

## Article

# Climate Change and the Spatiotemporal Variation in Survival of a Long-Distance Migrant (White Stork, *Ciconia ciconia*) across Western Europe

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**Simple Summary:** Although impacts of climate change at the population level are frequently reported in the scientific literature, the effects of global warming on particular individuals are not well-known, specifically when it comes to large spatial scales. However, understanding how the effects on individuals are translated into impacts in animal populations is key to getting insight into the consequences of climate change for species conservation. We used ring recoveries of White Storks across western Europe to assess the influence of different environmental factors on the survival of this long-distance migratory bird. We found that both the shape and the strength of the relationship between climate warming and survival differ across age groups, with juvenile White Storks more strongly affected. Furthermore, we found a decline in survival which is particularly marked for those storks breeding in southern Europe. The large-scale effect of climatic conditions identified in this widespread and common long-distance migrant species represents a highly likely scenario for other migratory birds in Europe.

**Abstract:** The spatial variation in the strength of climate change may lead to different impacts on migratory birds using different breeding areas across a region. We used a long-term data series of White Stork ring recoveries to study the temporal and spatial variation of annual survival rates of White Stork across western Europe between 1960 and 2009 in relation to climatic and environmental conditions at their breeding and wintering grounds. White Stork survival was estimated from the Cormack–Jolly–Seber (CJS) model using a cohort-based analysis. Our results support that climate change has caused a gradual decline in the survival performance of western European White Storks during the study period. Both the shape and the strength of the relationship between climate warming and survival differ among different life-stages of the individual development, with juvenile White Storks more strongly affected. The decline in survival is particularly marked for those storks breeding in southern Europe. The large-scale effect of climatic conditions identified in this widespread long-distance migrant species represents a highly likely scenario for other migratory birds in Europe.

**Keywords:** climate change; mark-recapture; NDVI; temperature anomaly; Cormack–Jolly–Seber



**Citation:** Martín, B.; Onrubia, A.; Ferrer, M. Climate Change and the Spatiotemporal Variation in Survival of a Long-Distance Migrant (White Stork, *Ciconia ciconia*) across Western Europe. *Birds* **2021**, *2*, 362–380. <https://doi.org/10.3390/birds2040027>

Academic Editor: Jukka Jokimäki

Received: 24 September 2021

Accepted: 29 October 2021

Published: 31 October 2021

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## 1. Introduction

Disturbances are events that can disrupt living organisms at any ecological level [1]. In this sense, human-driven climate change over the last years [2] is resulting in significant impacts on wild species around the world and has been considered a long-term threat for many of them [3,4]. Climate change and severe weather, defined as long-term climatic changes that may be linked to global warming and other severe climatic or weather events outside the natural range of variation that could wipe out a vulnerable species or habitat, are classified as first-level direct threats to biodiversity [5,6]. As warming occurs rapidly,

the survival of the species facing climate change may be compromised if they are unable to adapt to the new environmental conditions [3].

Habitat models are usually used for assessing the responses to climate change as a method to project potential distributions of species under different climate conditions [7]. Therefore, although shifts in the latitudinal and altitudinal ranges [8] of many species have been frequently reported as a common effect of climate warming, much less is known about the impacts of recent climate change at the level of particular individuals and populations [9]. However, habitat availability is not the only factor influencing species responses to climate change, since community composition [10], population-specific traits, as well as the potential interactions between demographic and landscape processes [11] also modulate the species responses [12].

The survival rate is one of the main demographic parameters determining population trends in living organisms [13], particularly in long-lived species [14,15]. In these species, in which demographic parameters change with age, responses to environmental variation, including climate change, may largely vary among populations, as different populations present different age-specific survival rates [16]. Moreover, there is marked spatiotemporal heterogeneity in the patterns of climate change, which differ not only over the seasons but also across different regions [17]; thus, different populations are subjected to different climate conditions. On the other hand, to properly describe climate effects, we need long-term monitoring of the demographic rates (e.g., a minimum 30-year period is generally regarded as required for describing current climate trends; [18]). How individuals' survival is shaped by environmental factors and life history is of major importance when predicting the future of a population [19] and the impact of climate change therein [20]. However, we know little about the relationship between climate and individual survival over such long temporal frames.

Long-lived long-distance migrants subject to a wide range of environmental conditions are expected to be particularly affected by climate change [21]. Since their annual survival is conditioned by the seasonal survival rates, migratory populations of a species using different breeding and wintering areas may be subjected to different impacts of climate change [22]. The White Stork (*Ciconia ciconia*, L.) is a long-distance migrant with a wide distribution throughout Europe [23,24]. Its popularity makes this species an appropriate model for large-scale and long-term studies [25–28]. In this species, former research has shown an impact of environmental and climatic conditions on survival [26,29,30]. It is well-known that the White Stork Western European population has been increasing in size during recent decades [27] after recovering from a sharp decline in the 19th and early 20th centuries, mainly due to industrialization and changes in farmland practices [31,32].

In this study, we linked time series of climate and landscape environmental variables with age-specific survival models to explore the spatiotemporal variation of the impacts of climate change on the populations of a long-lived long-distance migratory species. Specifically, we used data series of White Stork ring recoveries stored in the European Union for Bird Ringing database (EURING Data Bank) [33] across western Europe and climate and environmental conditions at the breeding and wintering grounds between 1960 and 2009. This period was selected because it is a relevant time frame in terms of climate change since considerable global surface warming has occurred in the years between the mid-1970s and the late 1990s [17].

Climate warming is expected to increase population growth and carrying capacity if populations are located close to the coolest limit of a species' distribution [34]. We predicted that White Stork survival at northern latitudes would be positively influenced by climate warming, whereas we expected either negative or no effect of climate change on the survival of individuals breeding in southern populations. On the other hand, adult survival rates in long-lived species commonly exhibit lower variability than juvenile ones because natural selection tends to favor a reduction in the variation of those demographic rates with a higher impact on population growth rate [13]. In this sense, we expected juveniles to be more sensitive to timing factors related to climatic variability [35], and

therefore we predicted a stronger climate change impact on young White Storks compared with adult birds.

To our knowledge, no previous study has assessed the importance of climate change on the vital rates of a long-distance migratory species across its life cycle, in the long-term and over regional spatial extents such as this. Determining the relationship between survival and climate change in the White Stork can illustrate how the effects of present and future warming may impact other species allowing us to better understand the vulnerability of different populations to climate change across Europe.

