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Effects of climate variables on the White Stork (*Ciconia ciconia* L.) productivity in a long term study

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Abstract We analysed the effects of weather and climatic patterns on the productivity of the White Stork in Hungary between 1958 and 2017, using i) linear mixed effect models (LMM), ii) LMM-s extended by a single random effect variable or a nested combination; iii) LMM-s extended by a single fixed effect variable and iv) using an additive model of the selected variables. As a preselection, the following climatic variables were identified with substantial support: March mean temperature, March precipitation, April mean temperature, June mean temperature, June precipitation (negative), July mean temperature. The slight increase of the mean number of fledged chicks over 59 years could be the result of the increasing mean temperature, but in itself it might not be strong enough to prove that climate change will overall benefit White Stork productivity. Higher temperature and precipitation values are favourable, probably because of the higher biomass, providing more prey, but high precipitation is unfavourable until the thermoregulation of chicks is not developed. Decreasing amounts of precipitation may cause loss of wetlands as suitable feeding sites. Extreme weather is important to complement the picture given by climate change.

Keywords: climate change, weather effect, White Stork, productivity

Összefoglalás Az időjárás- és klímamintázatok fehér gólya produktivitására gyakorolt hatásait elemeztük 1958–2017 közötti magyarországi adatsorokon i) lineáris kevert modellekkel (LMM), ii) LMM, kiterjesztve egyetlen random hatású változóval vagy beágyazott kombinációval, iii) LMM, kiterjesztve egyetlen fix hatású változóval és iv) a kiválasztott változókkal additív modellben. Az előzetes szelekció során a következő klimatikus változókat azonosítottuk alapvető jelentőségűnek: márciusi átlaghőmérséklet, márciusi csapadékösszeg, áprilisi átlaghőmérséklet, júniusi átlaghőmérséklet, júniusi csapadékösszeg (negatív előjellel), júliusi átlaghőmérséklet. A kirepült fiókák átlagos számának 59 év során bekövetkezett enyhe emelkedése lehet az átlaghőmérséklet emelkedésének következménye, de önmagában nem elég erős bizonyítéka annak, hogy a klímaváltozás általában pozitív hatással van a fehér gólya produktivitására. A magasabb hőmérséklet és a több csapadék kedvezőbb, valószínűleg a magasabb biomassza miatt, ami több táplálékkal szolgál, de a sok csapadék kedvezőtlen addig, amíg a fiókák hőszabályozása nem elég fejlett. A csökkenő csapadékmennyiség okozhatja az alkalmas táplálkozóterületnek számító vizes élőhelyek eltűnését. Az extrém időjárás hatásairól alkotott ismeretek fontosak abban, hogy kiegészítik a klímaváltozás által alkotott képet.

Kulcsszavak: klímaváltozás, időjárás hatása, fehér gólya, költési siker

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Introduction

The strong ecological effects of climate change has been demonstrated in a large number of studies (Doran & Zimmerman 2009, Scheffers *et al.* 2016, Sheldon 2019) and also its anthropogenic origin is widely supported (IPCC 2021). Responses of affected ecosystems manifested in phenological changes: flowering and leaf unfolding occur earlier in plants (Mo *et al.* 2017), migratory birds arrive earlier in spring (Csörgő *et al*. 2009, Pautasso 2011, Harnos *et al*. 2015), mismatch occurs in interacting species whose life cycle asynchronically shifted, which acts at community level (Nakazawa & Doi 2012), distribution of species changes in latitude (Tryjanowski *et al*. 2005b, Chamberlain *et al*. 2012, Moren-Ruenda *et al*. 2012, Chodkiewicz & Sikora 2020) and altitude (Popy *et al*. 2009, Freeman 2018), both in terrestrial and marine ecosystems (Poloczanska 2013).

The White Stork *(Ciconia ciconia)* is a large, long-distance migratory bird, a model species of population and breeding ecology with long-term datasets available (BirdLife International 2015, Kaatz *et al*. 2017, Lovászi *et al*. 2020), which makes it a perfect candidate to study climate change at different spatial scales. The European population increased in the last two decades of the 20th century, since then the smaller western populations increase and the Eastern core population decrease (Kaatz *et al*. 2017, PECBMS 2022).

