

# Nonlinear impact of climate on survival in a migratory white stork population

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## Summary

1. There is growing evidence that ongoing climate change affects populations and species. Physiological limitation and phenotypic plasticity suggest nonlinear response of vital rates to climatic parameters, the intensity of environmental impact might be more pronounced while the frequency of extreme events increases. However, a poor understanding of these patterns presently hampers our predictive capabilities.

2. A recent climatic shift in the Sahel, from droughty to less severe condition, offers a good opportunity to test for an influence of the climatic regime on the response of organisms to their environment. Using a long-term capture–mark–recapture data set on a white stork (*Ciconia ciconia*) population wintering in Sahel, we investigated potential change in the impact of environmental conditions on survival and recruitment probabilities between 1981 and 2003.

3. We observed a decrease in the strength of the link between survival and Sahel rainfall during the last decade, down to a nondetectable level. Whether Sahel climate was found to affect the survival of storks under droughty conditions, individuals did not seem to respond to climatic variation when precipitation was more abundant.

4. This result gives evidence to a nonlinear response of a migrant bird to wintering environment. Present climate seems to fluctuate within a range of condition providing enough resources to maximize stork's survival. It suggests that whereas inter-annual variability impacted individuals, pluri-annual average condition affected the intensity of this impact. Such pattern may be more widespread than thought, and its modelling will be crucial to predict the impact of future climate change on population dynamics.

**Key-words:** *Ciconia ciconia*, juvenile and adult survival, North Atlantic oscillation, recruitment, Sahel rainfall index

## Introduction

Global climate change has been reported to impact on phenology, distribution, dynamics and even selection processes of populations across a variety of ecosystems (Harrington, Woiwod & Sparks 1999; Hughes 2000; IPCC 2001; Walther *et al.* 2002; Root *et al.* 2003; Parmesan 2006). However, under the denomination of 'global climate change', substantial spatio-temporal heterogeneity has to be considered. For instance, current warming is generally larger over lands than over oceans (IPCC 2001; Moberg *et al.* 2005; Hansen *et al.* 2006). The importance of spatial heterogeneity for population dynamics is exemplified by Newton (2004), who showed that

contrasting trends in the dynamics of populations breeding at the same place could only be understood through differences in the conditions experienced at respective wintering grounds. Concerning the temporal heterogeneity, some changes in fish communities have been linked to major climatic shifts (Anderson & Piatt 1999) and demographic changes in some seabird species also coincided with changes in climate (Aglar *et al.* 1999; Weimerskirch *et al.* 2003; Ainley *et al.* 2005; Jenouvrier *et al.* 2005). However, very little is known about the temporal variability of the links between climate, vital rates and population dynamics over decadal scales (Durant *et al.* 2004). Extreme events are rare at this scale and the impact on demographic parameters appeared relatively stable. As a result, climatic impacts on life-history traits are largely described with linear relationships.

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Nonlinear responses of populations to their environment are highly suspected (Stenseth *et al.* 2004; Hsieh *et al.* 2005), but methodological limitation restricted their exploration. On one hand, organisms are shaped by a set of physiological constraints conditioning development to a given range of physio-chemical parameters. Phenotypic plasticity balances this response by providing organisms with a higher degree of tolerance to external fluctuations, leading to the numerous linear relationships reported in the literature. However, such a linear adjustment would only be possible for a limited amount of variation and could not sensibly be extrapolated outside the range of observed conditions. For instance, results from Nevoux, Weimerskirch & Barbraud (2007) suggest that an increase by 1.8 °C of the average sea surface temperature (realistic with most climatic predictions for the next century; IPCC 2001) would lead to a mean breeding success higher than one in the black-browed albatross (*Thalassarche melanophris*) at Kerguelen, which is not reasonable as this seabird lays one egg per breeding season. On the other hand, the influence of environment on individuals may also fluctuate over time, depending on the severity of the local conditions or on the health of the population. By strongly affecting all individuals at the same time, catastrophic weather events may have a huge impact on population dynamics even if the given climatic parameter only represent a negligible concern during regular years (Newton 2004; Altwegg *et al.* 2006; Wilson & Peach 2006). In the barn owl (*Tyto alba*), although normal snow condition had only a minor impact on survival, catastrophic harsh events were associated with major crashes in population size (Altwegg *et al.* 2006). Prolonged unfavourable weather, illustrated by any shift in local climatic regime, may result in a drastic change in the individuals' ability to face environmental fluctuations (Durant *et al.* 2004). In that respect, individuals might tolerate climatic constraints up to a certain level of perturbation based on plasticity and physiological limits. However, beyond a certain threshold some climatic constraints may start to affect the fecundity of individuals and/or their life expectancy, and eventually the dynamics of the whole population. Therefore, it can be predicted that the strength of the relationships between demographic and climate parameters should vary.

Most frequently, quadratic functions are used to model nonlinear responses, but more complex approaches such as nonparametric regression (Gimenez *et al.* 2006), self-excitatory threshold autoregressive (Tong 1990; Ellis & Post 2004) or generalized autoregressive conditional heteroskedasticity models (Bollerslev 1986) have been developed. Nevertheless, long-term data sets often contain insufficient extreme events to detect such nonlinearity (Altwegg *et al.* 2006). This subject is of particular importance to improve our understanding of long-term impacts of climatic changes on population dynamics. It also provides an opportunity to update the traditional linear view of the links between populations and their environment.

