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Altitudinal and temporal patterns of breeding of the white stork

Diploma thesis

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ZOOLOGY

Supervizor: **doc. RNDr. Tomáš Grim, Ph.D.**

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Prostorové a časové trendy v hnízdění čápa bílého

Diplomová práce

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Declaration

I declare that I elaborated this diploma thesis by my own under the supervision of doc. RNDr. Tomáš Grim, Ph.D and using only information sources listed in the References section.

In Olomouc ....

Signature

Prohlášení

Prohlašuji, že tato práce je mým původním autorským dílem. Práci jsem vypracovala samostatně pod vedením doc. RNDr. Tomáše Grima, Ph.D. Veškerou literaturu a další zdroje, z nichž jsem čerpala řádně cituji a jsou uvedeny v seznamu použité literatury.

V Olomouci ....

Podpis

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Data were provided by a Work group for research on the white stork and they are a property of the Czech Society for Ornithology.

Poděkování

Velký a upřímný dík patří mému vedoucímu Tomáši Grimovi, za odborné vedení, pomoc při náročném statistickém zpracování dat, vyhledávání a zapůjčení odborné literatury, poskytování konzultací a cenných rad. Děkuji také panu Davidu Lacinovi (AOKP ČR Praha), panu Bohumilu Rejmanovi (koordinátor sčítání čápa bílého) i Zdeňku Vermouzkovi, za poskytnutí přístupu k hnízdním kartám, zapůjčení odborné literatury, udělení cenných rad a přátelský přístup. Velký dík patří také všem pozorovatelům, kteří sledovali hnízda na Moravě pro pana Rejmana. Také bych chtěla poděkovat celé mojí rodině, která měla „svatou“ trpělivost při mojí práci na převádění dat do elektronické podoby.

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Abstract: In this study I analysed nest records of the white stork (*Ciconia ciconia*) in the Moravian region from the period 1980–2005. I studied the influence of global climatic changes on the phenology and breeding behaviour of the white stork. I predicted that new nests would be built in increasingly higher altitudes during this period. Further, I predicted that arrival dates, mating dates and egg laying dates will decrease whereas deparure dates of storks will increase in line with well known global climate changes.

Against expectations, the year of the nest establishment correlated negatively with the altitude. Therefore, storks colonized lowlands more frequently than higher altitudes. Further, I analysed phenological data regarding arrivals (male, female) and departures (old, young), mating dates, dates of egg laying, and numbers of eggs and young hatched and fledged. I found out that a different timing of stork arrival to different altitudes almost disappeared through the years – originally storks arrived later to higher than to lower altitudes but at the end of the study period they arrived at similar times to all altitudes. Analysing young and old storks departures, I found out that at the end of the observed period storks parents were nesting at higher altitudes with a similar success as at lower altitudes and young storks departures were not under this influence. I discovered that the storks mated at the same time - without any influence, but they laid eggs earlier. The influence on eggs count and hatched count was negative for laying – the earlier laying brings a higher number of eggs and young, but I did not verify the influence on the number of the hatched young. Generally, the ascend of temperatures during last 25 years may be responsible for changes in storks phenology (earlier arrival dates), on the other hand, I did not found predicted shift of stork populations to higher altitudes during the study period.

Keywords: global climatic changes, Moravian region, white stork (*Ciconia ciconia*)

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Abstrakt: V této prácí jsem analyzovala hnízdní záznamy čápa bílého pro území Moravy, které pokrývají období 1980–2005. Studovala jsem vliv změn klimatu na migrační a hnízdní chování čápů. Predikovala jsem, že nová hnízda vznikají během tohoto období postupně ve vyšších nadmořských výškách. Dále jsem předpověděla, že data příletů, prvního páření a snášení vajec se budou snižovat, naopak data odletů se budou zvyšovat v souladu s dobře známými globálními změnami klimatu.

Oproti očekávání rok založení hnízda koreloval s nadmořskou výškou negativně. V průběhu let čápi svá nová hnízda stavěli v průměru ve stále nižších nadmořských výškách.