Hungary is a particularly suitable area for such a study, as three climatic regimes (Mediterranean, continental, oceanic) influence the weather to a constantly varying extent and duration, therefore, significant differences in weather may occur despite the relatively small area and flat surface of the country. The absolute minimum temperature is –35 °C, the absolute maximum is +41.9 °C, the local annual precipitation varies between 203 and 1554.9 mm (Hungarian Meteorological Service 2022).

The aim of our study was to analyse whether there are differences in productivity (mean number of nestlings) between the regions, are the differences due to weather effects or caused by independent geographical factors, are the differences caused by mixed effects of these above mentioned factors, how extreme weather conditions affects the productivity.

Materials and Methods

We analysed White Stork breeding data recorded between 1958 and 2017, retrieved from two resources. For the 1958–1989 period, censuses were conducted every five years via printed questionnaires. Two types of protocols ran in parallel: simplified forms (po) sent out to post offices, filled out by post workers; and more detailed questionnaires (qu) sent out to amateur ornithologists, forestries, hunting companies, high schools, etc., filled out by their members or volunteers (Lovászi 1998). These data are archived in the Móra Ferenc Múzeum, Szeged. For the 1994–2017 period, volunteers of the MME/BirdLife Hungary collected the data. This database is now fully available in electronic format, provided by the Monitoring Centre of the MME/BirdLife Hungary. Since the repetition of observations were not expected and 100% coverage was not ensured, the number of White Stork pairs is probably underestimated and there could be also differences in productivity, but these estimates do not differ significantly from real values, as this study states (Aguirre & Vergara 2009).

For our study, we chose six out of the 19 Hungarian counties (namely Győr-Moson-Sopron, Somogy, Bács-Kiskun, Békés, Hajdú-Bihar and Szabolcs-Szatmár-Bereg County). We considered the following criteria: 1. data available from every year, 2. there are enough breeding pairs for the analysis, 3. they represent different geographical and socio-economical regions of Hungary.

Water permeability of soil types affects the amount of water covered areas which is in relation to the distribution of White Storks, therefore we present the soil types of the counties along with the main water bodies, the typical agricultural use and the human population density (Mezősi & Bata 2011, https://www.ksh.hu/).

– Győr-Moson-Sopron (GYMS): soil types: fluviosols, gleysols, phaeozems, chernozems (near rivers), luvisols (Transdanubian Mountains). Main waters: Danube, Rába, Rábca. Agricultural usage: 4.8% grassland, 53.5% arable land, 19.2% forest. Density: 107/km^2.
– Somogy: soil types: fluviosols, gleysols, phaeozems (near rivers and lakes), luvisols, arenosols, cambiosols. Main waters: Dráva, lake Balaton. Agricultural usage: 5.2% grassland, 42.2% arable land, 29.5% forest. Density: 52/km^2.
– Bács-Kiskun (BK): soil types: regosols, solonchaks, fluviosols (along Danube), chernozems (Bácska region). Main waters: Danube, alkaline, saline lakes. Agricultural usage: 12.3% grassland, 41.3% arable land, 20.9% forest. Density: 61/km^2.
– Békés: soil types: chernozems, rendzinas, phaeozems, vertisoils. Main waters: Körös, Berettyó. Agricultural usage: 5.5% grassland, 67.7% arable land, 4.6% forest. Density: 63/km^2.