## 2. Materials and Methods

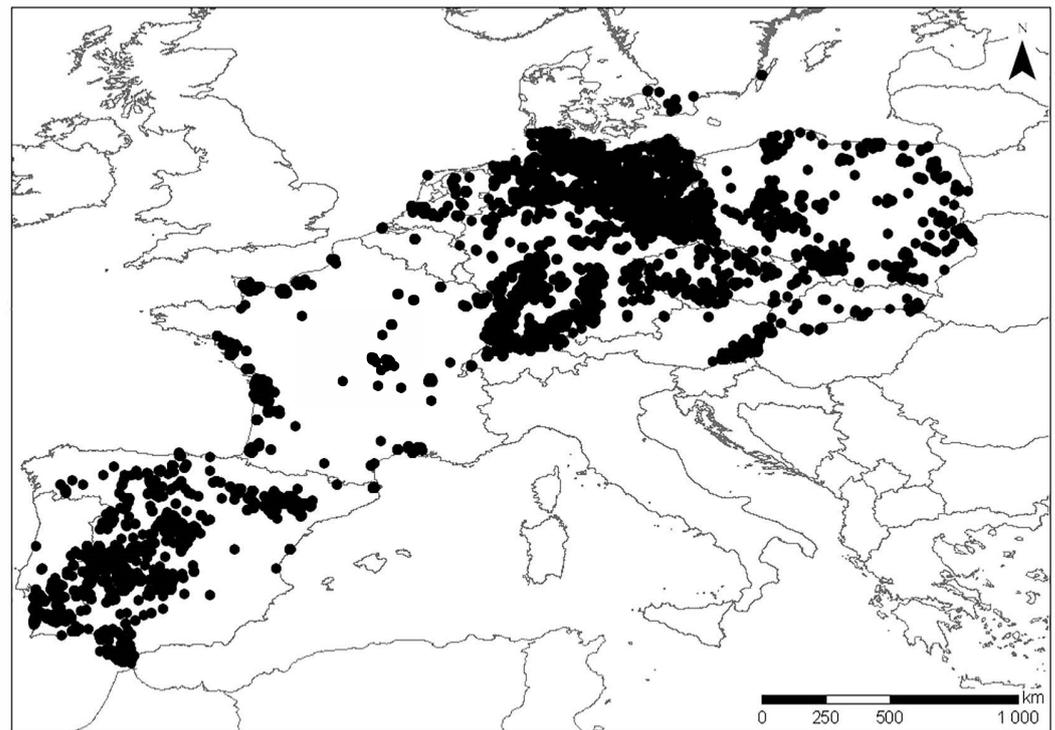
### 2.1. Study Species

The White Stork is a migrant species breeding in Europe and wintering in sub-Saharan regions [23,24]. The White Stork European population is estimated at 224,000–247,000 pairs [24]. Western European populations of White Stork winter in the Sahel region, whereas eastern European White Stork populations winter in eastern and southern Africa, although the Sahel region constitutes an important staging area for these birds when traveling South. This species has a delayed maturity, with first breeding at 3 years, although the probability of starting to breed increased from 2 up to a maximum at 4 years, an age when most storks reproduce. Before first breeding, some birds remain in the African wintering grounds, whereas other individuals may return to the breeding sites in Europe [29]. White Storks are strongly associated with wetlands, although they can inhabit highly human-transformed habitats [36].

### 2.2. Ringing Data

Ring recovery information was obtained from the EURING database [33] on different individual mark-reencounter histories of western European White Storks collected from 1960 to 2009 (Figure 1 and Figure S1 in the Supplementary Materials). This is a relevant time period in terms of climate change since considerable global surface warming has occurred between the mid-1970s and the late 1990s [17]. In addition, this period comprises a time span (i.e., 1993–2010) where climate change at the breeding grounds was particularly pronounced [37]. The reason for stopping the data analysis in 2009 was to count on recent evidence of substantial population changes, e.g., [23], as a consequence of the environmental effects that were detected in the study models (see below). To determine population decline according to IUCN criteria [38], population size has to be measured over 10 years or three generations, whatever is longer. White Storks generally begin breeding when they are about four years old. As generation time can be calculated (*sensu* [39]) as the weighted-mean age of the mothers at childbirth, three generations of White Storks are about 12 years, which comprises the period between 2009 (the end of our study) and the present time.

As indicated in Figure 1, the entire breeding range of the species within western Europe was covered. The data included information on the date and locality of any subsequent recovery (i.e., encountering of a ringed bird, both dead or alive, including resightings), elapsed time, distance, and direction between ringing and each recovery encounter for birds ringed (with metal and/or colored rings and other marks) as fledglings at their nests. The spatial location of the natal site for each individual was determined using package *geosphere* [40] in R [41]. Spatial coordinates at the time of ringing were based on the direction and the loxodromic distance (distance on a constant compass bearing) between ringing and recovery localities [42]. Birds were only included in the analysis if the accuracy of the recovery coordinates were within a 50-km radius, according to the EURING database. All records containing any other detectable errors and inaccuracies (i.e., wintering or resident birds; individuals intentionally or non-intentionally moved and/or transport) were omitted. With these restrictions, 23,874 individuals remained.



**Figure 1.** Spatial distribution of the White Stork ringing locations considered in the analysis (1960 to 2009;  $n = 23,874$ ).

### 2.3. Analyses

White Stork survival was estimated from the Cormack–Jolly–Seber (CJS) model, where  $\phi$  is the local survival and  $p$  is the recapture (or resighting) probability [43,44]. We estimated survival and recapture probabilities using a cohort-based analysis. A birth cohort consists of all the individuals born in a given breeding season. Since birds were ringed as fledglings, all released cohorts were of known age [45]. We modeled time- and age-specific survival and recapture probabilities of the successive cohorts. As a source of heterogeneity in survival probability among individuals, we also considered the latitude of the natal site (as a surrogate of the breeding region, [27]), the temporal trend in the productivity, and the distance to the closest dump area within the breeding sites as individual covariates [45]. In addition, we constrained variation in survival ( $\phi$ ) to be a linear function of climate change (i.e., temperature anomaly, Sahel precipitation anomaly). Recapture probability through the study period ( $p$ ) was constrained to be an exponential function of time (see below for a detailed description of the variables included in the models).

### 2.4. Predictors of Survival

**Age:** Adult survival in White Stork has been found to be dependent on age, but not sex [46,47]. Since behavioral differences between juvenile (<1-year), immature (1-year < 4-year), and adult (>4-year) White Storks may affect survival and recovery probabilities among individuals, we considered the age of birds both as a predictor of survival and recapture probability.

**Temporal constraints:** Previous studies have reported that survival rates of European White Storks are sensitive to Sahel rainfall during the wet season [29,46]. Climatic conditions on the breeding grounds are also a relevant survival constraint in this species [26]. We used anomalies in the Sahel Precipitation Index with respect to 1900–2016 (Deutscher Wetterdienst Global Precipitation Climatology Centre data, [doi:10.6069/H5MW2F2Q](https://doi.org/10.6069/H5MW2F2Q), accessed on 17 October 2021) as a surrogate of the annual climatic conditions in the wintering grounds. The term anomaly means a departure from the long-term average, which is the reference value. The Sahel index was computed from the annual rainfall over the sub-Saharan region (10–20N, 20W–10E) from June to October since the Sahel rainy season

is centered in these months. As an indicator of the climatic conditions faced by birds on their breeding grounds, we used an annual averaged value of the North Hemisphere land temperature anomaly (Jones et al., 1999), based on monthly temperature anomalies from March to May in a particular year. Anomalies were provided as departures from the 20th-century average (1901–2000). Temperature anomalies were downloaded from <ftp://ftp.ncdc.noaa.gov/pub/data/anomalies> (accessed on 15 May 2017).

