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The effect of extreme weather events on breeding parameters of the White Stork *Ciconia ciconia*

MARCIN TOBOLKA[1]*, KATARZYNA M. ZOLNIEROWICZ[1] and NICOLA F. REEVE[2]

[1]*Institute of Zoology, Poznań University of Life Sciences, Ul. Wojska Polskiego 71C, 60-025 Poznań*

[2]*Coventry University, Gosford Street, Coventry CV1 5DD*

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*Correspondence author. Email: marcin_tobolka@o2.pl

Summary

Although the White Stork avoids adverse weather conditions modifying its arrival and breeding, it cannot avoid extreme weather events during the breeding season.

Aims

To show how extreme weather conditions can influence breeding attempts of a large, long-lived species, the White Stork.

Methods

We analysed data on arrivals of White Storks in Western Poland from 2005 - 2013 and detailed breeding biology parameters from 2009 - 2013 in relation to weather conditions. We analysed breeding success and breeding failure rate from 1974 - 2013.

Results

In years with a cold March White Storks arrived later than when March was warmer. Frost during incubation negatively influenced the hatching success. Extreme weather events caused high late mortality even for nestlings older than 30 days. Data from 27 breeding seasons showed a significant increase of mean breeding success but also a significant increase of proportion of pairs which lost broods on the nestling stage.

Conclusion

The White Stork can modify its arrival in response to current weather conditions on the breeding grounds but it cannot respond to extreme weather events. Due to increasing frequency of extreme weather events caused by climate change, White Stork breeding success may decrease in future.

INTRODUCTION

Climate changes may be evident in different patterns of rainfall and temperature gradients (e.g. Zhang *et al.* 2012, Coumou & Rahmstorf 2012, IPCC 2013, Tang *et al.* 2013) and cause unfavourable habitat changes for many animal species (IPCC 2013). It causes migratory birds to avoid adverse conditions on breeding grounds in two main ways: to change breeding areas (Huntley *et al.* 2008) or to change the timing of migration (Hüppop & Winkel 2006, Rainio *et al.* 2006, Both & te Marvelde 2007, Charmantier & Gienapp 2014), arrival (Gordo *et al.* 2005, Tryjanowski *et al.* 2002, Tryjanowski *et al.* 2005, Macmynowski *et al.* 2007) and breeding (Both & te Marvelde 2007, Visser *et al.* 2009, Charmantier & Gienapp 2014). For long-distance migrants, climate changes can be more severe than for short-distance migrants because it is much more difficult to predict conditions on the breeding grounds from remote wintering areas in Africa than from closer regions such as Southern Europe (Both & Visser 2001, Both *et al.* 2010). Therefore in many long-distance migrants there is a phenology mismatch, i.e. mistiming of the main prey peak on the breeding grounds (Sanz *et al.* 2003, Both *et al.* 2006, Jones & Cresswell 2010). For short-distance migrants there is evidence of adaptation to changing food peak phenology (Visser *et al.* 1998). Moreover, species which did not show behaviour changes in response to climate conditions are declining (Møller *et al.* 2008). Although the long distance trans-African migratory birds seem to be more vulnerable to climate changes, some of them like the White Stork *Ciconia ciconia* can modify the timing of their arrival on the breeding grounds in response to the weather conditions (e.g. Ptaszyk *et al.* 2003).

Besides sustained global warming and changes in weather patterns, climate changes can also include more frequent extreme weather anomalies (Zhang *et al.* 2012, Coumou & Rahmstorf

2012, IPCC 2013, Tang *et al.* 2013). In particular, an increasing rate of hurricanes, droughts, cold weather spells and increased rainfall may influence bird population dynamics by reducing adults' survival and increasing frequency of reproduction failure (Robinson *et al.* 2007, Moreno & Møller 2011). Birds which build open exposed nests are theoretically more vulnerable to extreme weather events during egg laying, incubation or rearing of nestlings than hole-nesting birds. However, very severe weather anomalies can affect even hole-nesting birds (e.g. Bordjan & Tom 2014, Glądalski *et al.* 2014). Therefore long term studies focused on breeding biology of open-nesting long-lived birds are suitable to explain how a changing climate directly affects bird breeding biology. We can expect long term studies to reveal changes in arrivals and breeding but also an increase in brood failure rate in recent decades due to an increase in extreme unpredictable weather events.