In Africa, the Sahel represents a key ecosystem for a huge number of Eurasian migrant species. It is also characterized by long-term climatic oscillations known to impact on human and animal populations. A recent regime shift in the Sahel

occurred in the late 1970s, leading to a 30-year period of drought (L'Hote *et al.* 2002). Studies reported a strong impact of this dry climatic regime on a high number of Palaearctic migrant species wintering in sub-Sahara (see Newton 2004 for a review). Since the late 1990s, rainfall increased significantly (Ozer *et al.* 2003), presuming a change towards less severe environmental condition. This recent change thus offers a unique opportunity to investigate the influence of environmental severity on population dynamics under changing climatic conditions.

The white stork (*Ciconia ciconia* Linnaeus, 1758) is a migrant species breeding in Europe and wintering in sub-Saharan regions. In this species, demographic studies have largely demonstrated an impact of environmental condition over wintering areas on survival (Kanyamibwa *et al.* 1990; Kanyamibwa, Bairlein & Shierer 1993; Barbraud, Barbraud & Barbraud 1999; Schaub, Kania & Köppen 2005; Sæther *et al.* 2006). Using data from a long-term monitoring of a Western Europe population of white stork wintering in the Sahel, the aim of this study was to investigate temporal change in the demographic response of this population to recent environmental modification. Between 1980 and 2003, we investigated time variation in successive correlations between environmental parameters (for both winter and summer periods) and three key demographic parameters: juvenile survival, probability of starting to breed and adult survival. Since present wintering condition in the Sahel seems less severe than it was, we expected to detect a reduced impact of climate on life-history traits in this white stork population.

## Materials and methods

### SPECIES AND SITE

The white stork is a large wading bird inhabiting wetlands as well as some urban areas across Europe. According to their migratory pattern, East and West European populations are considered to be separate. During winter, western birds migrate to the western sector of the Sahel, whereas eastern storks migrate to the eastern Sahel and to South Africa (Géroutet 1994; Berthold *et al.* 2001). Recent census revealed a general increasing trend in white stork numbers across Europe (Schulz 1999; Kai-Michael Thomsen, Michael-Otto-Institut NABU: <http://bergenhusen.nabu.de/zensus/zensus2006/worldpopulation.pdf>).

Fieldwork was conducted in Brouage marshes, Western France, where a white stork population settled in the late 1970s. This area was the only breeding area for white storks in Western France in the late 1970s and early 1980s. In this marsh area, birds feed mainly on aquatic insects, anuran and crayfish (Barbraud *et al.* 1999). In winter, ring recoveries and resightings indicate that the birds from this population migrate through Spain and the Gibraltar Strait to the occidental Sahel in Africa (C. Barbraud, unpublished data). This route is the same as that followed by other Western European white stork populations (Géroutet 1994; Berthold *et al.* 2001).

At the start of the breeding season, all artificial platforms and known nest sites were checked with a telescope, pairs identified, their breeding status determined and breeding success monitored. Each year, where the nests were accessible, chicks were ringed just before fledging with a stainless steel band and a unique-numbered PVC (Darvic) band. The phylopatric behaviour of this increasing

population (Barbraud *et al.* 1999) combined with intensive monitoring of white storks in this marsh area has allowed virtually all breeding pairs to be located and all chicks to be ringed before 1996 (see Appendix 1). Sample size was small in early years primarily because the population was small too. Since all chicks born at this study area were ringed until 1996, the data are comprehensive with all birds sampled. Following the dramatic increase in population size in recent years, a growing number of natural nests were not accessible (on electric pylons) and their chicks were not ringed. As a consequence, and coupled with the settlement of unknown immigrants, an increasing proportion of the population is presently not ringed.

#### ESTIMATION OF THE DEMOGRAPHIC PARAMETERS

We used a capture–mark–recapture data set of known-age birds born on the study site and resighted during the 1980–2003 period ( $N = 1714$  individuals). Based on recent developments for recruitment analyses (Lebreton *et al.* 2003), we constructed a two-state model where birds are identified as pre-breeders (PB) or as breeders (B). Annual sample sizes are presented in Appendix 1 (see ‘chicks ringed’ and ‘marked individuals observed’ respectively). In this species with a delayed maturity, the probability of observing individuals in the PB stage was very low, enabling the use of a complete age-structured model. Recruitment, defined as an individual entering the breeding segment of the population, is the probability of surviving the PB period and starting breeding for the first time (transition from PB to B). The transition from B to PB was fixed at zero, as adult birds could not become immature again. We considered the initial Arnason–Schwarz (AS) model  $\{S[(PB, B) \cdot t] p[(PB, B) \cdot t] \Psi_{PB \rightarrow B}(t)\}$ , with survival (S) capture (p) and transition from PB to B ( $\Psi_{PB \rightarrow B}$ ) being a function of state (PB, B) and time ( $t$ ). We tested for age effects on capture, survival and transition by constraining these parameters to vary as a function of age classes. Previous studies on white storks (Kanyambwa *et al.* 1990, 1993; Barbraud *et al.* 1999) indicated that survival varied with age, and we suspected that in such a long-lived species with delayed maturity, capture and recruitment probabilities may vary with age. We also tested for a cohort effect on transition probabilities. Estimates of apparent survival and transition probabilities were obtained with the M-SURGE software (Choquet *et al.* 2004). Model selection among time-dependent models was carried out using an information theoretic approach (Burnham & Anderson 2002).

A goodness-of-fit test (GOF) was performed using the U-CARE software (Choquet *et al.* 2003) to assess the fit of the initial model (described above) to the data. For this multistate model, there is no formal GOF test for the AS model; thus, we considered the global GOF for the Jolly Move (JMV) model, calculated as the sum of tests  $WBWA + 3G.SR + 3G.SM + M.Itc + M.Ltec$ , as recommended by Pradel, Winterbert & Gimenez (2003). In case of potential lack of fit, a variance inflation factor was estimated to correct for over dispersion in the data, and a quasi-Akaike's Information Criterion (QAIC) was used (Burnham & Anderson 2002). Estimates are presented  $\pm 1$  SE.