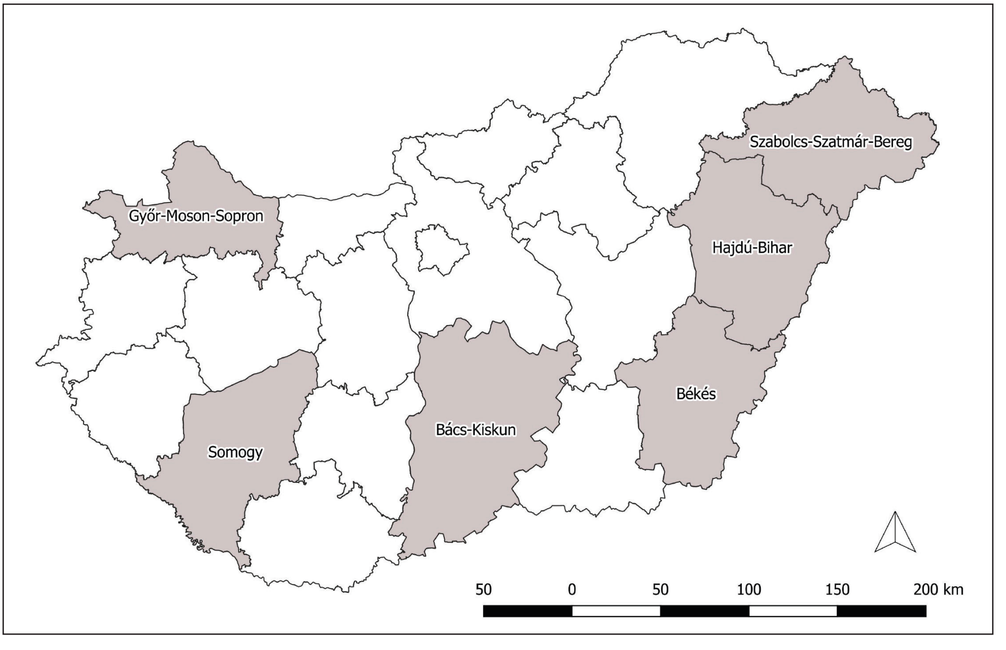

Figure 1. Map of Hungarian counties studied
1. ábra A vizsgált magyarországi megyék

- Hajdú-Bihar (HB): soil types: chernozems, solonetzes (Közép-Tisza region). Main waters: Tisza, Berettyó, alkaline-saline lakes. Agricultural usage: 17.7% grassland, 53.1% arable land, 11.1% forest. Density: 86/km^2.
- Szabolcs-Szatmár-Bereg (SZSZB): soil types: regosols, arenosols; phaeozems, fluviosols (along rivers). Main waters: Tisza. Agricultural usage: 10.8% grassland, 44.4% arable land, 21.1% forest. Density: 94/km^2 *(Figure 1)*.

Questionnaire data were digitized in MS Office Excel 2003 in .csv format, by county. The following variables were derived from the forms: year, settlement, address, number of adults, chicks hatched, chicks fledged, date. The postal forms up to 1989 only asked the number of nests (in the postal district) and their nest site and occupancy, but since many reported detailed breeding information, the exactly identifiable ones were included. We also marked the nesting status (successful pairs, pairs without young fledged, lonely stork, unoccupied) and redundancy (is the record identical to a previous one) for easier analysis. In case of the latter, the record with the most exact information was marked as nonredundant. The nonredundant successful pairs and pairs without young fledged were filtered from the paper data and merged with the successful pairs and pairs without young fledged from the electronic data (which was already nonredundant and in suitable format). The next step was to sum the presence of data by settlement and year. To examine the long-term effect of climate, we selected settlements which have data from at least 15 years. The productivity – the mean number of fledged chicks – was calculated for each settlement. To investigate whether there are regional differences in productivity, medium and microregions were assigned to each settlement (Marosi & Somogyi 1990). Number of records of the final dataset was assessed per year and county *(Table 1)*.

For the climate variables, we used the data of the following meteorological stations: Baja and Kecskemét (BK); Békéscsaba (Békés); Győr and Sopron (GYMS); Debrecen (HB); Siófok (Somogy); Nyíregyháza (SZSZB). Station data were retrieved from two sources: from the Hungarian Meteorological Service (HMS) for the 1958–1974 period, and from the Ogimet weather information service portal (http://www.ogimet.com/gsodc.phtml.en#est) for the 1979–2017 period. For analysis related to the breeding period, we used the mean temperature (°C) and the sum precipitation (mm) of months March–July, averaged (in case of mean temperature) and summed (in case of precipitation) for a whole month. Since HMS provided weekly, not daily data, the following month boundaries were made: 01.03–04.04., 05.04–02.05., 03.05–30.05., 31.05–27.06., 28.06–25.07. Otherwise, it was processed the same way as Ogimet data. In case of Bács-Kiskun and GYMS, where two stations were available, regions were assigned to the following stations: Bácskai-löszös síkság, Mohácsi-sziget, Kalocsai-sárköz to Baja; Kiskunsági-löszöshát, Solti-sík, Kiskunsági-homokhát and Dél-Tiszavölgy to Kecskemét; Kapuvári-sík, Ikva-sík, Répce-sík, Soproni-hegység, Fertő-medence and Fertőmelléki-dombság to Sopron; Csornai-sík, Mosoni-sík, Pápa-Devecseri-sík, Pannonhalmi-dombság, Szigetköz and Igmánd-Kisbéri-medence to Győr.

