Ardeola 57(2), 2010, 243-255

REPRODUCTIVE SUCCESS OF THE WHITE STORK *CICONIA CICONIA* POPULATION IN INTENSIVELY CULTIVATED FARMLANDS IN WESTERN POLAND

ÉXITO REPRODUCTIVO DE UNA POBLACIÓN DE CIGÜEÑA BLANCA *CICONIA CICONIA* EN ÁREAS INTENSAMENTE CULTIVADAS DEL OESTE DE POLONIA

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Summary.—*Reproductive success of the white stork* Ciconia ciconia *population in intensively cultivated farmlands in Western Poland.*

This work analyses reproductive data about the white stork in Western Poland, from 2003 to 2007 and shows how the main environmental factors (weather, habitat structure and NDVI) influence breeding parameters. Moreover, a meta-analysis of density and reproduction for 33 local populations in Central Europe was performed. The data come from 824 inspections of 227 nests. The population studied was characterised by the low density of breeding pairs 4.5 (2.8-6.6) pairs/100 km^2. The median of the first and second arrival dates was 1st and 11th April and differed significantly in different years. Clutch size (mean 3.81) and egg measurements (71.55 x 51.56 mm) did not differ among years, a result that may indicate low inter annual variance in feeding conditions at the onset of a breeding season. The highest seasonal differences in breeding output (mean 2.96 young per nest) were found during the nestling stage, which is a crucial period for nestling production and, in consequence, breeding output. The number of chicks was positively affected by weather conditions, i.e. air temperature, and negatively related to precipitation. Meta-analysis of local stork populations in Central Europe showed that, despite differences in breeding density, breeding success was similar in areas of low and high human population. In the case of the white stork, breeding density might be one of the key factors that affects overall breeding success by depending on strong competition for food as well as nest locations.

Key words: breeding success, *Ciconia ciconia,* clutch size, habitat structure, weather conditions, white stork.

Resumen.—*Éxito reproductivo de una población de cigüeña blanca* Ciconia ciconia *en áreas intensamente cultivadas del oeste de Polonia.*

Se estudió el éxito reproductivo de la cigüeña blanca en el oeste de Polonia, desde 2003 a 2007, en 227 nidos con 824 registros. Se demuestra cómo los principales factores ambientales (climatología, estructura del hábitat y NDVI) influyen en sus parámetros. Se realizó también un meta-análisis de la densidad y reproducción de 33 poblaciones de Europa Central. La población estudiada se caracteriza por la baja densidad de parejas reproductoras: 4,5 (2,8-6,6)/100 km^2. El tamaño medio de

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puesta (3,81) y las dimensiones de los huevos (71,55 x 51,56 mm) no difieren entre años. Existió una notable diferencia en el éxito reproductor interanual (media de 2,96 pollos por nido). Este número de volantones estuvo afectado por las condiciones climáticas: de forma positiva por la temperatura del aire y negativamente por la precipitación. El meta-análisis de las poblaciones centroeuropeas muestra que, a pesar de las diferencias en la densidad de población, el éxito reproductivo fue similar en áreas poco o muy humanizadas. La densidad de población del ave puede ser uno de los factores que afectan al éxito reproductivo, dependiendo de la fuerte competición por el alimento y de la localización de los nidos.

Palabras clave: estructura de hábitat, éxito reproductivo, *Ciconia ciconia,* cigüeña blanca, condiciones climáticas, tamaño de puesta.

Introduction

The white stork *Ciconia ciconia* is a large, conspicuous, soaring migrant with very obvious roosts and nest sites. It is well known to the general public, and in Central Europe it is considered as a harbinger of spring (e.g. Ptaszyk *et al*., 2003). The white stork is regarded as an indicator species of farmland conservation health, being a species with a long research history (Tryjanowski *et al*., 2005a; Profus, 2006). Most studies of the white stork have concentrated on several aspects, such as migration (Shamoun-Baranes *et al*., 2003; Chernetsov *et al*., 2005), phenology (Ptaszyk *et al*., 2003; Kosicki *et al*., 2004; Tryjanowski *et al*., 2004), fecundity (view Profus *et al*., 2004), diet (Pinowska and Pinowski, 1989; Alonso *et al*., 1991) and nestling development (Tortosa and Castro, 2003; Tsachalidis *et al*., 2005). The breeding biology of the white stork has been studied mainly in low altitude populated areas of human occupation, such as river valleys and areas with abundant meadows and pastures (e.g. Creutz, 1985; Profus, 1991; Goutner and Tashalidis, 1995; Profus *et al*., 2004).

