

# Timing of arrival at breeding grounds determines spatial patterns of productivity within the population of white stork (*Ciconia ciconia*)

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**Abstract** Early arrival at breeding grounds have important fitness consequences for migratory birds, both at individual and population level. The aim of this study was to investigate how the timing of arrival at the breeding territories affects the spatial patterns of reproductive success within a population of white storks (*Ciconia ciconia*). Data were gathered annually for ca. 200 pairs of storks breeding in central Poland between 1994 and 2011. Geostatistical analysis of data indicated that in years of delayed arrival of the population (measured by the first quartile arrival date), the reproductive output of storks was negatively autocorrelated, which indicated that there was a tendency for pairs of high breeding success to neighbour with pairs of low success. By contrast, in years when first storks returned in early dates to the breeding grounds, their reproductive success did not show any kind of spatial autocorrelation. These results suggest that delayed return of the first-arriving storks of the population may increase intensity of intra-specific competition to the level at which high-quality breeding pairs monopolize most of available resources at the expense of neighbouring low-quality pairs, which have lower reproductive success as a consequence. Such hypothesis was further supported with the analysis of nesting densities, showing that the late-arriving breeding pairs incurred greater fitness costs (or derived lower fitness benefits) while breeding in high densities comparatively to the early-arriving conspecifics.

**Keywords** Arrival dates · Competition · Geostatistics · Reproductive performance · Spatial autocorrelation

## Introduction

Fitness benefits that migratory birds derive from early arrival at breeding grounds are manifold (Smith and Moore 2005). Priority in access to a good quality breeding territory or nesting site is considered one of the major advantages of early return to the breeding grounds (Currie et al. 2000; Forstmeier 2002). The other advantages of early arrival include higher chances of acquiring a mate (Potti and Montalvo 1991), selecting mate of high phenotypic quality (Arvidsson and Neergaard 1991), and higher likelihood of obtaining extra-pair matings (Langefors et al. 1998; Møller et al. 2003). High fitness benefits of early arrival at breeding grounds lead to an intense selection pressure for advancing the timing of spring migration in birds (Kokko 1999). However, early arrival also incur certain costs on individuals and, in consequence, arrival dates should be viewed as the effects of optimization processes that takes into account all the benefits and costs of arriving at breeding territory at a particular time. Increased energetic expense of self-maintenance and higher mortality risk due to limited food resources and unfavourable environmental conditions are recognized as the major costs of early arrival at breeding grounds (Brown and Brown 2000). Since only individuals of high quality (expressed by best alleles, greater age, experience or better physical condition) are able to bear the costs of early arrival, the timing of spring migration can be considered a phenotype-dependent trait (Møller 1994).

Timing of arrival at breeding grounds may also have indirect consequences for reproductive output at the

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population level. We expect that in migratory species, including the white stork (*Ciconia ciconia*), arrival patterns may determine spatial distribution of reproductive success within population. Delayed arrival of the entire breeding population, usually caused by adverse weather conditions prior to departure from wintering grounds or along the migration route, may have profound consequences on the tightly regulated reproductive schedule of birds (Gunnarsson et al. 2006). Such situation may be described by the so called ‘domino effect’, assuming that the timing of one event determines the timing of the forthcoming events throughout the sequence of the life-cycle stages (Piersma 1987). Under such conditions, during years of delayed arrival the peak of the food requirements of the entire population may not match the peak of resource availability (Johansson and Jonzén 2012), which in turn may substantially increase intra-specific competition. Furthermore, since delayed arrival shortens the breeding season of birds (Reudink et al. 2009), we may expect higher breeding synchrony across the populations. Such synchronization could likely increase daily energy demand of the entire population during chick rearing period, leading to a lower per capita availability of food resources (Stempniewicz et al. 2000). Having assumed that, we could expect that delayed arrival at breeding grounds could affect the spatial distribution of breeding success within populations by increasing the intensity of exploitation and interference competition between neighbouring pairs.

This kind of pattern is especially expected in such species as the white stork, where high quality individuals have capabilities to monopolize available resources at the expense of the neighbouring low-quality pairs, thus reducing their reproductive output (Denac 2006). Under such conditions, a density dependence in reproductive success is likely to occur, which has already been reported for different European populations of white stork (Barbraud et al. 1999; Sasvári et al. 1999). It has also been demonstrated that storks from areas of high breeding densities arrive earlier in spring, indicating that intense competition takes place for attractive nesting territories (Gordo et al. 2007). Finally, there is strong empirical evidence for the fitness benefits associated with early arrival of storks (Tryjanowski et al. 2004; but see Janiszewski et al. 2013), which suggests that delayed arrival may coincide with less favourable environmental conditions and, possibly, with lower food availability.

