unknown which environmental factors have an impact on survival and whether there are common factors as in the western white storks that affect individuals from large areas and could thus be a reason for spatial survival synchrony. Eastern European white storks have potentially a much larger area available for wintering that is influenced by the northern and the southern tropical rainfall regime (eastern African Sahel and savannahs south of the equator), giving them the possibility to avoid temporally adverse areas by nomadic movements. Therefore, it is possible that temporal variation in survival is not induced significantly by environmental variation at the African wintering areas, but rather by environmental variation during breeding or migration.

Due to satellite telemetry and intensive ringing the spatio-temporal course of their migration is well understood (Creutz 1985; Kania 1985; van den Bossche *et al.* 1999; Berthold *et al.* 2001, 2002). Because white storks have to rely on thermal upwind for migration, they surround the Mediterranean Sea using narrow migratory pathways. They usually no longer make a stopover until they reach the central parts of Sudan and Chad in late September. White storks leave this staging area in November and conduct a further migration step of some thousands of kilometres to winter in eastern or southern Africa, where they stay until February. Within this vast wintering area white storks are then rather nomadic, and concentrate at places where food availability is high (Maclean, Gous & Bosman 1973). Significant mortality could be the result of food shortage at any of the areas visited for a longer time. We test whether survival rates of eastern white storks inhabiting a vast breeding area are spatially correlated, and hence could be attributed to environmental variation to which all individuals are exposed to. We estimate how much of the temporal variance in survival can be explained by environmental variation experienced during breeding and during several staging periods in the wintering areas. This allows us to infer at which spatio-temporal scale and by which reason variation in survival was induced. We provide evidence that survival rates of white storks from two countries are synchronized and the temporal variation is the result of variation of primary production at the Sahelian staging area. We discuss the population-dynamic consequences of these findings.

Materials and methods

DATA COLLECTION

We estimated survival rates from a combined analysis of capture–mark–resighting and capture–mark–recovery data of white storks ringed as nestlings during 19 years (1983–2001). This time period was selected to have a reasonable number of resightings, which has a major influence on the precision and reliability of survival estimates. Because not all white storks from eastern Germany migrate to eastern Africa (e.g. Schüz 1953; Fiedler 1998), we excluded most of the possible western migrants by considering only individuals which were born north of 52°N and east of 12°E.

With these restrictions, 16 217 nestlings from eastern Germany and 14 492 nestlings from Poland have been considered. Nestlings were ringed at the age of 4–7 weeks, 1–4 weeks prior to fledging. Rings were fixed either below or above the tarsal joint. The average ringing date, 30 June, was used as the annual divide, i.e. annual survival probability refers to the period between 30 June of year i to 29 June of year $i + 1$. Some white storks start to breed for the first time at the age of 3 years, and at the age of 4 years most reproduce (Schnetter & Zink 1960; Siefke 1981). Before first breeding they may stay in Africa, or they may return to the breeding grounds without breeding (Kania 1985; Köppen 2001). Hence, there are large behavioural differences between immature (< 4-year) individuals such that the resighting probabilities are not the same in all individuals, which violates an assumption of capture–mark–recapture models. We therefore included only

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resightings of individuals that were at least 4 years old and that were conducted in one of the two countries between 1 March and 30 September. With these restrictions, 694 individuals have been resighted 1495 times in eastern Germany and 59 individuals 105 times in Poland. No restriction was necessary for the recovery data. In total, 796 German and 346 Polish white storks have been recovered (EURING finding conditions codes 1–3, Speek *et al*. 2001).

STATISTICAL ANALYSIS

We used the model of Burnham (1993) to estimate survival probabilities. This model is parameterized with four different parameter types; S_i: the probability that a ringed individual survives from year i to year $i + 1$ (survival probability), F_i: the probability that a ringed individual does not emigrate permanently from the study area from year i to year $i + 1$ (fidelity probability), p_i: the probability that a ringed individual that is alive and in the study area at i is seen at i (resighting probability), r_i: the probability that a ringed individual that has died between year i and $i + 1$ is found and its ring reported to the ringing office (recovery probability).

The most general model included separate survival (S), fidelity (F) and recovery (r) parameters for each year (t), country of ringing (c) and age class (a; two age classes: juveniles from ringing to next summer, and adult in all subsequent years) and separate resighting (p) parameters for each year (t), country of ringing (c) and position of the ring (pos). No age effect was considered in the resighting rate, because only resightings of white storks older than 3 years were included. Following Lebreton *et al*. (1992) we denote this model as (S_{a*t*c}, F_{a*t*c}, $p_{t*c*pos}$, r_{a*t*c}).