As an initial step, the same monthly temperature and precipitation values of the different stations were compared with Pearson's correlation. After that, we used linear mixed effect models to further investigate the effects of climate variables (which were the fixed effects,

Table 1. Number of White Stork productivity records per year and county
1. táblázat A fehér gólya produktivitási adatsorok száma évre és megyére lebontva

year	Békés	BK	GYMS	HB	Somogy	SZSZB	sum / year
1958	6	0	57	1	3	14	81
1963	15	4	44	1	5	43	112
1968	22	0	38	3	3	29	95
1974	18	10	46	2	6	33	115
1979	29	9	47	3	3	59	150
1984	33	6	47	2	9	66	163
1989	40	8	65	3	10	57	183
1994	0	2	51	0	7	76	136
1999	0	5	54	5	7	92	163
2000	0	1	0	0	1	67	69
2001	1	6	54	0	1	73	135
2002	33	1	1	2	1	85	123
2003	6	4	9	2	10	87	118
2004	16	9	62	5	11	111	214
2005	14	6	62	3	11	97	193
2006	36	5	59	5	11	110	226
2007	42	9	6	5	11	108	181
2008	42	7	4	2	10	114	179
2009	42	8	54	5	9	109	227
2010	41	6	50	4	8	108	217
2011	42	10	61	5	9	50	177
2012	42	10	59	3	9	102	225
2013	42	8	60	2	4	115	231
2014	41	10	63	5	7	111	237
2015	41	9	60	4	10	89	213
2016	41	10	62	4	3	83	203
2017	41	8	64	5	1	74	193
sum /county	726	171	1239	81	180	2162	
total sum							4559

along with the year variable) and spatial variables (which were the random effects) on productivity. Before building more complex models, a preselection was made by applying a Linear Mixed Model (LMM). lmer(productivity ~ year) was considered a null model (Bates *et al.* 2015). Models extended by a single random effect variable or a nested combination of those were compared to find the one with the lowest AIC value. Models extended by a single fixed effect variable were investigated and the ones with a |t-value| > 2 – as a rule of thumb for significance, using a conservative approach (Siegel 2012) – were considered. As a final step, an additive model of the selected variables were build and investigated. Models were tested in R programming environment (R Core Team 2015).

Table 2. The Pearson's correlation of climatic variables between the studied weather stations
2. táblázat A klimatikus változók Pearson-korrelációja a vizsgált meteorológiai állomások között

