

Migration timing responses to climate change differ between adult and juvenile white storks across Western Europe

Beatriz Martín^{1,*}, Alejandro Onrubia¹, Miguel Ferrer²

¹Fundación Migres, Ctra. N-340 Km. 96.7, Huerta Grande, Pelayo, 11390 Algeciras, Spain

²Ethology and Biodiversity Conservation, Doñana Biological Station (CSIC), Avda. Américo Vespucio s/n, 41092 Seville, Spain

ABSTRACT: Our goal in this study was to identify age- and population-specific responses to climate change in the autumn migration phenology of a long-lived bird species, the white stork *Ciconia ciconia*, at the macroscale of its entire migration route in western Europe. We used a 40 yr data series of ring recoveries of adult (>1 yr) and juvenile (<1 yr) white storks to determine the date of autumn passage through the Strait of Gibraltar. We then modelled geographical variability in the timing of autumn migration between age classes across Europe from environmental conditions at the breeding grounds using age-specific generalized additive model (GAM) analysis. Best-fit models accounted for up to 31 % of the variability in the data and indicated a progressively earlier passage date over the course of the 40 yr dataset. However, responses varied among populations and age classes. A trend towards earlier migration in juvenile storks was observed, whereas in adults the trend was highly variable between years. In addition, advances in autumn passage dates of juvenile birds were larger in southwestern Europe. Differences between white stork age classes in response to environmental conditions on the breeding grounds are likely caused by different mechanisms for migration adjustment governing adult and young bird behaviour. Overall, plasticity in adapting to new environmental conditions has allowed western European white storks to rapidly respond to, and even benefit from, recent climatic and environmental changes.

KEY WORDS: Bottleneck · Global change · Long-term study · Phenotypic plasticity · Soaring bird · Spatial patterns · Temporal trends

— Resale or republication not permitted without written consent of the publisher —

1. INTRODUCTION

Migratory birds are subject to a wide range of environmental conditions throughout the year, and are particularly vulnerable to climatic and human-induced environmental changes (Fiedler et al. 2004). Over the last 40 yr, shifts in migratory behaviour due to climate change have become evident in a wide range of bird species all over the world (e.g. Lehikoinen et al. 2004, Beaumont et al. 2006, Newton 2008, Hurlbert & Liang 2012). Earlier arrival at the breeding grounds is one of the most commonly reported effects of climate change on migration phenology

(e.g. Rubolini et al. 2007, Végvári et al. 2010). However, data on temporal trends in autumn migration are less abundant, with some species advancing and others delaying their date of departure from the breeding grounds (Lehikoinen et al. 2004, Gordo & Sanz 2006, MacMynowski & Root 2007, Van Buskirk et al. 2009, Martín et al. 2014). Such behaviours are probably driven by species-specific annual strategies (e.g. Smallegange et al. 2010); however, previous evidence suggests that a change in migration phenology is a timing response to specific environmental conditions at a particular site (e.g. Lehikoinen et al. 2004).

*Corresponding author: bmartin@fundacionmigres.org

Among the general warming effects caused by global climate change, there is substantial spatio-temporal heterogeneity, and effects vary across different regions and seasons (IPCC 2007). Moreover, research has shown that spatial variation in avian migratory phenology follows climatic and geographical gradients (Gordo et al. 2007b, Ambrosini et al. 2014). Therefore, phenological responses in migration to climate change may vary among populations (Rubolini et al. 2007) as a result of environmental conditions experienced by birds in different breeding, passage, and wintering areas (Gordo & Sanz 2006, 2008, Both & te Marvelde 2007, Gordo et al. 2007b). These findings suggest that interactions between biotic and abiotic environmental characteristics shape the phenological response within each population (Gordo et al. 2007b).

Despite the spatial heterogeneity that exists in migration phenology, the geographical aspects of migration timing have received relatively little attention (but see Gordo et al. 2007b, Hurlbert & Liang 2012, Ambrosini et al. 2014) and remain unknown for most species. Moreover, heterogeneity in the phenological responses of migratory birds does not arise solely from spatial variation among populations. In many species, migration timing may vary among different fractions of the overall population (such as age and/or sex classes; e.g. Sparks et al. 2005, MacMynowski & Root 2007, Martín et al. 2014). Differences in the phenological response of migratory birds among populations and fractions within the same population (Cristol et al. 1999) imply differential costs of climate change (Wood & Kellermann 2015), leading to differential selection among populations and among groups within the same population. Thus, identifying shifts in the migration phenology of different populations or segments of the same population is critical to further our understanding of how birds may (or may not) persist under the current scenario of climate change. Intra-population differences in phenological responses of migratory birds, however, have received limited attention in climatic change research (but see MacMynowski & Root 2007, Balbontín et al. 2009).

The study of bird migration relies on data collected by various means such as direct observation, ringing, or more recently, information provided by electronic devices (Newton 2008). Data provided by ring recoveries has inherent weaknesses, mainly due to the large spatial and temporal heterogeneity in ringing and bird recoveries (Körner-Nievergelt et al. 2010). However, this type of data is highly valuable in the study of large scale and long term variations in spa-

tial patterns of bird populations (Tellería et al. 2012), such as changes in migratory behaviour (e.g. Ambrosini et al. 2014, Martín et al. 2014). Compared with data from other sources such as direct observation (Gordo et al. 2007a,b, Gordo & Sanz 2008), ringing recoveries provide accurate information on sex, age, timing of life-history events or breeding population (du Feu et al. 2009), which allows for the exploration of differential effects among specific fractions of the migratory population.

The white stork *Ciconia ciconia*, L. has a wide distribution throughout Europe, and its popularity makes this migratory bird an appropriate model for large-scale and long-term phenological studies (Gordo et al. 2007b, Flack et al. 2016). Previous studies have highlighted the importance of environmental and climatic variables in predicting spatial patterns of migration timing (mainly spring migration) in many bird species (Gordo et al. 2007a, Hurlbert & Liang 2012, Ambrosini et al. 2014), including white storks (Gordo et al. 2007b, Gordo & Sanz 2008). In this study, we used a long-term data series of white stork ring recoveries stored in the European Union for Bird Ringing database (EURING Data Bank; du Feu et al. 2009). With this dataset, we modeled shifts in autumn migration phenology in response to changes in environmental conditions across western Europe over the last 40 yr. Based on conditions at the storks' breeding grounds, we identified underlying ecological patterns explaining the potential spatial variation among populations and age classes. Although there have been previous studies assessing the effects of age on the migratory phenology of long-distance migratory birds at the population level (e.g. Møller 2004, Balbontín et al. 2009, Gordo et al. 2013), to our knowledge this is the first attempt to identify different responses to climate change in different age classes of a long-lived migratory bird at the macroscale of its entire migration route.

2. MATERIALS AND METHODS

2.1. Study area and species

The white stork is a Palearctic soaring species that generally breeds in Europe and winters in sub-Saharan Africa. This species breeds in most of continental Europe, with Belarus and Ukraine as the eastern boundary, and southern Scandinavia as the northern boundary of its distribution in Europe. White storks may also breed in North Africa (northern Algeria and Morocco) (BirdLife International 2015). White storks

are reproductively mature between 2 and 7 yr and can live up to 30 yr in the wild (Cramp et al. 1977). The breeding season is February to April, and its main departure from the European breeding grounds is in August, arriving in Africa by early October (Fernández-Cruz 2005). Eastern and western European populations can be distinguished by their migratory route: during autumn, western storks travel to the western sector of the Sahel, whereas the eastern population settles in the eastern Sahel and in South Africa (Berthold et al. 2001).

The Strait of Gibraltar in southern Spain has long been recognized as the most important bottleneck in western Europe for soaring bird migration (Bernis 1980, Finlayson 1992) in terms of number of individuals and species diversity (Porter & Beaman 1985). The passage is used by most western European and Iberian long-distance migrants (De Juana & García 2015). The Strait of Gibraltar is a key site for long-distance migrant birds, since it is the first European territory reached during the spring migration, and the last abandoned before returning to overwinter in Africa during autumn (Gordo & Sanz 2008), making it an ideal location to study migration phenology.

