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ORIGINAL ARTICLE

White stork nest altitude decreases as global temperatures increase

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Abstract

Climate change causes altitudinal shifts of animal distributions and this effect can potentially be accentuated or altered due to human agricultural activities. Because of the availability of uniquely long-term monitoring data, we chose the white stork (*Ciconia ciconia*) as a model species. We analyzed large data sets (record cards from 1191 nests) covering the long-term period from 1875 to 2005 in the Czech Republic, central Europe. We analyzed nest altitude during years of founding of the nest, temperature, land use variables and types of nests (natural vs. human provided nest pads). Consistent with findings from previous studies we predicted a temporal increase in the altitude of white stork nests. Surprisingly, we found that the altitude of nests was decreasing, despite an increase in local mean spring temperatures. The altitude of nests was higher when the proportion of arable land, water areas and developed land was lower and when the proportion of grass and forest cover was greater. The decrease in altitude was significant in natural nests (built by storks) but non-significant in nests on nest platforms (built by humans). Thus, human agricultural activities might potentially override the opposing effects of global climate change on animal altitudinal distribution shifts.

Keywords Altitude · Climate change · *Ciconia ciconia* · Temperature · Land use

Introduction

Global temperatures have changed dramatically over the last century throughout the world (Ahas and Aasa 2006; Bartošová et al. 2014; Roth et al. 2014; Hansen et al. 2016), and climatic changes are now a generally accepted phenomenon (Konvicka et al. 2003; Ahas and Aasa 2006; Parmesan 2006; Reif and Flousek 2012). Mean global surface temperatures rose by 0.6 ± 0.2 °C over the twentieth century (IPCC 2001). The effects of global climate change are well documented for terrestrial organisms (Konvicka et al. 2003; Tryjanowski et al. 2005a; Ahas and Aasa 2006; Gordo et al. 2013; Roth et al. 2014). For example, species of vascular plants bloom earlier and shift their distributions to higher altitudes (Ahas and Aasa 2006; Roth et al. 2014). These shifts in distribution ranges are not as common in animals (Konvicka et al. 2003; Tryjanowski et al. 2005a; Roth et al. 2014). However, animal ranges are also known to shift to higher altitudes in response to global climate change (Konvicka et al. 2003; Tryjanowski et al. 2005a). These range shifts are direct or indirect responses of species to exploit ranges that meet their habitat requirements and have been documented in a variety of taxa (invertebrates: Konvicka et al. 2003; Jore et al. 2011; Roth et al. 2014; fishes: Jung et al. 2013; birds: Valiela and Bowen 2003; Brommer 2004; Tryjanowski et al. 2005a; Zuckerberg et al. 2009; Popy et al. 2010; Paprocki et al. 2014; and mammals: Levinsky et al. 2007).

Here we focused our attention on the population of white storks (hereafter stork) in the Czech Republic. Increasing temperatures across the Czech Republic (Bartošová et al. 2014) may have increased the altitude at which white storks (*Ciconia ciconia* Linnaeus, 1758) nest, as they have in Poland (Tryjanowski et al. 2005a). The stork is ideally suited for examining these patterns, because long-term monitoring of this species in Europe and also in Czech Republic provides a

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detailed account of breeding times and locations (Rejman and Lacina 2002; Thomsen 2013). Storks are familiar, easily identified and historically nest within close proximity to human populations (Tobolka et al. 2012; Jerzak et al. 2016).

White stork nests are most commonly found near areas that match their habitat requirements (Tryjanowski et al. 2009; Jagiello et al. 2018). They require wet pastures near nests (Olsson and Rogers 2009; Olsson and Bolin 2014), open meadows and grasslands (Olsson and Rogers 2009; Tobolka et al. 2012; Janiszewski et al. 2013), and an abundant rodent population (Tryjanowski and Kuzniak 2002; Hušek et al. 2013). However, agricultural practices with dry areas (Janiszewski et al. 2013) can negatively affect nesting success. For example, the mortality of young storks was greater when they were reared in nests found on, or in the vicinity of, electricity poles (Kaluga et al. 2011). An additional factor affecting the location of white stork nests is the increasing availability of man-made nesting platforms (Tryjanowski et al. 2009), which may be placed in slightly different habitats than natural nests.