The European White Stork is an example of a long-lived trans-African migratory bird. It nests in a rural landscape, mostly on the top of human-made structures such as electricity posts, roofs, chimneys (Tryjanowski *et al.* 2009) and also on trees (Yavuz & Yavuz 2012). It is known that weather conditions prior to arrival on the breeding grounds may strongly influence arrival dates. In years with a very cold spring birds arrive later (Ptaszyk *et al.* 2003), mainly due to conditions during the route back to the breeding grounds (Shamoun-Baranes *et al.* 2003). The White Stork does not always profit from early return to the breeding grounds because very early arriving individuals can meet with severe weather conditions in the beginning of the breeding season which can reduce reproductive success (Tryjanowski *et al.* 2004, Janiszewski *et al.* 2013). The number of cold days before egg laying can influence the clutch size (Sasvári & Hegyi 2001) and weather conditions during egg incubation, especially in the second half of the incubation period is crucial, with temperatures below zero a potential cause of embryo death (Jovani & Tella 2004, Kosicki 2011). However, it has been shown that White Stork hatching success and the number of cold days during incubation were not correlated (Sasvári & Hegyi 2001). In Poland, where a more continental climate occurs, minimum temperatures in May (when most of White Storks are in the second half of incubation) can be much lower than in Southern or Western Europe, and in extreme cases temperatures as low as -8 ^{o}C during the night and in the morning may be recorded (Woś 1999). Hence, in this study we considered the mean minimum temperature in May as a key factor influencing hatching success of the White Stork. Rainy, windy and cold weather during chick rearing can significantly affect breeding success by reducing chick survival (Sasvári & Hegyi 2001, Jovani & Tella 2004, Denac 2006), until young storks develop their thermoregulatory ability (Tortosa & Castro 2003). Therefore, the highest mortality risk occurs when nestlings are young and not feathered. It decreases with age and feather development (Kosicki 2011).

In this study we analysed data of the White Stork breeding biology in Western Poland during nine breeding seasons under different weather conditions. We hypothesised that (1) temperature prior to arriving on the breeding grounds can influence arrival dates of pair members and the clutch size; (2) extremely low temperature during incubation can negatively affect hatching success and (3) extremely high precipitation can reduce survival rate of well feathered nestlings even in the final period of nestling life. Finally, based on long term data of White Stork breeding success from the study area we tested (4) if the reproductive failure rate has changed during last forty years.

MATERIALS AND METHODS

Study area

The study was conducted during 9 breeding seasons (2005-2013) in Western Poland near the town of Leszno (51°51′N, 16°35′E) in a 4 154 km^2 area. This is a rural area of arable fields (54%) interspersed with meadows (7%), pastures (less than 1%), human settlements (10%) and forests (17%). The White Stork is a solitary nester, but sometimes it forms small aggregations of up to five pairs, mainly in small river valleys or lakelands. The population density has declined from 8.86 pairs/100 km^2 in 1974 to 5.27 in 2009 with a small increase to 6.72 in 2010-2013 (e.g. Kuźniak & Tobółka 2010, Tobolka *et al.* 2013).