Dále jsem analyzovala fenologická data, týkající se příletů (samec, samice) a odletů čápů (staří, mladí), data páření a snášení a počty vajec a mláďat (vylíhlích a vyvedených). U fenologických dat jsem zjistila vliv intrakce mezi nadmořskou výškou a roky – na začátku studovaného období čápi přilétali do vyšších nadmořských výšek později než do nižších, ale na konci období přilétali do všech výšek v podobnou dobu. Při analýze odletů mladých a starých čápů jsem zjistila, že čapí rodiče hnízdili na konci sledovaného období s podobnou úspěšností ve vyšších nadmořských výškách jako v nižších nadmořských výškách a odlety mladých čápů nebyly nijak ovlivněny. Objevila jsem, že čápi se pářili ve stejnou dobu – bez ovlivnění, ale snášeli dříve. Vliv na počet vajec a počet vylíhlých mláďat mi byl negativní pro snášení – dřívější snášení znamená větší počet vajec a mláďat, ale vliv na počet vylítlých mláďat jsem nepotvrdila.

Celkově se zdá, že stoupající teploty během posledních 25 let by mohly být zodpovědné za změny v čapí fenologii (časnější přílety), na druhé straně jsem nepotvrdila běžně uváděný předpoklad o výstupu čapích populací do vyšších nadmořských výšek během sledovaného období.

Klíčová slova: globální změny klimatu, Morava, čáp bílý (*Ciconia ciconia*)

Content

Note: This Diploma Thesis is presented as a manuscript of a scientific paper.

Altitudinal and temporal patterns of breeding of the white stork (*Ciconia ciconia*) in the Eastern part of Czech Republic

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Abstract

I explored a possible influence of climate changes on an altitudinal distribution and phenology of the white stork. I analysed large data sets (742 nests in the area of approx. 27 000 km^2) based on nest record cards covering the period 1980–2005 in Moravia (eastern part of the Czech Republic, central Europe). In contrast to a prediction based on recent climate changes I found a significant decrease of altitude of both newly established stork nests and all breeding records as well. Thus, storks increasingly colonized lowlands but not highlands. Analyses of phenological data showed that arrivals of storks from wintering grounds were affected by an interaction between the altitude and the years – at the beginning of the study period storks were arriving to lowlands earlier than to highlands but at the end of the study period the difference disappeared. The departure analysis showed no across year changes but succesful breeders departed later than unsuccessful breeders and storks from lower altitudes departed on average sooner than those from higher altitudes. Young storks departures were not affected as well as the dates of first mating. However, the eggs laying occurred earlier throughout years. Number of eggs and hatched young decreased during the season, but number of the fledged young was not affected. Most importantly, this study provides compelling evidence of medium geographic scale changes in distribution of an avian species that are contrary to expectations based on global climate changes.

Keywords: global climatic changes, Moravian region, phenology, White stork (*Ciconia ciconia*)

Introduction

Climate change during the second half of the twentieth century has resulted in a mean increase of global temperatures by 0.6℃, with particularly large changes during spring in temperate and Arctic regions of the world (IPCC 2001). This involves the melting of polar ice caps, raising sea levels and expansion of arid and desert areas (Gralla 1995). However, this phenomenon does not concern only the melting of glaciers and desertification, in fact it is a global environmental problem. The analysis by Luterbacher et al. 2004 of monthly and seasonal temperature for Europe back to 1500 shows, that the late 20th and early 21th century European climate is very likely warmer than it was at any time during the past 500 years for the entire Northern Hemisphere. Detailed analyses provided some evidence for increasing trends of air temperatures at smaller spatial scales, e.g., in the Southern Urals (Sokolov & Gordienko 2008), Poland (Tryjanowski et al. 2005) and the Czech Republic (Tkadlec et al. 2006).

Climate change affects not only humans, but also all kinds of animals and plants anywhere on the Earth. Major effects of global climate changes include shifts of animal ranges to higher altitudes (Konvička et al. 2003, Tryjanowski et al. 2005), earlier arrival from wintering grounds to temperate breeding grounds (Hušek & Adamík 2008, Gordo & Sanz 2008, Møller et al. 2008, Sokolov & Gordienko 2008, Askeyev et al. 2009), later departure from temperate breeding grounds to wintering areas (Rejman et al. 2002, Kosicki et al. 2004, Adamík & Pietruszková 2008).