Here, using a long-term dataset, we compare two hypotheses that may explain the temporal changes in stork nesting altitude in the Czech Republic. First, increasing temperature and changes in agricultural land use may influence the altitude of white stork nests, with storks nesting at higher altitudes during warmer years. Alternatively, man-made platforms may affect the altitude of white stork nests. Specifically, if nesting platforms were created by humans at lower altitudes, we expect that storks will nest lower over time.

Material and methods

Long-term dataset

We used long-term national census data compiled by the Czech Society for Ornithology, which conducts annual national censuses (Rejman 1990; Rejman and Štollmann 1986). This dataset documents white stork nests ($n = 1191$) founded from 1875 to 2005. It covers 50 out of the 77 districts (Fig. 1.) where white storks are known to breed across the Czech Republic (i.e., contemporary political boundaries). There are five districts (Capital city Prague, Prague west, Prague east, Most, Jablonec nad Nisou) that contain no white stork breeding records.

For each nest, we included in our analyses its year of founding (i.e., each nest represented one data point, thus there was no pseudoreplication: Hurlbert 1984). Since the quality of the data varied, we coded the year of founding of each nest either as "estimated" or as "known". When the year of

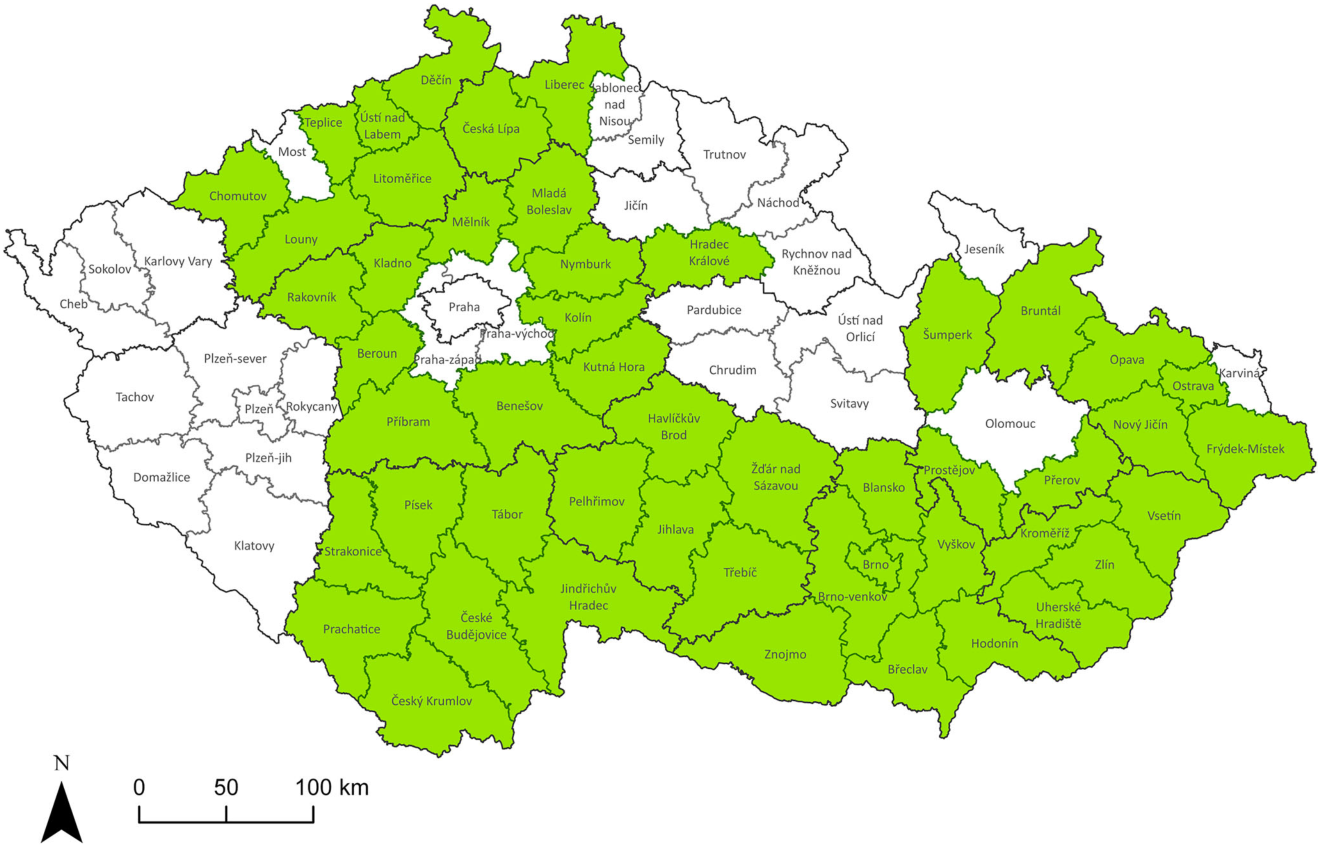

Fig. 1 Districts included in the present study (green) in the Czech Republic (white districts not included)

Table 1 Trend in altitude of white stork nests in the year of founding for nests where the year of founding is known (1907–2005)

Period	Estimate± SE	DF	t	*p*
$r^2 = 0.03$	−1.39 ± 0.24	978	−5.82	<0.0001

founding was estimated, we either used the year of the first observation or we calculated the average year of founding from the range of years reported on the nesting cards documenting storks breeding at each nest (mean ± SE = 1968 ± 1.5, min = 1864, max = 2004); data quality "estimated"). For each nest, we then recorded the altitude above sea level of the closest village using Google Earth (Google 2012).

Environmental data

We used free temperature data from the Czech Hydrometeorological Institute (www.chmi.cz), which are available from 1961 to present day. We used the mean temperature for each region within the months of March, April and May of the year when the nest was founded. We calculated mean temperature during this period because it corresponds with the arrival of white storks to their nests (Fulin et al. 2009).