There exists no goodness-of-fit test for this model. In order to judge approximately the goodness-of-fit we first considered only the mark–recovery data and performed a goodness-of-fit test of the simple recovery model (S_{a*t*c}, r_{t*c}) (Brownie *et al*. 1985). The test indicated that this model fitted the recovery data ($\chi^2_{38} = 51{\cdot}4$, $P = 0{\cdot}07$). Secondly, we considered the mark–resighting data from Germany (from Poland there were too few) and tested the goodness-of-fit of a model with different survival and resighting probabilities for each time period, cohort and ring position ($S_{cohort*t*pos}$, $p_{cohort*t*pos}$) using U-CARE (Choquet *et al*. 2001). The cohort model is a generalization of the two-age class model ($S_{a*t*pos}$, $p_{a*t*pos}$) and did clearly not fit the data ($\chi^2_{146} = 357{\cdot}4$, $P < 0{\cdot}001$). The cause for the lack of fit is 'immediate trap response' behaviour of the white storks (Pradel 1993), as evidenced by the significant directional test of 2.Ct ($Z = -13{\cdot}97$, $P < 0{\cdot}001$) and by a non-significant goodness-of-fit of a model which accounts for immediate trap response behaviour ($\chi^2_{56} = 54{\cdot}4$, $P = 0{\cdot}53$). Thus, individuals that have been observed in year i had a higher chance of being observed in year $i + 1$ than individuals that have not been observed in year i. The reason is that observers tended to visit places more often where ringed white storks have been detected in the previous year.

To account for this observer effect we adjusted our model in such a way that ringed individuals that were seen in year i had a different resighting probability in year $i + 1$ than individuals that have not been seen in year i. This observer effect is denoted with a m in the model. To fit the observer effect model together with age-dependent survival rates requires a special arrangement of the data (see Schmidt, Schaub & Anholt 2002). We considered a model with an additive structure (denoted with '+'), meaning that the resighting probability of individuals that have been seen in the previous year varies in parallel over time with the resighting probability of individuals that have not been seen in the previous year. We think that it is very unlikely that the position of the ring had a different effect each year on the resighting probability. Consequently we considered only an additive effect of the ring position on the resighting probability, resulting in the new general model (S_{a*t*c}, F_{a*t*c}, $p_{(t+m+pos)*c}$, r_{a*t*c}).

To make inferences from the data we a priori formulated different models, each representing a hypothesis about survival and the nuisance parameters. These models were fitted using program MARK (White & Burnham 1999) and the models were ranked according to the small sample-size adjusted Akaike's information criterion (AIC_c, Burnham & Anderson 1998). To reduce the list of reasonable models, we conducted modelling in two steps (Lebreton *et al*. 1992). First we looked for a model that describes the nuisance parameters (F, p, r) in the most parsimonious way. The survival part of the model was kept at the most complex structure in this step. Secondly, we assessed different models about survival while always retaining the most parsimonious structure of the nuisance parameters.

CANDIDATE MODELS AND HYPOTHESES

The resighting effort has certainly changed over time, because observers were asked by the ringing scheme to look for ringed white storks in recent years. Due to different numbers of observers in the two countries it was also clear a priori that the resighting probabilities were different, hence time and country effects were retained in all models. As it is unknown whether the position of the ring had a significant effect on the resighting rate, we considered a model with an effect ($p_{(t+m+pos)*c}$) and one without ($p_{(t+m)*c}$). Distances of natal dispersal are longer than distances of breeding dispersal in white storks (Zink 1967; Siefke 1981; Kania 1985), and hence fidelity was considered to be age-dependent in all models. Furthermore, as the size of the countries and the distribution of observers within the countries affect fidelity probability we always maintained a country effect on this parameter. As fidelity might have been variable or constant across time, three different structures for the fidelity parameter were considered (F_{a*t*c}; $F_{(a+t)*c}$; F_{a*c}). A priori knowledge about the recovery

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rate (r) is limited. The recovery rate may be dependent on age, as the mortality causes may differ among age classes (Schaub & Pradel 2004), it may vary over time and it may be different depending on the place of recovery (Kania & Busse 1987). We are not aware of statistical models allowing the estimation of finding place-specific recovery rates. Because most Polish storks were recovered in Poland and most German storks in Germany, we modelled the recovery rates as a function of the country of ringing. This seems to be a useful approximation. We identified 11 different reasonable structures for the recovery probability

$$r_{a*t*c};\ r_{(a+t)*c};\ r_{a*t};\ r_{a+t};\ r_a;\ r_t;\ r;\ r_{t*c};\ r_{a*c};\ r_{t+c};\ r_c.$$

The resulting set of 2*3*11 = 66 models for the nuisance parameters was obtained by considering all combinations of the different model fragments.

Modelling survival was divided into two complementary parts. First, we assessed the general shape of the temporal variation in survival. Secondly, we estimated how much of the temporal variation in annual survival could be explained by the variation of environmental covariates by variance decompositions (Burnham & White 2002).