Changes in phenology and range shifts resulting from climate change are currently the subject of a lot of attention. Phenological changes were studied very often in many species of animals and plants whereas range shifts received much less attention.

Recent data show of earlier arrival dates in 54 out of 56 studied species during the last 30 years (Sparks 1999). Gordo & Sanz (2008) studied the influence of food conditions on wintering site on arrival date of migrating birds and they found out, that during a period of two decades the birds from Africa wintering areas were arriving to Iberian Peninsula progressively earlier. Phenology changes are documented in northern Italy, migrant species and resident birds arrive earlier and trends in first egg laying dates showed a tendency towards earlier onset of reproduction (Rubolini et al. 2007).

The influence of climate changes on the phenology of birds was documented in both passerines and non-passerines. During the last four decades such changes in the beginning of reproduction became detectable in various species, e.g., several European thrushes (Najmanová & Adamík 2009), collared flycatcher (*Ficedola albicollis*) (Weidinger & Král 2007) and also red-backed shrike (*Lanius collurio*) (Hušek & Adamík 2008), these changes were described by Adamík & Pietruszková (2008) with wading migrating birds. Finally, phenology of white storks was analyzed by Ptaszyk et al. (2003). They found earlier arrival associated with warmer spring weather.

Range shifts due to climate changes were studied and documented in various taxa, e.g., in butterflies (Konvička et al. 2003), birds (Tryjanowski et al. 2005). Studies of altitudinal range shifts seem to be rare (e.g., Konvička et al. 2003, Tryjanowski et al. 2005) in comparison to works dealing with phenological changes (e.g., Hušek & Adamík 2008, Gordo & Sanz 2008, Møller et al. 2008, Sokolov & Gordienko 2008, Askeyev et al. 2009, Najmanová & Adamík 2009). Therefore, in my work I focused not only on phenology, as typically done by other studies, but also on possible changes in average altitude of breeding areas.

In this study, I examined temporal and altitudinal trends in breeding in the white stork. I employed a large data set of 742 nests regularly observed during the last quarter of century in Moravia (the Eastern part of the Czech Republic). The study area covered approx. 27 000 km^2 and altitudinal extremes (min. = 148 m asl; max. = 1492 m asl) provide an ample opportunity for storks to shift their ranges altitudinally.

The white stork (*Ciconia ciconia*) is an ideal model species for a study of climate-driven changes in phenology and range shifts for several reasons.

1) The white stork is probably the most well known and easily recognized species of any bird in Europe. The simple fact that any layperson can unequivocally recognize this species (in contrast to great majority of other avian taxa) means that large amount of data can be gathered with the help of public.

2) The white stork is one of the largest, the most conspicuous and the most unmistakable birds breeding in Europe. Thus, both breeding and non-breeding records of this species most likely contain no false positives (i.e., mistaken species identification) and no false negatives (i.e., birds being overlooked).

3) White stork nests are by far the most conspicuous and least concealed avian nests in Europe. Thus, it is virtually impossible to overlook breeding birds and also extremely easy to determine whether they bred successfully.

4) White storks mostly breed close to human settlements and this further makes recording of breeding data much easier than in any other bird species.

5) The white stork breeds in both lowland and middle/higher altitudes making it an excellent model for the study of elevational changes in avian ranges.

All these facts mean that the white stork can provide data of much higher quantity and much larger quantity than virtually any other avian taxon. For example, monitoring of the white storks has a long tradition in a central European country, the Czech Republic, where all observers follow clearly defined guidelines for several decades. Storks breed across most parts of the Czech Republic.

I predicted that the newly found nests will occur at higher altitudes than previously established nests. Further, I predicted a negative relationship between spring arrival dates and advancing years. Additionally, I examined covariation of temporal and altitudinal explanatory variables with breeding performance and phenological data. Here, I expected negative relationships (earlier mating, laying, departure of young and old storks) (as indicated in studies of, e.g., Weidinger & Král 2007, Hušek & Adamík 2008).

Methods

Study area

Data about nesting of the white stork were collected in 22 counties (Fig. 1). Before the end of the period of data collection (1980–2005) administrative division changed. Thus, before 2000, the counties included in the present work (Fig. 1) belonged to South Moravian and North Moravian region. After 2000, the same counties are currently covering the whole area of the South Moravian, Zlín, Olomouc, Moravian-Silesian regions and an Eastern part of Vysočina region.