	Tmean.mar	Prec.mar	Tmean.apr	Prec.apr	Tmean.may	Prec.may	Tmean.jun	Prec.jun	Tmean.jul	Prec.jul
Baja_Bekes	0.899	0.804	0.902	0.836	0.840	0.224	0.842	0.463	0.823	0.623
Baja_BK	0.938	0.820	0.889	0.899	0.849	0.476	0.909	0.419	0.886	0.537
Baja_GYMS	0.933	0.642	0.874	0.565	0.813	0.391	0.899	0.135	0.828	0.652
Baja_HB	0.875	0.687	0.920	0.684	0.786	0.522	0.829	0.406	0.802	0.343
Baja_Somogy	0.945	0.745	0.881	0.674	0.803	0.506	0.869	0.340	0.839	0.163
Baja_Sopron	0.907	0.357	0.797	0.421	0.788	0.505	0.860	0.315	0.800	0.350
Baja_SZSZB	0.862	0.606	0.893	0.673	0.750	0.278	0.808	0.433	0.829	0.062
Bekes_BK	0.947	0.869	0.939	0.654	0.971	0.253	0.960	0.363	0.954	0.380
Bekes_GYMS	0.859	0.802	0.913	0.539	0.902	0.143	0.927	0.057	0.901	0.559
Bekes_HB	0.973	0.819	0.981	0.669	0.976	0.578	0.964	0.712	0.958	0.634
Bekes_Somogy	0.931	0.868	0.903	0.572	0.918	0.330	0.947	0.380	0.929	0.209
Bekes_Sopron	0.829	0.521	0.836	0.625	0.899	0.165	0.900	0.248	0.828	0.178
Bekes_SZSZB	0.957	0.766	0.953	0.639	0.928	0.057	0.923	0.323	0.914	0.170
BK_GYMS	0.913	0.661	0.939	0.509	0.898	0.947	0.955	-0.040	0.917	0.284
BK_HB	0.962	0.844	0.958	0.740	0.965	0.408	0.932	0.465	0.945	0.212
BK_Somogy	0.963	0.883	0.935	0.457	0.920	0.361	0.960	0.402	0.939	0.150
BK_Sopron	0.900	0.370	0.894	0.323	0.888	0.508	0.920	0.192	0.881	0.207
BK_SZSZB	0.959	0.844	0.933	0.655	0.892	0.372	0.876	0.388	0.934	0.133
GYMS_HB	0.870	0.649	0.917	0.743	0.916	0.370	0.885	0.103	0.926	0.235
GYMS_Somogy	0.955	0.779	0.944	0.522	0.941	0.334	0.980	0.258	0.967	0.527
GYMS_Sopron	0.970	0.837	0.962	0.710	0.973	0.553	0.977	0.331	0.962	0.634
GYMS_SZSZB	0.884	0.588	0.899	0.678	0.893	0.401	0.837	0.139	0.909	0.087
HB_Somogy	0.944	0.776	0.902	0.590	0.925	0.727	0.920	0.526	0.961	0.031
HB_Sopron	0.857	0.502	0.846	0.627	0.907	0.246	0.844	0.397	0.870	0.026
HB_SZSZB	0.989	0.863	0.967	0.884	0.964	0.491	0.977	0.569	0.969	0.347
Somogy_Sopron	0.948	0.612	0.946	0.483	0.967	0.316	0.965	0.378	0.930	0.049
Somogy_SZSZB	0.942	0.818	0.901	0.541	0.852	0.494	0.875	0.232	0.922	0.018
Sopron_SZSZB	0.871	0.411	0.838	0.457	0.872	0.137	0.800	0.305	0.871	0.208
mean	0.921	0.705	0.909	0.620	0.893	0.396	0.905	0.330	0.900	0.286

Table 3. Comparison of null models with different random spatial variables. npar = number of parameters, AIC = Akaike information criterion, BIC = Bayesian information criterion, logLik = log-likelihood, Chisq = Chi-square test statistic, Df = degree of freedom, Pr(>Chisq) = significance of Chi-square test statistics, reg.med = medium region, reg.small = microregion

3. táblázat Nullmodellek összehasonlítása különböző random térbeli változókkal. npar = paraméterek száma, AIC = Akaike-kritérium, BIC = Bayes-kritérium, logLik = log-likelihood, Chisq = khí-négyzet próba, Df = szabadságfok, Pr(>Chisq) = a khí-négyzet próba szignifikancia-szintje, reg.med = középtáj, reg.small = kistáj

random variable	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
county	4	12668	12694	-6330.1	12660			
reg.med	4	12654	12679	-6322.8	12646	11.6182	0	
reg.small	4	12687	12713	-6339.5	12679	0	0	
settlement	4	12725	12751	-6358.6	12717	0	0	
county/reg.med	5	12653	12685	-6321.6	12643	73.9936	1	< 2.2e-16 ***
county/reg.small	5	12663	12696	-6326.7	12653	0	0	