Data collection

In 2005-2013 arrival dates of 591 pairs from 168 nests (42 - 86 breeding attempts yearly) were recorded by farmers living in the vicinity of the nests, using special questionnaires for each studied nest (details in Ptaszyk *et al.* 2003). In 2009-2013 for 101 accessible nests (23 - 58 broods yearly) we collected more detailed data (clutch size, hatching success and nestling survival rate) on 239 broods based on direct inspections using a 16 m ladder, cherry-picker or climbing equipment (depending on the availability of the nest). Each nest was visited directly at least three times and at least twice from the ground. The inspections were conducted as follows: first, in April, in the beginning of the breeding season to detect pairs which had occupied the nests and to collect the questionnaire forms; second, in the beginning of May to record clutch size. Based on observations of pairs, arrival dates and interviews with nest hosts we estimated the phase of incubation. Clutch size was recorded in the second half of incubation (which for most pairs is in the beginning of May) to avoid abandonment risk. In the case of eggs being rejected for example due to fights, we excluded the record from the analyses. Due to storks nesting in close proximity to humans nearly all cases of egg rejection could be detected. The third visit was conducted to record hatching success. For most pairs it took place in the second half of May. During this visit nestlings up to 7 days old were individually banded by colourful non-toxic markers. Older nestlings were banded by rings used for poultry marking, provided their tarsus was thick enough. The fourth visit took place in the second half of June to ring the nestlings which were at least 30 days old. In 2013 the fourth inspection was conducted in 26-28th June, just after two days of continuing rainfall. Dead chicks were found no longer than one-three days after death. The fifth visit was conducted from the ground to record breeding success, consisting of counting the number of fledglings standing on the nest and able to fly, which is a standard method to estimate White Stork breeding success (Tryjanowski *et al.* 2006). We recorded breeding success and productivity in each nest in the study area through these detailed investigations. The last visit was conducted between 1st and 25th of July (depending on when storks started breeding) and in some very late broods, in August. All doubtful records were supplemented by interviews with farmers living near the nest. If they did not clarify what happened, we excluded the brood from the breeding parameters analyses. The time of nest investigations was modified according to the beginning of the breeding season. Although the Eastern migratory White Stork breeding time is strongly synchronized, in some cases additional inspections were needed. When any eggs were found unhatched at the time of the visit we came back after several days to record the final hatching success. If there were still any unhatched eggs we visited the nest again to ensure that the clutch remained partially unhatched. The White Stork can prolong incubation and unhatched eggs can remain in the nest for a long time (Wuczyński 2012). We did not record any brood abandonment due to our disturbance or other causes. We defined clutch size as the number of eggs recorded during the first inspection of the nest when the clutch was completed; hatching success as the percentage of hatched eggs; nestling survival rate as the percentage of hatched nestlings which survived and left the nest. During the nest visit we measured the bill length of each nestling using callipers with accuracy 0.01mm.

For long term analyses we incorporated existing data collected in 27 breeding seasons between 1974 and 2013 as partially published by, for example, Kuźniak & Tobółka (2010) and Tobolka *et al.* (2013). Number of breeding pairs (HPa), pairs with success (HPm) and pairs which failed reproduction (HPo) were available.

Weather conditions

To assess the influence of weather on White Stork breeding attempts we obtained data from the TuTiempo.net database (http://www.tutiempo.net/en/Climate/LESZNO/124180.htm). The mean temperature in March was 3.2°C (range: -2.0 - 6.4) and differed significantly between study years (ANOVA: F_8=13.3, P<0.0001). To compare arrival dates in years with different temperatures we divided years into two groups: 1 (with warm March) - mean temperature in March greater than the mean temperature in March during the whole study period and 0 (with cold March) – below the overall mean. The mean minimum temperature in May for five breeding seasons when detailed breeding biology data were collected was 7.7°C (range: 6.3 - 9) and varied significantly between years (ANOVA: F_4=3.9, P=0.004). The lowest recorded temperature was -3.7^{o}C in 2011 and locally even -6^{o}C was observed. We defined years with frost in May as 'cold May years' - 1, and years without frost in May as 'normal May years' - 0. Mean and mean minimum temperature in June were respectively 16.9 and 11.0°C (range: 15.5 - 18.5 and 10.8 - 12.1) and differed significantly between years (ANOVA resp.: F_4=3.7, P=0.007 and F_4=2.89, P=0.024). The lowest recorded temperature was

1.9°C. Total precipitation differed significantly between years during the incubation period (15th of April - 15th of May) but not during nestling rearing periods (16th of May - 15th of July) (Kruskal-Wallis: χ^2=12.1, P=0.02 and χ^2=7.2, P=0.12). On the 25th - 26th of June 2013 very intensive continuing rainfall with a high total precipitation (50 mm, while total yearly is ca. 600) was recorded. The weather in 2013 was extreme compared to other research years both in spring and summer (e.g. Glądalski *et al.* 2013).

Data processing and statistical analyses

The age of nestlings was estimated during the first visit after hatching as a mean from two available linear regression models of bill length (Kania 1988, Tsachalidis *et al.* 2005).

The effect of weather conditions on the arrival date, clutch size, hatching success and fledging success was estimated using a generalised linear mixed model, including the year as a random effect to account for variation between years. Each model included an additive effect of temperature and precipitation as it has been suggested that a combination of these factors may be important (Bairlein & Hennenberg 2000). We also considered an interaction between temperature and precipitation. This was removed from the final model for arrival date, clutch size and hatching success because it was not significant. The interaction term was retained in the model for fledging success.