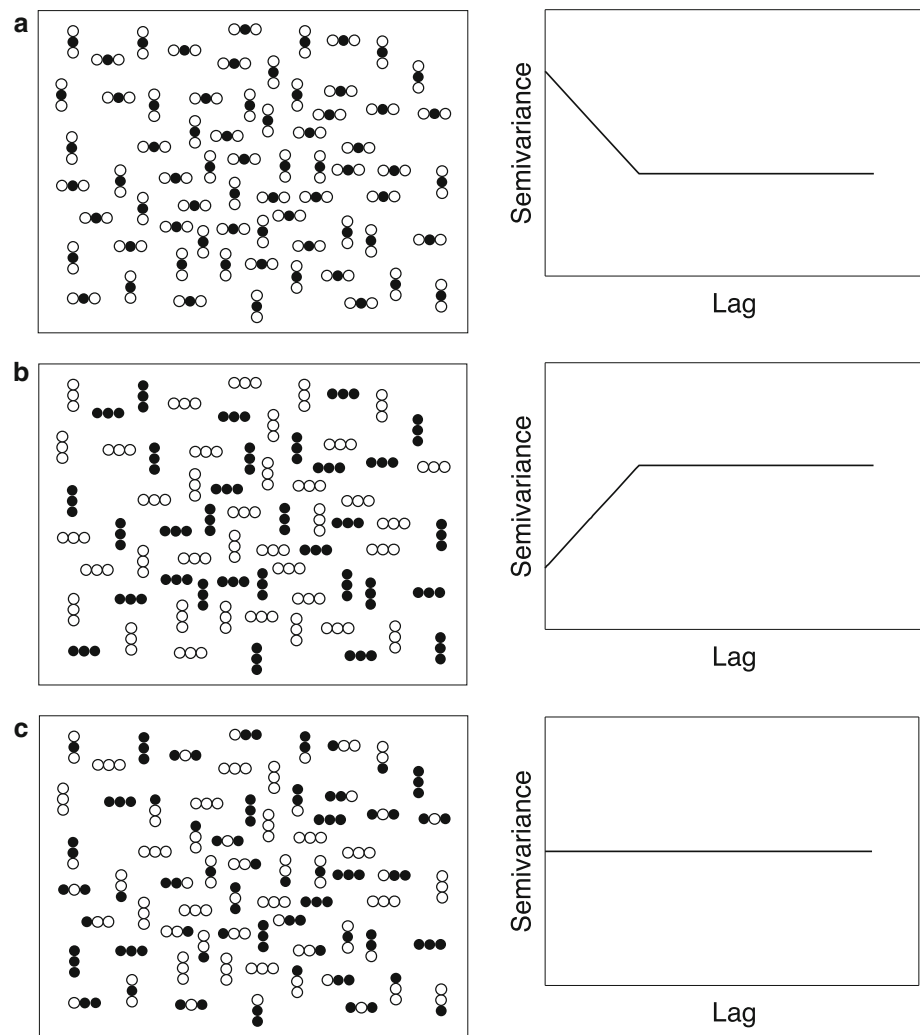
The aim of this study was to investigate whether the timing of arrival exerts impact on spatial patterns in reproductive performance within a population of a migratory bird, the white stork. For this purpose, we analysed a long-term data on arrival and breeding success of storks with geostatistical tools. With this method we could describe the degree of spatial dependence of the data by

relating the values of reproductive success of each breeding pair to the parameters of neighbouring pairs located in varying distances, i.e., within the lags of different radii. We assumed that high intra-specific competition should be associated with negative autocorrelation of reproductive success across the population. This means that variation in reproductive output (measured by semivariance) should be high within short distances (lags), as pairs of high success tend to neighbour with pairs of low success (satellite model of distribution, Fig. 1a). In contrast, lack of competition-related effects should result in non-negative spatial autocorrelation of reproductive success, and its spatial distribution should be consistent with a clumped or a random theoretical model (Fig. 1b, c). The clumped pattern assumes a positive spatial autocorrelation where values of semivariance are low at short distances (Fig. 1b), as pairs of certain reproductive output neighbour with pairs of similar breeding success, suggesting high and low quality breeding regions. Finally, the random pattern of distribution is associated with lack of any autocorrelation and a constant level of semivariance at all lags (Fig. 1c), which means that quality of breeding territories and quality of breeding pairs would be randomly distributed across the study area. In order to support the results of autocorrelation analysis we also searched for any density-dependence patterns in reproductive success within the studied stork population.