#### SELECTION OF ENVIRONMENTAL COVARIATES

To test whether environmental variability could explain a significant part of the temporal variability on demographic parameters, we integrated environmental information as temporal covariates in models. We suspect that environmental variability will impact on demographic parameters through changes in food availability. Unfortunately, no data were available describing the temporal

variation in abundance of prey consumed by storks. Thus, climatic indices were used to characterize the environmental fluctuations faced by individuals. Based on the annual life cycle of the white stork and using previous findings for this species, we selected a set of indices to describe environmental variability on breeding and nonbreeding grounds. The winter North Atlantic Oscillation (wNAO) (Hurrell 1995; data: <http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html>) has been reported to influence the size of Eastern European stork populations (Sæther *et al.* 2006) and describes large-scale conditions faced by birds on breeding grounds in Europe. It has been demonstrated that precipitation during spring affects the size of Eastern European populations (Sæther *et al.* 2006), so we used precipitation in the vicinity of the breeding area (45.0–47.5°N, 2.5–0°W) as the key parameter controlling resource availability in this marsh ecosystem. Data were averaged over the 3-month spring period (February to April) (Chen *et al.* 2002; data: <http://iridl.ldeo.columbia.edu/SOURCES/NOAA/NCEP/CPC/PRECL/prcp>). The Sahel index, computed from the amount of precipitation over the sub-Saharan sector (10.0–20.0°N, 20.0°W–10.0°E), is known to affect storks' survival during winter (Kanyambwa *et al.* 1990, Barbraud *et al.* 1999). Data were averaged over the rainy season (July to September) (Janowiak 1988; data: <http://jisao.washington.edu/data/sahel/>). The normalized difference vegetation index (NDVI) reflects primary productivity (Tucker *et al.* 2005; data since 1982: <http://iridl.ldeo.columbia.edu/SOURCES/UMD/GLCF/GIMMS/NDVI/global/ndvi/>). NDVI over wintering areas in Africa has already been linked to the survival of Eastern European storks' populations (Schaub *et al.* 2005). To test for density-dependent effects, we used data from an annual census of the breeding pairs ( $N$ ) on the study site. The inter-annual variability of these parameters is presented in Appendix 2. Covariates were standardized over the study period. Correlations between covariates were tested using Pearson correlation test with a Bonferroni correction for multiple correlations, under the R software (R Development Core Team 2004).

#### MODELS WITH ENVIRONMENTAL COVARIATES

Vital rates were modelled over 22 years as linear function of a covariate on a logit scale, as  $\text{Logit } \theta = \alpha + \beta \times x$ , where  $\theta$  is the vital rate,  $\alpha$  the intercept and  $\beta$  the slope of the relationship with the covariate  $x$ . Nonlinear effects were tested using a quadratic model:  $\text{Logit } \theta = \alpha + \beta_1 \times x + \beta_2 \times x^2$ . The contribution of a covariate to the model was assessed using an analysis of deviance (ANODEV) and the amount of variation in the focal rate explained by the covariate was evaluated by  $R^2$ ; (Skalski, Hoffmann & Smith 1993). To test for long-term effect, the probability of starting to breed was constrained with covariates referring to both actual condition (the year preceding the first breeding decision) and natal condition (during the early development of birds). The influence of natal condition was modelled as a cohort effect on the transition from PB to B.

Nonlinear relationships may be difficult to detect with a quadratic function on a 22-year data set due to a lack of extreme events (Altwegg *et al.* 2006). In order to explore this in depth, we conducted correlation analyses over 13 successive 10-year windows moving along the time series by a 1-year step ( $t_1$  to  $t_{10}$ ,  $t_2$  to  $t_{11}$ , ...  $t_8$  to  $t_{17}$ , Durant *et al.* 2004). Obtaining the same correlation between a demographic parameter and a covariate for all windows would describe a single linear relationship over the whole study period. Otherwise, nonlinear processes may be supported. The length of the sliding window referred to the 10-year period used in Barbraud *et al.* (1999) who described a correlation between survival and Sahel index

for this population. It is a good trade-off between the number of successive windows available and the number of points in each window. Preliminary analyses highlighted the persistence of the signal in smaller or larger windows. As we were more interested in the progressive change of the correlation over time rather than by its absolute significance, we only considered the slope parameter ( $\beta \pm 95\%$  CI) to avoid statistical irrelevance due to multiple testing between non-independent windows.

## Results

### TIME-DEPENDENT MODELS

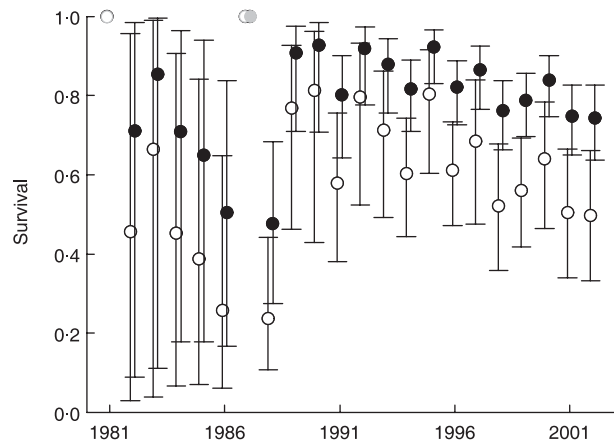
The GOF of the initial JMV model did not correctly fit the data ( $\chi^2 = 261.66$ , d.f. = 132,  $P < 0.001$ ). Principally, the absence of capture heterogeneity required for CMR models was not met (Test 3G:  $\chi^2 = 155.59$ , d.f. = 57,  $P < 0.001$ , Lebreton *et al.* 1992). We thus used an over-dispersion factor,  $\tau = 1.982$  (Lebreton *et al.* 1992).