For the long term data, we used a generalised linear model to assess whether the reproductive failure rate has changed during the last forty years, testing the number of fledglings per pair, the proportion of pairs with no offspring and the proportion of pairs failing at the nestling stage.

To avoid the confounding effect of clutch size in the analysis of hatching success we used the proportion of eggs that hatched and modelled it using a binomial distribution. Similarly, fledging success, the proportion of pairs with no offspring and the proportion of pairs failing at the nestling stage were modelled using a binomial distribution.

All analyses, transformations and figures were prepared using R 3.1.1, MS. Excel 2007 and IBM SPSS Statistics 20 for Windows.

RESULTS

The arrival date of the first bird of the pair varied between the 75th and 150th day of the year (16th of March - 30th of April) and the second bird of the pair varied between the 77th and the 157th day of the year (18th of March - 7th of May). Based on annual means, the mean arrival date of the first bird on the nest was the 94th day of the year (4th of April, median - 92) and for the second bird from the pair, the 99th day (9th of April, median - 97). Both the first and the second pair member arrived significantly earlier in years with a warm March (resp. 92 and 96) than in years with a cold March (mean resp. 99 and 104); Table 1. The significant effect of temperature became marginal when precipitation was added to the model. Precipitation also had no significant effect.

We did not find a significant relationship between temperature in March on the breeding grounds and clutch size, with warm and cold March both having a mean clutch size of 4.4 (Table 1). Mean hatching success was 89% (range: 69–93%) and differed significantly between years with very low temperatures in May (86%) and normal years (90%) (Table 1). Again, no significant difference was found when also including precipitation, for either temperature or precipitation.

Mean survival rate of nestlings was 74% (range: 16-84%). No significant relationship was found between temperature in May and fledgling success. However, temperature in June did have a significant effect on fledgling success (Table 1) when combined with precipitation. When there is a mean precipitation of 1.65mm (average for the whole study period), there is a mean fledgling success of 72% in years with a cold June and 78% in normal years. When there is a mean precipitation of 3mm (close to the maximum for the study period), there is a mean fledgling success of 73% in years with a cold June and 16% in normal years, indicating an increase in fledgling success when cold weather is combined with high precipitation.

The mean number of fledglings per breeding pair was 2.31 (range: 0.59-3.04). The number of fledglings per breeding pair (HPm) had no significant long term trend (P=0.44, N=27 years, Table 3). However, when excluding the year 2013, there was a significantly increasing trend in the mean number of fledglings (P=0.025, N=26, Figure 2, Table 3). Most of the nestlings in 2013 died after two days of continued rain, low mean temperatures (12°C, min. 7°C) and strong winds (maximum sustained wind speed 35-43 km/h). The average age of nestlings when the high mortality occurred in 2013 was 32 days.

Long term data showed that the mean percentage of pairs which failed in their reproduction attempts during 27 breeding seasons was 22.0% (range: 5.4-65.6). We did not find a significant increase of percentage of pairs without offspring in the period 1974-2013 (Table 3) but after excluding 2013, we did find a significant relationship (Figure 3, Table 3). In contrast, the percentage of pairs which failed in reproduction during nestling stage increased significantly during the study period (Table 3) but no significant effect was observed when 2013 was excluded (Table 3).

DISCUSSION

The arrival pattern of storks was similar to results from earlier studies from western Poland where in warmer springs White Storks were arriving earlier (Tryjanowski *et al.* 2004) possibly because of overall climate warming. Another study suggests more frequent overwintering in Europe as a factor influencing earlier return to the breeding ground (Ptaszyk *et al.* 2003). However, while in the western migratory White Stork population overwintering is becoming more frequent (Gordo *et al.* 2007), in the eastern migratory Stork population this phenomenon is still relatively rare (Nankinov 1994, van den Bossche 2002) and needs more detailed studies incorporating telemetry methods to assess the scale of its occurrence. As a long-distance migrant, the White Stork cannot respond immediately to the weather conditions on the breeding areas from remote wintering grounds. However, during the last part of the route back via SE Europe, birds are influenced by the weather (which is correlated with weather on the breeding grounds), especially by the wind and temperature (Shamoun-Baranes *et al.* 2003) and they can shorten the time of migration in good conditions (in warm springs). Arrival time on the breeding grounds plays a significant role in the spatial pattern and reproduction of the population (Kokko 1999; Janiszewski *et al.* 2013, 2014). Birds that arrive earlier usually have higher breeding success (Tryjanowski *et al.* 2004) but in some cases a very early return does not provide a benefit due to unfavourable weather conditions at the beginning of spring (Janiszewski *et al.* 2013). Therefore, earlier arrival is a trade-off between nest (territory) occupation, avoidance of adverse weather conditions and mismatch avoidance (in this case between the arrival date which influences breeding time and the time of spring meadow mowing). Short-distance migrants like Tits Paridae have also been shown to adjust their time of reproduction and clutch size to local weather conditions (Møller *et al.* 2008, Bordjan & Tome 2014, Glądalski *et al*. 2014).