2.2. Ringing data

Ringing information was obtained from the EURING database (du Feu et al. 2009) on 79 832 recoveries of white storks rings made between 1960 and 2008. Data included information on date of ringing and location of any subsequent recovery, and elapsed time, distance, and direction between ringing and each recovery encounter for birds ringed as either adults or nestlings. The data encompassed most of the breeding range of the white stork in western Europe (Fig. 1). From the initial set of recoveries, only those individuals ringed on their breeding grounds and recovered that year or in subsequent years at the Strait of Gibraltar during the autumn migration period were considered in this analysis. Data from birds recovered in subsequent years (i.e. elapsed time between ringing and recovery >1 yr) were also included in the analysis since mature birds exhibit philopatric behaviour and high fidelity to the breeding grounds (Vergara et al. 2006), and juveniles typically travel only moderate distances during natal dispersal (Chernetsov et al. 2006). We defined

breeding and migration periods based on Del Hoyo et al. (1994) and Fernández-Cruz (2005). Since the timing of breeding varies among European populations, birds ringed between 20 April and 31 July (Del Hoyo et al. 1994) were included for breeding areas in northern and central Europe, whereas for southern Europe (i.e. Iberian Peninsula) we included birds ringed between 1 February and 15 June (Fernández-Cruz 2005). Recoveries during autumn migration from 5 July to 10 October (Bernis 1980) were selected within the Strait of Gibraltar area (between 34–38° N and <6° W). Using this new subset of recoveries, spatial location of the breeding site for each individual was determined using package 'geosphere' (Hijmans et al. 2010) in R (R Development Core Team 2011). Spatial coordinates at the time of ringing were based on the direction and loxodromic distance (distance on a constant compass bearing) between ringing and recovery (Imboden & Imboden 1972). 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 or inaccuracies were omitted. If there was >1 recovery record for a single bird, only the first record was included.

2.3. Spatial predictive model of the timing of migration

Generalized additive models (GAMs) were used to analyze autumn migration passage dates through the Strait of Gibraltar (i.e. recovery date at the Strait). Before GAM modeling, we checked for possible multicollinearity among predictors by means of Variance Inflation Factors (VIFs) using the AED package in R. In order to avoid multicollinearity, the pre-selection of variables was accomplished by sequentially dropping explanatory variables in a hierarchical way until all VIF values were <5 (Rogerson 2001). The GAMs in-

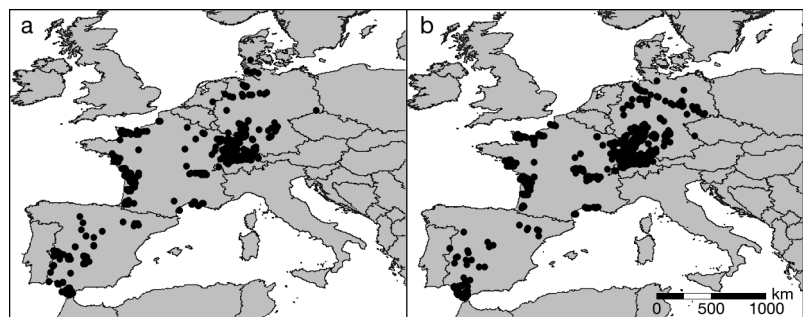


Fig. 1. Recoveries of (a) juvenile and (b) adult white stork *Ciconia ciconia* (n = 2281) considered in the analysis

cluded a Gaussian response and an identity link function using the *mgcv* package (Wood 2011) in R; the restricted maximum likelihood method (REML) was used for smoothing parameter estimation. Splines were only calculated for the variables that showed non-linear relationships with autumn passage date. Akaike's information criteria (AIC) was used to identify the most robust model (i.e. the model with variables having the greatest impact on outcomes), as well as the most parsimonious (avoiding over-fitting); the model with the lowest AIC was considered to have the best fit (Burnham & Anderson 2002).

Environmental variables (see Table 1) determined for the storks' breeding sites were considered as predictors of the autumn migration passage date of each bird. We used WorldClim data (www.worldclim.org), which is a set of data layers representing current (1950–2000) climate conditions generated as smooth maps of averaged monthly climate data obtained from thousands of weather stations (Hijmans et al. 2005). Averaged climate data provide information on the climatic characteristics of an area over time, allowing us to detect spatial variation in migratory phenology across Europe. Additionally, we used the 'human footprint' dataset (Sanderson et al. 2002) to assess the spatial relationship between stork migration timing and human presence and ease of access to humans. Averages and standard deviations of the normalized difference vegetation index (NDVI) for this study were also derived from the Global Inventory Modeling and Mapping Studies (GIMMS) for the period 1981–2006 (Tucker et al. 2005), as well as topographic diversity, calculated from the SRTM digital elevation map (USGS 2004). All data were resampled using package 'raster' (Hijmans & van Etten 2011) in R so that all layers had the same grid size with a resolution of 0.33° (~ 40 km). This grid size corresponds to the 50 km accuracy of the coordinates for ring recoveries selected from the EURING database.

In contrast to averaged climatic conditions, weather data in a particular year provide information on inter-annual variation in weather conditions and on the impact of climate change throughout the study period. As an indicator of climate conditions within a particular breeding season, we used an averaged value of the Northern Hemisphere land temperature anomaly, based on monthly temperature anomalies from February to April in that particular year. The Northern Hemisphere land temperature anomaly was considered as an indicator of climate change (Jones et al. 1999). The term 'temperature anomaly' means a departure from a long-term average, which is the reference value. Anomalies were provided as departures

from the 20th century average (1901–2000). The averaged value of temperature anomalies from June to August in a particular year was also included as a measure of climate conditions during departure. Temperature anomalies were downloaded from ftp://ftp.ncdc.noaa.gov/pub/data/anomalies/usingGHCNMv2/monthly.land.00N.90N.df_1901-2000mean.dat.

As an additional source of yearly weather conditions, we used annual spring NDVI based on a 5 mo period (February–June). NDVI is a surrogate for primary productivity, and its value is controlled by climate drivers (precipitation and temperature). Annual spring NDVI data were downloaded from <http://iridl.ldeo.columbia.edu/SOURCES/UMD/GLCF/GIMMS/NDVIg/global/ndvi/> and were resampled using package 'raster' (Hijmans & van Etten 2011) in R following a GIS 'moving window' approach based on an aggregation by means of averaging 8 km cells so the layers had a final grid size of ~ 50 km. However, annual NDVI was only available for the period from 1982–2006. A preliminary model selection based on data from 1982–2006 showed that the best-fit model, both for adult and juvenile birds, did not include annual NDVI. Analysis of deviance supported this result, showing that the annual NDVI term was not significant ($p > 0.1$). According to these results, and since a longer temporal frame is more appropriate for assessing climate change effects, we rebuilt our models using the total available sample (1960–2008) without including spring annual NDVI as a predictor.

We considered the ring recovery year as an additional predictor to account for temporal trends in the autumn passage date at the Strait during the study period. We also included the interaction term between year and latitude (i.e. latitudinal coordinates of each individual breeding location) to control for spatial effects.

Considering a bird's age is essential in the study of the migration timing of this species in order to avoid the potential bias caused by behavioural differences between age-classes (Vergara et al. 2007). Therefore, to examine differences in migration phenology among different age classes, separate models for juvenile and adult white storks were created. Since storks do not reach sexual maturity for 2 yr (Cramp et al. 1977), we included the additional predictor 'elapsed time between ringing and recovery' as an indicator of the bird's age. Elapsed time was preferred instead of age at ringing (reported in EURING data base) because exact age was only recorded for a few adult individuals ($n = 125$); correlation between age and elapsed time for those birds of known age was high ($r = 0.97$; $p < 0.01$).