For modelling survival we always retained the age structure, because survival of white storks has been found repeatedly to be age-dependent (Kanyamibwa *et al*. 1990; Barbraud *et al*. 1999; Schaub, Pradel & Lebreton 2004). We tested whether survival probabilities varied over time and between countries. The reasoning behind the 15 formulated candidate models (Table 1) is the following: the hypothesis that environmental variation over a large area (in the breeding and/or the non-breeding area) has a significant influence on survival is represented by models without a time × country interaction. Significant environmental variation at country scales during breeding time must result in a significant time–country interaction. Furthermore, if no time effect on survival were present we would conclude that survival is not sensitive to environmental variation. The hypothesis that the two age classes are differentially sensitive to environmental variation is represented in a significant time × age interaction. Finally, if only the juvenile age class is sensitive to environmental variation, juvenile survival would be time-dependent and adult survival constant over time.

Next we estimated how much of the possible temporal variation of survival is due to variation in food supply in either the wintering areas or the breeding areas. We considered the normalized difference vegetation index (NDVI) at winter staging areas as an integrative correlate of food supply variation during non-breeding and the amount of rainfall at the breeding area as a correlate of food supply variation during breeding. We expect the survival rate to be reduced in years with low availability of food, hence to be low in years with low NDVI and in years with low amount of rainfall.

The NDVI is a measurement of chlorophyll density obtained by infrared pictures from satellites of the US National Oceanic and Atmosphere Administration (NOAA). High values indicate high chlorophyll density (Tucker, Dregne & Newcomb 1991), thus dense vegetation and hence high availability of phytophagous insects, which is the most important prey during non-breeding (Dallinga & Schoenmakers 1987; Mullié, Brouwer & Scholte 1995). For example, abundance of locust depends on rainfall (Cheke & Holt 1993; Todd *et al*. 2002), and temporal variation in rainfall is transformed into temporal variation of NDVI. The NDVI values were obtained at http://edcw2ks21.cr.usgs.gov/adds/(15 December 2003). To identify the range of staging areas and time-period of its use, we used published results of ring recoveries and satellite telemetry of white storks from eastern Germany and Poland (Kania 1985; Oatley & Rammesmayer 1988; van den Bossche *et al*. 1999; Berthold *et al*. 2001). We identified three staging areas (Fig. 1). The first one is in the Sahel and is visited during October and November. Later white storks move to eastern or southern Africa and stay there from December to February. Due to their nomadic behaviour during this time, the definition of the staging areas is less clear. We divided the large area into two parts (Fig. 1). For each year and staging area we calculated the mean NDVI over the period visited. Within a staging area we allocated the years where the average NDVI was lower than the 25% quartile as dry, in years where the average NDVI was higher than the 75% quartile as wet and the other years as medium.

Important prey during breeding includes earthworms and amphibians whose access is reduced during dry weather, hence the amount of precipitation was

Table 1. The 15 models used to explain temporal variation of survival probabilities in two age classes of the white storks. They are classified according to the scale of environmental variation and to the sensitivity of the age classes to it. Table entries are the survival models considered. S stands for survival, subscript a refers to an age effect (two age classes), subscript t refers to time-dependence, subscript c refers to a country effect, subscript. refers to constancy, subscript *juv* refers to the first age class (first year of life), subscript *ad* refers to adults (all age classes older than one year); * indicates that the effects are interacting, and + indicates that the effects are additive (i.e. vary in parallel among all age or country classes)

	Environmental variation		
Sensitive survival parameter	Large scale	Country scale	None
Age classes differentially sensitive	S_{a*t} S_{a*t+c}	S_{a*t*c}	–
Age classes equally sensitive	S_{a+t} S_{a+t+c} S_{a*c+t}	$S_{(a+t)*c}$	–
Only juveniles sensitive	$S_{\text{juv: } t;\ \text{ad:.}}$ $S_{\text{juv: } t;\ \text{ad: } c}$ $S_{\text{juv: } t+c;\ \text{ad:.}}$ $S_{\text{juv: } t+c;\ \text{ad: } c}$	$S_{\text{juv: } t*c;\ \text{ad:.}}$ $S_{\text{juv: } t*c;\ \text{ad: } c}$	–
–	–	–	S_a S_{a*c}