**Individual covariates:** To test whether the survival probability has changed spatially across western Europe, we used the latitude of the ringing location as a surrogate of the White Stork breeding region [27]. Since White Storks exhibit philopatric behavior and high fidelity to the breeding grounds year after year when they are mature [48], and a moderate natal dispersal distance when juveniles [49], we expected the natal site to be a close indicator of the later breeding region.

**High primary productivity:** is associated with a high density of primary consumers [50]. Therefore, food availability for White Storks seems to be related to levels of primary productivity [26]. The normalized difference vegetation index (NDVI) is a commonly used surrogate of primary productivity [51]. We used trends in the NDVI at each individual natal site as a surrogate of the environmental changes that took place on the breeding grounds over the study period. Specifically, we measured the linear trend in annual NDVI during spring based on averages from a five-month period (February–June). The trend was quantified for the period 1982–2006 because there was no data available prior to this period. Monthly spring NDVI data were downloaded from <http://iridl.ldeo.columbia.edu/SOURCES/.UMD/.GLCF/.GIMMS/.NDVIg/.global/.ndvi/> (accessed on 20 October 2021) and were resampled using package raster [52] in R following a GIS moving window approach based on aggregation by means of averaging 8 km cells, so these layers had a final grid size of ~50 km.

**Human activities:** such as rubbish dumps [53,54], may benefit European White Storks by providing new feeding opportunities that increase bird survival due to the exploitation of a new resource. We measured a surrogate of these human activities in the breeding grounds based on data from CORINE land cover 1990, 2000, and 2006 projects [55–57]. Particularly, as a proxy of this non-natural source of food, we measured the averaged distance (averaged value for 1900–2006) between the ringing site of each individual and the closest dump location (<https://land.copernicus.eu/user-corner/technical-library/corine-land-cover-nomenclature-guidelines/html/index-clc-132.html>, accessed on 25 October 2021) since the use of rubbish dumps by White Storks depends on the distance between the nest and the rubbish dump [58].

### 2.5. Recovery Rates

The recovery rate in western European White Storks is likely to be dependent on age due to the behavioral differences present among age classes [59]. To test whether the resighting effort changed spatially (see Figure S2 in the Supplementary Materials), we modeled the recovery rates as a function of the latitude of the ringing site [60]. Since we knew that the resighting effort had increased exponentially over time (see Figure S3 in the Supplementary Materials), we also constrained recapture probabilities to follow an exponential temporal trend [45].

### 2.6. Models

Survival and recapture rates were modeled over 49 years as linear and/or quadratic functions of the temporal constraints and covariates on a logit scale. Quadratic terms were used to model nonlinear responses. We fitted models where the strength and the shape of the effect of the covariate were dependent on age (i.e., models with different slopes of the covariate for each age class), as well as additive models where only the strength of the effect of the covariate was affected by age. According to previous studies on this species [26,29], we identified 13 different reasonable structures for the survival and recovery probabilities (Table 1). The models were then ranked according to the small

sample-size adjusted Akaike's information criterion (AICc, [61]). Since there is no method for testing the fit of models with individual covariates, following [45]'s recommendations, we performed GOF testing on the most general model that did not include individual covariates and used the overdispersion value (c-hat) for this general model on all of the other models. Analyses were performed using the software program MARK [62].

**Table 1.** Description of the models that were assessed. Naming convention from [43];  $(t)p(t)$  as a model with full time-dependence (t) for both survival ( $\phi$ ) and recapture (p). \* a3: three age classes (juvenile (first)/ immature (second)/ adult (third)); tma: Northern Hemisphere Temperature Anomaly; sahel: Sahel index anomaly; ylat: latitude of the ringing site; ndvi: trend (1982–2006) in NDVI in the ringing site; dump: mean distance to dump from the ringing site (1990–2016). Additive effect (+) and interaction term (:); 2: quadratic term.

Model *	Description
$\{\phi(a3-tma2/tma2/tma2+sahel+ylat+ndvi+dump+sahel:ylat+ndvi:ylat+dump:ylat)p(a3(ylat/ylat/ylat)+trend)\}$	3 age-classes for survival (a3), all age classes time-constrained, constrained by quadratic Northern temperature anomaly -tma-, and constrained by Sahel index (sahel; additive effect); additive effect on survival of the covariates (ylat, ndvi, and dump) and interaction terms between covariates (sahel:ylat, ndvi:ylat, dump:ylat). 3 age-classes for recapture, all age classes dependent on latitude in the ringing site (ylat); exponential temporal trend in recapture (additive effect)
$\{\phi(a3-tma2/tma2/tma2+sahel+ylat+sahel:ylat+ndvi+dump+ndvi:ylat+dump:ylat)p(a3+ylat+trend)\}$	3 age-classes for survival (a3), all age classes time-constrained, constrained by quadratic Northern temperature anomaly -tma-, and constrained by Sahel index (sahel; additive effect); additive effect on survival of the covariates (ylat, ndvi, and dump) and interaction terms between covariates (sahel:ylat, ndvi:ylat, dump:ylat). 3 age-classes for recapture, exponential temporal trend in recapture (additive effect), additive effect of latitude in the ringing site
$\{\phi(a3-tma2/tma2/tma2+sahel+ylat+ndvi+dump+sahel:ylat+ndvi:ylat+dump:ylat)p(a3+trend)\}$	3 age-classes for survival (a3), all age classes time-constrained (constrained by quadratic Northern temperature anomaly -tma- and constrained by Sahel index (sahel; additive effect); additive effect on survival of the covariates (ylat, ndvi, and dump) and interaction terms between covariates (sahel:ylat, ndvi:ylat, dump:ylat). 3 age-classes for recapture, exponential temporal trend in recapture (additive effect)
$\{\phi(a3-tma2/tma2/tma2+sahel+ylat+ndvi+dump+ndvi:ylat+dump:ylat)p(a3+trend)\}$	3 age-classes for survival (a3), all age classes time-constrained, constrained by quadratic Northern temperature anomaly -tma-, and constrained by Sahel index (sahel; additive effect); additive effect on survival of the covariates (ylat, ndvi, and dump) and interaction terms between covariates (ndvi:ylat, dump:ylat). 3 age-classes for recapture, exponential temporal trend in recapture (additive effect)
$\{\phi(a3-tma2/tma2/tma2+sahel+ylat+ndvi+dump+ndvi:ylat)p(a3+trend)\}$	3 age-classes for survival (a3), all age classes time-constrained, constrained by quadratic Northern temperature anomaly -tma-, and constrained by Sahel index (sahel; additive effect); additive effect on survival of the covariates (ylat, ndvi, and dump) and interaction term between covariates (ndvi:ylat). 3 age-classes for recapture, exponential temporal trend in recapture (additive effect)
$\{\phi(a3-tma2/tma2/tma2+sahel+ylat+ndvi+dump)p(a3+trend)\}$	3 age-classes for survival (a3), all age classes time-constrained, constrained by quadratic Northern temperature anomaly -tma- and time-constrained by Sahel index (sahel; additive effect); additive effect on survival of the covariates (ylat, ndvi, and dump). 3 age-classes for recapture, exponential temporal trend in recapture (additive effect)
$\{\phi(a3-tma2/tma2/tma2+sahel+ylat)p(a3+trend)\}$	3 age-classes for survival (a3), all age classes time-constrained, constrained by quadratic Northern temperature anomaly -tma-, and time-constrained by Sahel index (sahel; additive effect); additive effect on survival of the covariate 'latitude' (ylat). 3 age-classes for recapture, exponential temporal trend in recapture (additive effect)