The first white storks to arrive at the breeding areas in spring are usually males (Ptaszyk et al. 2003). However, the small sample size containing information on individual's sex prevented us from exploring sex effects in our models. Nevertheless, a preliminary analysis based on the small subset of recoveries of adult individuals of known sex ($n = 38$) suggested that the date of passage over the Strait was similar in both sexes (ANOVA, $F_{1,36} = 0.625$; $p = 0.434$). Supporting this result, median arrival date in Slovakia during 1977–2003 showed similar timing patterns (differences of only days) in both sexes (Gordo et al. 2013).

Finally, we quantified a national white stork population trend (between 1990–2000) based on data from BirdLife International (2004). The trend was measured from data corresponding to each European country in which the recorded bird bred. We estimated the trend as the number of breeding pairs in 2000 divided by the number in 1990 (Visser et al. 2009).

2.4. Map production

A grid layer for western Europe with a resolution of 0.33° (~ 40 km) was constructed to spatially predict the dates of passage of white stork at the Strait of Gibraltar according to the specific environmental conditions at breeding grounds across Europe. Using the best-fit GAM models, the date of passage over the Strait in each 40 km breeding cell was calculated using package 'raster' in R. Six different phenological maps were generated from measures based on averaged values for the predictors over the following periods: (1) adult passage dates during 1960–1970, (2) adult passage dates during 1980–1990, (3) adult passage dates during 2000–2010, (4) juvenile passage dates during 1960–1970, (5) juvenile passage dates during 1980–1990, and (6) juvenile passage dates during 2000–2010.

3. RESULTS

We analyzed 2281 ring recoveries (834 adults and 1447 juveniles) from the original EURING database. Based on the multicollinearity assessment, a final set of 10 explanatory variables was used, which provided information on environmental conditions at the breeding sites (Table 1). Since variability in the predictors among adult and young birds was too large to be incorporated in a single model, we created sepa-

rate models for juvenile and adult migration phenologies (Table 2). Inspection of deviance residuals against year of the best-fit models predicting date of passage showed the absence of a marked temporal correlation for either adult or juvenile birds. Furthermore, inspection of the spatial correlogram of the residuals showed no spatial correlation patterns in any age class. The best-fit model for juvenile passage dates accounted for almost 33% of variability; the adult best-fit model accounted for nearly 30%.

Between 1960 and 2008, the western European population of white storks (adult and juvenile birds included) exhibited a significant trend towards progressively earlier autumn migration. The trend in adult birds, however, did not follow a linear trend but rather was highly variable between years. Environmental conditions at the breeding sites affected both juvenile and adult stork passage dates. According to the best-fit models (Table 3), white storks breeding in areas with high precipitation seasonality (BIO15) exhibited earlier migration dates. In contrast, breeding areas with high precipitation during the wettest month (BIO13) and large seasonality in temperature (BIO4) were related to delayed migration in juvenile storks. Overall, climatic variables involving seasonality determined the difference between earlier and later migration for juvenile birds. In contrast, mean diurnal range had a negative effect on adult birds, advancing their autumn passage date. In young storks, the temporal trend in passage dates was determined by latitude, whereby birds that originated in lower latitudes (i.e. southern Europe, closer to the Strait of Gibraltar) had more advanced passage dates over the study period than those from breeding locations farther from the Strait. Human footprint also contributed to predicting earlier adult passage dates. There was a slight but significant effect of the age of the bird on the timing of migration in adults (which was indirectly shown by the significant effect of the elapsed time between ringing and recovery); with older birds tending to have earlier passage dates. Temperature anomalies influenced the passage date of both adults and juveniles, indicating an impact of climate change on autumn migration. However, this effect differed between adult and juvenile age classes. In adult birds, there was a tendency towards earlier migration when the previous spring was warmer. However, this effect was only noticeable when spring temperatures did not depart from the 20th century average. In contrast, when spring temperatures exceeded the long-term average, both adult and juvenile storks tended to delay their passage dates at the Strait. Autumn migration of juve-

Table 1. Variables considered for predicting white stork *Ciconia ciconia* passage dates over the Strait of Gibraltar. Environmental predictors were measured at the breeding grounds. VIFs: Variance Inflation Factors (environmental predictors with values <5 were included in the models)

Variable name	Description	Source	VIFs
BIO1	Annual mean temperature	WorldClim (www.worldclim.org)	
BIO2	Mean diurnal range (mean of monthly max. temp – min. temp)	WorldClim (www.worldclim.org)	X
BIO4	Temperature seasonality (SD × 100)	WorldClim (www.worldclim.org)	X
BIO5	Max. temperature of warmest month	WorldClim (www.worldclim.org)	
BIO6	Min. temperature of coldest month	WorldClim (www.worldclim.org)	
BIO7	Temperature annual range (BIO5 – BIO6)	WorldClim (www.worldclim.org)	
BIO10	Mean temperature of warmest quarter	WorldClim (www.worldclim.org)	
BIO11	Mean temperature of coldest quarter	WorldClim (www.worldclim.org)	
BIO12	Annual precipitation	WorldClim (www.worldclim.org)	
BIO13	Precipitation of wettest month	WorldClim (www.worldclim.org)	X
BIO14	Precipitation of driest month	WorldClim (www.worldclim.org)	
BIO15	Precipitation seasonality (coefficient of variation)	WorldClim (www.worldclim.org)	X
BIO18	Precipitation of warmest quarter	WorldClim (www.worldclim.org)	
BIO19	Precipitation of coldest quarter	WorldClim (www.worldclim.org)	
ANNUAL_NDV	Annual spring normalized difference vegetation index (NDVI) in a particular year (1982–2006) based on a 5 mo period (Feb–June) (see 'Methods')	IRI/LDEO Biblioteca de Datos Climáticos (http://iridl.ldeo.columbia.edu/)	X
HUMAN_FOOT	Human footprint: human presence and accessibility over the period 1950–2000	Sanderson et al. (2002)	X
NDVI_AVERA	Average of the normalized difference vegetation index (NDVI) for the period 1981–2006	Global Inventory Modelling and Mapping Studies (GIMMS; Tucker et al. 2005)	X
TOPO_DIVER	Topographic diversity	Calculated from the SRTM digital elevation map (USGS 2004)	X
ANO_FMA	Average temperature anomaly from Feb to Apr (annual departures from the period 1901–2000). Northern hemisphere land temperature anomaly	ftp://ftp.ncdc.noaa.gov/pub/data/anomalies	X
ANO_JJA	Average temperature anomaly from Jun to Jul (annual departures from the period 1901–2000). Northern hemisphere land temperature anomaly	ftp://ftp.ncdc.noaa.gov/pub/data/anomalies	X
ELAPTIME	Elapsed time between ringing and recovery as an indicator of individual age in birds ringed as adults	EURING (www.euring.org)	
Pop.trend	National population trend (1990–2000)	BirdLife International (2004)	
YEAR	Year of recovery	EURING (www.euring.org)	
YEAR:Y_RINGING	Interaction term between year of recovery and latitude of the ringing location	EURING (www.euring.org)	

Table 2. Akaike's information criterion (AIC) selection of the best-fit models predicting autumn migration passage of juvenile (<1 yr) and adult (>1 yr) white storks *Ciconia ciconia* at the Strait of Gibraltar. See Table 1 for variable descriptions