Results

The average correlation coefficients between two meteorological stations for temperatures and precipitation are: Tmean.mar = 0.9208, Prec.mar = 0.7050, Tmean.apr = 0.9094, Prec.apr = 0.6202, Tmean.may = 0.8927, Prec.may = 0.3961, Tmean.jun = 0.905, Prec.jun = 0.3299, Tmean.jul = 0.8997, Prec.jul = 0.286 (for the full table for each individual pairs, see *Table 2*). The preselection on the random effects in the linear mixed effect models showed that among spatial variables, the medium region nested within the county has the lowest AIC value: 12643 (for table of all models, see *Table 3*). As for the preselection of fixed effects, the following climatic variables were found with t values > 2: year = 13.38, Tmean.mar = 7.025, Prec.mar = 7.233, Tmean.apr = 8.342, Tmean.jun = 9.099, Prec.jun = –5.310, Tmean.jul = 4.659. The final full model was: m_full = lmer(fled.mean ~ Tmean.mar + Prec.mar + Tmean.apr + Tmean.jun + Prec.jun + Tmean.jul + (1 | county/reg.med)). The t values for the fixed effects were: Tmean.mar = 5.359, Prec.mar = 9.313, Tmean.apr = 5.868, Tmean.jun = 4.090, Prec.jun = –3.693, Tmean.jul = –1.771. The variance for the random effects was: regmed:county = 0.05057, county = 0.05835 with total variance = 1.0033 (see *Table 4*).

Discussion

Climate is one of the stochastic environmental factors affecting populations: unpredictable, uncontrollable and involves all individuals. It can influence individuals directly, for example through their development or survival, or indirectly, for example through the availability of food (Kaatz *et al*. 2017). The White Stork, as a large, long-lived bird species, is mainly affected through its prey (Nevoux 2008), however, weather has a direct influence for the survival of the chicks up until their thermoregulation fully develops at three weeks old (Denac 2010).

Table 4. The statistics of model with the preselected fix and random variables. AIC = Akaike information criterion, BIC = Bayesian information criterion, logLik = log-likelihood, residual df = residual degree of freedom, std. error = standard error, rel. variance = relative variance

4. táblázat A kiválasztott fix és random változókat tartalmazó modell statisztikái. AIC = Akaike-kritérium, BIC = Bayes-kritérium, logLik = log-likelihood, residual df = reziduális szabadságfok, std. error = standard hiba, rel. variance = relatív variancia

Model criterions					
	AIC	BIC	logLik	deviance	residual df
	12408.2	12478.8	-6193.1	12386.2	4515
Number of observations					
medium region:county					22
county					6
total					4526
Fixed effects					
	estimate	confidence intervals		std. error	t value
intercept	-15.174	-20.074	-10.274	2.498	-6.074
year	0.008	0.005	0.010	0.001	6.040
march mean temperature	0.085	0.054	0.116	0.016	5.359
march sum precipitation	0.141	0.111	0.171	0.015	9.313
april mean temperature	0.096	0.064	0.128	0.016	5.868
june mean temperature	0.075	0.039	0.111	0.018	4.090
june sum precipitation	-0.056	-0.085	-0.026	0.015	-3.693
july mean temperature	-0.031	-0.066	0.003	0.018	-1.771
Random effects					
			std deviation	variance	rel. variance
medium region:county			0.225	0.051	0.050
county			0.242	0.058	0.058
residual			0.946	0.894	0.891

The food supply of the White Stork is also influenced by various descriptors of climatic variability on its breeding and wintering grounds and on the migration route as well. There is a connection between the NDVI (the most commonly used vegetation index to estimate phytomass) and the survival of individuals on the wintering grounds (Schaub *et al*. 2005, Nevoux 2008). There is a difference between the sexes in how much weather affect the timing of arrival: females are more dependent on temperature (Gordo 2013). The outcome of spring migration affects breeding success of the population: the ratio of successful breeding pairs is lower in years with delayed arrival. Adverse weather circumstances during migration result weaker condition and lower body mass at arrival, so fewer pairs start to breed, and breeding pairs have fewer eggs (Profus 1991). Storks breeding in Hungary use the eastern migration route (Lovászi & Rékási 2009), where bird are more exposed to weather conditions during wintering and migration compared to western populations (Kaatz *et al*. 2017). The influence of the Sahel on the western stork population has decreased in recent decades (Nevoux 2008).

The amount of food that can be collected by storks also depends upon the density of prey animals and the vegetation cover. Warmer temperatures in March and April facilitates the earlier development of the vegetation and thus the higher amount of insects and rodents as prey animals. Warmer June and July weather may increase the activity of prey. Models showed no significant correlation between May mean temperature and productivity of storks, maybe because of the very variable weather of this month. Precipitation is also important for the development of the vegetation, but with two possible opposite impact. Higher precipitation in March facilitates vegetation. Precipitation in June regularly occurs together with colder weather, causing increased mortality of the offspring.