Nowadays, however, intensively cultivated farmlands prevail in European Union countries where large-monoculture arable fields dominate. Many meadows and pastures in western Poland, for example, were transformed into arable fields. Consequently, the density of breeding pairs living in highly populated areas is smaller than that of those breeding in low populated areas (Barbraud *et al*., 1999; Dziewiaty, 2002; Nowakowski, 2003; Denac, 2006).

Intensively used farmlands offer different breeding conditions to storks, which are strongly connected with food and nesting structures (Alonso *et al*., 1991; Tryjanowski *et al*., 2009a). Rapid mechanisation, the use of herbicides, and monoculture cultivation have a negative effect on access to potential food resources (Ryszkowski *et al*., 1973; Pinowski *et al*., 1991). Recent studies on in highly populated areas may reveal the situation of breeding storks to be worse than estimated. In addition to a complete picture of reproduction ecology of the studied population, it is essential to consider weather factors which often indirectly influencing populations, as well as critical periods that occur in each reproductive cycle, which consequently determine breeding output. During breeding, both adult white storks and their nestlings are affected by weather conditions (e.g. temperature and precipitation), as are adults during migration, wintering (Sæther *et al*., 2006) and after arrival at the breeding grounds (Tryjanowski *et al*., 2004). Until young storks develop their thermoregulatory ability (Tortosa and Castro, 2003), rainy and cold weather can significantly reduce breeding success by causing low chick survival (Jovani and Tella, 2004). Therefore, a study that includes complex analysis of both the habitat and weather conditions will define critical periods and determine factors influencing reproductive success.

The aims of this paper are to:

(i) Describe the basic parameters of white stork breeding biology in intensively cultivated farmlands.
(ii) Explore the main environmental factors influencing breeding performance.
(iii) Compare results with other research carried out in areas of both in low populated areas and high human densities.

METHODS

The study was conducted in western Poland between 51º 68' to 51º 98' N and from 16º 10' to 17º 34 'E near the town of Leszno, in an area of 990.3 km^2. The research area covers agricultural landscape characterised by intensive farming. Average altitude is 78 m. a.s.l. The largest part is covered by homogenous arable fields (57.9%). There are also numerous forests (22.7%), grasslands (5.4%), farming areas with a large participation of natural vegetation (9.4%), built-up areas (2.9%), reservoirs and flooded areas (1.7%), as well as wastelands (0.02%). There are no large rivers, but there are several small reservoirs surrounded by forests in the northeastern part. In recent years some meadows have been forested or turned into arable land.

Fieldwork

Fieldwork was carried out during five breeding seasons (March-July) in 2003-2007. Most nests were found at the beginning of March. Arrival dates of the white stork to the nest were recorded in a special questionnaire by farmers living near nests and delivered directly to the author. The return rate of record sheets varied annually: 2003: 89%, 2004: 81%, 2005: 94%, 2006: 93% and 2007: 92%.

Where climbing up to the nest was possible, it was inspected directly. This method was used for nests situated on buildings, chimneys or pylons that were not directly connected to electricity. Inaccessible nests were checked by means of a camera attached to a tube.

The data comes from 824 inspections of 227 nests. The mean (±SD) number of inspections per nest per season was 5.1 ± 7.9. It was not possible to acquire the whole history for all inspected nests. Thus, sample size may differ in different analyses. Complete data from egg laying up to fledging or failure were obtained for 55 nests.

The size of a breeding population was estimated on the basis of nests with breeding pairs found in the study area. A total of 192 eggs from 55 nests were examined during five breeding seasons. Egg length and breadth were measured exact to 0.1 mm using sliding callipers.

Data processing and analysis

The nest occupancy by each breeding pair was defined according to first (FAD) and second bird arrival date (SAD), knowing that the sexes migrate separately.