We did not find a relationship between mean temperature in March and clutch size, despite a relatively large sample size but a longer time series might reveal a stronger relationship. This is in contrast to the earlier study on White Stork in Hungary where low temperatures before egg laying were a main factor reducing clutch size (Sasvári & Hegyi 2001). Similarly, Nol *et al.*(1997), for example, found a significant relationship between clutch size variation and summer temperatures for the more northern, ground nesting Semipalmated Plover *Charadrius semipalmatus*. However, it is not entirely clear when and where females accumulate resources for egg production. Conditions on wintering grounds or on migratory routes may also influence a females' fitness through the number and size of laid eggs, through carry-over effects (Norris 2005, Norris & Taylor 2006, Hahn *et al.* 2009). Clutch size and its range in our study were larger than in earlier research from a study site located in the middle of our study area (Kosicki 2010, Kosicki & Indykiewicz 2011) and in contrast to Kosicki & Indykiewicz (2011) it differed significantly between study years. However, other studies from this part of Europe reveal similar results to ours (e.g. Profus 1991, Sasvári & Hegyi 2001).

We found a significant influence of weather conditions (i.e. minimum ambient temperature) on hatching success which other studies on White Stork and related species have not shown (Sasvári & Hegyi 2001, Kosicki 2011, Polak & Kasprzykowski 2013). However, it seems to be logical that very severe weather conditions may affect embryo development and extremely low temperatures may be a cause of their death (Jovani & Tella 2004). Events with very low temperatures in May in Poland are relatively rare and occur irregularly (Woś 1999). Therefore, to record extremely low temperatures during the incubation phase is difficult during any short term research focused on breeding biology. Long-term breeding biology monitoring may show a clearer relationship between hatching success and temperature during incubation. We found a much larger number of hatchlings than in earlier studies conducted on the smaller site in the middle of our study area (Kosicki 2010, Kosicki & Indykiewicz 2011) but similar to other studies from Poland (Profus 1991). This is probably an effect of difference in sample size.

Mean survival rate of nestlings in our study was lower than that found by Kosicki (2011) where it was near 90%, but we found a much broader range of survival rates between study years, with one year of extremely low nestling survival (only 16%). Nestling survival is strongly dependent on food availability: storks are known to reduce their broods when food availability is low (Zieliński 2002). This can be by infanticide, nestling removal or starvation (Klosowski *et al.* 2002, Valkama *et al.* 2002, Zieliński 2002, Denac 2006, Massemin-Challet *et al.* 2006, Zduniak 2009, Dugas 2010, Moreno 2012). During our study we only recorded a few cases of infanticide but this is difficult to record without permanent nest monitoring via cameras (e.g. Dolata 2006). Unfavourable weather conditions (e.g. strong wind and heavy rain) may strongly reduce breeding effectiveness even in good feeding conditions (Jovani & Tella 2004, Pipoly *et al.* 2013). Kosicki (2011) showed that temperature negatively influenced nestling survival, while Bairlein & Hennenberg (2000) suggested that high precipitation and low temperature occurring simultaneously are a major driver of the nestling survival. We also found a combination of precipitation and temperature was significant, with our results suggesting perhaps counter-intuitively that high precipitation combined with low temperature increased survival. Other studies on open nesting birds indicate rainy, windy and cold weather during chick rearing are key factors reducing chick survival (Sasvári & Hegyi 2001, Jovani & Tella 2004, Denac 2006, Polak & Kasprzykowski 2013). Even for secondary hole nesting birds, weather is the major driver of breeding success but for these birds weather does not directly affect the nestlings, instead it reduces parents' mobility and their foraging abilities (Bordjan & Tome 2014, Glądalski *et al.* 2014). Furthermore, in some local White Stork populations weather conditions may be a main factor affecting population distribution (Radović *et al.* 2014).