Table 1. Cont.

Model *	Description
$\{\phi(a3-tma2/tma2/tma2+sahel)p(a3+trend)\}$	3 age-classes for survival (a3), all age classes time-constrained, constrained by quadratic Northern temperature anomaly -tma-, and constrained by Sahel index (sahel; additive effect); latitudinal additive effect on survival (ylat). 3 age-classes for recapture, exponential temporal trend in recapture (additive effect)
$\{\phi(a3-tma2/tma2/tma2)p(a3+trend)\}$	3 age-classes for survival (a3), all age classes time-constrained, constrained by quadratic Northern temperature anomaly -tma-, and constrained by Sahel index (sahel; additive effect). 3 age-classes for recapture, exponential temporal trend in recapture (additive effect)
$\{(a3-././.)p(a3+trend)\}$	3 age-classes for survival (a3), all age classes constant (././.) - juvenile (first)/ immature (second)/ adult (third)- through time
$\{\phi(t)p(t)\}$	Standard CJS model; time dependence in survival and recapture
$\{(t)p(.)\}$	Time-dependent survival; constant recapture through time
$\{\phi(.)p(.)\}$	Constant survival and recapture through time

### 3. Results

#### 3.1. Description of the Best Fit Model

Model selection was based in quasi-AICc (QAICc) values, (i.e. AICc values corrected for the c-hat from the standard CJS model: (t) p(t); c-hat = 1.86). Estimates, standard errors, and confidence intervals were also corrected for this c-hat. The best fit model (model with the lower QAICc) was strongly supported according to the QAICc weights (Table 2).

Table 2. Model selection. QAICc: Corrected AICc; wi: QAICc weights; np: number of parameters in the model; QDeviance: Corrected deviance. Estimates corrected for c-hat = 1.93 (c-hat from CJS standard model -(t) p(t))-, see Methods and Table 1).

Model	QAICc	Delta QAICc	w <sub>i</sub>	np	QDeviance
$\{\phi(a3\ tma2/tma2/tma2+sahel+ylat+sahel:ylat+ndvi+dump+ndvi:ylat+dump:ylat)p(a3(ylat/ylat/ylat)+trend)\}$	21,569.35	0.00	1.00	22	21,525.32
$\{\phi(a3\ tma2/tma2/tma2+sahel+ylat+sahel:ylat+ndvi+dump+ndvi:ylat+dump:ylat)p(a3+trend+ylat)\}$	21,591.17	21.82	0.00	20	21,551.14
$\{\phi(a3\ tma2/tma2/tma2+sahel+ylat+sahel:ylat+ndvi+dump+ndvi:ylat+dump:ylat)p(a3+trend)\}$	21,636.69	67.34	0.00	19	21,598.66
$\{\phi(a3\ tma2/tma2/tma2+sahel+ylat+ndvi+dump+ndvi:ylat+dump:ylat)p(a3+trend)\}$	21,672.07	102.72	0.00	18	21,636.05
$\{\phi(a3\ tma2/tma2/tma2+sahel+ylat+ndvi+dump+ndvi:ylat)p(a3+trend)\}$	21,718.74	149.39	0.00	17	21,684.72
$\{\phi(a3\ tma2/tma2/tma2+sahel+ylat+ndvi+dump)p(a3+trend)\}$	21,831.62	262.26	0.00	16	21,799.60
$\{\phi(a3\ tma2/tma2/tma2+sahel+ylat)p(a3+trend)\}$	22,844.18	1274.83	0.00	15	22,814.16
$\{\phi(a3\ tma2/tma2/tma2+sahel)p(a3+trend)\}$	22,844.47	1275.12	0.00	14	22,816.45
$\{\phi(a3\ tma2/tma2/tma2)p(a3+trend)\}$	23,123.97	1554.61	0.00	13	23,097.95
$\{\phi(a3)p(a3+trend)\}$	23,448.88	1879.53	0.00	7	23,434.88
$\{\phi(t)p(t)\}$	23,541.65	1972.30	0.00	96	23,349.00
$\{(t)p(.)\}$	23,933.62	2364.26	0.00	50	23,833.44
$\{\phi(.)p(.)\}$	24,952.57	3383.22	0.00	2	24,948.57

#### 3.2. Parameters in the Best Fit Model: Additive and Interaction Terms

Survival estimates from the best fit model differed among age classes and were nonlinearly time-constrained by the Northern temperature anomaly (i.e., climate conditions at the breeding grounds) in all the age classes, and linearly time-constrained by the Sahel index anomaly (i.e., climate conditions at the wintering grounds). The effect of the temperature anomaly (i.e., climate conditions at breeding sites) on survival rates was different among juvenile, immature, and adult individuals (i.e., different slopes), whereas the relationship between survival and the Sahel index (i.e., climate conditions at the wintering grounds) varied in parallel (i.e., additive model) among the three age classes on a logit scale. The best fit model also included an additive effect of the covariates (latitude of the breeding

site, trend in NDVI-i.e., trend in vegetation productivity in spring at the breeding site-, and mean distance to dump) on the survival rate of all age classes (i.e., same effect of the variables on the survival of different age classes), as well as interaction terms between the trend in NDVI, the distance to dump and latitude (ndvi:ylat, dump:ylat), indicating that the effect of the environmental conditions in the breeding site (trend in the vegetation productivity and mean distance to dump over the study period) on survival differed along environmental gradients in latitude.