The time of brood initiation is the moment the first egg is laid in the nest. The length of the breeding season was defined as the time from the date when the earliest egg was laid in the population until the date when the last juvenile left the nest. For each nest, the relative date of nest initiation was calculated as a residual from the yearly population median.

Egg volume (EV) was calculated in mm^3 from egg length (L) and breadth (B) following Profus *et al.*, (2004): $EV = 1.1203 + 0.4820 (B + 1.1)^2 \times (L + 1.1)$. Only eggs from complete clutches were considered in the analysis. The number of nestlings was estimated during the first inspection of the nest after hatching. Mean (±SD) age of chicks during the first inspection was 3.5 ± 4.2 (N = 55). The number of fledglings was defined as the number of nestlings present in the nest during the last visit, providing they were older than 50 days.

The impact of several environmental factors possibly influencing the number of chicks in the nest, such as mean daily air temperature, mean daily precipitation, NDVI (http://free.vgt.vito.be/), and habitat structure (Cover, 2000) was tested. The nearest meteorological station to the study site was the IŚRiL in Turew [52° 01' N, 16° 49 E] which provided access to daily weather data.

Independent variables (e.g. air temperature and precipitation) expressed as mean values for ten-day periods were computed for each brood. The analysis of habitat structure and NDVI was conducted in a circle of 1.5 km radius from the nest, which is the distance from the nest covered by the majority of foraging flights (Alonso *et al*., 1991; Nowakowski, 2003; Denac, 2006). Six types of habitats were distinguished in each territory. The most frequent were environments classified as large-area, homogenous arable fields (54.6%), then grasslands (21.8%), farming areas with a large participation of natural vegetation (9.2%), forests (8.3%), built-up areas (3.4%), reservoirs and flooded areas (2.4%). NDVI, expressed as mean monthly value for each territory (NDVI-April, NDVI-May, NDVI-June, NDVI-July), was calculated from three measurements taken every ten days.

Differences in the breeding success between years were most probably connected with different environmental conditions occurring during particular seasons. Thus, it was directly investigated how these conditions, but not a "year factor", influenced breeding success in the studied population and data from the six years were pooled.

To analyse the effect of environmental factors on breeding success, a General Linear Model (GLM) was applied with the number of nestlings in nests as the dependent variable and twelve environmental factors as independent variables. Moreover, time (year) was included in the model as a covariate. The significance of tested factors as well as the significance of the model was estimated during forward selection using the Monte Carlo Permutation test set for 1,000 permutations.

For the meta-analysis of low populated areas and highly populated areas in Western Europe data about breeding parameters of 33 studied populations were used (table 1). Only populations that were studied in 2000-2003 were analysed. The habitat structure analysis was conducted in a circle of 15 km radius from the location's centre of the population (table 1). Data about the habitats structure comes from Corine Land Cover (2000). Habitats are divided into two groups: low population areas composed of large-area, homogenous arable fields (22.3%), grasslands (13.5%), farming areas with a large participation of natural vegetation (12.0%), forests (42.2%), built-up areas (3.6%), reservoirs and flooded areas (1.6%), wastelands (4.8%); and highly populated areas composed of large-area, homogenous arable fields (43.4%), grasslands (6.3%), farming areas with a large participation of natural vegetation (6.5 %), forests (31.2 %), built-up areas (7.8%), reservoirs and flooded areas (0.9%), wastelands (3.4). For meta-analyses a GLM was applied to mean density (first model) and the mean number of local population (second model) as dependent variables. Latitude of the local population and the habitat type were included as independent variables. Moreover, the year of study was included in the model as a covariate.

Mean values are presented with 95% confidence limits (95% CL).

TABLE 1

Localization, latitude (Lat), longitude (Long), altitude (Alt), log of density (Den), mean breeding success (Suc), source and separate type of feeding habitat of local breeding populations of white stork in Western Europe.
[Localización, latitud (Lat), longitud (Long), altitud (Alt), log. de la densidad (Den), media del éxito reproductor (Suc), referencia y tipo de hábitat de la población reproductora local de cigüeña blanca en el oeste de Europa.]