In 2013 we observed relatively late nestling mortality. A Cox proportional hazard model for the White Stork reveals that the lowest hazard of death for chicks is in the second half of the time spent in the nest and achieves its asymptote just after 20 days (Kosicki 2011). Stork nestlings achieve homeothermy when they are 15 days old (Jovani & Tella 2004). Surprisingly, nearly 70% of observed nestlings in our study died in the final period of their nestling life with mean age of death of 32 days, with fledging normally occurring at 55-60 days old (Kosicki 2011). This extremely high late mortality is likely due to other factors in addition to weather conditions. During continuing heavy rainfall adults are not able to forage effectively and they cannot meet the food requirements of their nestlings, which constitute near 1 kg per day per one nestling with body mass ca. 3 kg (Kosicki *et al.* 2006). During this study we observed adults which could not even return to the nest because of their wet feathers. The breeding failure rate in 2013 was the highest since 1974, when monitoring of this population was established.

In this paper we have shown that the White Stork as an example of a large, long-lived bird can avoid very adverse weather conditions in the beginning of the breeding season but due to the long period of rearing nestlings it cannot avoid extreme events like unusually heavy rainfall. We found a significantly higher proportion of pairs failing in their reproduction in recent years. Extreme weather events are becoming more frequent and the pattern of rainfall and temperature gradient is changing due to climate change (IPCC 2013). This may suggest that nestling mortality could increase in the near future.

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Table 1. Results from generalised linear mixed models showing effect of temperature and precipitation on breeding behaviour, total number of pairs=591 over 9 years. Note: estimates for Binomial models are given on the logit scale.

Model	Parameter	Estimate	Std. Error	Test statistic	P
Arrival 1	Cold March	7.4	2.4	3.1	0.017
Arrival 2	Cold March	8.0	2.7	3.0	0.021
Arrival 1, including	Cold March	4.9	2.4	2.1	0.088
precipitation	Precipitation	-0.13	0.066	-2.0	0.10
Arrival 2, including	Cold March	5.7	3.0	1.9	0.11
precipitation	Precipitation	-0.12	0.083	-1.4	0.21
Clutch size	Cold March	0.15	0.18	0.8	0.47
	Precipitation	0.004	0.005	0.9	0.46
Hatching success	Frost May	-0.44	0.22	-2.0	0.048
Hatching success,	Frost May	0.16	0.50	0.3	0.76
including precipitation	Precipitation	0.34	0.27	1.3	0.20
Fledging success	Frost May	-1.7	2.0	-0.9	0.39
	Precipitation	-1.4	1.0	-1.4	0.18
Fledging success	Cold June	-4.2	0.52	-8.1	< 0.001
	Precipitation	-2.2	0.21	-10.1	< 0.001
	Cold June: Precipitation	2.4	0.26	9.3	< 0.001

Table 2. Breeding parameters of the White Stork *Ciconia ciconia* in agricultural landscape in Western Poland.

Year	N	Mean clutch size (±SD)	Mean no of hatchlings (±SD)	Mean no of fledglings (±SD)
2009	23	4.30±0.77	3.87±0.62	3.04±0.93
2010	61	4.28±0.82	3.97±0.91	2.75±1.27
2011	58	4.43±0.70	3.83±0.94	2.71±0.99
2012	53	4.09±0.65	3.71±0.72	2.49±0.87
2013	44	4.42±0.66	4.00±0.95	0.59±0.95
Total	**239**	**4.30±0.73**	**3.87±0.86**	**2.31±1.32**

Table 3. Results from generalised linear models showing long term trend in breeding success, total number of pairs=7988, from 27 breeding seasons. Note: estimates for Binomial models are given on the logit scale.

Model	Parameter	Estimate	Std. Error	Test statistic	P
No. Fledglings per pair (all years)	year	0.0060	0.0074	0.8	0.44
Prop. no offspring (all years)	year	-0.0029	0.0022	-1.3	0.19
Prop nestling failure (all years)	year	0.052	0.0040	12.8	< 0.001
No. Fledglings per pair (excluding 2013)	year	0.014	0.0059	2.4	0.025
Prop. no offspring (excluding 2013)	year	-0.019	0.0024	-7.6	< 0.001
Prop nestling failure (excluding 2013)	year	0.0072	0.0050	1.5	0.15

Figure. 1. Arrival dates of the first bird in a pair of nesting White Storks *Ciconia cicocnia* in years with colder temperatures than the mean in March (0) and warmer than the mean in March (1), with ±2 standard errors.