Predictors in the model	AIC	ΔAIC	R adjusted	Deviance explained
Juveniles				
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO4)+s(BIO15)+(BIO13)+(YEAR:Y_RINGING)	11081.30	0.00	0.321	33.3
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO13)+s(BIO15)+(BIO4)+Pop.trend+ (YEAR:Y_RINGING)	11083.04	1.74	0.321	33.3
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO2)+(BIO4)+(BIO13)+s(BIO15)+(TOPO_DIVER)	11095.42	14.12	0.315	32.7
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO2)+(BIO4)+(BIO13)+s(BIO15)	11096.50	15.20	0.315	32.6
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO2)+(BIO4)+s(BIO15)+(TOPO_DIVER)+(BIO13)+(ndvi_range)	11096.87	15.57	0.315	32.7
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO2)+(BIO4)+s(BIO15)+(TOPO_DIVER)+(BIO13)+(NDVI_AVERA)	11097.41	16.11	0.315	32.7
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO2)+(BIO4)+(BIO13)+s(BIO15)+(HUMAN_FOOT)	11098.08	16.78	0.314	32.7
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO2)+(BIO4)+(BIO13)	11247.20	165.90	0.236	24.5
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO2)+(BIO4)	11250.22	168.92	0.233	24.2
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+(BIO2)	11353.00	271.70	0.177	18.6
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)	11410.62	329.32	0.143	15.2
s(YEAR)+s(ANO_FMA)	11471.64	390.34	0.104	11.1
s(YEAR)	11543.05	461.75	0.055	5.86
Adults				
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)+s(BIO15)+(HUMAN_FOOT)	6678.28	0.00	0.27	29.5
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)+(BIO4)+s(BIO15)+s(NDVI_AVERA)+(HUMAN_FOOT)+(YEAR:Y_RINGING)	6679.57	1.28	0.28	30.1
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)+(BIO4)+s(BIO15)+s(NDVI_AVERA)+(HUMAN_FOOT)+(TOPO_DIVER)	6680.56	2.27	0.28	30.0
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)+(BIO4)+s(BIO15)+s(NDVI_AVERA)	6685.85	7.56	0.27	29.1
s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)+(BIO4)+s(BIO15)+s(NDVI_AVERA)+(HUMAN_FOOT)	6688.32	10.04	0.27	28.8
s(YEAR)+(Slope)+s(ANO_FMA)+s(ANO_JJA)+(HUMAN_FOOT)+s(ELAPTIME)+(BIO2)+s(BIO15)	6691.63	13.35	0.26	28.1
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)+(BIO4)+s(NDVI_AVERA)+(HUMAN_FOOT)	6692.53	14.25	0.26	28.7
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)+(BIO4)+s(BIO15)	6694.64	16.36	0.26	27.6
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)+(BIO4)	6699.93	21.65	0.25	27.3
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)+(BIO4)+(BIO13)	6700.35	22.06	0.25	27.4
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)+(BIO2)	6713.78	35.50	0.24	25.8
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)+s(ELAPTIME)	6720.72	42.44	0.23	25.1
s(YEAR)+s(ANO_FMA)+s(ANO_JJA)	6759.94	81.65	0.19	20.2
s(YEAR)+s(ANO_FMA)	6766.73	88.45	0.18	19.4
s(YEAR)	6829.99	151.71	0.11	12.1

Table 3. Generalized additive model (GAM) predicting autumn migration passage of juvenile (<1 yr) and adult (>1 yr) white storks *Ciconia ciconia* at the Strait of Gibraltar based on environmental factors measured at the breeding areas. edf: estimated degrees of freedom for each model parameter; Ref.df.: approximate degrees of freedom for the *F* distribution.

See Table 1 for variable descriptions

Parametric coefficients	Estimate	SE	<i>t</i> -value	p-value
Juveniles				
(Intercept)	168.500	11.940	14.12	<0.001
BIO4	0.001	6.40×10^{-4}	1.95	0.051
BIO13	0.049	0.016	3.02	<0.001
YEAR:Y_RINGING	6.80×10^{-4}	1.19×10^{-4}	5.74	<0.001
Approximate significance of smooth terms	edf	Ref.df	<i>F</i>	p-value
s(YEAR)	4.525	5.290	5.299	<0.001
s(ANO_FMA)	6.448	7.108	10.574	<0.001
s(ANO_JJA)	4.877	5.662	13.441	<0.001
s(BIO15)	5.532	6.459	6.041	<0.001
Parametric coefficients	Estimate	SE	<i>t</i> -value	p-value
Adults				
(Intercept)	267.875	4.970	53.895	<0.001
BIO2	-0.170	0.054	-3.147	0.002
HUMAN_FOOT	-0.089	0.042	-2.137	0.033
Approximate significance of smooth terms	edf	Ref.df	<i>F</i>	p-value
s(YEAR)	7.253	7.748	6.197	<0.001
s(ANO_FMA)	4.191	4.894	10.064	<0.001
s(ANO_JJA)	3.912	4.661	6.603	<0.001
s(ELAPTIME)	3.535	4.434	3.164	0.011
s(BIO15)	2.652	3.312	12.300	<0.001

niles was earlier in years with higher summer temperature anomalies (ANO_JJA). In adults, however, higher summer temperature was related to later autumn passage dates (Table 2, Fig. 2).

Fig. 3 shows temporal trends and age effects on the geographical patterns of autumn migration dates at the Strait of Gibraltar. Passage over the Strait follows a general southwestern spatial gradient over Europe, both for adult and juvenile birds, showing 3 roughly separate spatial regions that can be differentiated by the autumn passage dates of the individuals breeding in (1) southern Europe (southwest Iberian Peninsula), (2) central Europe (from northeast Iberian Peninsula to northern Germany), and (3) northern Europe (Scandinavian countries). Passage dates of adult white storks were consistently later than those of juvenile birds in all regions. Only the juvenile birds exhibited a clear shift towards earlier migration dates across all regions of Europe.

4. DISCUSSION

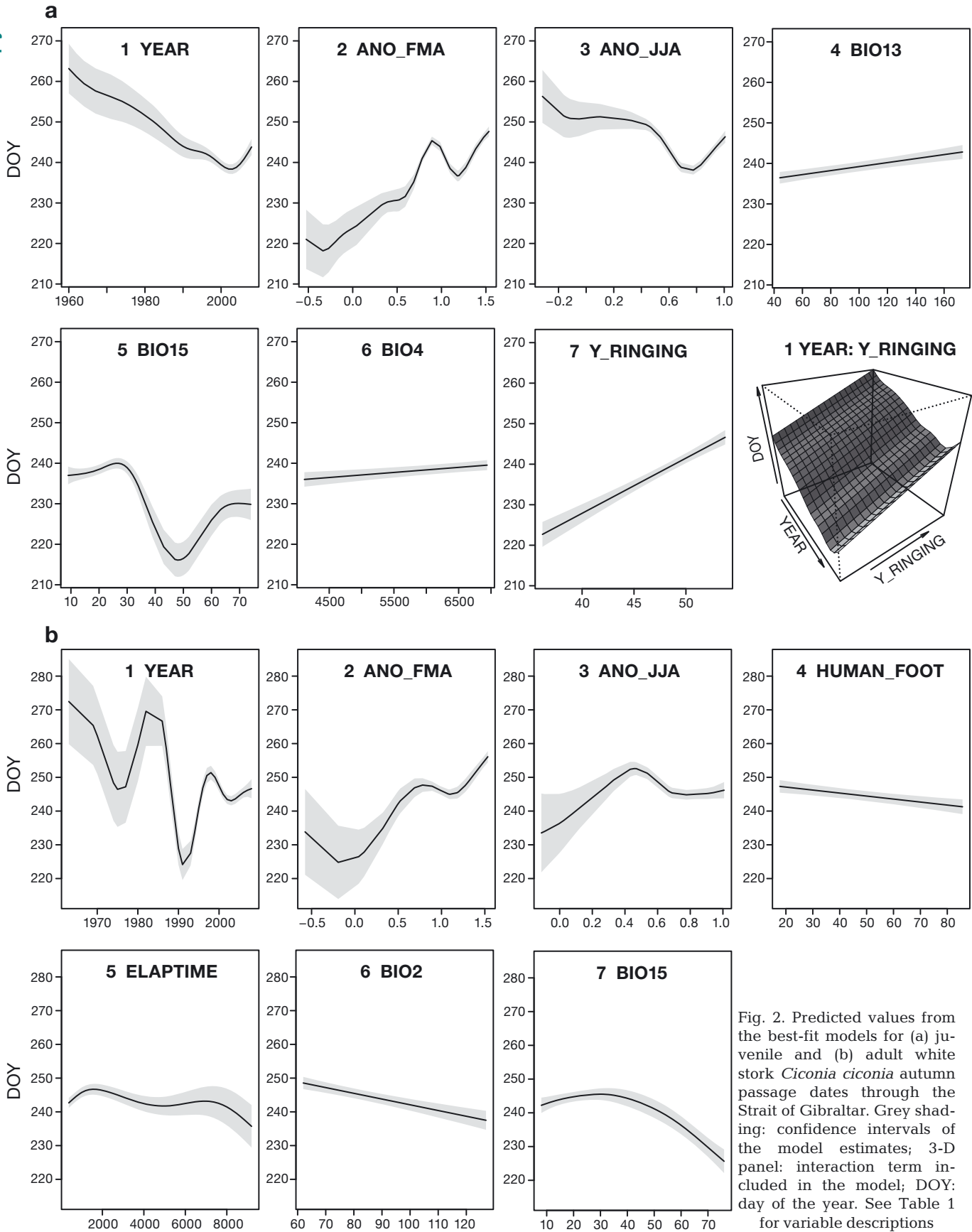
Our analysis of ringing and recoveries of white storks migrating through the Strait of Gibraltar revealed that the timing of autumn passage in this species advanced significantly throughout Europe between 1960 and 2008. Phenological estimates from our models were consistent with the timing of autumn passage detected by visual observations at the Strait (De la Cruz et al. 2011). Earlier spring arrival dates of white storks in relation to climate change have been reported since the mid-1970s throughout Europe (e.g. Ptaszky et al. 2003, Gordo & Sanz 2006, Vaitkuviene et al. 2015). However, in contrast to spring migration, the only studies investigating autumn migration phenology in this species (Gordo & Sanz 2006, Gordo et al. 2007b) were restricted to southern Europe, and did not find significant temporal trends in white stork departure dates from the breeding grounds.