Localization	Lat	Long	Alt	Den	Suc	Source
Low populated areas						
Kłopot	52.075	14.422	26	1.38	2.33	Tryjanowski *et al.*, 2009b
Terespol	52.050	23.340	129	1.74	1.68	Tryjanowski *et al.*, 2009b
Perleberg	53.035	11.500	86	1.04	1.2	Latus and Kujawa, 2005
Żywiec	49.412	19.110	603	0.64	1.78	Tryjanowski *et al.*, 2009b
Nowy Targ	49.281	20.016	855	0.57	1.89	Tryjanowski *et al.*, 2009b
Dzierżoniów	50.435	16.394	268	0.53	1.66	Tryjanowski *et al.*, 2009b
Stara Lubova	49.180	20.413	645	0.43	2.33	Tryjanowski *et al.*, 2009b
Frydek-Mistek	49.410	18.190	359	0.42	1.81	Tryjanowski *et al.*, 2009b
Chyżne	49.253	19.403	1129	0.34	2.24	Tryjanowski *et al.*, 2009b
Jindrichuv Hradec	49.080	14.490	479	0.25	2.28	Tryjanowski *et al.*, 2009b
Ceske Budejovice	48.580	14.280	470	0.16	2.15	Tryjanowski *et al.*, 2009b
Poprad	49.032	20.182	814	0.06	2.38	Tryjanowski *et al.*, 2009b
Highly populated areas						
Kosice	48.400	21.153	217	1.33	2.29	Tryjanowski *et al.*, 2009b
Wielichwo	52.065	16.211	72	1.08	2.17	Tryjanowski *et al.*, 2009b
Leszno	51.503	16.355	101	0.80	2.03	Tryjanowski *et al.*, 2009b
Breclav	48.450	16.530	163	0.72	2.07	Tryjanowski *et al.*, 2009b
Forst	51.362	14.392	436	0.67	1.4	Latus and Kujawa, 2005
Poznań	52.242	16.553	84	0.61	1.84	Tryjanowski *et al.*, 2009b
Hodonin	48.510	17.070	161	0.61	1.83	Tryjanowski *et al.*, 2009b
Rimavska Sobota	48.226	20.011	226	0.59	2.49	Tryjanowski *et al.*, 2009b
Bad Freinwalde	52.466	13.015	78	0.59	1.4	Latus and Kujawa, 2005
Bardejov	49.172	21.164	490	0.59	2.2	Tryjanowski *et al.*, 2009b
Opava	49.560	17.540	261	0.42	1.73	Tryjanowski *et al.*, 2009b
Sabinov	49.060	21.052	384	0.41	2.4	Tryjanowski *et al.*, 2009b
Spisska Nova Ves	48.564	20.341	858	0.37	2.3	Tryjanowski *et al.*, 2009b
Strausberg	52.343	13.532	58	0.33	1.1	Latus and Kujawa, 2005
Zdar nad Sazavou	49.330	15.560	547	0.20	2.29	Tryjanowski *et al.*, 2009b
Roznava	48.394	20.321	500	0.14	2.3	Tryjanowski *et al.*, 2009b
Juterborg	51.591	13.043	88	0.02	1.5	Latus and Kujawa, 2005

RESULTS

Breeding density and distance among nests

The mean density of breeding pairs was 4.5 (95% CL: 2.8-6.6) pairs per100 km^2, and it varied from 3.5 in 2005 to 6.0 in 2003 pairs per 100 km^2, but the difference among years was not significant (χ^2_4 = 2.92, NS).

The effect of the habitat type (sparsely populated areas or highly populated areas), latitude and altitude on the mean density of breeding pairs in Central Europe was analysed. The GLM model was significant (F = 6.53, P < 0.01, R^2 = 0.35). Two factors included in the model were significant, i.e. altitude (F = 4.65, P < 0.04, β ± SE = –0.44 ± 0.20, fig. 1) and habitat structure (F = 4.22, P < 0.04, fig. 2). Latitude was not significant (F = 1.36, NS).