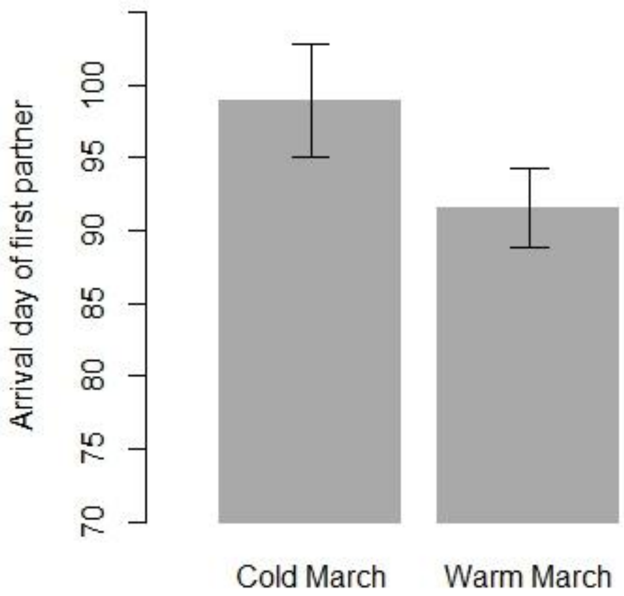

Figure. 2. Mean breeding success (points, JZa - no of fledglings per breeding pair) of White Stork *Ciconia ciconia* breeding population in Western Poland in years 1974 – 2013, with fitted line from the generalized linear model in Table 3 (solid line).

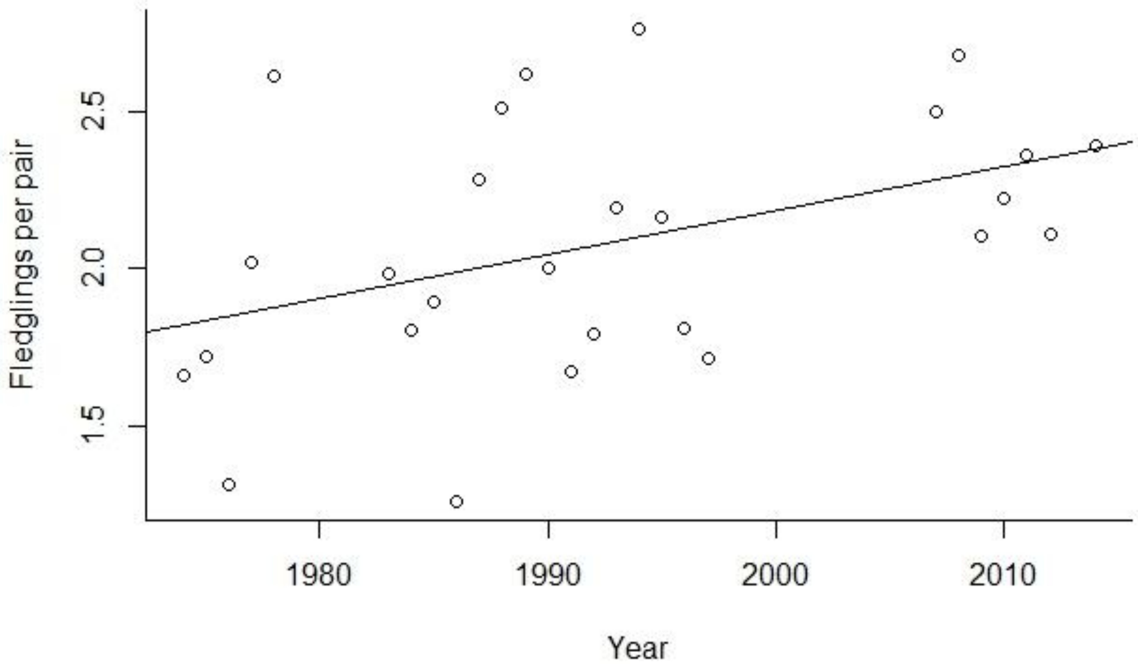

Figure. 3. Proportion of pairs with no offspring (points) of White Stork *Ciconia ciconia* breeding population in Western Poland in years 1974 – 2013, with fitted line from the generalized linear model in Table 3 (solid line).