As an estimate of available nesting habitats, we used long-term records of land use (arable land, cover of grassland, forest, water areas, and developed land) from State Administration of Land Surveying and Registry (www.cuzk.cz). These data were not sampled regularly over time; therefore, we used land use from 1966 to 2005. These data represent the area of land use (in hectares), and we calculated the proportion of land use for each district (proportions of arable land, grassland, forest, water areas, and developed land within each district). From our 1191 nests in years of founding (first year of existence), five were platforms on electricity pylons and 119 were natural nests on electricity pylons.

Statistical analyses

We used linear models to predict the altitude of stork nests by year of founding using all stork nests (both "estimated" and "known", hereafter "pooled"; 1875–2005), and where the year of founding was known (data quality "known"; 1907–2005). Then we predicted the altitude of stork nests by the year of founding, temperature during the year of founding in region and land use separately using datasets containing all stork nests ("pooled") and stork nests with a known year of founding (data quality "known"; 1907–2005). Finally, one analysis predicted the altitude of all stork nests ("pooled") by the year of founding ("pooled"; 1875–2005) and stork nests with a known year of founding (data quality "known"; 1907–2005) by platforms and natural nests.

Because the land use predictors (proportions of different land use types) were strongly correlated with each other (arable land correlated with grassland $r_s = -0.81$, $p \leq 0.0001$, forest $r_s = -0.85$, $p \leq 0.0001$, water areas $r_s = 0.01$, $p = 0.58$, developed land $r_s = 0.44$, $p \leq 0.0001$; developed land correlated with grassland $r_s = -0.47$, $p \leq 0.0001$, forest $r_s = -0.46$ $p \leq 0.0001$, water areas $r_s = -0.09$ $p \leq 0.0001$; water areas correlated with grassland $r_s = -0.05$, $p \leq 0.0001$, forest $r_s = -0.29$, $p \leq 0.0001$; forest correlated with grassland $r_s = 0.66$, $p \leq 0.0001$) we summarized variation in these land use variables (proportions of arable land, grassland, forest, water areas, and developed land within each district) using principal component analysis (PCA), and used a single principal component (see Results).