Phenology and time of breeding

In the study area the first arrival day of the white storks varied between 12 March and 15 May (median: 1 April), and differed significantly among years (Kruskal-Wallis test: H_4 = 62.5, P < 0.001). The second arrival day varied between 18 March and 29 May (median: 11 April), and also differed significantly among years (Kruskal-Wallis test: H_4 = 69.7, P < 0.0001, fig. 3). The first and second arrival dates were strongly correlated (Spearman correlation: r_s = 0.86, N = 238, P < 0.001). Arrival repeatability was 0.19 (95% CL: 0.06-0.53) for the first arrival day per nest, and 0.42 (0.13-0.84) for the second arrival day per nest; however, there were no significant differences between arrivals.

The day of the second partner's arrival was negatively correlated with breeding success (r = –0.33, N = 238, p = 0.0001). Temperature and precipitation did not influence the arrival day of the second partner (F = 1.28, NS).

The median date of laying the first egg did not differ among years (Kruskal-Wallis test: H_4 = 12.72, NS). The time of arrival was strongly correlated with the date of egg laying (r = 0.87, p = 0.001, n = 55). During five breeding seasons no replacement clutches were recorded.

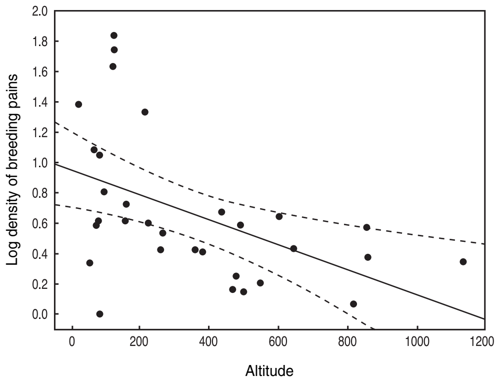

FIG. 1.—Relationship between density of breeding pairs and the altitude breeding locations of white storks in Central Europe (y = –0.08x + 0.94).
[Relación de la densidad de parejas reproductoras y la altitud del núcleo reproductor de cigüeña blanca en Europa Central (y = –0,08x + 0,94).]

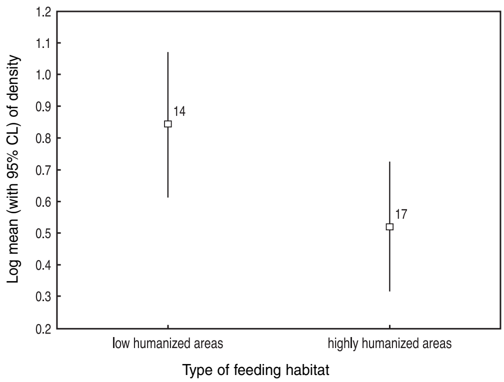

FIG. 2.—Differences in mean density of breeding pairs of white storks between low populated and highly populated areas in Western Europe.
[Diferencias en la densidad media de parejas reproductoras de cigüeña blanca en áreas poco y muy humanizadas de Europa Occidental.]

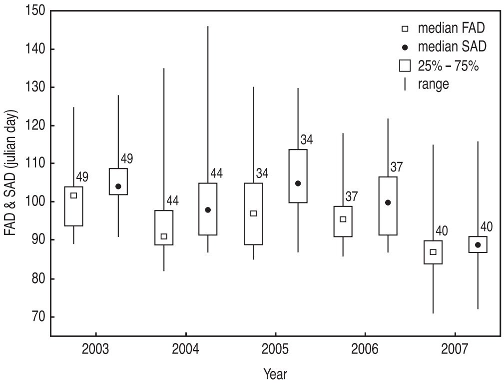

FIG. 3.—Median date of first (FAD) and second (SAD) arrival dates of white storks to Western Poland in 2003-2007. Numbers represent sample size.
[Fechas medias de la primera (FAD) y segunda llegada (SAD) de las cigüeñas blancas al oeste de Polonia en 2003-2007. Los números indican el tamaño de muestra.]

Clutch size and egg measurements

In 51 visited nests, 198 eggs were laid, i.e. an average of 3.81 (3.6-4.0) per nest. The most common clutch has 4 eggs (number of mode = 34), and the clutch varied from two to five eggs. No differences were recorded in the mean clutch size among years (Kruskal-Wallis test: $H_4 = 2.38$, NS). Clutch size did not decrease during the breeding season (GLM model with "year" as co-variate F = 1.39, NS).