The climate correlations between stations within Hungary showed that differences were higher in the precipitation than in the temperature. According to IPCC predictions, precipitation patterns will become more unpredictable and variable due to climate change (IPCC 2021), which means the differences will more likely grow, so it is crucial to consider spatial variation at various scales to see how it affects the White Stork population. The slight increase in mean number of fledged chicks over 59 years (estimate: 0.008, see *Table 4*) could be the result of the increasing mean temperature, but in itself it might not be strong enough to prove that climate change will overall benefit White Stork productivity. Moreover, the results of Martín *et al*. (2021) show that there has been a gradual decrease in survival of Western European populations as a result of climate change, affecting juvenile birds more strongly.

The weather of the breeding areas determines the local food conditions, which mainly affects productivity. Winter precipitation is positively correlated with the mean number of chicks (Lovászi 2013), as the number and size of areas covered with shallow water preferred by storks increase. The correlation between the May and June NDVI values of the feeding areas around the 1.5 km radius of the nest and the average number of chicks is also positive (Kosicki 2010). The temperature and precipitation conditions of the spring-summer months affect small mammals, e.g. for the behaviour of the Common Vole *(Microtus arvalis)*: they move more in warmer weather, so storks are more likely to prey on them. However, in rainy years earthworms can be found in larger masses, that are more favorable for young chicks (Thomsen 1995).

Habitat quality can also modify the impact of weather on productivity: more chicks hatch in a better habitat, they can heat each other more efficiently, and as they are in better condition, reach the body weight needed for homeothermality sooner, the weather has less effect on them (Denac 2006). Due to the unpredictability, the effect of precipitation out of the climatic factors is more critical: while temperature rise steadily each year (regardless of baseline), a heavy storm, more rainfall can occur at any stage of breeding (Bert & Lorenzi 1999). Depending on latitude, the temperature conditions of which month have the greatest effect on productivity may vary, but the role of May precipitation is equally important in each region (Moritzi *et al*. 2001, Jovani & Tella 2004).

According to research in Poland and Slovakia, global warming reduce the differences in altitude for storks: higher, cooler regions's climate become milder and thus more habitable by storks (Tryjanowsky *et al*. 2005a, Gordo 2013). The same is true for latitude: in the last 30 years, the White Stork may have spread in the Baltic States due to global warming

(Kosicki 2010, Kaatz *et al*. 2017). Moreover, the impact of weather on productivity may diminish, as storks feed more and more on landfills (both in their breeding and wintering grounds), making their survival less and less dependent on local natural vegetation (Djerdali *et al*. 2016, Gilbert *et al*. 2016, López-Garcia *et al.* 2021), although number of breeding pairs affected mainly by anthropogenic environmental factors do not automatically reflects for the breeding success (Bachir 2013).

One of the reasons for the increase in the mean number of offsprings in our study is climate change: the positive effect of temperature variables on productivity is clear in all climate models. According to our results, the maximum temperature is the strongest explanatory variable among the temperature components. In previous studies, a relationship was found with the mean temperature (Moritzi *et al*. 2001, Jovani & Tella 2004, Kosicki 2010). While this is a good indicator of the temperature throughout the day, extreme values are likely to be of even greater biological significance. It is possible, for example, that during the heat-sensitive period it is particularly important how well the chicks can warm up, which is determined by the maximum temperature.

Precipitation also proved to be a significant positive variable in the three strongest models, which was also expected from the results of previous studies, as local precipitation conditions affect the vegetation index of the breeding area and thus the number of hatching chicks through the food supply (Schaub *et al*. 2005). However, the interaction of precipitation with each temperature variable is negative, i.e. the higher the temperature, the less the precipitation. An increase in temperature and precipitation is also favourable for storks, but they do not usually rise at the same time. While higher temperatures are likely to be favourable at all stages of breeding, high precipitation can be detrimental in the heat-sensitive period of the chicks. Examining the months of extreme weather is therefore important to complement the picture given by climate change. The distribution of precipitation has a significant effect on productivity, but with different signs for each month: in March, for example, rainy weather is strongly positive and drought is strongly negative (Cuadrado *et al*. 2016). Storks are not yet in the breeding area for most of March, arriving at the end of the month: the cold may delay the arrival of storks, but does not affect breeding success (Kosicki 2010). The rains in March establish the food base of storks as in Hungary there are a lot of temporary wet grasslands and other wetlands with shallow water, which in certain years can be dry all year round.