Geographic coordinates:

North limit – 50°26´ N and 16°54´ E

South limit – 48°37´ N and 16°55´ E

East limit – 49°31´ N and 18°49´ E

West limit – 49°18´ N and 15°23´ E

(source: http://amapy.centrum.cz/#x=3546969@y=5521970@cs=2@sidx=2@pg=1,5@pl=@app=0@sbar=c)

Data

I analysed the data-sets that were collected by accredited or voluntary observers in the period from 1980 to 2005 in the Moravian region in the Czech Republic (Central Europe). Overall 742 nests were monitored. During the study period, some nests were deserted (i.e., storks stopped to breed there), or destroyed (e.g., nest fell down after a storm). Destroyed nests were either restored by humans at the same or nearby place. In some cases, this involved the change of nest substrate (e.g., natural nest placed on a chimney fell after a storm and an artificial nest pad was established at a nearby house). Summary data-sets were published annually (e.g., Rejman 1995).

Observations from each nest were recorded in a standartized nest record card that included following descriptive information: quadrate, location (village, town, etc.), county, altitude (m), watershed, year when the nest was founded, substrate on which the nest was placed, height of the nest above ground (m), and any changes in location of the nest (e.g., nest was removed from a roof and placed on an artificial nest pad).

Nest cards further contained information on following phenological and behavioural parameters: male arrival date, female arrival date, first mating date, first egg laying date, clutch size, original brood size (number of chicks hatched), first feeding of young date, fledging date (i.e., when young took first flight), final brood size (number of chicks fledged), parental departure date, and young departure date.

Statistical analyses

I analysed following variables with coding as given here:

Studied variables

The year of founding of the nest: the exact year was given for most nests in the nest record cards. For some other nests only a range of years was given. Here, I used midpoint of that range as an estimate of the year when the nest was founded. For nests with no explicit information I considered the year of first breeding as a year of founding of the nest. Because of varying quality of this information I analysed both (a) whole data-set (precise data plus estimates) and (b) only nests with exact founding year information (excluding estimates).

Year: the year of observing, continual variable.

Altitude: altitude of village, town, or other place where the nest was placed. The atlitude of nests was given for most nests in nest record cards, the missing altitudinal data were searched in Google Earth. I also did a cross-check on altitudes, given in nest cards in Google Earth.

Male arrival date: date of male arrival to the nest.

Female arrival date: date of female arrival to the nest.

Population size: the total number of active nests for a given year. This is a surrogate measure of current population size.

The number of available nesting pads: the total number of artificial nesting pads provided by humans that were available in the given year.

Mating date: date of the first mating of storks.

Laying date: date of the first egg laying.

All dates were converted into sequential calendar dates with 1 = 1st January

Nesting succes: categorical binary variable; successful = at least one chick fledged, unsuccessful = no chicks fledged.

Clutch size: number of eggs.

Brood size – hatchlings: number of chicks.

Number of fledged young: number of young storks, which survived nesting and left the nest.

Parental departure data: date of parents departure from the nest. Both members of the pair leave breeding grounds at the same time.

Young departure date: date of young storks departure from the nest. In white storks, offspring leave after parental departure.

In altitudinal analyses, I tested for possible effects of the year of the founding of the nest on altitude. I also tested for effects of population size and availability of nesting pads.

In phenological analyses, I included the influence of all independent variables (altitude and year and interaction between these two variables, nesting success – only in models for departure of old storks) on the dependent variable (female/male arrival dates, young/old departure dates, mating date, first egg laying date, number of eggs, number of hatched chicks, the number of fledged young).

Always starting with the altitude*year interaction (Grafen and Hails 2002), I removed an independent variable, if it was not significant ($P>0.05$). Final models contained only significant variables ($P<0.05$).

I analysed the data with general linear models or general linear mixed models. Because storks repeatedly occupy the same nest across several years, data from the same nest from various years are not independent. To avoid pseudoreplication (Hurlbert 1984), I analyzed the data with general linear mixed models (GLM) with nest identity as a random effect.