The capture probability differed between PB and B (Table 1, model 1 vs. model 2), being time-dependent in PB (model 3 vs. model 4) and constant over time (model 1 vs. model 4) but increased with age from 1 to 4 years old (model 4 vs. model 5) in B. On average, the capture probability was  $0.056 \pm 0.005$  and  $0.891 \pm 0.016$  for PB and  $B \geq 4$  years old, respectively.

Survival probability differed among states (models 5 and 6 vs. model 7) and varied with time (models 5 and 6 vs. model 8). A model with an interaction between state and time was not preferred to an additive model (model 5 vs. model 6), indicating that temporal fluctuations of PB and B survival were parallel on a logit scale. When removing the first 7 years of the study to prevent potential bias due to small sample size, this additive pattern persisted. Finally, a two age-class model (juveniles of age 0 and adults of age  $\geq 1$ ) was a more parsimonious description of the data than a two-state model (model 6 vs. model 9). Juvenile survival ( $0.598 \pm 0.041$ ) was lower than

adult survival ( $0.784 \pm 0.013$ , Fig. 1). That is to say most of the mortality occurred during the first year of life and survival of PB  $\geq 1$  year old was assumed to be equal to B.

A constant model (Table 1, model 10) was preferred to a time- or a cohort-dependent model (respectively models 9 and 10) to describe the probability of starting to breed. Finally, an age-dependent model was a more parsimonious description of the data (model 12). The first breeding event never occurred at 1 year old and the probability of starting to breed increased from 2 up to a maximum at 4 (transitions

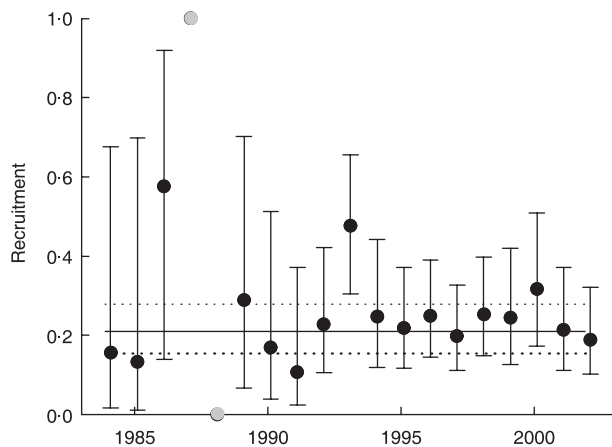


**Fig. 1.** The survival probability of juveniles and adults. Estimates of survival were obtained from a model with two age classes where survival of juveniles (the probability to survive from fledging to age 1, open circles) and of adults (the probability to survive from age 1 to age 2 and older, full circles) varied in parallel with time on a logit scale (Table 1, model 12). Grey circles indicate non-estimable parameters. Bars indicate  $\pm 0.95$  CI. Note: among the four chicks ringed in 1980, at least two of them were observed breeding several years later and entered the adult class in 1981, allowing estimates of adult survival since 1981.

**Table 1.** Model selection between time- and age-dependent models for capture, survival and transition. The model selected is presented in bold characters

No.	Capture	Survival	Transition (PB→B)	np	Deviance	QAIC	$\Delta$ QAIC
1	(PB, B) * t	(PB, B) * t	t	99	4699.2	2571.3	197.4
2	t	(PB, B) * t	t	84	5229.8	2809.3	435.3
3	(PB, B)	(PB, B) * t	t	68	4941.3	2631.6	257.6
4	(PB) * t + (B)	(PB, B) * t	t	85	4727.7	2557.7	183.8
5	(PB) * t + (B) * a <sub>1-4</sub>	(PB, B) * t	t	89	4538.0	2469.9	95.9
6	(PB) * t + (B) * a <sub>1-4</sub>	(PB, B) + t	t	72	4601.4	2467.9	94.0
7	(PB) * t + (B) * a <sub>1-4</sub>	t	t	71	4745.5	2538.7	164.8
8	(PB) * t + (B) * a <sub>1-4</sub>	(PB, B)	t	52	4716.8	2486.2	112.2
9	(PB) * t + (B) * a <sub>1-4</sub>	a <sub>1-2</sub> + t	t	72	4494.5	2414.0	40.0
10	(PB) * t + (B) * a <sub>1-4</sub>	a <sub>1-2</sub> + t	t	51	4540.5	2395.2	21.2
11	(PB) * t + (B) * a <sub>1-4</sub>	a <sub>1-2</sub> + t	coh	71	4507.3	2418.4	44.5
<b>12</b>	<b>(PB) * t + (B) * a<sub>1-4</sub></b>	<b>a<sub>1-2</sub> + t</b>	<b>a<sub>2-5</sub></b>	<b>54</b>	<b>4486.6</b>	<b>2374.0</b>	<b>0.0</b>
13	(PB) * t + (B) * a <sub>1-4</sub>	a <sub>1-2</sub> + t	a <sub>2-5</sub> + t	73	4451.3	2394.1	20.1
14	(PB) * t + (B) * a <sub>1-4</sub>	a <sub>1-2</sub> + t	a <sub>2-5</sub> + coh	73	4529.4	2433.6	59.6
15				3	6292.9	3184.2	810.2

np, number of parameters estimated by the model. Notation for effects: PB and B, pre-breeder and breeder states; t, time; a<sub>1-4</sub>, four age classes (from 1 to 4); coh, cohort; '.', constant; '+' and '\*', additive effect and interaction