None of the egg measurements (table 2) differed significantly among over the years (one-way ANOVA, in all cases P > 0.06), and they were independent of clutch size (in all cases P > 0.07).

Hatching and breeding success

Mean hatching success was 76% (66.0-85.0) and it did not vary among years ($\chi^2_4 = 7.20$, NS). In 75 visited nests, 222 eggs hatched, which gave the mean of 2.96 (2.67-3.24) nestlings per nest and 3.17 (2.93-3.20) per nest with hatching success.

The mean number of nestlings per nest did not differ among years (Kruskal-Wallis test: $H_4 = 5.91$, NS, fig. 4), but differences were recorded for nests with hatching success (Kruskal-Wallis test: $H_4 = 10.82$, $P < 0.05$, fig. 4). The differences were due to differences between 2003 and 2007 (value *p* for the multiple comparisons of mean ranges, P = 0.02). Mean breeding success was 0.80 (0.73-0.86) and differed among years ($\chi^2_4 = 32.2$, $P < 0.001$).

TABLE 2

Means and range of the white stork eggs measurements in study area during 2003-2007.
[Medias y rango de las medidas de los huevos de cigüeña blanca en la zona de estudio durante 2003-2007.]

Measurements	**Mean (95% CL)**	**Range (clutch mean)**	**Range (all eggs)**
N	192	51	192
Length (mm)	71.55 (71.10-71.99)	68.07-77.40	64.6-80.4
Breadth (mm)	51.56 (51.32-51.80)	48.55-55.62	47.4-56.4
Elongation (cm^3)	1.38 (1.370-1.39)	1.29-1.55	1.23-1.60

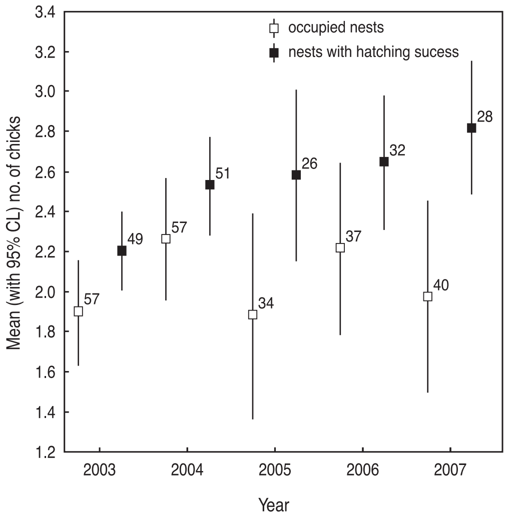

FIG. 4.—Mean breeding success of white storks in Western Poland in the consecutive years of study (2003-2007); per occupied nests (black point) and for nests with hatching success (white point). Means are given with 95% CL and numbers represent sample size.

[Media del éxito reproductor de la cigüeña blanca en Polonia occidental durante los años de estudio (2003-2007), según nidos ocupados (puntos negros) y nidos con éxito (puntos blancos). Las medias se ofrecen con el 95% de LC y los números representan el tamaño de la muestra.]

The GLM model with all environmental factors (mean daily air temperature, mean daily precipitation, the NDVI and the habitat structure) on the number of nestlings in nests was significant (the Monte Carlo permutation test: $F = 15.3$, $P < 0.0001$, $R^2 = 0.30$). Only four factors included in the model after forward selection were significant (the Monte Carlo permutation test; temperature: $F = 3.98$, $P < 0.005$, $\beta \pm SE = 0.19 \pm 0.11$; precipitation: $F = 16.68$, $P = 0.0001$, $\beta \pm SE = -0.47 \pm 0.11$; NDVI-May: $F = 11.43$, $P = 0.001$, $\beta \pm SE = 0.32 \pm 0.34$; NDVI-June: $F = 17.58$, $P = 0.0001$, $\beta \pm SE = 0.52 \pm 0.76$ and meadows $F = 12.88$, $P = 0.001$, $\beta \pm SE = 0.21 \pm 0.90$). The number of nestlings per nest was positively related to mean daily air temperature, the NDVI (May and June) and meadows, but it was negatively related to mean daily precipitation.