### 3.3. Beta Estimates of the Model Predictors

The Sahel index anomaly (i.e., climate conditions at the wintering grounds), the latitude, and the trend in NDVI in spring at the breeding site showed a positive linear relationship with survival (i.e., larger survival rates with positive trends in vegetation productivity, at higher latitudes and with larger anomalies in the Sahel precipitation index) in all age classes, whereas the distance to dump was negatively related to survival probability (i.e., the larger the distance to dump, the lower the survival in all age classes; see Table 3). According to the negative effect of the interaction terms between latitude and the climate conditions in wintering sites (i.e., sahel:ylat) and between latitude and the trend in vegetation productivity at the breeding site (i.e., ndvi:ylat), the positive effect on survival of both the Sahel index and the trend in vegetation productivity were lower at higher latitudes compared with southern ringing locations, whereas the negative relationship between the distance to dump and survival was stronger for birds breeding in northern populations. Latitude “per se” was only almost significant (95% CI:  $-0.013$ – $-0.032$ ) whereas confidence intervals for the slope of all other estimates did not include zero, indicating significant effects for their corresponding predictors (Table 3).

**Table 3.** Beta estimates for survival  $-\phi$  and recapture  $-p$  (i.e., logit link function parameters) derived from the best fit model (lower QAICc), see Table 2. Standard Error (ES) and Confidence Intervals (CI) were corrected for  $\hat{c} = 1.932$ . Parameters: age 1: juveniles (<1 year); age 2: immature (2–3 year); age 3: adult (>3 year); tma: Northern Hemisphere Temperature Anomaly; sahel: Sahel index anomaly; ylat: latitude of the ringing site; ndvi: trend (1982–2006) in NDVI in the ringing site; dump: mean distance to dump from the ringing site (1990–2016). Interaction term (:); 2: quadratic term.

Parameter	Beta	E.S.	Lower	Upper
<b>Survival-<math>\phi</math>-</b>				
age 1	-1.182	0.584	-2.327	-0.037
tma (age 1)	-0.317	0.275	-0.857	0.223
tma2 (age 1)	-1.276	0.201	-1.670	-0.882
age2	-0.475	0.579	-1.610	0.659
tma (age 2)	1.180	0.367	0.459	1.900
tma2 (age 2)	-1.924	0.271	-2.455	-1.394
age3	0.185	0.586	-0.963	1.333
tma (age 3)	1.353	0.365	0.638	2.069
tma2 (age 3)	-1.942	0.278	-2.486	-1.398
sahel	1.809	0.349	1.125	2.494
ylat	0.010	0.011	-0.013	0.032
sahel:ylat	-0.040	0.007	-0.054	-0.026
ndvi	2313.312	270.802	1782.540	2844.084
ndvi:ylat	-53.876	5.684	-65.016	-42.736
dump	-1.391	0.209	-1.802	-0.981
dump:ylat	0.051	0.005	0.042	0.060

Table 3. Cont.

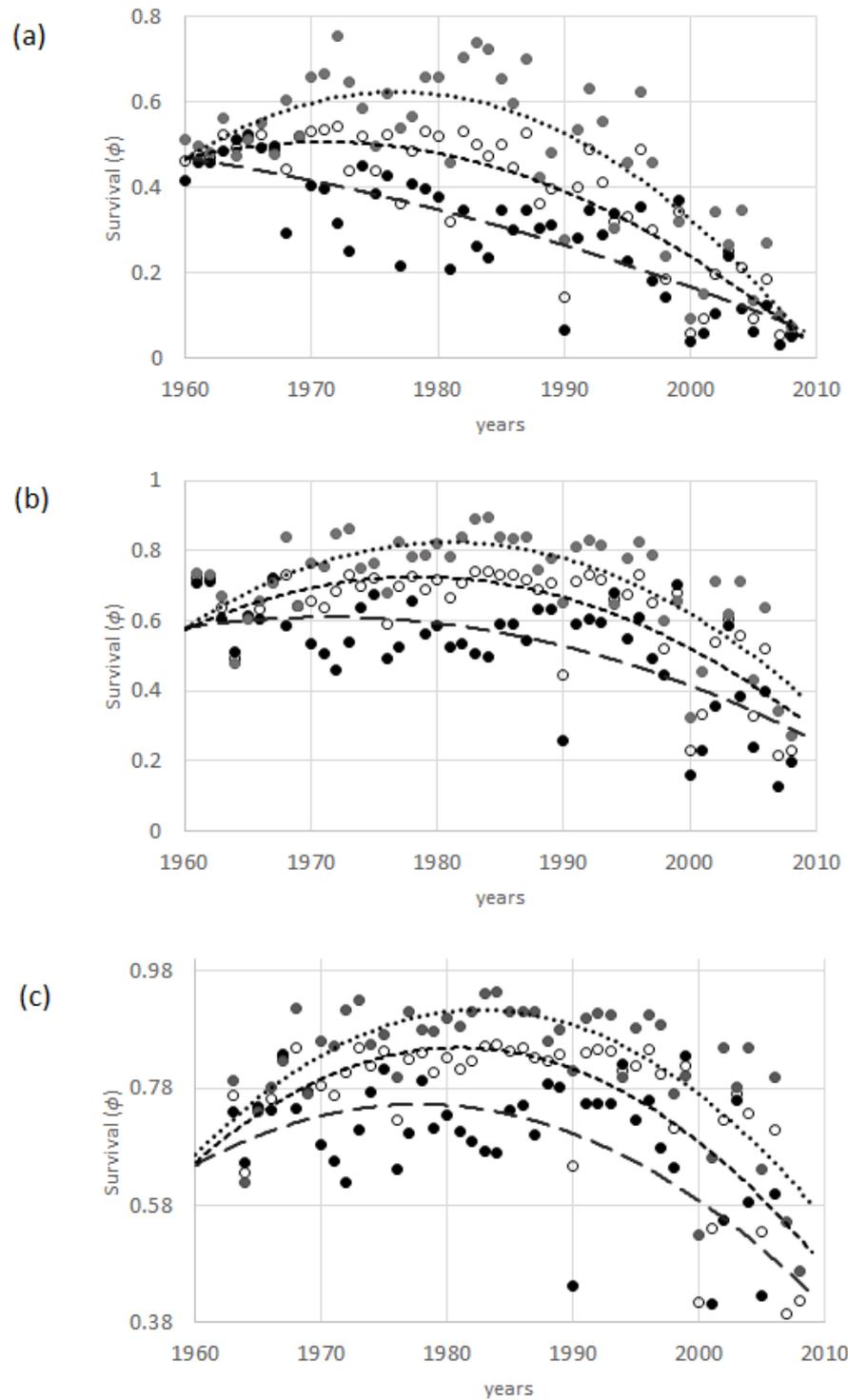
Parameter	Beta	E.S.	Lower	Upper
		<b>Recapture -p-</b>		
age1	-0.513	0.748	-1.979	0.953
ylat	-0.049	0.015	-0.078	-0.020
age2	2.707	0.844	1.052	4.361
ylat	-0.107	0.017	-0.141	-0.074
age3	5.060	0.843	3.409	6.712
ylat	-0.149	0.017	-0.183	-0.115
exponential				
temporal trend	3.580	0.417	2.763	4.396