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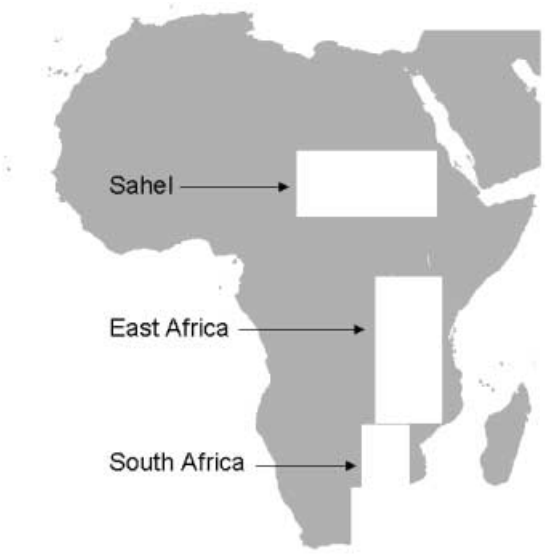

Fig. 1. The staging areas used by white storks within Africa as identified by published results on satellite tracking and ring recoveries of individuals from eastern Germany and Poland. White storks are present in the Sahel from October to November and in east and south Africa from November to February.

considered to be a suitable correlate of availability of this prey. Data on anomalies of precipitation during breeding are provided by NOAA at http://lwf.ncdc.noaa.gov/oa/climate/research/ghcn/ghcngrid_prcp.html (16 March 2004). We considered the mean of the months June–August of the area between 47·5°N to 57·5°N and 12·5°E to 27·5°E. We allocated the years where the average amount of precipitation was lower than the 25% quartile as dry (low food availability), in years where the average rainfall anomaly was higher than the 75% quartile as wet (high food availability) and the other years as medium (intermediate food availability).

We estimated first the temporal variation in juvenile and adult survival by variance decompositions. This method allows the separation of sampling variance from process variance (Burnham & White 2002). As in large mammals, we expect juvenile survival to be more variable over time than adult survival (Gaillard, Festa-Bianchet & Yoccoz 1998). We then estimated the proportion of the temporal variation in survival explained by the variation of NDVI in the three African staging areas and of precipitation in the breeding grounds. To do so, we used the best model without constraints on the survival rates (i.e. S_{a*c*t}) and calculated separately for each of the four age–country groups the proportion of temporal variance explained by a particular covariate and the mean survival rate for each environmental condition (see Loison *et al*. 2002).

Results

MODELLING NUISANCE PARAMETERS

Modelling of the nuisance parameters clearly favoured the model with age- and country-specific fidelity probabilities, time- and country-specific recovery probabilities and with time-, country- and position-dependent resighting probabilities (Table 2). The average recovery probabilities were lower in Polish than in German white storks (Germany: 0·0478 (SE = 0·0018); Poland: 0·0261 (SE = 0·0009)). The resighting probabilities were higher in Germany than in Poland [mean resighting probability of individuals that were marked above the tarsal joint and that have been seen in the preceding year: Germany, 0·547 (SE = 0·014); Poland, 0·390 (SE = 0·029)] and increased over time in both countries. Individuals that were seen in the preceding year were more likely to be seen in the current year than individuals that were not seen in the preceding year [difference on the logit scale: Germany, 1·680 (SE = 0·100); Poland, 2·879 (SE = 0·507)]. White storks with rings below the tarsal joint were less likely to be resighted than white storks with rings above the tarsal joint, but the difference was not large [difference on the logit scale: Germany, 0·375 (SE = 0·140); Poland, 0·158 (SE = 0·397)].

Table 2. Modelling recovery (r), fidelity (F) and resighting (p) probabilities of white storks as functions of age (a), country (c), time (t), observer effect (m) and the position of the ring (pos); + indicates an additive effect (parallelism), * indicates that the two effects interact (no parallelism). For all models the most general structure of the survival rate S_{a*t*c} was used. This model part is not shown in the table. Of the 66 models fitted, only the best nine and the most general one (model 10) are shown

Model	Deviance	Parameters[a]	ΔAIC_c[b]	AIC_c-weight[c]
1 F_{a*c}, $p_{(t+m+pos)*c}$, r_{t+c}	8612·2	134	0·00	0·74
2 F_{a*c}, $p_{(t+m)*c}$, r_{t+c}	8619·7	132	3·46	0·13
3 F_{a*c}, $p_{(t+m)*c}$, r_{a*c}	8652·0	116	3·52	0·13
4 F_{a*c}, $p_{(t+m+pos)*c}$, r_{t+a}	8626·9	133	12·70	0·00
5 F_{a*c}, $p_{(t+m)*c}$, r_{t*c}	8594·1	150	14·22	0·00
6 $F_{(a+t)*c}$, $p_{(t+m+pos)*c}$, r_a	8668·3	115	17·84	0·00
7 F_{a*c}, $p_{(t+m+pos)*c}$, r_{t*c}	8596·5	151	18·62	0·00
8 $F_{(a+t)*c}$, $p_{(t+m+pos)*c}$, r_{t+c}	8566·0	167	20·47	0·00
9 F_{a*c}, $p_{(t+m+pos)*c}$, r_t	8637·3	132	21·04	0·00
10 F_{a*t*c}, $p_{(t+m+pos)*c}$, r_{a*t*c}	8514·7	255	147·52	0·00

[a]Number of estimated parameters.
[b]Difference in AIC_c of the actual model and the best one ($\Delta AIC_c = AIC_{ci} - AIC_{cmin}$).
[c]Computed as $\exp(-0{\cdot}5AIC_{ci})/\Sigma\exp(-0{\cdot}5AIC_c)$.