The effect of the habitat type (low populated areas and highly populated areas), latitude and altitude on mean breeding success in Central Europe was not significant (GLM model: $F = 1.20$, NS).

DISCUSSION

The breeding density of the studied population was lower than those densities recorded in low populated areas in Polish river valleys: in the valley of the Nurc river – 89.2 pairs/100 km^2 (year of study: 1995, Pugacewicz, 2000), the valley of the Narvia river – 69.2 pairs/100 km^2 (year of study: 2000; Nowakowski and Górski, 2004); the valley of the Bug river – 78.7 pairs/100 km^2 (years of study: 1984-1985, 1994; Kasprzykowski and Goławski, 1998); the valley of the Obra river – 12.9 pairs/100 km^2 (years of study: 1983-1992; Kuźniak, 1994a); as well as on intensively farmed areas near the city of Poznań – 4.6 pairs/100 km^2 (years of study: 1984-1985; Ptaszyk, 1994), and near the town of Kościan – 6.9 pairs/100 km^2 (years of study: 1974-1990; Kuźniak, 1994b).

During the last 30 years the white stork has increased its elevation range in Eastern Europe (Janaus and Stipniece, 2004; Ots 2009). East European countries, e.g. Lithuania, Latvia, Estonia, offer storks a lot of meadows, pastures and extensively used arable fields. This, along with climatic factors (changes in temperatures and precipitation), has created new habitats, offering them new foraging opportunities.

In the 1930s, in Western Poland, white storks arrived on average between 30 March and 4 April (Slywinsky, 1938), similar to the dates recorded at the end of the 19th century

(Slywinsky, 1938). In the 1950s storks arrived on average on 1 April (Zabłocka, 1959). In the years 1983-2002 the first arrival day occurred between 11 March and 1 April (Ptaszyk *et al*., 2003). These results suggest that nowadays the first white storks return from Africa *ca.*10 days earlier than they did a hundred years ago. Similarly, Tryjanowski *et al*. (2004) found that white storks changed their spring arrival date during the study period. According to Ptaszyk *et al*. (2003) and Tryjanowski *et al*. (2004), I concentrated on the arrival dates of the second partner assuming that it was the most important event in the studied area. In other areas, where nest sites could be limited, the arrival of the first bird at the nest site might have been more important. A long-term phenological study showed that the white stork delayed its arrival in years when weather was adverse (snow and heavy rains), but it did not influence breeding success (Tryjanowski *et al*., 2004). During this study there were no cases of such sudden changes of weather. Therefore, weather had no significant influence on the second arrival date.

Data about the clutch size of the white stork in other geographical zones of Central Europe are of historical interest only; therefore a statistical meta-analysis had low biological importance. Mean clutch size was lower than previously recorded in Estonia (3.91; Veromann, 1980), German (3.94; Kaatz and Stachowiak, 1987), Southern Poland (4.23; Profus, 2006), Hungary (4.20; Sasvári and Hegyi, 2001), and the reintroduced population in Switzerland (5.02; Bloesch, 1982). This means that clutch size in the study area is the smallest among the previously studied ones. The observed range of clutch size was wider than generally established for the white stork (1 to 5 eggs; Cramp, 1998), but 6 and 7 eggs were also possible for the species (Creutz, 1985).

Egg measurements were smaller than those reported by Profus (2006) in Southern Poland (72.1 x 52.19 mm), and Graumann and Zöllick (1977) in Mecklenburg (Germany) (72.56 x 52.55 mm), Profus (1991) in Hungary (72.44 x 51.82 mm) and Bloesch (1982) in Switzerland (72.52 x 51.01 mm). On the other hand, egg measurements in Africa were smaller than those reported in the study area in Tunisia 70.45 x 50.95 mm (Lauthe, 1977) and in Morocco 71.4 x 51.2 mm (Schierer, 1972). Thus, if the weight of the egg depends on the size of the female (Bennet and Owens, 2002), it suggests that birds living in Africa are smaller than birds nesting in Eastern Europe. Consequently, the smaller weight of bird's eggs in lower latitudes is compliant with Bergman's rule (Krebs, 2001). No analysis of weather influence on egg measurements was performed because it is not known when storks accumulate components for laying.