### 3.4. Recapture Probabilities

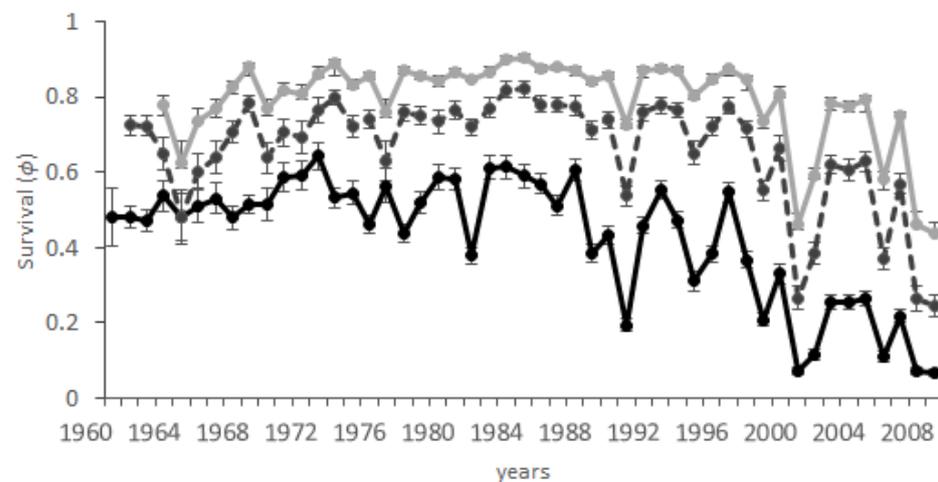
Recapture probabilities increased exponentially over the study period and were different across the spatial study range (i.e., latitude). Recapture probabilities were also different for the three age classes, although the effect of the exponential temporal trend on the recapture rates varied in parallel (on a logit scale) among the three age classes (i.e., additive model). The beta estimate for latitude was negative, showing lower probabilities of recapture for birds ringed at northern breeding areas. Recapture probabilities were larger for adult birds (age 3) compared to immature (age 2) and juvenile (age 1) birds, with juveniles showing the lowest recapture probability. However, differences in recapture probability between juveniles and all other age classes were not statistically significant (95% CI for the slope estimates included zero). In contrast, all other beta estimates were statistically significant (95% CI for the slope estimates did include zero), indicating significant effects for their corresponding predictors (Table 3).

### 3.5. Differences among Age Classes

The Northern temperature anomaly (i.e., climate conditions at the breeding grounds) showed a hump-shaped relationship with survival which differed in its shape between age classes, particularly between juveniles and birds older than 1 year (i.e., immature and adult birds) (Figure 2). Both survival and recapture probabilities increased with age (see Table S1 in Supplementary Materials). Most of the mortality occurred during the first year of life, whereas the difference in the survival of immature and adult individuals was lower (Figure 3). Variation in the survival of younger birds over the years was larger (almost double) than that in older birds. On average, the survival probability was  $0.428 \pm 0.028$  (mean  $\pm$  ES) for juveniles,  $0.662 \pm 0.029$  for immatures and  $0.791 \pm 0.016$  for adult birds (estimates based on average values of the individual covariates). The recapture probabilities were  $0.09 \pm 0.007$  for juvenile birds;  $0.125 \pm 0.008$  for immatures, and  $0.167 \pm 0.008$  for adult individuals, respectively. The nonlinear relationship between temperature anomaly and survival of immature birds was non-significant (95% CI for the slope estimates included zero).



**Figure 2.** Age-specific survival rates ( $\phi$ ) across main geographical regions over the study period. (a): Juveniles; (b): Immatures; (c): Adults in different latitudinal regions: South (dark dots): 40°; Centre (white dots): 46°; North (grey dots): 52°. Temporal trends (second-order polynomial) in the age-survival probabilities. Survival estimates were derived from the best fit model (lower QAICc) in Table 2, where survival of all age classes was time-constrained by the quadratic Northern temperature anomaly and linearly constrained by the Sahel index (additive effect). The model also included an additive effect on the survival of the covariates (latitude, trend in NDVI, mean distance to dump) and interaction terms between covariates and latitude. The model also included three age classes for recapture probabilities. Recapture rates were dependent on latitude in the ringing site and followed an exponential temporal trend (additive effect). Estimates were based on average values of the individual covariates.



**Figure 3.** Survival probabilities ( $\phi$ ) for the different age classes. Juveniles <1 year (dark solid line); immatures 2–3 year (dashed line); Adult >3 year (grey line). Estimates were obtained from the best fit model (lower QAICc) in Table 2, where survival of all age classes was time-constrained by the quadratic Northern temperature anomaly and linearly constrained by the Sahel index (additive effect). The model included an additive effect on the survival of the covariates (latitude, trend in NDVI in the ringing site, mean distance to dump) and interaction terms between covariates and latitude (see Table 1). The model also included three age classes for recapture probabilities (see Table S1 in the Supplementary Materials). Recapture rates were dependent on latitude in the ringing site and followed an exponential temporal trend (additive effect, i.e., parallel slopes among age classes). Estimates were based on the average values of the individual covariates. Vertical bars indicate  $\pm$  standard error.

#### 4. Discussion

Our results provided evidence on how recent climate change, in complex conjunction with other environmental and human-induced changes, has shaped the survival of a long-lived, long-distance migratory species across western Europe over 1960–2009. Although previous research had shown that survival in local populations may vary over time in relation to the variation in the climatic conditions [63], to our knowledge, this is the first attempt to identify large scale effects of climate change on the survival of a long-lived species at the macroscale of its entire latitudinal breeding range. Supporting previous findings, our models showed that survival rates of long-lived, long-distance migratory species could be strongly constrained by recent climatic changes, both in their breeding as well as in their wintering grounds. However, according to our results, the vulnerability of European White Storks to climate conditions, and probably of other long-lived migrant species, varies among different life-stages and across different populations.