I checked all models for linearity of effects, normality of errors, and homogeneity of variances and I found them to perform satisfactorily (Grafen and Hails 2002). To satisfy these assumptions, I log-transformed some variables (as indicated in Results). Because not all information were available for all nests samples, sizes differ between analyses. All analyses were done in JMP 8. I using only variable with N > 100 observations.

Results

Altitudinal distribution of the white stork

First, I tested a relationship between altitude and the year of founding of new nests. Analysis, in which each nest stood out as one data point, confirmed the dependence of altitude of newly found nests on the year of foundation; however, in contrast to expectations, the correlation was negative (Table 1, Fig. 2). This result was independent of the quality of data (i.e., analyses with estimated years of founding excluded or included) and the span of years studied (1920–2005 vs. 1980–2005; Table 1).

In an additional analysis I used all breeding records (repeated measurements at each nest) to explore whether year of observation (i.e., year when storks were breeding at the particular nest) covaries with altitude and population size. Altitudinal changes could be potentially confounded by population changes (e.g., increasing population trends) and/or supply of artificial nesting pads by humans (Table 1). Number of available nest pads was highly correlated with population size across years ($r = 0.94$, $n = 26$, $P < 0.0001$). Therefore, I analyses using nest pads or population size gave virtually identical results. In this analysis I entered year as a response and altitude as an explanatory variable because using altitude as a response and year as a predictor (as in the analyses of year of nest founding) led to meaningless results due to the inclusion of random effects (altitude of each particular nest cannot change across years, thus, random effects explain 100% of variance). Results were in line with previous analyses of years of founding: relationship between years and altitude was neagative which mean that in the past more active nests existed in higher altitudes than in lower altitudes and vice versa. This relationship was robust because either number of nest pads or population size did not explain any statistically significant variation (Table 1).

Phenology and reproduction of the white stork

In phenological analyses, I tested the effects of altitude, year and interactions between these variables to changes in storks behaviour (time of arrival and departure, laying, mating and numbers of chicks and eggs).

Arrival dates of males depended on altitude but this relationship changed during years (Table 2). At the start of the study period males arrived later to higher altitudes than to lower altitudes but arrival dates decreased at higher altitudes throughout the study period. Thus, at the end of the period males arrived at similar time to both high and low altitudes. I reached the same conclusions for female arrival too (Table 2).

When analysing departure of old and young storks the results were different (Table 2). Analysing departure of stork parents, the influence of successful nesting was included, and this variable in interaction with altitude had a significantly positive influence (Table 2) on departure of old storks. Overall, succesful breeders departed later than unsuccessful breeders (average departure date with 1 = 1st January: successful = 238.3 ± 2.1, unsuccesful = 220.3 ± 2.8). Storks from higher altitudes departed on average later than those from lower altitudes but the relationship was more pronounced (i.e., steeper) for unsuccessful breeders. In contrast, departure dates of young storks did not vary significantly with any of the tested variables (Table 2).

Further, I analysed timing of breeding of white storks (Table 3). While there was no influence of any variables on mating dates. Still, storks laid their eggs progressively earlier throughout years and this trend did not depend on altitude (Table 3).

Finally, I found seasonal trends in clutch and brood sizes (Table 4). Trends were negative – earlier laying resulted in higher numbers of eggs and hatched young. However, this seasonal trend disappeared when young storks left their nests – number of fledglings did not covary with the laying date in the season (Table 4).

Discussion

In this study I found that average altitude of nests of the model species, the white stork, gradually decreased during the recent years in the eastern part of the Czech Republic. This contradicts expectations based on global climate changes. In contrast, changes in phenological parameters of white storks either conformed to climatic-based expectations or did not change statistically significantly. The present work showed that Czech birds responded to global climate changes as reflected by their timing of migration and phenology and a shift of altitude of their nests.

Altitude of nests

I tested relationship between altitude and year of founding of nest. The hypothesis that the nests in later years will be founded in higher altitudes than nests founded earlier, was rejected. My analysis showed exactly opposite trend – average altitude of new stork nests through the years dramatically decreased (Fig. 2).