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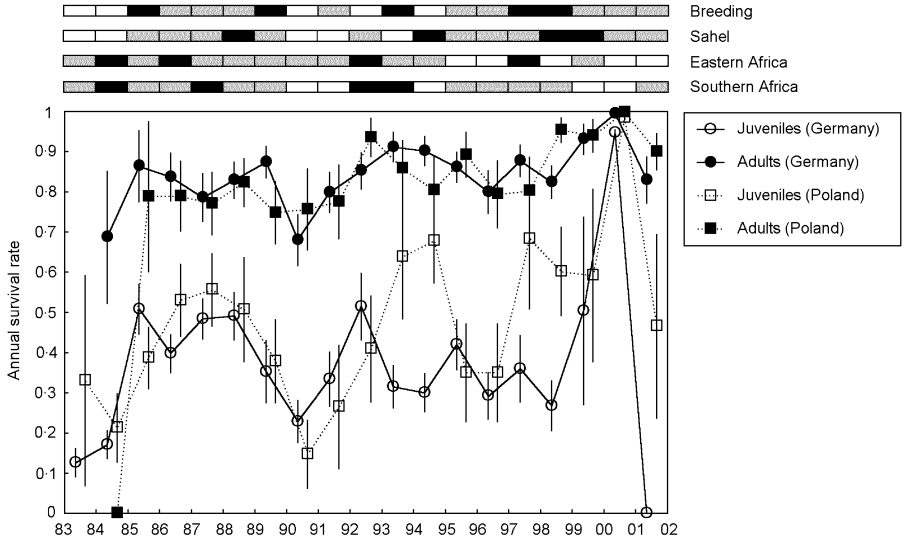

Fig. 2. Annual survival rates of juvenile and adult eastern white storks from eastern Germany and Poland from 1983 to 2001. The estimates are from the most general survival model (S_{a*t*c}, F_{a*c}, $p_{(t+m+pos)*c}$, r_{t+c}) (model 1 in Table 3). Vertical lines indicate standard errors. The rectangles above the graph indicate the categories of the four environmental covariates for each year. The open rectangles refer to years with low NDVI and to low rainfall, the black rectangles to years with high NDVI and rainfall, and the grey rectangles to years with medium NDVI and rainfall.

Table 3. Modelling survival probabilities (S) of white storks as functions of age (a), country (c) and time (t). A + in the model notation indicates an additive effect (parallelism), a * indicates that the two effects interact (no parallelism). For all models the most parsimonious structure for F, p and r was used (F_{a*c}, $p_{(t+m+pos)*c}$, r_{t+c}) as identified in Table 2. This model part is not indicated in the table below

Model	Deviance	Parameters[a]	ΔAIC_c[b]	AIC_c-weight[c]
11 S_{a*c+t}	8680·9	83	0·00	0·66
12 $S_{\text{juv: } t;\ \text{ad: } c}$	8686·0	82	3·07	0·14
13 $S_{\text{juv: } t+c;\ \text{ad: } c}$	8684·1	83	3·13	0·14
14 $S_{\text{juv: } t+c;\ \text{ad:.}}$	8689·0	82	6·06	0·03
15 S_{a+t+c}	8690·4	82	7·46	0·02
16 $S_{\text{juv: } t;\ \text{ad:.}}$	8692·8	81	7·86	0·01
17 $S_{[a+t]*c}$	8659·0	100	12·31	0·00
18 $S_{\text{juv: } t*c;\ \text{ad: } c}$	8662·6	100	15·86	0·00
19 $S_{\text{juv: } t*c;\ \text{ad:.}}$	8666·5	99	17·72	0·00
20 S_{a*t}	8669·6	98	19·37	0·00
21 S_{a*t+c}	8669·6	99	20·88	0·00
22 S_{a+t}	8708·1	81	23·16	0·00
1 S_{a*t*c}	8612·2	134	33·94	0·00
23 S_{a*c}	8823·1	64	104·00	0·00
24 S_a	8832·6	62	109·45	0·00

[a]Number of estimated parameters.
[b]Difference in AIC_c of the actual model and the best one ($\Delta AIC_c = AIC_{ci} - AIC_{cmin}$).
[c]Computed as $\exp(-0{\cdot}5AIC_{ci})/\sum\exp(-0{\cdot}5AIC_c)$.