Environmental factors such as air temperature and precipitation may have reduced stork nestling numbers and growth in two ways. First, by directly influencing the nestling's survival in the first days of its life. Rainy days with low temperature are much more dangerous for small nestlings with reduced thermoregulation (before the age of 20 days) than days without rain (Jovani and Tella, 2004). Second, air temperature and precipitation indirectly affect potential food resources available to storks, such as insects, amphibians, small mammals and small passerine birds (Dallinga and Schoenmakers, 1987; Tryjanowski and Kuźniak, 2002). Indeed, the white stork in the continental biogeographic region (Sackl, 1987; Antczak *et al*., 2002) is less active in cold and wet weather than in warm and dry weather (Stokes *et al*., 2001). Reduced food availability may cause starvation of the chicks or hamper their growth, and due to chilling made them directly more susceptible to mortality. In addition, reduced food availability and severe weather constitute stress factors often associated with parasite infections (Newton, 1998), which additionally might have increased mortality of white stork chicks. In low population areas, weather did not affect reproductive success and it appears that it plays a role only in densely populated areas (*sensu* Denac, 2006). Thus, since the study area is a highly populated area, it means that weather is the most important factor affecting the number of nestlings.

Potential food abundance depends on vegetation whose determinant is NDVI (Schaub *et al.*, 2005). In intensively used farmlands, grazing within large dairy farms probably supports constancy and repeatability of food over the years (Tryjanowski *et al.*, 2005b). In case of this study, farming activity was not analysed, but Tryjanowski *et al.*, (2005b) suggest that dairy farming is positively affected with NDVI and meadows and pasture areas. Møller, (2001) reported that the number of breeding barn swallows *Hirundo rustica* had been decreasing for several years after farming had ceased. White storks isolate their nests with cow dung to minimise chick heat loss (Tortosa and Villafuerte, 1999), indicating that retarding heat loss is a very important factor in the early period of chick growth.

In the last few years, following Poland's accession to the EU, intensive farming has increased significantly compared to previous years. Livestock farming practices have changed dramatically (*sensu* Sanderson *et al.*, 2009). In western Poland many meadows and pastures have been transformed into arable fields. Clearly, the potential impact of changes in farming practices needs further investigation. From the conservation point of view, changes in management practices, e.g. increased livestock farming, may improve demographic parameters not only of local breeding white storks, but also other species of farmland avifauna in Poland.

The meta-analysis shows that in low population areas breeding pairs of the white stork have high densities in comparison with highly populated areas, but no such relationship was found with respect to the number of chicks. The data did not enable identification of a demographic mechanism leading to density dependence of reproductive success. High regional density (NE Europe) probably affects productivity through competition between individuals in foraging areas. In high density areas, storks need more time to find food. High density involves competition (Begon *et al.*, 1996) and predation (Sinclair and Pech, 1996), its occurrence depends on environmental conditions and thus is likely to vary in space and over time.

To conclude, the study covers all breeding stages of the white stork from arrival to fledgling. Weather and habitat conditions do not influence the arrival date. Therefore, the cost of an early return from wintering area is low, and reproductive success is shaped in later stages when nestlings need more energy to develop. Clutch size and egg measurements did not differ over the years and this result may indicate low inter annual variance in feeding conditions at the onset of the breeding season. The highest seasonal differences in breeding output were found during the nestling stage and this period is crucial for nestling production and, in turn, for breeding output. On a large geographical scale, in low population areas breeding white stork pairs create higher densities when compared with highly populated areas, but breeding success is not different in these two kinds of habitat. In areas of high density, the time necessary for finding food and predation probably increases.

ACKNOWLEDGEMENTS.—I would like to express my thanks to J. Grześkowiak, P. Tryjanowski, P. Zduniak, A. Nowak, S. Kuźniak and M. Antczak for their assistance, and anonymous reviewer for comments, which improved the manuscript. My gratitude is due to IŚRiL in Turew for providing access to meteorological data. The study was supported by MNiSW grant N N304 025936.

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[Recibido: 27-11-2009]
[Aceptado: 25-03-2010]