Furthermore, our results provide evidence that the changes in autumn migration phenology in white storks are related to temperature anomalies caused by climate change. Date of autumn migration varied non-linearly over the study period in accordance with recent changes in temperatures recorded in western Europe: an overall increase of 0.61°C during 1980–2006 followed by a period of relative cooling between 2006–2010 (Jaffré et al. 2013). The shifts in

autumn migration phenology that we observed occurred mainly between 1980–2000, whereas little to no change was observed in the 1960s and 1970s, and a partial return to pre-1980 migration phenology was observed in the migration phenology decades. Other long-distance migrants such as the barn swallow *Hirundo rustica* also showed earlier arrival dates during the 1970s, and then returned to the initial timing of spring arrivals (Ambrosini et al. 2014).

4.1. Climate change and autumn migration

Genes determining migratory behaviour, especially those related to migration direction, can be modified by local environmental conditions (Shepherd et al. 2013). However, studies examining changes in the timing of autumn migration have frequently shown no definitive correlation between cli-



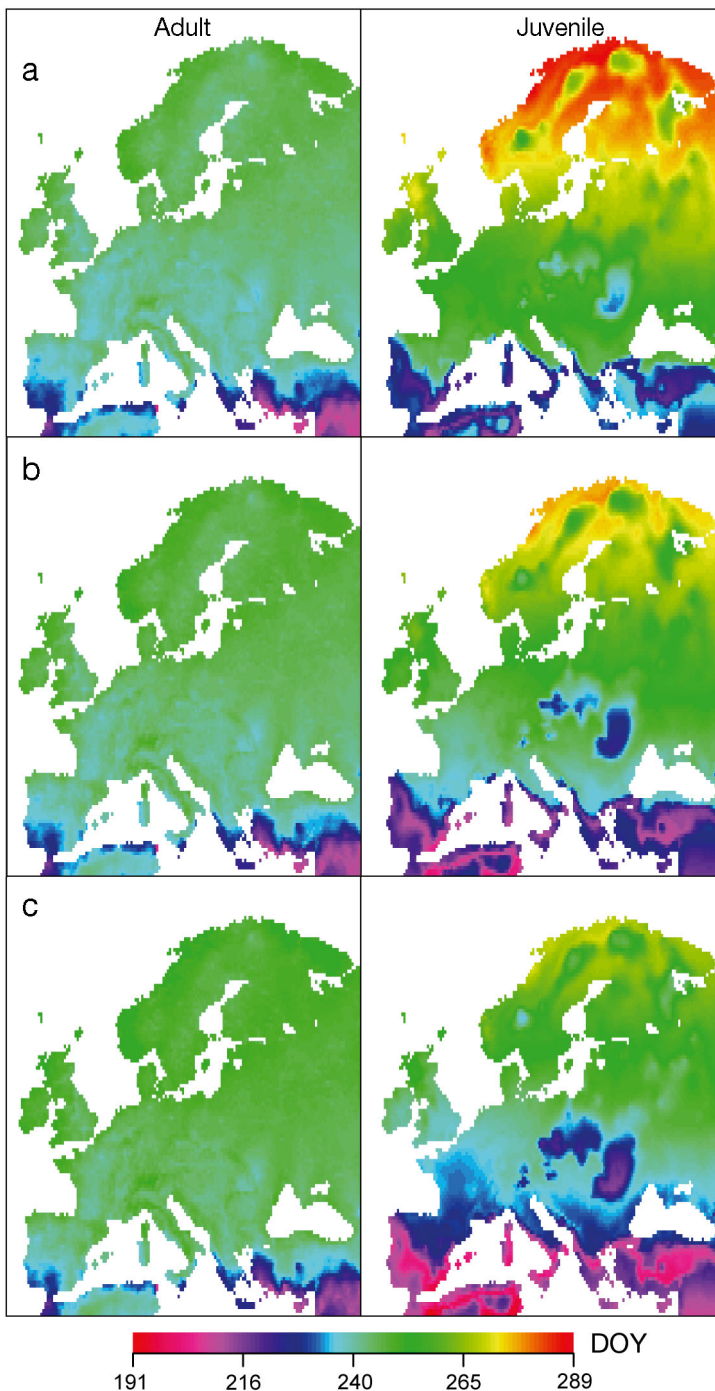


Fig. 3. Temporal trends and age effects on the geographical patterns of white stork *Ciconia ciconia* autumn migration passage dates through the Strait of Gibraltar during (a) 1960–1970, (b) 1980–1990, and (c) 2000–2010. Spatial predictions for autumn migration timing (DOY) are from the best fit models reported in Table 2

mate change and migration dates (e.g. Gordo & Sanz 2006). The differences found in the shifts between spring and autumn migration phenology have been related to the competitive nature of spring migration

(i.e. high degree of competition for the best breeding sites) (Vergara et al. 2006, 2007), which is not a factor during autumn migration. Furthermore, in contrast to the marked increasing trend in spring temperatures over the last decade, the trend observed in autumn temperatures across Europe has been much smaller (Easterling et al. 1997). However, there may be selective pressure for earlier departures in autumn if early-departing individuals have higher survival rates as a result of acquiring higher quality wintering areas (Bêty et al. 2004). Spring temperatures may also modulate autumn migration phenology; previous studies have found that white storks arrive and depart earlier in years with warmer springs (Ptaszyk et al. 2003, Gordo & Sanz 2006). Variation in spring temperatures may have a cascading effect (Tøttrup et al. 2012) on the timing of autumn migration if earlier arrival to the breeding grounds occurs without a change in the length of stay, leading to an advance in the timing of all subsequent events (Lehikoinen et al. 2004). Since the white stork is a single-brooded species, earlier spring arrival does not translate into additional breeding attempts (Møller 2002); thus, earlier arrival in spring should also lead to earlier departure in autumn (Gordo et al. 2007a).

In contrast to previous research (Gordo & Sanz 2006, Gordo et al. 2007b), we found that spatial variation in environmental factors on the breeding grounds lead to a clear south-western gradient in the autumn migration of western European white storks. Our results may differ from previous studies because of the larger spatial scale used here compared to the more restricted region studied in Gordo et al. (2007b). Furthermore, we also used a different data source (ring recoveries) than Gordo & Sanz (2006) and Gordo et al. (2007b), who analyzed volunteer observer sightings. Compared to other data sources, ring recoveries provide more accurate information on specific features of the migrating individuals, such as sex, age, and breeding location. Even though we cannot reject the influence of scale and data source on the divergences among studies, however, we suggest that the main differences between our results and those of the previous researchers are

due to the separate analysis for different age classes that we included in this study. These separate models allowed us to quantify both the different phenological patterns in environmental and climatic conditions among European populations of white storks, as well as the specific responses between birds of different ages within a population.