TEMPORAL PATTERNS IN SURVIVAL

The most general survival model (S_{a*t*c}) yielded survival estimates that varied astonishingly in parallel over time (Fig. 2). This impression is confirmed by the model selection which clearly favoured the model with the survival rates of the two age classes and the two countries constrained to vary in parallel over time (Table 3). Thus, individuals of both age classes and from both countries were similarly sensitive to environmental variation. However, because there was an additive (to time) country effect, regional differences affecting survival were present as well. Because models using the second and third best structure of the nuisance parameters (Table 2) were clearly worse than the most parsimonious model [(S_{a*c+t}, F_{a*c}, $p_{(t+m)*c}$, r_{t+c}): $\Delta AIC = 5{\cdot}66$; (S_{a*c+t}, F_{a*c}, $p_{(t+m)*c}$, r_{a*c}): $\Delta AIC = 8{\cdot}00$], the conclusions about survival are robust.

The mean and the temporal variance of survival was estimated by a variance decomposition for each age and country group separately and based on the unconstrained survival model (model 1, Table 3). All survival rates in 2000 were biased high, as the recovery rates of the corresponding year were estimated to be 1. Survival rates of adults from Poland in 1984 and of juveniles in 2001 from Germany were boundary estimates (Fig. 2).

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Table 4. Residual temporal process variance ($\hat{\sigma}^2_{res}$) of survival and the proportion explained by the normalized difference vegetation index (NDVI) in the Sahel, NDVI in eastern Africa, NDVI in southern Africa and the amount of rainfall during the breeding season

	Poland juveniles		Poland adults		Germany juveniles		Germany adults	
Model	$\hat{\sigma}^2_{res}$	Variability explained	$\hat{\sigma}^2_{res}$	Variability explained	$\hat{\sigma}^2_{res}$	Variability explained	$\hat{\sigma}^2_{res}$	Variability explained
$S_{.}$	0·0109		0·0020		0·0103		0·0015	
$S_{\text{NDVI Sahel}}$	0·0013	0·88	0·0013	0·37	0·0046	0·55	0·0014	0·04
$S_{\text{NDVI E-Africa}}$	0·0139	0·00	0·0014	0·31	0·0123	0·00	0·0019	0·00
$S_{\text{NDVI S-Africa}}$	0·0134	0·00	0·0027	0·00	0·0117	0·00	0·0020	0·00
S_{rainfall}	0·0104	0·05	0·0027	0·00	0·0074	0·29	0·0017	0·00

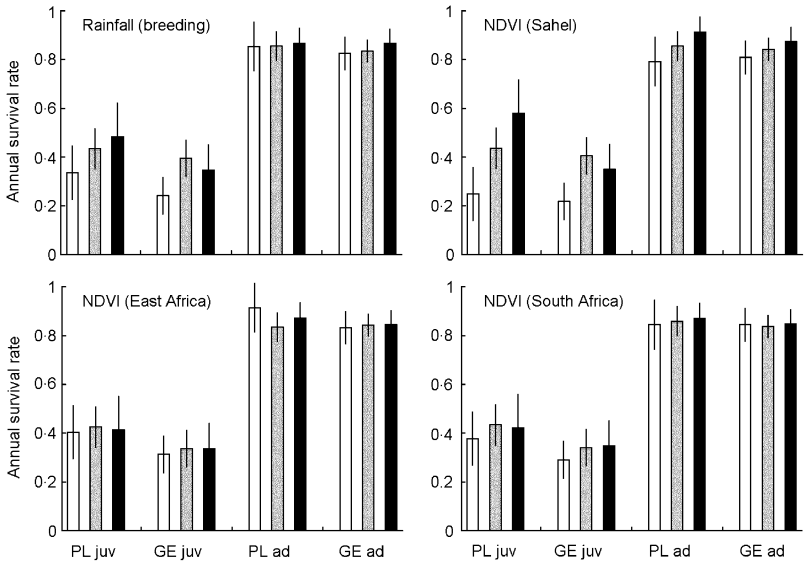

Fig. 3. Estimates of annual survival of the four groups of white storks (PL juv: juveniles from Poland; GE juv: juveniles from eastern Germany; PL ad: adults from Poland; GE ad: adults from eastern Germany) in relation to variation of rainfall during breeding, to the normalized difference vegetation index (NDVI) in the Sahel, eastern Africa and southern Africa. The estimates are from a random effects model. The vertical lines indicate the limits of the 95% confidence intervals. The open bars refer to years with low NDVI and to low rainfall, the black bars to high NDVI and rainfall, and the grey bars to medium NDVI and rainfall.