##### 4.1. Latitude and Asynchrony in Survival

In migratory bird species, many individuals from different breeding populations are affected by similar environmental conditions through staging or wintering areas [64]. Like other long-distance migrant species, western European White Storks share a similar latitudinal range during the non-breeding season, and previous studies have described a spatial synchronization in the annual survival probability of different European White Stork populations [29]. In contrast to these findings, based on two breeding populations in Germany and Poland located at a similar latitude, we found that the environmental and climatic conditions in the breeding grounds in western Europe differed across a latitudinal gradient, leading to an asynchrony in the annual survival rates of White Storks ringed at different latitudinal locations. Species exhibiting wide thermal tolerance, such as the White Stork, may breed in climates that are currently cooler than their physiological optima. Therefore, in these species, climate warming is expected to particularly benefit animals occurring at higher latitudes [65,66] by increasing population growth and carrying capacity

in the areas close to the coolest limit of the species distribution [34]. The reason is that warmer springs are expected to provide better ecological breeding conditions, benefit the body condition of the individuals, and therefore affect not only survival but other life-history traits, such as breeding success or migration phenology [27,67]. However, when the spring temperature exceeded the long-term average, which is becoming a frequent event as a consequence of global warming since the 1980s, our results showed that higher spring temperatures negatively affected White Stork survival. This negative effect was stronger in the individuals breeding in southern populations. Apart from the spring season, the annual survival of White storks is the product of other seasonal survival rates (i.e., survival during migration and wintering). According to our results, there was a high correlation between seasonal temperatures within a year, thus increases caused by climate warming are also affecting other seasonal temperatures in Europe. While warmer temperature may be beneficial during the breeding period, survival can be reduced by rising temperatures during the post-fledging and postnuptial periods, because of a reduction in food abundance [27]. Actually, in Mediterranean climates, such as those in southern Europe, the most unfavorable and limiting season is the summertime, when temperature is closely related to productivity. According to the current climatic predictions, large temperature increases are projected over southern Europe during summer, whereas annual precipitation is generally projected to decrease in this region [68]. If these climatic predictions take place, the differences in White Stork survival between northern and southern regions will be enhanced.

#### 4.2. Latitude and Land Use Changes

For higher-level consumers, such as the White Stork, the influence of climate on survival is mainly mediated by an indirect mechanism, through the climate disruption of lower trophic levels on which birds feed [63,69]. However, apart from climate change, food availability for White Storks is also markedly impacted by other human-induced changes. White storks are strongly associated with wetlands [36], and one of the main causes for their decline is grasslands and wetlands losses [23]. During the last century, about two-thirds of the wetlands that originally existed in Europe have been lost due to regulation and drainage [70], although some wetlands have been recently restored [58]. NDVI can be a surrogate for the presence of marshes and, therefore, a good indicator of food availability for White Storks [46,71]. Our results showed that breeding sites with positive trends in NDVI in spring exhibited higher survival rates in all White Stork age classes. The benefits of a positive trend in the primary productivity on survival were stronger in southern Europe, where the vulnerability of marshes to climate change is higher due to the more pronounced effect of climate warming [68]. On the other hand, the exploitation of rubbish dumps [53,54] has benefitted European White Stork populations by providing new feeding opportunities and an increased food supply. Therefore, it was not surprising that the long-term trend in the survival of western European White Storks was also affected by the presence of dumps. Breeding in areas closer to dumps is likely to reduce the daily energetic costs of storks due to the shorter foraging movements [60]. In contrast to trends in primary productivity (i.e., trend in NDVI), the benefits of dumps in the vicinity of the breeding area were particularly positive in northern populations, where food availability must be a more limiting factor than in populations occurring at medium-low latitudes.

#### 4.3. Age-Dependent Survival

Mean survival derived from our models was similar to those estimated from other previous studies on White Storks [26,29,72] and followed the general and predicted pattern of increments in survival, such as bird age, as described for other long-lived species [73]. Adult survival rates in long-lived species commonly exhibit lower variability than juvenile ones because natural selection tends to favor a reduction in the variation of those demographic rates with a higher impact on the population growth rate [13]. For this reason, we expected juveniles to be more sensitive to timing factors related to climatic variability [35],

and a stronger climate change impact on young White Storks compared with adult birds was expected. Previous research has shown that the phenological response to climate change in White Stork migrants also differs between adult and juvenile individuals [27]. Our results support that both the shape and the strength of the relationship between climate warming and survival differ at different life-stages of individual development [9]. Overall, we showed that survival was reduced when the temperature in the breeding area was too high, yet juvenile White Storks were more strongly affected than other age classes. Individuals in the first age class (i.e., juveniles) are younger and less experienced. Thus, they are expected to experience a higher impact of the climate and environmental changes compared to older individuals [74]. In contrast to the results provided by previous research [26], our models, which are based on a longer temporal frame study, support that the difference in the strength of the effect of climate change on survival between juveniles and older individuals has increased during the study period.

#### *4.4. Consequences at the Population Level*

Although the number of storks recorded in western Europe has largely increased since the 1980s [24,75], their numbers have not yet reached the figures recorded at the beginning of the 20th century (i.e., 1934, [76]). The population growth rate of White Storks is very sensitive to changes in survival [29]. Indeed, it seems that the effects on White stork survival, and particularly on the survival of juvenile birds, of climatic as well as environmental conditions described in the present study, have already been translated into changes at the population level. In agreement with the results from our models, pointing out that White storks breeding at lower latitudes in western Europe have lower survival rates, increases in population size over the past 20 years have mainly taken place in White storks breeding at central and northern Europe, whereas most of the Iberian populations remained stable [23]. On the other hand, previous studies showed that White Storks appear to follow habitat and climatic alterations. Thus, shifts in the altitudinal distribution range of this species have been reported in relation to climate change [8]. Supporting this fact, predictive models about changes in the distribution range of White storks in relation to global warming predict losses in southern and western Europe, whereas extensions in the distribution range in northeastern Europe are expected [77]. According to our results, as the climate gets warmer, environmental conditions for White Storks in southern–western Europe become less suitable for breeding. Simultaneously, these southern areas are becoming more and more frequently wintering grounds for White Storks [78,79]. These two parallel processes will probably lead to a northerly shift in the future distribution range of this species across western Europe [77] and could make this long-distance migratory species become a partially short-distance migratory bird in the long-term.

#### *4.5. Other Factors and Caveats beyond Climate Change*

Hot extremes are now more frequent in all Europe, but the vulnerability to human-induced climate change across the continent differs substantially between subregions [68,80]. In this regard, compared to other European areas, Southern Europe (i.e., the Mediterranean region) has been subject to larger impacts as a result of both decreased precipitation and increased temperature. Furthermore, these impacts are expected to be even worse in the future. Actually, large increases in heat extremes and lower water availability (both because of decreases in water precipitation as well as in river flow) are key-past and projected climate change impacts in this region. Higher temperatures (via increased land evapotranspiration) and lower water availability are also increasing the risk of droughts and leading to decreases in vegetation productivity in Southern Europe. To a lesser extent, temperature extremes and a decrease in summer precipitation are also key-past and projected climate change-related impacts in Central and Eastern Europe. In contrast, climate change may even benefit Northern Europe by increasing vegetation productivity [68,81,82]. The latitudinal gradient in White Stork survival rates across western Europe found in our models therefore matched the North–South divergence in climate change effects observed and pro-

jected in Europe [82]. However, although our models showed a consistent pattern between White Stork survival and climate change over time (measured as the Northern temperature anomaly in Europe and Sahel precipitation anomaly), this does not necessarily imply causation (i.e., direct relationship between survival and climate) because other factors not considered in the study may have an effect on survival. However, food availability at the breeding and wintering grounds as well as in the migration routes have been described as determinants of the global and regional changes in the population size of this species [83]. In this sense, the relationship between survival and climate change-related variables found in our models could be mediated by feeding conditions that are directly related to vegetation productivity. For instance, mismatches between the timing of food requirements and food availability have been shown to cause population declines in long-distance migrants in seasonal habitats [84]. Furthermore, other climate change impacts, such as increases in the frequency of droughts in the wintering areas in Africa [30,85], together with shifts in the weather conditions at the breeding grounds in spring [86], have also been described as factors affecting White Stork population dynamics. In this sense, according to our best-fit model, the trend in vegetation productivity in spring at the breeding site of the bird is also a determinant factor related to White Stork survival over the study period, supporting the link between temporal climate trends, food availability, and stork survival.