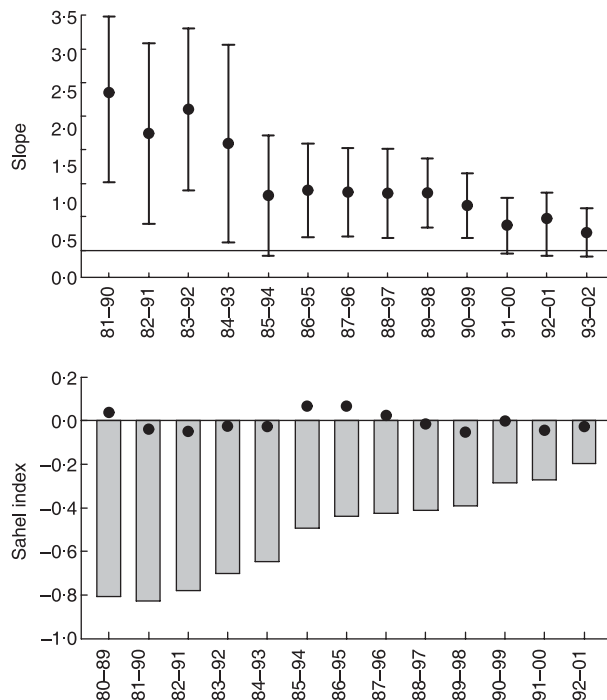
**Fig. 2.** The probability of starting to breed. Time dependent (dot) and constant (line) probabilities for 4-year-old storks. Estimates were respectively obtained from models 13 and 12 (Table 1). Grey circles indicate non-estimable parameters. Bars and dotted lines indicate  $\pm 0.95$  CI.

from PB to B at age 2 and at age 4 and older were respectively  $0.062 \pm 0.010$  and  $0.209 \pm 0.032$ ). However, neither time (model 13) nor cohort (model 14) appeared to affect the age-specific decision to start breeding (Fig. 2). Model selection remained unchanged when adjusting the over dispersion factor from 1 to 3, and model 12 was always ranked first.

#### MODELS WITH COVARIATES

The density of storks on the breeding ground was correlated with both the Sahel index (Pearson = 0.546,  $P_{\text{Bonferroni}} = 0.016$ ) and the NDVI (Pearson = 0.832,  $P_{\text{Bonferroni}} < 0.001$ ) over the study period. However, Sahel index, NDVI and  $N$  all follow a positive linear trend from 1980 to 2002 (respectively Pearson = 0.603,  $P_{\text{Bonferroni}} = 0.006$ , Pearson = 0.880,  $P_{\text{Bonferroni}} < 0.001$  and Pearson = 0.935,  $P_{\text{Bonferroni}} < 0.001$ , see Appendix 2), which may potentially explain this observed correlation. A principal component analysis supported this hypothesis since the first axis explained all the variance (proportion of variance explained by axes: PC1 = 0.995, PC2 = 0.005). To disentangle the effect of Sahel index, NDVI and  $N$ , we de-trended these covariates to focus on their own inter-annual variability. Residuals from linear (Sahel index and NDVI) or quadratic ( $N$ ) regression were used. No significant correlation was found between either these de-trended covariates or the wNAO and  $P_p$ .

The covariates were incorporated into the best model selected above (Table 1, model 12). As juvenile and adult survival varied in a parallel way in this model, the impact of climate on both parameters was similar. Over the 22 years of the study, we detected neither linear nor quadratic relationship between survival or the probability of starting to breed and the covariates (Table 2). Correlations over successive 10-year sliding windows highlighted changes in the slopes between successive windows. A positive impact of the Sahel index was detected, explaining up to 70% of the variability on survival during some early periods of the study, but this impact decreased thereafter (Table 3, Fig. 3a). In recent years, the



**Fig. 3.** Correlations over the successive 10-year windows between survival and Sahel index. Upper panel: values of the slopes of the relationships between survival and the de-trended Sahel index (bars indicate  $\pm 0.95$  CI). Lower panel: Sahel index: row (bars) and de-trended (dots) data averaged over the 10 years of each window considered. Note: the 1-year shift between the  $x$ -axis of the two graphs comes from the use of the climatic index the previous winter ( $t - 1$ ) to explain variation in the survival of individuals in year  $t$ .

Sahel index did not explain a significant part of the variation in survival (95% CI for the slope estimates included zero). This pattern was robust to changes in the length of sliding windows from 7 to 13 years. Winter NAO appeared to positively influence survival at the beginning of the study. By contrast, no clear pattern was observed with the probability of starting to breed.

#### Discussion

In this study, we detailed the influence of some climatic indices on different vital rates in the white stork, using data from a long-term monitoring programme conducted in Western France. In large animals, the regulation of population dynamics by climate is mostly considered to operate *via* an indirect mechanism, through the climatic perturbation of lower trophic levels on which organisms feed (Stenseth *et al.* 2002). In white storks, which are strongly associated with wetlands (Géroutet 1994), precipitation appeared to be a good indicator of food availability (Barbraud *et al.* 1999; Sæther *et al.* 2006). Whereas neither linear nor quadratic relationships identified a significant impact of covariates on vital rates over the whole study period, the sliding windows analysis revealed some interesting patterns at a smaller time-scale. The decreasing impact of winter climate on survival during the last decade may coincide with a recent change in environmental conditions.