To ensure a proper estimation of the mean and the temporal variance, we did not consider biased and boundary estimates for the following estimations (Burnham & White 2002). On average, the annual survival rates of both age classes of Polish white storks were slightly higher than those of German white storks [Polish juveniles: 0·415 (SE = 0·043); Polish adults: 0·862 (SE = 0·026); German juveniles: 0·330 (SE = 0·034); German adults: 0·843 (SE = 0·018)]. As expected, the temporal variance of annual survival was five to seven times larger in the juveniles than in adults (Poland, juveniles: $\hat{\sigma}^2 = 0{\cdot}0109$ (CV = 25·1%); Poland, adults: $\hat{\sigma}^2 = 0{\cdot}0020$ (CV = 5·2%); Germany, juveniles: $\hat{\sigma}^2 = 0{\cdot}0103$ (CV = 30·7%); Germany, adults: $\hat{\sigma}^2 = 0{\cdot}0015$ (CV = 4·6%)).

ENVIRONMENTAL EFFECTS ON SURVIVAL

The four environmental covariates were not intercorrelated temporally (highest correlation between NDVI Sahel and NDVI South Africa: $r = -0{\cdot}43$, $P = 0{\cdot}07$; all other correlations $r < |0{\cdot}27|$). Of all environmental covariates considered, NDVI Sahel explained the largest amount of temporal variation in survival in all groups of white stork (Table 4). Four of the 5 years with low NDVI Sahel values coincided with the lowest annual survival probabilities (Fig. 2). The mean annual survival rates were lowest in years with a low primary production in the Sahel, and highest with a high primary production (Fig. 3). The other two covariates of the environmental variation in Africa explained much less of the temporal variance and the result was not consistent among groups. The covariate rainfall during breeding explained some of the temporal variance in juveniles. The survival probabilities slightly increased with increasing rainfall on the breeding grounds (Fig. 3).

Discussion

The results of our study is one of the few examples demonstrating that environmental variation experienced in an area that is visited during only a short time

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significantly affect survival of individuals originating from a large breeding area – thus provoking synchrony of survival at the population level. Survival probabilities of juvenile and adult white storks from eastern Germany and Poland varied in parallel over a 19-year period, indicating that the temporal variation in survival was caused largely by environmental effects which affected all individuals from the two countries. We identified the variation of the primary production at the Sahelian staging area as an important source for the temporal variation in annual survival in both age classes. Annual survival was high when primary production in the Sahel was high, and low when the primary production in the Sahel was low. In addition, the variation of rainfall during the breeding season contributed slightly to temporal variation in annual survival in juveniles. In contrast, variation in primary production at other non-breeding staging areas in eastern and southern Africa did not contribute significantly to temporal variation of annual survival.

We predicted that survival of white storks to be negatively influenced by low availability of food at all staging areas. An explanation for the essential sensitivity of storks to environmental condition in the Sahel and not in other staging areas is the spatio-temporal pattern of rainfall in Africa. The Sahel is under the northern tropical rainfall regime, i.e. rainfall occurs from June to September. The savannahs in east and south Africa are under the southern tropical rainfall regime, with regular rainfall occurring from November to April (Brown, Urban & Newman 1982). Consequently, the vegetation in the Sahel is well developed when the white storks arrive in October, but the area dries out quickly and food supply declines (Mullié *et al*. 1995). In east and south Africa the vegetation starts to grow with the rain only in November, and the food supply increases thereafter. Hence, white storks have to stay in an environment of decreasing food supply in the Sahel until the increasing food supply in eastern and southern Africa is sufficient. In years with low primary production in the Sahel food is less abundant and depleted quickly, which then has adverse effects on survival. The rainfall in east and south Africa is spatially irregular (Brown *et al*. 1982) and white storks are nomadic there (Schulz 1988; Berthold *et al*. 2002). They can thereby exploit efficiently localized areas with high food availability, and reduce mortality. Eastern white storks depend thus in a similar way on the environmental condition in the Sahel as the western ones. However, because the western white storks have to spend the entire winter in the Sahel, their survival is likely to be affected more strongly by environmental variation in the Sahel than that of eastern white storks.

As predicted, survival was reduced when the amount of precipitation in the breeding area was low, yet only juvenile white storks were affected. While rainfall was beneficial during the post-fledging period because food availability is enhanced, it is adverse during the early nestling period because chick survival is then reduced (Jovani & Tella 2004). Survival during the early nestling period was not included in our estimates of annual survival. The population-dynamic consequences due to variation of precipitation during breeding are therefore complex; they depend on the timing of precipitation relative to the timing of breeding.

Some of the temporal variance in survival was not explained by the environmental covariates considered. Possibly mortality during migration may have contributed to this unexplained variation. Individuals from different populations migrate in large flocks on well-defined, narrow pathways (van den Bossche *et al*. 1999). Consequently, localized adverse weather conditions could cause the death of many individuals leading to synchronization of survival. Despite our conservative data selection some of the German white storks considered might have migrated to western Africa. Because they would be affected by differential environmental conditions they would contribute to the unexplained temporal variance.