Other factors apart from climate change could also be responsible for the trends in survival observed in our results. For example, land-use changes in relation to farmland intensification [87] may also affect White Stork population dynamics. Although farmland intensification was not explicitly considered in our study, farmland intensification has been previously related to NDVI variation [88]; thus, to a certain extent, changes in farmland regimes in the breeding sites have been indirectly considered in the models through NDVI trends in spring. However, density-dependence effects were not considered in our models since it is impossible to obtain such detailed information (e.g., carrying capacity at the population level for each ringed bird) in the whole of Europe. However, the strong density-dependence of the White Stork [71,89] also links population trends with intra-specific factors, such as age structure. Therefore, more densely populated areas present lower changes in abundance (as is the case of many populations in the Iberian Peninsula and Central–Eastern Europe), whereas smaller and unsaturated populations are subjected to Allee effects and can experience larger changes in a short time. This could be the case of Sweden, Finnish, or Danish White Stork populations [23]. However, density-dependent effects act at the local level and would hardly have led to the overall long-term consistent trend in survival found in our study. The use of organochlorine pesticides (e.g., DDT) from the 1940s until they were banned in the 1970s–1980s has also been identified as a factor affecting the population dynamics of this species in Europe [90]. However, this variable was not included in our models.

On the other hand, open-air rubbish dumps are being progressively replaced by covered waste processing facilities inaccessible to birds due to the European Union Landfill Directive (1993/31/EC). In July 2018, the European Union (EU) adopted new laws to reduce waste and promote higher recycling targets. Among the approved measures, a 10% cap on landfill by 2035 was included. In our study, we did not take into account recycling centers or abandoned dump sites. However, the application of EU waste legislation is likely having impacts on White Stork survival due to the reduction in the availability of food waste [58] that was not considered in our study. The reduction in food waste, together with the reduction in natural food resources associated with climate change, could lead to larger negative impacts on White Stork survival in the long term.

Finally, it is well-known there are multiple biases in ringing and recovery data, especially at large spatial and temporal scales, such as the one in our study. Under this scenario, direct comparison of the recovery sites and dates are not enough to reach robust conclusions on long-term changes across the range of the marked population in a particular period [30]. The most important reason is the temporal and spatial variation in the probability of recapture, which is impossible to calculate with simple approaches [30]. To overcome

this problem, in our study, we explicitly considered the spatiotemporal heterogeneity of ringing and recovery probabilities over time by taking into account time-constrained models that included spatially explicit covariates (e.g., trend in the vegetation productivity in spring at the breeding site; distance of the breeding site to the nearest rubbish dump) as well as latitude at the breeding site itself [60]. In this sense also, the increases in the activity of the White Stork observers through the study period (i.e., higher number of recoveries in recent time) was explicitly considered in the recapture estimates of the model as an exponential trend over time, according to the real observed trend in the number of recoveries between 1960–2009. As recovery probabilities have increased over the study period, the increased recovery probabilities within the life span of individuals may have led to an overestimation of survival since the assumption made in mark–recapture models that recovery probability is independent of the age at which an individual is recovered may be violated (the frequencies of the age at the recovery can be inspected in Figure S4 in the Supplementary materials). However, as we are not interested in the absolute survival estimates but in the effect of several covariates, the model assumption should not bias our results [60]. Furthermore, the recovery rate can depend on the type of ring, its position on a bird’s leg, and recovery circumstances. For instance, previous studies have found that the recovery rate of rings put on the tibia was much higher than that of metal rings on the tarsus [30]. However, according to the information reported in the EURING Database, 99.64% of the ringed birds considered in our study were only marked with metal rings, and less than 1% were also provided with additional marks (such as color or numbered leg-rings, flags, or other types of marks). This proportion remains in the recovery sample, where we found 99.93% of the recoveries belonging to birds ringed only with metal rings, whereas less than 1% also had other types of marks, supporting the lack of a significant effect on the recovery probability by the type of ring.

## 5. Conclusions

Our results support that climate change has caused a gradual decline in the survival performance of western European White Storks during the last years. This decline in survival is a real risk for the future long-term persistence of western European White Stork populations, in particular for those storks breeding in southern Europe. According to future climatic predictions, climate changes are expected to increase the existing vulnerabilities and deepen the differences in White Stork survival across Europe in years to come. The large-scale effect of climatic conditions identified in this widespread and common long-distance migrant species represents a highly likely scenario for other migratory birds in Europe.

**Supplementary Materials:** The following are available online at <https://www.mdpi.com/article/10.3390/birds2040027/s1>, Figure S1. Annual ringing effort of the juvenile white storks considered in the study, Figure S2: Spatial distribution of the annual recoveries (i.e., encountering a ringed bird, both dead or alive, and including resightings) of White Storks (1960–2009). Data source: EURING Data Bank, Figure S3: Annual recoveries of White Storks (1960–2009) and their exponential trend over time. Data source: EURING Data Bank, Figure S4. Frequency histogram of the age at the recovery (1960–2009). Data source: EURING Data Bank, Table S1: Parameter estimates ( $\Phi$ : survival;  $p$ : recapture) based on mean individual covariate values. Standard Error (SE) and Confidence Intervals (CI).

**Author Contributions:** Conceptualization and writing: B.M., A.O.; Review and supervision: M.F.; data acquisition: A.O.; Methodology, software, data curation, formal analysis and interpretation, investigation, writing—original draft preparation, review, and editing: B.M. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Data used in the study can be obtained after request at the EURING Data Bank, <http://www.euring.org/> (Accessed date 29 June 2010).

**Acknowledgments:** We are grateful to the European Union for Bird Ringing (EURING), which made the recovery data available through the EURING Data Bank and to the many ringers and ringing scheme staff who gathered and prepared the data. We would also like to thank the editor and three anonymous referees for providing us with comments and suggestions which helped to improve the manuscript.

**Conflicts of Interest:** The authors declare no conflict of interest.

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