**Table 2.** Test for linear and quadratic impact of climatic indices and density on survival and transition from pre-breeder to breeder state over the 22 years of the study period. Sahel index, NDVI and  $N$  are de-trended, all covariates are standardized

	$np$	Deviance	ANODEV	$P_{ANODEV}$	$R^2$
Actual conditions on survival probability					
wNAO	34	4532.7	1.42	0.247	0.07
wNAO + wNAO <sup>2</sup>	35	4523.9	3.08	0.070	0.24
Precipitation	34	4533.4	1.10	0.306	0.05
Precipitation + precipitation <sup>2</sup>	35	4529.3	1.49	0.417	0.03
Sahel index	34	4531.6	1.98	0.174	0.09
Sahel index + Sahel index <sup>2</sup>	35	4530.8	1.12	0.347	0.11
NDVI	36	4535.0	0.00	1.00	0.00
NDVI + NDVI <sup>2</sup>	37	4535.0	0.42	0.524	0.02
$N$	34	4536.0	0.01	0.913	> 0.01
$N + N^2$	35	4536.0	0.01	0.989	> 0.01
Actual conditions on transition (PB→B) probability					
wNAO	55	4470.2	1.44	0.244	0.07
wNAO + wNAO <sup>2</sup>	56	4469.2	1.27	0.272	0.12
Precipitation	55	4470.6	1.00	0.330	0.05
Precipitation + precipitation <sup>2</sup>	56	4469.8	0.88	0.360	0.08
Sahel index	55	4471.3	0.20	0.660	0.01
Sahel index + Sahel index <sup>2</sup>	56	4471.3	0.10	0.755	0.01
NDVI	57	4470.9	0.18	0.673	0.01
NDVI + NDVI <sup>2</sup>	58	4469.7	0.69	0.517	0.07
$N$	55	4468.8	3.15	0.091	0.14
$N + N^2$	56	4468.5	1.70	0.209	0.16
Natal conditions on transition (PB→B) probability					
wNAO	54	4485.8	0.62	0.441	0.03
wNAO + wNAO <sup>2</sup>	55	4484.7	0.68	0.419	0.07
Precipitation	54	4486.1	0.34	0.564	0.02
Precipitation + precipitation <sup>2</sup>	55	4486.1	0.16	0.687	0.02
Sahel index	54	4485.7	0.67	0.432	0.03
Sahel index + Sahel index <sup>2</sup>	55	4481.6	2.06	0.166	0.18
NDVI	56	4484.8	1.31	0.268	0.07
NDVI + NDVI <sup>2</sup>	57	4484.5	0.75	0.486	0.08
$N$	54	4486.2	0.30	0.590	0.02
$N + N^2$	55	4486.1	0.17	0.847	0.02

In the first part of the study, we identified the signal of a positive impact of rainfall in the Sahel on survival as previously described by Kanyambwa *et al.* (1990, 1993) and Barbraud *et al.* (1999) for different white stork populations. Survival probability refers to an apparent survival estimate since we were not able to disentangle true survival from permanent emigration in this open population (Lebreton *et al.* 1992). Permanent emigration from this growing population was close to zero [per year, < 2% established breeders in this population were recorded in other populations, although this was slightly higher for juveniles (C. Barbraud, unpublished data)]. In light of this, it is highly probable that Sahel index mainly affected true survival. In addition, emigration should be primarily dependent on resources at breeding site rather than at wintering ground. Interestingly, our approach provided an updated view of this well-known relationship between storks and African climate: the influence of Sahel rainfall on survival had progressively decreased during the last decade, down to an undetectable level. This observed change coincided with a gradual shift in precipitation patterns in recent years (Ozer *et al.* 2003) from a drought-dominated regime towards more favourable conditions for storks and their aquatic prey

species. From a mechanistic point of view, phenotypic plasticity should allow individuals to face limited variability, without putting their survival in jeopardy. In response to less taxing environmental constraints, the selection pressure exerted by climate severity on phenotypic plasticity (Reed *et al.* 2006) on this stork population may have decreased, supporting the observed loss of Sahelian signal on adult survival. From Fig. 3, we could define a threshold in climatic condition corresponding to an upper limit above which survival started to be affected. This threshold of  $-0.4$  corresponds to a minimum of 5400-mm rainfall per rainy season (averaged over the 14 stations of the Sahel index) that would be required to maintain sufficient resources for storks. Where adverse environmental conditions are sporadic, the impact on the stork population may be minimal. In contrast where these conditions are prevalent in successive years, the consequences may be far more severe. This idea of an accumulation of stress was supported by the positive relationship between wNAO and survival, observed at the beginning of the study period, where winter condition strongly affected survival. It suggests that both wNAO and Sahel index may interact. In case of harsh winter condition in the Sahel, followed by dry weather in Western

**Table 3.** The impact of climatic indices and density on survival and transition from pre-breeder to breeder state over successive 10-year periods. \* indicates 95% CI of slope estimates that do not include zero. Sahel index, NDVI and *N* are de-trended, all covariates are standardized over each 10-year window