I also analysed if there was an influence on altitude by the number of nest pads placed by people. Availability of nest pads did not affect the altitude of new nests. However, in another analysis I found out that through observed years there was an increasing number of active stork nests (stork population grew) (Table 1). Again, however, population size did not explain any significant variation in altitudinal trends.

The similar observation was done by Grúz (1994), who recorded storks shifts from southern parts of Czech Republic to the north locations, it is possible to observe this reality very distinctively on shift of couples from the southern Moravia to Opavsko and Ostravsko. The author describes the reality of stork shifting to the Krkonose and Podkrkonosi, where he firstly noticed several new nests of storks. He does not give an opinion on the altitude, he just refers to appearance of new nests in his region and Podkrkonosi. In years 1973-1977 storks did not almost occure, but in the period from 1985-1989 there was recorded a growth in appearance. Tthis can be related with an overall growth of storks nests in all the Czech Republic during 1985-1989. Though, his conclusions are based only on a small sample of nests (4 vs. 742 in my work).

Shift of storks to the higher altitude was detected by Tryjanowski et al. (2005a) in the southern Poland in the period of 1931–2003. In 1931 the first nest was recorded, in the year 1933 there were found seven nests, all of them in the area under 650 meters above sea level, through years 1974–2003 a location of nests was becoming higher. In 1974 there was detected a nest at the height of 650 meters above sea level and by the year 1999 the stork attained maximum of 890 meters above sea level. Tryjanowski associates this phenomenon with increasing number of young storks and their need to settle in new areas.

Shift up to the higher altitude was observed with 15 species of Czech butterflies, which were situated at the higher average altitude through the years 1995–2001, than during the period of 1951–1980 (Konvička et al. 2003).

These works came to the opposite conclucions (shift up to higher altitudes) than to which I came in my analysis (descent to lower altitudes). However, works dealing with a shift within altitude are not too common.

Phenology

In the next analyses I tested for spatial and temporal trends in arrivals and departures of storks, time of laying and mating and clutch and brood sizes.

Stork arrivals were analyzed for male and female separately. With these phenological data I found out the influence of interaction between the altitude and years, which means that a different stork arrival up to the different altitudes has almost disappeared through the years.

A similar research concerning arrivals of the white stork to nesting sites was done by Ptaszyk (2003) in the western Poland during the period of 1983–2002. He recorded earlier arrivals of storks on an average of 10 days earlier during last 20 years. Earlier arrivals were connected with warmer spring weather and a longer arrival period. Tryjanowski et al. (2004) reported about a relationship between arrival dates and cold and normal years, They found significant difference in the median arrival date of the first partner in cold years was 7 April (± 0.7 days) and 3 April (± 0.5 days) in normal years.

Arrival dates of storks were also studied in Slovakia by Fulin et al. (2009), they found differences in arrival dates during years 1978–2002. Earlier spring arrivals of storks were also noted in years 1997–1999 by Hubálek et. al (2005) in southern Moravia. They were monitoring a short period, but observing more bird families. There is a correspondency with my work but I studied much larger dataset for this species and longer period. In other paper Hubálek (2004) described trend towards earlier arrival date of white storks during 1881–2001 in Moravia. That analysis included a long time period but the data were not so detailed for this species (he tracked only arrival of storks).

The analysis of the first arrival dates (FAD) of Tryjanowski et al. (2005b) in Western Poland during the period of 1983–2003 recorded a negative trend of FAD for 24 of the 30 migrating bird species within these years, including for the white stork. But 6 species showed a trend towards later arrival. This study agrees with my work in that sense, that the Polish storks arrive earlier in recent years.

In contrast, Weidinger & Král (2007) did not find in European populations of collared flycatcher (*Ficedula albicollis*) any shift on the date of arrival during the period of 1973–2002. Askeyev et al. (2009) studied arrival of *Sylvia* warblers during 1957–2008 in Tatarstan Republic, however only two of the four species were arriving significantly earlier.

Also in Eastern Ireland, during period 1969–1999, there were migratory birds observed, Donnelly et al. (2009) tested trends in the data of arrival. They found the evidence of earlier arrival times in 9 out of the 11 long distantce migrant species.