Our results confirmed the temporal differences in migration with age previously described for this species, with juvenile birds migrating earlier than adults (Fernández-Cruz 2005). According to our results, this age pattern in autumn migration was consistent among populations across Europe. While juvenile birds commence autumn migration upon fledging, adult birds require more time on the breeding grounds in order to recover from the reproductive cycle and regain an optimal body condition to migrate (Alonso-Álvarez et al. 2002). This is supported by previous studies, which report a larger number of adult birds in the early migrating flocks of juvenile storks in years when many adult birds failed to breed (Van den Bossche et al. 2002). The conclusion is that even if birds breeding the furthest distance from the Strait of Gibraltar passed over the Strait later in migration on average (Gordo et al. 2007b), there will still be juvenile and adult birds originating from different European breeding populations passing over the Strait simultaneously.

Clear advancements in passage dates throughout the study period, however, were only observed in juvenile storks, whereas the magnitude of the tendency for early passage in adult birds was highly variable between years. Recent research shows a lack of relationship between departure date and final destination reached by white storks (Flack et al. 2016). However, we found that the responses to climate change of western European white storks differed in intensity among breeding populations such that juvenile birds that originated in southern Europe advanced their passage dates over the study period to a greater extent than those from breeding sites farther from the Strait of Gibraltar.

According to our results, adult white storks initiated autumn migration earlier when the previous spring was warmer (Ptaszyk et al. 2003, Gordo & Sanz 2006), at least when spring temperatures did not depart from the 20th century average. Warmer springs provide better ecological conditions, which results in individuals being in better body condition and consequently affects not only arrival date, but also departure time and the progression of migration (i.e. speed of migration and time spent on stopovers), which ultimately affects the autumn passage date

that we observed at the Strait. In contrast, when spring temperatures exceeded the long-term average (which is becoming a more frequent event as a consequence of global warming), both adult and juvenile storks tended to delay their migration dates over the Strait. The latter pattern is likely a consequence of global change, but it probably does not reflect the only influence on autumn migration timing. In conjunction with climate change, anthropogenic factors such as rubbish dumps (which storks can exploit as food sources) (Tortosa et al. 2002, Kruszyk & Ciach 2010), new livestock farming practices (Tryjanowski et al. 2005), changes in agricultural landscapes (Dallinga & Schoenmakers 1989), and a reduction in the use of pesticides (Newton 2008) have benefited European white stork populations by providing new feeding opportunities. Because of these human-induced benefits, it is widely known that a change in the migratory behaviour is occurring in the western European population, with a growing number of white storks overwintering in southern Europe during the last 2 decades (Molina & Del Moral 2005). Individuals overwintering at the Strait of Gibraltar area may be counted as migrating birds, leading to an overestimation of migrants crossing the Strait (Gordo et al. 2007b). On the other hand, the changes in climate that have occurred over the last century have improved weather conditions for storks during the breeding season in central and northern European populations where spring temperatures are colder (Martín et al. 2014), shortening the time invested in breeding, and increasing chick survival (Gordo et al. 2013). The expected population increases in these areas likely enlarged the pool of storks breeding in central Europe that were included in our sample. This may have biased the migration dates recorded in the last decades of the study period (coinciding with the increases in temperatures across Europe) in favour of those individuals passing over the Strait at a later date. Nevertheless, these effects did not completely mask the observable differences among populations and the trend towards earlier autumn migration.

On the other hand, the change in climate patterns differ greatly (IPCC 2007) not only temporally but also spatially, and different populations may experience different effects of climate change depending on where and when they breed, migrate, or overwinter (Sparks & Tryjanowski 2007). The Mediterranean region is especially vulnerable to global climate change. Models for climate change over the Mediterranean region predict a decrease in precipitation, especially in the warm season, as well as more frequent high temperature events during summer (Giorgi &

Lionello 2008). Summer temperature anomalies are closely related to productivity during the summer, which is the most unfavorable and limiting season in Mediterranean climates (Gordo et al. 2007a) such as those in southern Europe. Perhaps not surprisingly then, white stork spatial patterns of autumn migration are markedly affected by precipitation—and specifically by, seasonal variables related (directly or indirectly) to the availability of water during summer. Both adult and juvenile autumn passage dates were earlier in years with higher summer temperatures. The meteorological triggers of soaring-bird migration are related to deteriorating living and migratory flight conditions (Shamoun-Baranes et al. 2006). Earlier migration allows birds to avoid unfavorable environmental conditions during the summer, particularly in southern Europe, which can negatively affect their survival (Gordo et al. 2007a). The large sensitivity of Mediterranean basin to climate change is supported by our models, which found the greatest advances in autumn juvenile passage dates over the study period in southern Europe.

4.2. Different responses to climate change between age classes

The phenological response of adult birds was highly variable from year to year because individual adult storks seemed to respond differently to the ecological conditions on their breeding grounds compared to juvenile birds. This variation highlights the ability of adult storks to adapt to the complex interactions emerging between reproductive constraints and environmental conditions during the breeding season. Previous studies have reported that high productivity in one year is usually followed by lower productivity and delayed arrival the next spring for white storks (Tryjanowski et al. 2004), suggesting that storks are able to modulate their breeding investment in a particular year depending on their sex, age, body condition, and status (Gordo et al. 2013). Supporting this, regardless of environmental conditions, white storks in optimal physical condition or in high quality sites may start reproduction earlier (Tryjanowski et al. 2004), and breeding date may affect their autumn departure (Kosicki et al. 2004). Although breeding success in white storks is affected by breeding date and nest site selection in any age class (Tobolka et al. 2013, 2015), other studies have shown that age is related to earlier spring arrivals (Vergara et al. 2007), and older individuals have been reported to be more successful breeders than younger ones (Vergara et al.

2006, 2007), which will affect the subsequent departure date in autumn. Our model suggests that individual adult birds may shift their autumn migration to earlier dates as they age. Besides environmental conditions, social flocking behaviour (Kosicki et al. 2004), and the reproductive cycle itself, autumn migration phenology may also depend on the timing of moult (Barta et al. 2008). Adult white storks exhibit a complete postbreeding moult, starting during the breeding period and finishing in winter. Juvenile storks, however, do not initiate their post-juvenile moult until December (Blasco-Zumeta & Heinze 2015). Thus, in contrast to most passerine birds, moulting in this species does not appear to affect the timing of autumn migration (Barta et al. 2008).

Beyond environmental and life-history constraints, differences in the phenological response between white stork age classes are likely caused by the different mechanisms for migration adjustment governing adult and young bird behaviour. Genetic variability and phenotypic plasticity allow birds to adjust their migration strategies according to changes in climate and environmental conditions (Ambrosini et al. 2014). Although the two mechanisms are not mutually exclusive and could act simultaneously, phenotypic plasticity seems to be more important than microevolutionary change (Both et al. 2005). In fact, long-lived animals like the white stork are expected to be more flexible in their behavioural responses to environmental changes during migration (Newton 2008), and rely more on their plasticity than on microevolutionary changes. However, the source of such plasticity may vary among age classes; only adult birds can rely on information acquired during previous migration journeys (Berthold 2003), whereas inexperienced juvenile birds on their first migration must rely on an inherited migratory programme controlled by endogenous rhythms that depend on environmental cues (Coppack & Both 2002). Circannual clocks can be synchronized with the environment by changes in photoperiod, light intensity, and likely temperature and precipitation patterns (Wikelski et al. 2008). According to our results, juvenile white storks base their decision to depart on favourable weather conditions, at least to some extent, since the timing of autumn migration is correlated with latitudinal gradients and shows a trend consistent with an effect of climate change. The ability of juvenile storks to alter their migratory patterns according to environmental conditions (Berthold et al. 1992, Pulido et al. 1996) allows these inexperienced birds to respond to climate change. However, white storks may adopt more flexible

migration behaviours as they gain more experience in subsequent migration journeys (Thorup et al. 2007). Besides the climatic and environmental constraints, adult storks exhibit great plasticity in terms of adapting to annual specific conditions, since other variables such as bird age or parental investment also play a role (Vergara et al. 2006, 2007). Thus, adult storks cannot simply advance their departure dates and must respond in a more complex way to account for the negative impacts of climate change.