The warmth of early spring also has a positive effect: it accelerates the development of vegetation and the appearance of herbivorous insects. The key role of early spring temperatures may be indicated by that the effect of the extreme cold was only significantly negative in March; chicks are not affected, negative effects affect only vegetation. At first glance, the positive correlation of cold extremes of the other months, especially the significant values in April and May, seem surprising. A possible explanation for this is that cold extremes are rarely coupled with rainfall, and low temperatures alone do not risks chicks (hatching is typical during this period and small chicks can be covered by the parents to keep them warm). Nevertheless, it is true that the effect of warm extremes is more favourable than that of cold, as less energy is needed to heat eggs or chicks (Denac 2010). An exception to this is July, when the positive effect of cool weather is significantly greater than heat: probably because higher temperatures in this month tend to reduce the amount of food by increasing the evaporation and the vegetation can dry out without rainfall, which has a negative effect on the food supply. However, our results do not support that the lack of rainfall in the summer months would have an overall negative effect on the average number of hatching chicks through the vegetation index (Schaub *et al*. 2005), but the positive trend in dry weather is declining from May onwards. It is more favourable for the chicks if the rainfall conditions tend to shift towards dry land, but they require more and more food, that can only be provided by a habitat in the right condition. Extreme heat is therefore harmful to the habitat, not to the chicks: the heatwave is not only tolerated by the chicks, but we have a significantly positive effect according to our results. Studies in Spain show that extremely high temperatures do not affect their survival, as they occur at the end of the breeding season, when the mortality of the chicks is already low (Jovani & Tella 2004). In Poland, the growth rate of chicks was different in particular years affected by temperature and precipitation (Kosicki & Indykiewicz 2011), and the most critical period during the breeding period was the time of incubation and the first days after hatching (Kosicki 2012).

Climate models for the entire breeding period show that the level of significance of climate variables and their interactions decreases compared to the original climate model: the weather of the months of the breeding period together better explains productivity than the maximum temperature, precipitation, and their interaction together. This shows that different weather conditions are optimal for storks at different stages of their development. Based on our results, for example, a higher precipitation in March, a lack of precipitation in May, a cold in April, and a warm in June plays key role, and cooler period in July is also important (for good vegetation conditions).

Overall, the average number of nestlings has increased in most of the counties studied since 1958, and our models suggest that this may be due to the warming of recent decades. The higher the temperature, the higher the productivity of the storks: the relationship with the minimum, average and maximum temperatures is significantly positive, but the effect of the maximum temperature is the strongest. This is an important result as it draws attention to the importance of extreme values. In the case of precipitation, productivity in generally better with increasing amount, but its distribution is significant: more precipitation is favourable in March because it establishes the water supply of the vegetation, thus increasing the area's food base, but rains in May and June can perish chicks. A more detailed examination of the weather in the months of the breeding season reveals how extreme the various stages of spending affect productivity: in July and April, for example, the influence of precipitation is significantly smaller than in the other months. The variance between counties is low for all climate models: this means that the influence of weather is independent of the region.

On a large scale, warming is predicted, which is favourable for productivity; however, on a small scale, extreme weather events are expected to become more frequent and, as our results show, even a short period extreme weather can significantly reduce the productivity. If there are more frequent years in which very few young fly out due to an extreme weather period, the age group dynamics of the population will change.

It should be noted, however, that the present study only examines the effects of weather on productivity and therefore its results may in themselves be misleading for future population developments. During the period under review, Hungary's stork population decreased from about 16,000 pairs to 4,000 pairs, presumably due to unfavourable changes in nesting sites and feeding grounds (Lovászi *et al*. 2020), and population development of the last two decades is similar to other East-European populations (Lovászi 2022).

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