Based on these results, two questions relevant for understanding white stork population dynamics emerge. First, which effect has the variation of the Sahelian primary production on population dynamics, and secondly, to what extent could survival rate synchrony induce population synchrony? The impact of the variation of a vital rate on population dynamics depends on the sensitivity of the population growth rate to variation in the vital rate and on the magnitude of variation in this trait. Ignoring correlations among vital rates, the proportional contribution of variation in vital rates to variation in population growth rate can be calculated as the product of the square of the vital rate sensitivity and the temporal variance of the vital rate (Caswell 2000). Based on data on reproductive success of white storks from six different areas in Poland and eastern Germany from 1983 to 2001 with totally 42 407 breeding attempts (Kuźniak 1994a,b; Ptaszyk 1994; Zöllick 1996; Kaatz & Kaatz 2001; Ludwig 2001; Kuźniak and Ptaszyk, personal communication) we calculated the mean reproductive output (Poland: 2·08 fledglings per breeding attempt, eastern Germany: 1·91) and its temporal variation (Poland: $\hat{\sigma}^2 = 0{\cdot}1451$; eastern Germany: $\hat{\sigma}^2 = 0{\cdot}1154$). Using the age-classified matrix population projection model described in Schaub *et al*. (2004) parameterized with the mean reproductive output and survival rates, we calculated the sensitivity of population growth to variation of reproduction (Poland: 0·07; eastern Germany: 0·07), of juvenile survival (Poland: 0·37; eastern Germany: 0·40) and of adult survival (Poland: 1·09; eastern Germany: 1·07). The relative contribution of the vital rate's variances to population dynamics in Polish white storks was then 17%, 32% and 51% for reproduction, juvenile and adult survival, respectively (corresponding figures for eastern Germany: 14%, 42%, 44%). As 88% and 37% of the variation in juvenile and adult survival in Polish white storks was explained by variation of the primary production in the Sahel (corresponding figures for eastern

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German white storks: 55% and 4·3%), about 47% (eastern Germany: 25%) of the variation in population size was due to environmental variation in the Sahel.

These estimates are rough, based on simplistic assumptions, and probably underestimations. They were built on a combination of prospective (sensitivities) and retrospective (observed vital rate variation) analyses which may result in slightly biased estimates. We ignored the covariance between the vital rates. The covariance between adult and juvenile survival was positive (Fig. 2, Table 3), meaning that environmental variation in the Sahel would have a stronger impact on population dynamics than estimated. Furthermore, there is evidence that the reproductive success is correlated negatively with the amount of rainfall in the Sahel in the previous winter (Dallinga & Schoenmakers 1987), which renders the covariance between survival and reproductive success positive and thereby further increases the significance of environmental variation in the Sahel on population dynamics. These considerations show that the environmental conditions in the Sahelian staging area, which is visited for only 1–2 months, had an important impact on the population dynamics of eastern white storks.

Because the population dynamics of white storks is driven largely by variation in juvenile and adult survival, synchronized survival rates have the potential to induce population synchrony. This would have important consequences for conservation, as population synchrony reduces the persistence of metapopulations (Palmqvist & Lundberg 1998). Indeed, there is empirical evidence of population synchrony in white storks (Zink 1967; Dallinga & Schoenmakers 1987; Bairlein 1991), although explicit analyses are still lacking.

There is increasing empirical evidence that environmental variation experienced by migratory bird species in wintering areas has significant consequences on fitness components and thus on population dynamics. For example, annual survival rates of sedge warbler *Acrocephalus schoenobaenus* (Peach, Baille & Underhill 1990), willow warbler *Phylloscopus trochilus* (Peach, Crick & Marchant 1995) and sand martin *Riparia riparia* (Szép 1995) increase with the increasing amount of rainfall in their western African wintering areas. In addition, the reproductive output can be worse following a year with adverse conditions during wintering (Dallinga & Schoenmakers 1987; Marra, Hobson & Holmes 1998; Saino *et al*. 2004). Here we provide a further example and showed in addition that survival of individuals inhabiting large areas during breeding are affected by conditions during wintering which probably result in population synchrony, and thereby increase the risk of local population extinction. We also demonstrated that such mechanisms are not restricted to species or populations spending the whole winter in the narrow extent of the Sahel in western Africa (Newton 2004), but also apply to a species which only stops for a short period of time in the Sahel and spends the longest part of the winter in eastern and southern Africa. To better population understand dynamics of long-distance migrants it is therefore crucial to focus research not only on mechanisms operating during breeding, but also to those operating during wintering and migration.

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