Period	wNAO		Precipitation		Sahel index		NDVI		<i>N</i>	
	Slope	<i>R</i> <sup>2</sup>	Slope	<i>R</i> <sup>2</sup>	Slope	<i>R</i> <sup>2</sup>	Slope	<i>R</i> <sup>2</sup>	Slope	<i>R</i> <sup>2</sup>
Actual conditions on survival probability										
1981–90	0.78	0.35	0.87*	0.48	2.35*	0.64			–0.22	0.12
1982–91	0.47*	0.35	0.96*	0.61	1.74*	0.38			–0.17	0.06
1983–92	0.63*	0.27	0.09	0.01	2.10*	0.50	–0.52	0.07	–0.29	0.23
1984–93	0.67*	0.32	–0.13	0.02	1.5*	0.34	–0.32	0.02	–0.26*	0.28
1985–94	0.50*	0.29	0.02	0.00	0.81	0.14	–0.18	0.01	–0.15	0.12
1986–95	0.54*	0.30	0.11	0.02	0.89*	0.30	0.00	0.01	0.00	0.01
1987–96	0.19	0.03	0.12	0.03	0.87*	0.36	0.07	0.00	–0.03	0.02
1988–97	0.06	0.01	0.12	0.03	0.85*	0.35	0.06	0.00	–0.03	0.01
1989–98	0.09	0.04	0.25	0.22	0.86*	0.77	0.33	0.08	0.00	0.00
1990–99	0.15	0.11	0.10	0.03	0.7	0.39	0.42	0.11	–0.01	0.00
1991–00	0.10	0.07	0.01	0.00	0.37	0.19	0.36	0.09	0.01	0.01
1992–01	0.05	0.01	–0.10	0.05	0.48	0.27	0.41	0.09	0.02	0.04
1993–02	0.10	0.06	–0.13	0.13	0.26	0.10	0.43	0.07	0.02	0.04
Actual conditions on transition (PB→B) probability										
1981–90	–0.04	0.50	–0.04	0.01	0.11	0.01			–0.18	0.10
1982–91	0.02	0.41	0.30	0.10	0.71	0.10			–0.30	0.22
1983–92	–0.04	0.48	0.21	0.08	0.49	0.06	0.26	0.12	–0.13	0.09
1984–93	–0.04	0.19	–0.27	0.26	–0.46	0.03	0.69	0.37	–0.32*	0.55
1985–94	–0.06	0.19	–0.27	0.19	–0.32	0.03	0.65	0.37	–0.22*	0.34
1986–95	–0.06	0.15	–0.19	0.20	–0.24	0.04	0.39	0.08	–0.17*	0.30
1987–96	–0.08	0.13	–0.21	0.22	–0.24	0.04	0.37	0.07	–0.09	0.17
1988–97	–0.03	0.07	–0.03	0.10	–0.15	0.02	0.40	0.09	–0.03	0.02
1989–98	–0.06	0.08	0.02	0.06	–0.08	0.01	0.35	0.08	–0.02	0.02
1990–99	–0.17	0.08	0.01	0.06	–0.09	0.01	0.34	0.07	–0.02	0.02
1991–00	–0.18	0.21	–0.30	0.13	0.11	0.02	0.42	0.13	–0.03	0.18
1992–01	–0.23	0.26	–0.35	0.16	0.10	0.03	0.41	0.12	–0.03	0.15
1993–02	–0.10	0.25	–0.22	0.13	0.05	0.01	0.03	0.00	–0.03	0.16
Natal conditions on transition (PB→B) probability										
1981–90	–0.40	0.03	–0.03	0.02	–0.23	0.07			0.13	0.65
1982–91	–0.43	0.10	–0.06	0.12	–0.34	0.27			0.09	0.56
1983–92	–0.50	0.49	–0.11	0.66	–0.17	0.50	–0.34	0.71	0.00	0.83
1984–93	–0.43	0.60	–0.03	0.70	–0.12	0.63	–0.29	0.78	0.03	0.47
1985–94	–0.15	0.11	0.02	0.10	0.33	0.24	–0.15	0.13	–0.05	0.40
1986–95	–0.21	0.16	0.01	0.14	0.13	0.18	–0.14	0.18	–0.06	0.22
1987–96	–0.15	0.05	–0.03	0.01	0.16	0.08	–0.14	0.04	–0.07	0.34
1988–97	0.10	0.01	–0.02	0.01	0.16	0.08	–0.13	0.04	–0.06	0.37
1989–98	0.10	0.05	–0.05	0.04	0.09	0.05	–0.15	0.07	–0.06	0.37
1990–99	0.11	0.37	0.03	0.29	0.17	0.33	–0.27	0.35	–0.04	0.32
1991–00	0.12	0.32	0.02	0.23	0.06	0.23	–0.31	0.30	0.00	0.13
1992–01	0.12	0.11	–0.08	0.02	0.30	0.12	–0.21	0.03	0.01	0.01
1993–02	0.16	0.10	–0.05	0.09	0.25	0.16	0.07	0.08	0.02	0.08

Europe, storks might not be able to recover a sufficient body condition to reproduce and survive.

Surprisingly, we were not able to detect any long- (initial condition) or short- (present condition) term effect of climate or density on the probability of starting to breed. In this expanding population, the probability of entering the breeding part of the population did not appear to be limited by environmental factors. Nevertheless, our measure of density may not be entirely appropriate to investigate density dependence on the decision to start breeding. Our census at  $t_{-1}$  includes individuals that may die between  $t_{-1}$  and  $t$ , but considering a census at  $t$  would still consider new recruits. As a

consequence, not being able to detect density dependence does not necessarily mean that carrying capacity was not already reached in this increasing population.

Could other factors, unrelated to climatic conditions, explain the observed change in survival that we have attributed to rainfall in the Sahel? The age structure of the population varied over the study period, being biased towards young individuals as the population became established. An increasing proportion of older and more experienced individuals in the second age-class could have led to a decreasing impact of Sahel environment on this population over time (Coulson *et al.* 2001). By contrast, performance of juveniles (first age-class)

could remain constant over time. Thus, the difference (in term of mean survival and impact of climate) between juveniles and older individuals should have increased during the study period. This pattern was not supported by the model selected. Alternatively, a change in the migratory behaviour of storks, suggested by the growing number of birds wintering in southern Europe (Tortosa, Caballero & Reyes-Lopez 2002; Archaux *et al.* 2004) could explain the observed decrease in Sahel impact on survival. However, recent band recoveries in Sahel (C. Barbraud, unpublished data) indicate that a proportion, although unknown, of our population continues to winter in Africa. Furthermore, decadal censuses of white storks indicate that the number of breeding pairs recorded in Western Europe (Spain, Portugal, Germany and France) increased by 74.8% between 1984 and 2004 (respectively 11 702 and 46 356 breeding pairs, Schulz 1999, Thomsen, Michael-Otto-Institut NABU: <http://bergenhusen.nabu.de/zensus/zensus2006/worldpopulation.pdf>). In the meantime, the number of white storks counted over the Gibraltar Strait en route to Africa has increased by 86.4% (27 414 and 20 1639 individuals in 1985 and 2005 respectively, Fernandez-Cruz, SEO/birdlife, programme Migres: [http://www.seo.org/programa\\_seccion\\_ficha.cfm?idPrograma=11&idArticulo=458](http://www.seo.org/programa_seccion_ficha.cfm?idPrograma=11&idArticulo=458)). Although the number of storks wintering in Europe has increased, the number of migrant storks has also increased in a relatively similar proportion to the number of breeding birds. Thus, the proportion of storks reaching the African ground each winter would have remained quite constant since the mid-1980s, therefore supporting the idea of a change in climatic condition in Sahel becoming more favourable for wintering storks.