MacMynowski & Root (2007) in Chicago, USA (1979–2002) focused on relationship between climate variables and diferences in arrival timing between sexes and diferences in arrival timing between species too. All in all, the arrival dates of 16 of 22 of the species studied correlated with NAO or regional temperature in the early phase of species' migratory period. NAO was significantly correlated with the initial migration phase of males for nearly a third of all species examined. The arrival dates of 75% of males from long-distance migrant species negatively correlate with NAO. The arrival dates of males for all of short-distance migrant species are correlated with regional temperature.

I also studied departure dates of storks. I analysed departure dates for old storks and for young storks. I found an influence of the interaction between altitude and nesting, that means storks from higher altitudes departed later than those from lower altitudes and the succesful breeders departed later than unsuccessful breeders. But departure dates of young storks did not significantly change with any predictor variables. Departures of old storks were observed by Rejman et al. 2002 and Kosicky et al. 2004, but they investigated average day of departure of old storks from nesting ground or provided a relation between number of the young and date departure (Kosicki et al. 2004).

Assessing the influence of altitude or years on the departure of young storks was not done before. Thus, to my knowledge, my analysis is the first one to study this issue.

There was no influence of any variables or their interactions on the mating dates, but the egg laying dates showed some changes – this variable was negatively correlated with years. Thus, storks did not shift timing of their mating, but they did shift their egg-laying – they were laying eggs earlier when in previous years. This finding is surprising, because the mating and egg laying are connected with each other. Interestingly, trends in laying were under study often, but I did not find any studies on the changes in timing of mating. It might by caused by the fact that my model species seems to be observed very easy while it is almost impossible to observe mating in other, especially passerine species.

Earlier trends in first egg laying dates were detected by Rubolini et al. (2007) in Italy. Najmanová & Adamík (2009) described in European thrushes a shift in breeding phenology for thrushes. Weidinger & Král (2007) tracked the dates of egg laying of collared flycatcher and since 1980 laying started earlier. Dunn (2006) carried out a research of monitoring laying date and he found out, that 79% (45/57) of studied species lay eggs earlier. All these works cited came to the same results as I did in my work.

Testing influences on number of eggs and hatched young I found a negative influence of laying – earlier egg laying means more eggs and more young. I did not confirm any influence of studied variables on the number of hatched young. Articles dealing with number of eggs and young storks in such details as my work are not common. Sæther et. al (2006) observed variation in the population dynamics in storks, they showed trends (positive and negative) in population in many European countries. Tryjanovski et al. (2005c) were dealing only with varying number of storks on the territory of Poland. Paper focused on storks eggs comes from Southern Poland, here Profus et al. (2004) studied variation of eggs size, but they did not study number of eggs. Fulin et al. 2009 noted shifts in Slovakia, early arriving storks mean earlier breeding and higher breeding success (number of fledglings per successful pair). This work evaluates a population growth of storks, size of storks eggs or arrival time and their influence on a final number of young storks. However, no one analysed varying numbers of eggs and the young so fairly as this work.

In this work, I evaluated changes in migratory behaviour and reproduction of white storks during the last quarter of century in a Central European country. Suprisingly, white stork population did not shift to higher altitudes but clearly moved to lowlands. This conclusion was supported by analyses of both newly founded nests and also all breeding records. Further, I found out, that both male and female storks arrive to the territory of Moravia in the spring earlier than in the past. During the study period, the difference between old storks departures from different altitudes gradually disappeared. Some breeding parameters also changed, e.g., egg laying shifted to earlier times in the year.

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Table 1 Relationship between altitude (log-transformed) and the year of founding of the nest. I analysed either whole data set (including nests founded before 1980) or only data from the intense study period of 1980–2005 (i.e., sparser data from 1920–1980 were excluded). Additionally, I run both analyses for all nests (including nests with estimated year of founding) and only nests with known exact year of founding. Further, I used all breeding records to test whether year of observation (i.e., year when the particular nest was active) covaries with altitude and population size (I controlled for repeated measurements by including nest identity as a random effect). See Results for explanations of different analyses.