4.3. Consequences for the white stork population in Europe

Recent censuses have shown a general increasing trend in white stork numbers across Europe (BirdLife International 2015). Phenology mismatches seem to drive migratory bird declines (Jones & Cresswell 2010); however in contrast to other bird species, breeding success in the white stork does not depend on a temporal match with seasonal peaks of resources (Gordo et al. 2013). Furthermore, non-climatic changes (e.g. rubbish dumps, land use changes) which provide large and predictable food supplies for storks (De Juana & García 2005) have probably decreased the strength of the link between stork survival and climatic conditions during the last decade. The potential negative impacts of climatic and environmental changes may be reduced if birds are able to better cope with them or even take advantage of these conditions.

In order to draft suitable management plans that affect migratory birds, particularly long-lived species, we need to have a clearer picture of the impacts of climate change. Further studies should investigate the potential divergences among effects and responses in migratory behaviour related to global change (climatic and non-climatic changes) that may arise between different fractions within a population (i.e. age, sex classes) at large geographical scales beyond the population level.

Acknowledgements. 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 have gathered and prepared the data. We are also grateful to the Board of the Migres Foundation and to Andrea Feltro Grassi and Emily A. Tyrrell who helped in the early stages of the manuscript. Special thanks to Karen A. Prisby for her kind revision of the language of the manuscript. We would like to thank the editor and anonymous referees for providing us with comments and suggestions that helped to improve the manuscript.

LITERATURE CITED

- Alonso-Alvarez C, Velando A, Ferrer M, Veira JAR (2002) Changes in plasma biochemistry and body mass during incubation in the yellow-legged gull. *Waterbirds* 25: 253–258
- Ambrosini R, Borgoni R, Rubolini D, Sicurella B and others (2014) Modelling the progression of bird migration with conditional autoregressive models applied to ringing data. *PLoS ONE* 9:e102440
- Balbontín J, Møller AP, Hermosell IG, Marzal A, Reviriego M, De Lope F (2009) Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. *J Anim Ecol* 78:981–989
- Barta Z, McNamara JM, Houston AI, Weber TP, Hedenström A, Feró O (2008) Optimal moult strategies in migratory birds. *Philos Trans R Soc Lond B Biol Sci* 363:211–229
- Beaumont LJ, McAllan IAW, Hughes L (2006) A matter of timing: changes in the first date of arrival and last date of departure of Australian migratory birds. *Glob Change Biol* 12:1339–1354
- Bernis F (1980) La migración de las aves en el Estrecho de Gibraltar (Epoca Posnupcial). Vol 1. Aves planeadoras. Universidad Complutense, Madrid
- Berthold P (2003) Genetic basis and evolutionary aspects of bird migration. *Adv Stud Behav* 33:175–229
- Berthold P, Helbig AJ, Mohr G, Querner U (1992) Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360:668–670
- Berthold P, Bossche WVD, Fiedler W, Kaatz C and others (2001) Detection of a new important staging and wintering area of the white stork *Ciconia ciconia* by satellite tracking. *Ibis* 143:450–455
- Bêty J, Giroux JF, Gauthier G (2004) Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behav Ecol Sociobiol* 57:1–8
- BirdLife International (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge
- BirdLife International (2015) Species factsheet: *Ciconia ciconia*. www.birdlife.org/datazone/speciesfactsheet.php?id=3835 (accessed 10 Sept 2015)
- Blasco-Zumeta J, Heinze G (2015) White stork: aging and sexing. http://aulaenred.ibercaja.es/wp-content/uploads/46_WhiteStorkCiconia.pdf (accessed 15 Oct 2015)
- Both C, te Marvelde L (2007) Climate change and timing of avian breeding and migration throughout Europe. *Clim Res* 35:93–105
- Both C, Bijlsma RG, Visser ME (2005) Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. *J Avian Biol* 36:368–373
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY
- Chernetsov N, Chromik W, Dolata PT, Profus P, Tryjanowski P (2006) Sex-related natal dispersal of white storks (*Ciconia ciconia*) in Poland: How far and where to? *Auk* 123: 1103–1109
- Coppack T, Both C (2002) Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* 90: 369–377
- Cramp S, Simmons I, Ferguson-Lees IJ, Gillmor P and others (eds) (1977) Handbook of the birds of Europe the Middle

- East and North Africa. Oxford University Press, Oxford
- Cristol D, Baker M, Carbone C (1999) Differential migration revisited: latitudinal segregation by age and sex class. In: Nolan V, Ketterson E, Thompson C (eds) Current ornithology. Plenum Publishers, New York, NY, p 33–88
- Dallinga H, Schoenmakers S (1989) Population changes of the white stork since the 1950s in relation to food resources. In: Rheinwald G, Ogden J, Schulz H (eds) Weißstorch—white stork. Proc 1st Int Stork Conserv Symp, Schriftenreihe des DDA 10:231–262
- De Juana E, García E (2015) The birds of the Iberian peninsula. Bloomsbury Publishing, London
- De la Cruz A, Onrubia A, Pérez B, Torralvo C and others (2011) Seguimiento de la migración de las aves en el estrecho de Gibraltar: resultados del Programa Migres 2009. Revista Migres 2:65–78
- Del Hoyo J, Elliot A, Sargatal J (eds) (1994) Handbook of birds of the world, Vol 2: new world vultures to guineafowl. Lynx Edicions, Barcelona
- du Feu CR, Joys AC, Clark JA, Fiedler W and others (2009) EURING data bank geographical index 2009. www.euring.org/edb
- Easterling DR, Horton B, Jones PD, Peterson TC and others (1997) Maximum and minimum temperature trends for the globe. Science 277:364–367
- Fernández-Cruz M (2005) La migración otoñal de la cigüeña blanca (*Ciconia ciconia*) por el estrecho de Gibraltar. In: Molina B, Del Moral JC (eds) La cigüeña blanca en España. VI. Censo internacional (2004). SEO/BirdLife, Madrid, p 162–201
- Fiedler W, Bairlein F, Köppen U (2004) Using large-scale data from ringed birds for the investigation of effects of climate change on migrating birds: pitfalls and prospects. Adv Ecol Res 35:49–67
- Finlayson JC (1992) Birds of the Strait of Gibraltar. Academic Press, London
- Flack A, Fiedler W, Blas J, Pokrovsky I and others (2016) Costs of migratory decisions: a comparison across eight white stork populations. Sci Adv 2:e1500931
- Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. Glob Planet Change 63:90–104
- Gordo O, Sanz JJ (2006) Climate change and bird phenology: a long-term study in the Iberian Peninsula. Glob Change Biol 12:1993–2004
- Gordo O, Sanz J (2008) The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. J Ornithol 149:199–210
- Gordo O, Sanz JJ, Lobo JM (2007a) Environmental and geographical constraints on common swift and barn swallow spring arrival patterns throughout the Iberian Peninsula. J Biogeogr 34:1065–1076
- Gordo O, Sanz JJ, Lobo JM (2007b) Spatial patterns of white stork (*Ciconia ciconia*) migratory phenology in the Iberian Peninsula. J Ornithol 148:293–308
- Gordo O, Tryjanowski P, Kosicki JZ, Fulín M (2013) Complex phenological changes and their consequences in the breeding success of a migratory bird, the white stork *Ciconia ciconia*. J Anim Ecol 82:1072–1086
- Hijmans RJ, van Etten J (2011) Package 'raster': geographic analysis and modeling with raster data. R package version 1.9-5. <http://cran.r-project.org/web/packages/raster/raster.pdf>
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978
- Hijmans RJ, Williams E, Vennes C (2010) Package 'geosphere': spherical trigonometry. <http://cran.r-project.org/web/packages/geosphere/geosphere.pdf>
- Hurlbert AH, Liang Z (2012) Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. PLoS ONE 7:e31662
- Imboden C, Imboden D (1972) Formel für Orthodrome und Loxodrome bei der Berechnung von Richtung und Distanz zwischen Beringungs- und Wiederfundort. Vogelwarte 26:336–346
- IPCC (2007) Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the fourth assessment report of the Intergovernmental Panel on Climate Change. IPCC, Geneva
- Jaffré M, Beaugrand G, Goberville É, Jiguet F and others (2013) Long-term phenological shifts in raptor migration and climate. PLoS ONE 8:e79112
- Jones T, Cresswell W (2010) The phenology mismatch hypothesis: Are declines of migrant birds linked to uneven global climate change? J Anim Ecol 79:98–108
- Jones PD, New M, Parker DE, Martin S, Rigor IG (1999) Surface air temperature and its changes over the past 150 years. Rev Geophys 37:173–199
- Körner-Nievergelt F, Sauter A, Atkinson PW, Guélat J and others (2010) Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. J Avian Biol 41:8–17
- Kosicki J, Sparks T, Tryjanowski P (2004) Does arrival date influence autumn departure of the white stork *Ciconia ciconia*? Ornithol Fenn 81:91–95
- Kruszyk R, Ciach M (2010) White storks, *Ciconia ciconia*, forage on rubbish dumps in Poland—a novel behaviour in population. Eur J Wildl Res 56:83–87
- Lehikoinen A, Sparks T, Zalakevicius M (2004) Arrival and departure dates. Adv Ecol Res 35:1–31
- MacMynowski DP, Root TL (2007) Climate and the complexity of migratory phenology: sexes, migratory distance, and arrival distributions. Int J Biometeorol 51:361–373
- Martín B, Onrubia A, Ferrer M (2014) Effects of climate change on the migratory behavior of the common buzzard *Buteo buteo*. Clim Res 60:187–197
- Molina B, Del Moral JC (eds) (2005) La cigüeña blanca en España. VI. Censo internacional (2004). SEO/BirdLife, Madrid
- Møller AP (2002) North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. J Anim Ecol 71: 201–210
- Møller AP (2004) Protandry, sexual selection and climate change. Glob Change Biol 10:2028–2035
- Newton I (2008) The migration ecology of birds. Academic Press, London
- Porter R, Beaman M (1985) A resume of raptor migration in Europe and the Middle East. ICBP Tech Publ 5:237–242
- Ptaszyk J, Kosicki J, Sparks T, Tryjanowski P (2003) Changes in the timing and pattern of arrival of the white stork (*Ciconia ciconia*) in western Poland. J Ornithol 144:323–329
- Pulido F, Berthold P, Van Noordwijk AJ (1996) Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. Proc Natl Acad Sci USA 93:14642–14647
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