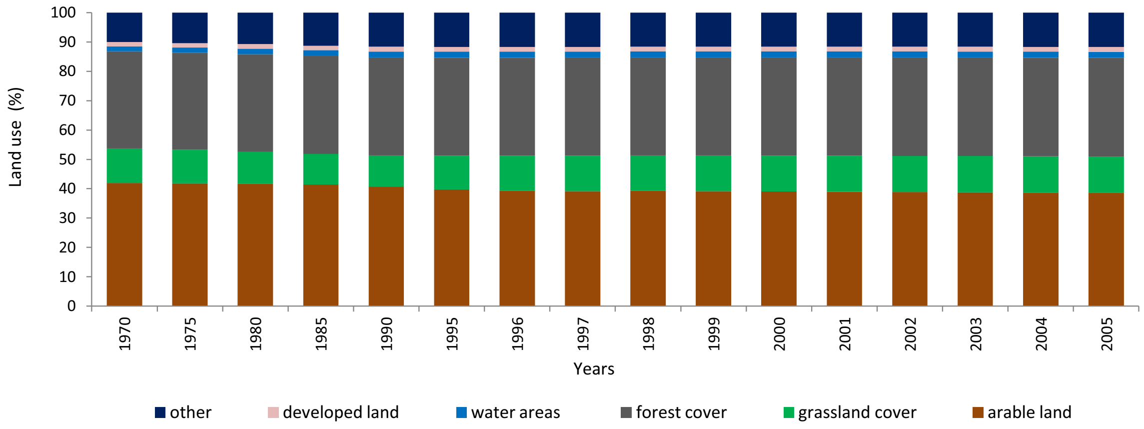

Fig. 2 Proportion of land use in the Czech Republic from 1970 to 2005

Table 2 Trend in altitude of nests affected by year of founding, temperature and land use. We separately analyzed full data set (1875–2005, see Results) and then the data about the nests with exactly known year of founding (1907–2005), influenced by temperature and land use (see Methods)

Period	Estimate± SE	DF	t	*p*
Full model				
$r^2 = 0.41$; DF = 193; $p < 0.0001$				
Year of founding *	−0.94 ± 1.07	1	−0.88	0.38
Temperature	−29.29 ± 5.74	1	−5.10	<0.0001
PC1	55.86 ± 7.55	1	7.40	<0.0001
Final model				
$r^2 = 0.41$; DF = 195; $p < 0.0001$				
Temperature	−31.85 ± 4.92	1	−6.47	<0.0001
PC1	55.74 ± 7.51	1	7.43	<0.0001

We predicted the altitude of each founded nest as the response variable by "temperature" (continuous), "land use" (continuous; represented by PC1) and "type of nest" (dichotomous; natural nest or platforms). Then, we used backward elimination of non-significant predictors until we obtained a final model containing only significant variables (as recommended by Grafen and Hails 2002). All analyses were performed for all data ("pooled") and for exactly known years of founding (quality "known" only). The rationale for using quality "estimated" data was that including these less precise data had the benefit of a larger sample size and better temporal and spatial coverage.

Results

The average nest altitude (±SD) of our study area was 363.4 ± 136.9 m above sea level (range: 139 to 792 m). These nest records came from both natural nests (345.7 ± 138.2 m) and artificial platforms (358.5 ± 139.9 m). We found that the altitude of newly founded white stork nests decreased over the years in the full dataset (1875–2005; $r^2 = 0.03$, estimate ± SE = −1.21 ± 0.2, DF = 1175, t = −5.94, $p < 0.0001$). The result was the same when the analysis included only known years of nest founding (1907–2005; Table 1).