Expanatory variable	Effect size	R^2	F	DDF	P
Data set 1920–2005					
Year – all data	−2.21 ± 0.312	0.07	50.46	709	0.0001
Year – excluding estimates	−2.45 ± 0.328	0.08	55.69	620	0.0001
Data set 1980–2005					
Number of nest pads			0.72	526	0.40•
Population size	0.30 ± 0.12	0.15	6.50	528	0.01
Year of founding	−5.43 ± 1.90		8.12	528	0.005
Year of observation					
Altitude	−0.003 ± 0.004	0.81	47.06	148.2	0.0001
Population size	0.056 ± 0.0004	0.81	22523.15	4417	0.0000

• = variable was removed, the model was recalculated for remaining variables.

Table 2 Trends in the phenology of the white stork. Models for arrival of males and females and departure of young included effects of altitude, year and their interaction. Models for departure of the whole pair additionally included effects of nesting (nominal: successful = at least one chick fledged, unsuccessful = no chicks fledged) and its intearctions with other variables. DDF = denominator degrees of freedom from GLM controlling for repeated measures at particular nests (nest identity was included as a random effect in all models).

Expanatory variable	Effect size	R^2	F	DDF	P
Arrival – males					
Altitude*Year	−0.0009 ± 0.0003	0.18	9.62	1175	0.002
Arrival – females					
Altitude*Year	−0.0008 ± 0.0003	0.18	5.48	1042	0.019
Departure – old					
Altitude*Year*Nesting			0.29	434.6	0.59•
Altitude*Year			2.20	470.9	0.14•
Year*Nesting			2.81	410.9	0.09•
Altitude*Nesting	0.02 ± 0.009	0.57	5.50	418.2	0.02
Departure – young					
Altitude of nest*Year			0.97	261.3	0.33•
Altitude			62.51	0.67	0.42•
Year			287.1	2.67	0.10

• = variable was removed, the model was recalculated for remaining variables.

Table 3 Trends in the breeding bahaviour of the white stork. Models included predictors of altitude, years and an interaction of both. DDF = denominator degrees of freedom from GLM controlling for repeated measures at particular nests (nest identity was included as a random effect in all models).

Expanatory variable	Effect size	R^2	F	DDF	P
Date of first mating					
Altitude*Year			0.005	151	0.95•
Year			0.54	65.27	0.46•
Altitude			0.43	57.85	0.51
Date of laying					
Altitude*Year			0.30	82.84	0.59•
Altitude			0.18	60.32	0.68•
Year	–0.305± 0.129	0.45	5.63	69.76	0.02

• = variable was removed, the model was recalculated for remaining variables.

Table 4 Changes in breeding performance of the white stork. Number of eggs, young and hatched young and influencing of these numbers by variables – altitude, year, laying date and interaction of all these. DDF = denominator degrees of freedom from GLM controlling for repeated measures at particular nests (nest identity was included as a random effect in all models).

Expanatory variable	Effect size	R^2	F	DDF	P
Clutch size					
Altitude*Year*Laying date			0.68	117	0.41•
Altitude*Laying date			0.12	115.2	0.74•
Altitude*Year			0.09	72.57	0.78•
Year*Laying date			0.18	117.8	0.67•
Altitude			0.12	64.13	0.73•
Year			0.11	74.61	0.74•
Laying date	−0.026 ± 0.010	0.036	6.20	119.3	0.01
Brood size – hatchlings					
Altitude*Year*Laying date			0.68	117	0.41•
Altitude*Laying date			0.12	115.2	0.74•
Year*Laying date			0.18	116.5	0.68•
Altitude*Year			0.09	116.9	0.76•
Altitude			0.12	64.13	0.73•
Year			0.11	74.61	0.74•
Laying date	− 0.026 ± 0.010	0.036	6.20	119.3	0.01
Brood size – fledglings					
Altitude*Year*Laying date			0.05	114.5	0.83
Year*Laying			0.03	112.9	0.86
Altitude*Year			-	-	-
Altitude*Laying			0.20	113	0.65
Altitude			2.35	50.41	0.96
Year			0.16	55.53	0.69
Laying			2.25	113.6	0.14

• = variable was removed, the model was recalculated for remaining variables.

– = could not be calculated, model was reduced based on F-values.

Figure 1 Study area (source: http://www.zemepis.com/okresycr.php)

Figure 2 Relationship between altitude and the year of founding of the nest (including nests established before 1980)