- Rogerson PA (2001) Statistical methods for geography. Sage Publications, London
- Rubolini D, Møller A, Rainio K, Lehikoinen E (2007) Intra-specific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Clim Res* 35:135–146
 - Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. *BioScience* 52:891–904
 - Shamoun-Baranes J, Van Loon E, Alon D, Alpert P, Yom-Tov Y, Leshem Y (2006) Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? *Glob Ecol Biogeogr* 15:541–552
 - Shephard JM, Ogden R, Tryjanowski P, Olsson O, Galbusera P (2013) Is population structure in the European white stork determined by flyway permeability rather than translocation history? *Ecol Evol* 3:4881–4895
 - Smallegange IM, Fiedler W, Köppen U, Geiter O, Bairlein F (2010) Tits on the move: exploring the impact of environmental change on blue tit and great tit migration distance. *J Anim Ecol* 79:350–357
 - Sparks T, Tryjanowski P (2007) Patterns of spring arrival dates differ in two hirundines. *Clim Res* 35:159–164
 - Sparks TH, Bairlein F, Bojarinova JG, Hüppop O and others (2005) Examining the total arrival distribution of migratory birds. *Glob Change Biol* 11:22–30
 - Tellería JL, Santos T, Refoyo P, Muñoz J (2012) Use of ring recoveries to predict habitat suitability in small passerines. *Divers Distrib* 18:1130–1138
 - Thorup K, Bisson IA, Bowlin MS, Holland RA, Wingfield JC, Ramenofsky M, Wikelski M (2007) Evidence for a navigational map stretching across the continental US in a migratory songbird. *Proc Natl Acad Sci USA* 104:18115–18119
 - Tobolka M, Kuźniak S, Zolnierowicz KM, Sparks TH, Tryjanowski P (2013) New is not always better: low breeding success and different occupancy patterns in newly built nests of a long-lived species, the white stork *Ciconia ciconia*. *Bird Study* 60:399–403
 - Tobolka M, Zolnierowicz KM, Reeve NF (2015) The effect of extreme weather events on breeding parameters of the white stork *Ciconia ciconia*. *Bird Study* 62:377–385
 - Tortosa F, Caballero J, Reyes Lopez J (2002) Effect of rubbish dumps on breeding success in the white stork in southern Spain. *Waterbirds* 25:39–43
 - Tøttrup AP, Klaassen RHG, Kristensen MW, Strandberg R and others (2012) Drought in Africa caused delayed arrival of European songbirds. *Science* 338:1307
 - Tryjanowski P, Sparks T, Ptaszyk J, Kosicki J (2004) Do white Storks *Ciconia ciconia* always profit from an early return to their breeding grounds? *Bird Study* 51:222–227
 - Tryjanowski P, Jerzak L, Radkiewicz J (2005) Effect of water level and livestock on the productivity and numbers of breeding white storks. *Waterbirds* 28:378–382
 - Tucker CJ, Pinzon JE, Brown ME, Slayback DA and others (2005) An extended AVHRR 8 km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. *Int J Remote Sens* 26:4485–4498
 - USGS (2004) Shuttle Radar Topography Mission, 1 Arc Second scene SRTM_u03_n008e004, Unfilled Unfinished 2.0. Global Land Cover Facility, University of Maryland, College Park, MD, Feb 2000
 - Vaitkuvienė D, Dagys M, Bartkeviciene G, Romanovskaja D (2015) The effect of weather variables on the white stork (*Ciconia ciconia*) spring migration phenology. *Ornis Fenn* 92:43–52
 - Van Buskirk J, Mulvihill RS, Leberman RC (2009) Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Glob Change Biol* 15:760–771
 - Van den Bossche W, Berthold P, Kaatz M, Nowak E, Querner U (2002) Eastern European white stork populations: migration studies and elaboration of conservation measures. Final Report of the F+E-Project. Bundesamt für Naturschutz (BfN)/German Federal Agency for Nature, Bonn
 - Végvári Z, Bókonyi V, Barta Z, Kovács G (2010) Life history predicts advancement of avian spring migration in response to climate change. *Glob Change Biol* 16:1–11
 - Vergara P, Aguirre JI, Fargallo JA, Dávila JA (2006) Nest-site fidelity and breeding success in white stork *Ciconia ciconia*. *Ibis* 148:672–677
 - Vergara PI, Aguirre J, Fernández-Cruz M (2007) Arrival date, age and breeding success in white stork *Ciconia ciconia*. *J Avian Biol* 38:573–579
 - Visser ME, Perdeck AC, van Balen JH, Both C (2009) Climate change leads to decreasing bird migration distances. *Glob Change Biol* 15:1859–1865
 - Wikelski M, Martin LB, Scheuerlein A, Robinson MT and others (2008) Avian circannual clocks: adaptive significance and possible involvement of energy turnover in their proximate control. *Philos Trans R Soc Lond B Biol Sci* 363:411–423
 - Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc Series B Stat Methodol* 73:3–36
 - Wood E, Kellermann J (eds) (2015) Phenological synchrony and bird migration: changing climate and seasonal resources in North America. CRC Press, Boca Raton, FL

Editorial responsibility: Mauricio Lima,
Santiago, Chile

Submitted: October 26, 2015; Accepted: March 15, 2016
Proofs received from author(s): May 20, 2016