In addition, we analyzed the potential effects of temperature, land use and the year of founding of the nests on nest altitude. The first principal component (PC1) on land-use data (Fig. 2) explained 54.2% of variance in the data. PC1 was correlated negatively with the proportion of arable land ($r_s = -0.92$, $p < 0.0001$), water areas ($r_s = -0.16$, $p < 0.0001$) and developed land ($r_s = -0.57$, $p < 0.0001$) and positively with the proportion of grassland ($r_s = 0.89$, $p < 0.0001$) and forest ($r_s = 0.91$, $p < 0.0001$). The results of this model showed similar trends for 1875–2005 (final model $r^2 = 0.44$, DF = 215, $p < 0.0001$, temperature: estimate ± SE = −37.51 ± 4.79, t = −7.83, $p < 0.0001$; PC1: estimate ± SE = 56.49 ± 7.55, t = 7.48, $p < 0.0001$) and 1907–2005 (Table 2). The year of founding of the nests was not significant in any of the models. The final model showed a negative influence of spring temperatures and a positive influence of land use i.e., mean altitude of newly founded nests increased with increasing proportion of available grassland (i.e., meadows) and decreasing proportion of arable land. The altitude of natural nests was significantly negatively correlated with year of founding. For platforms, we found no significant patterns (Table 3).

Discussion

Global and local (Czech Republic) temperatures have been increasing across our entire long-term dataset (Bartošová et al. 2014; Hansen et al. 2016), and we expected that these environmental changes would lead to white storks nesting at higher altitudes. Such patterns have been found for animals across Europe, where numerous species have shifted their ranges to higher altitudes in response to global climate change (Konvicka et al. 2003; Tryjanowski et al. 2005a; Lehikoinen et al. 2014; Roth et al. 2014). By contrast, we found that Czech white storks have decreased their nesting altitude over the past century. Our analyses suggest that long-term human agricultural landscape transformations over the past century have had a significant impact on stork nesting altitudes. From 1952 to 2009, the Czech Republic's landscape has

Table 3 Temporal trends (predictor: year of founding) of altitude of newly found white stork nests at natural nests (data available for the period 1875–2005) and platforms (data available for the period 1920–2005). Data analyzed separately for the full data set (including estimated data, see Methods) and only nests with exactly known year of founding

Nest type	Year of founding of the nest	Estimate± SE	DF	t	*p*
Platforms	estimated ($r^2 = 0.002$)	−0.51 ± 0.88	147	−0.58	0.56
	known ($r^2 = 0.004$)	−0.67 ± 0.94	133	−0.71	0.48
Natural nests	estimated ($r^2 = 0.04$)	−1.37 ± 0.21	1022	−6.44	<0.0001
	known ($r^2 = 0.04$)	−1.57 ± 0.25	841	−6.27	<0.0001

dramatically changed, marked by a substantial reduction in the proportion of farmland (Sklenicka et al. 2014). Newly founded natural nests decreased across this period while such changes for artificial platforms were not detected.

Both temperature (Kosicki 2012) and altitude (Tryjanowski et al. 2005a) are related to white stork productivity, positively and negatively, respectively. Thus warm, low altitude nesting sites are likely preferred by this species, but in the Czech Republic lower altitudes were also subject to more intensive agriculture than higher altitude locations (Potop et al. 2012). Thus, as agricultural practices (generally found at lower altitudes) decreased in the Czech Republic, new preferred stork habitats with wet pastures and livestock became available (Tryjanowski et al. 2005b, c).

Storks may be actively selecting newly available habitats and abandoning less preferred sites at higher altitude (Olsson and Bolin 2014). Alternatively, storks nesting at higher altitudes may suffer greater mortality or lower productivity (Tryjanowski et al. 2005a; Lehikoinen et al. 2014) than those that exploit newly available low altitude areas, which is opposite to the pattern of many European birds (Lehikoinen et al. 2014). We acknowledge that a range of additional climatic variables likely predict stork nesting habitats, because stork nest choice requires a complex combination of both habitat and climatic conditions (i.e., temperature, weather patterns and extreme weather conditions). Nonetheless, ultimately, we illustrate an important example where human land use practices alter avian breeding ranges.

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Compliance with ethical standards

Conflict of interest We have no conflicts of interest to disclose.

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