Our modelling and conclusions are based on very small sample sizes in the early part of the study, which explains some of the large confidence intervals in Figs 1 and 2. Low sample sizes may have favoured simpler models, potentially increasing bias in parameter estimates and inaccuracy in our conclusions. Despite this apparent limitation in the data, we want to stress that until the mid-1990s, all the chicks born in the entire study area were ringed and the entire breeding population studied (see Appendix 1). Even during the later part of the study, most (~70% to 90%) chicks were ringed, and most breeding adults monitored (Appendix 1). Thus, sample sizes were low because the population size was low. Therefore, the data are comprehensive with all birds sampled and mean estimates of vital rates are very unlikely to be biased due to unrepresentative sampling of the population. When focusing on the last 10 years of the study where sample sizes were much higher, the model selection procedure also retained an additive model between juvenile and adult survival.

Results suggest that the intensity of the links between demographic parameters and environmental conditions may vary over time, in relation to the severity of the local climatic regime. Climatic changes occurring over the Sahel seem to result from a long-term process acting at large spatial scales (Janowiak 1988; L'Hote *et al.* 2002), and Sahel rainfall condition is known to affect a large variety of Palaearctic migrant species (Newton 2004). Thus, the patterns described

in this white stork population may be of great use to better understand the dynamics of other trans-Saharan migrant species. The nature and the spatial implication of factors affecting individuals have changed over time, as well as the underlying processes driving population dynamics. Being able to detect and model such nonlinear processes will be crucial to predictions of the impact of environmental changes on populations and species using population models. The current development of new analytical tools (Gimenez *et al.* 2006) may facilitate testing for these nonlinear patterns.

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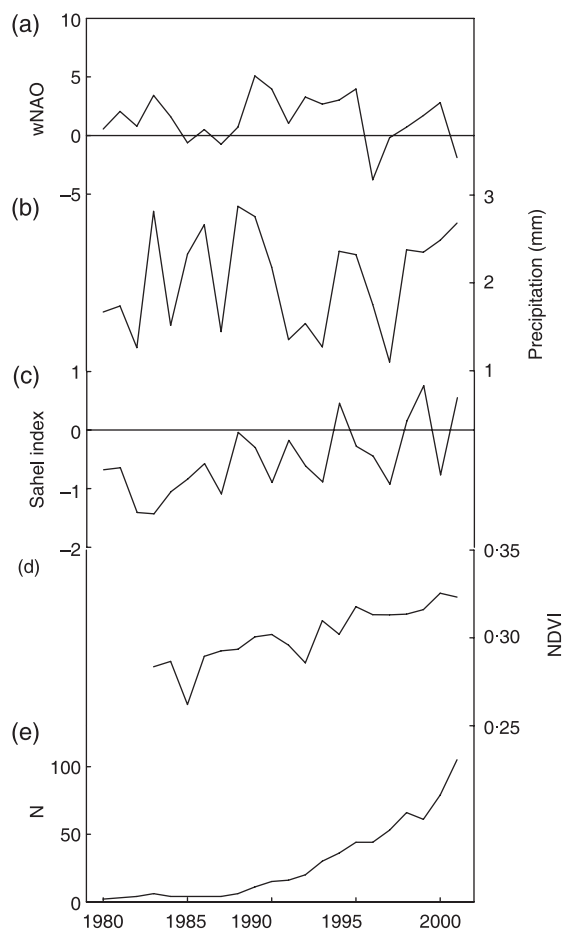
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**Appendix 1.** Total number of breeding pairs detected over the study area, number of known (ringed) individuals observed, number of chicks fledged, number of chicks ringed, and proportion of chicks ringed for each breeding season in the white stork population of Brouage

Season	Number of breeding pairs	Marked individuals observed	Chicks fledged	Chicks ringed	Proportion of chicks ringed (percentage)
1980	2	0	4	4	100.0
1981	3	0	4	4	100.0
1982	4	0	14	14	100.0
1983	6	0	21	21	100.0
1984	4	2	14	11	78.6
1985	4	4	9	9	100.0
1986	4	4	13	13	100.0
1987	4	4	18	18	100.0
1988	6	6	21	21	100.0
1989	11	6	35	35	100.0
1990	15	19	45	45	100.0
1991	16	24	50	50	100.0
1992	20	38	65	65	100.0
1993	30	49	97	95	97.9
1994	36	55	109	103	94.5
1995	44	89	123	114	92.7
1996	44	91	100	97	97.0
1997	53	145	136	129	94.9
1998	66	117	196	175	89.3
1999	61	165	237	214	90.3
2000	79	154	254	216	85.0
2001	105	169	252	183	72.6
2002	115	166	183	143	78.1
2003	121	148	240	171	71.3

**Appendix 2.** Temporal variation of the indices used in this study: (a) wNAO, (b) precipitation, (c) Sahel Index, (d) NDVI over the Sahel region and (e) *N*