## Methods

The study took place in a white stork population occupying an area of ca. 1120 km<sup>2</sup> of agricultural landscape within the borders of the Łowicz county (Poland, 52°06′N, 19°56′E) between 1994 and 2011. Each year, all existing nests from the previous seasons were visited and the whole area was searched for new breeding pairs. Effective location of new territories was possible due to the high conspicuousness of nests, which are frequently built on electricity poles, chimneys, building roofs or high trees (Tryjanowski et al. 2009). Reproductive success was assessed in all active nests by binocular observation of fledglings in the second half of July. Active nests were defined as those where both pair members were recorded during the breeding season. The number of breeding pairs ranged from 161 to 209 and the number of fledglings were recorded in a total of 3,352 breeding attempts. Since 2000, arrival dates of the first- and the second-arriving pair members were recorded using special forms filled by farmers living in the nearest surroundings of each occupied nest. This methodology is widely used in ecological studies on white stork (Tryjanowski and Sparks 2008). Timing of arrival was recorded for both adult birds per pair with the accuracy of 1 day; however, in the analyses we only used

**Fig. 1** Three theoretical distributions of breeding pairs with high (*filled circles*) and low (*open circles*) reproductive success. Spatial distribution shown at *left*: satellite pattern indicates a negative autocorrelation (**a**), clumped pattern indicates a positive autocorrelation (**b**), and random pattern indicates lack of autocorrelation (**c**). Standardized variograms for each model shown at *right*. Semivariances are shown in each lag, with high values indicating a negative autocorrelation and low values a positive autocorrelation. Figure adapted from Minias et al. (2012)



data for the first recorded bird from each pair. Each year, we managed to obtain accurate data on the timing of arrival for 52.5–66.7 % of all breeding pairs. For each year, we expressed arrival time at the population scale with the first and the third quartile values of all recorded arrival dates (only first-arriving pair members included). We assumed that the first quartile value of arrival dates was likely to express time of the year at which the first storks were able to return to the breeding territories (arrival of early-breeders). Consequently, this variable should be determined by environmental factors such as weather conditions and/or food availability along the migration route and at the breeding grounds (Tryjanowski et al. 2004). In contrast, the third quartile value should reflect arrival of birds of low phenotypic quality that are known to return to the breeding grounds later in the season (Møller 1994). Quartile-based division on early- and late-breeders is commonly applied in the studies on avian migration phenology (e.g., Lourenço et al. 2011). Both variables (the first and the third quartiles) were subjected to the Box–Cox transformation to improve

normality and standardized to equal unit variances (*z* scores) prior to analyses.

Every year, all active nests were mapped with a hand held global positioning system (GPS) unit (Garmin Gps-Map 60Cx, Olathe, KS, USA). Nest coordinates were used to calculate distances between all the nests. Basing on the constructed nest distance matrix we calculated two spatial characteristics: nest density (number of active nests within the radius of 2 km from each nest) and nearest neighbour distance (km). We have decided to choose the radius of 2 km to ensure that we investigate interactions solely between the closest neighbours. In the studied population, most of pairs (64.8 %) had between one and three neighbouring pairs within the radius of 2 km from their nests. Both nest density and nearest neighbour distance were calculated for all active nests recorded within the study area throughout each breeding season, as there was no time-gap between breeding activities of the earliest and the latest pairs (i.e., all the clutches were laid before the first chicks fledged).

Spatial distribution of reproductive success was analysed with geostatistical tools summarized by Rossi et al. (1992). We started analysis by constructing omni-directional variograms that presented semivariance values  $\hat{\gamma}(h)$  for the chosen lags of distance ( $h$ ) according to the following equation:

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_i + h)]^2$$

where  $N(h)$  is the number of pairs of nests separated by lag  $h$ ,  $z(x_i)$  and  $z(x_i + h)$  are the values of the variable recorded for the pair  $i$  of nests separated by lag  $h$ . For the purpose of analysis, we have set lags to 4 km with a tolerance of 2 km, with the first lag of 0–2 km. The length of lag was chosen to produce a sufficiently large sample size of pair comparisons in the first lag. All the variograms were calculated using the geostatistical software VARIOWIN (Pannatier 1996). To estimate spatial autocorrelation of data in the first lags of variograms we have calculated Pearson product-moment correlation according to the following equation:

$$r(h) = \frac{1}{N(h)} \frac{\sum_{i=1}^{N(h)} [z(x_i) - m_x][z(x_i + h) - m_{x+h}]}{S_x S_{x+h}}$$

where,  $r(h)$  is a product-moment correlation coefficient estimated for lag  $h$ ,  $N(h)$  is the number of pairs of nests separated by lag  $h$ ,  $z(x_i)$  and  $z(x_i + h)$  are the values of the variable recorded for the pair  $i$  of nests separated by lag  $h$ ,  $m_x$  and  $S_x$  are respectively mean value and standard deviation calculated for all  $z(x_i)$ ,  $m_{x+h}$  and  $S_{x+h}$  are respectively mean value and standard deviation calculated for all  $z(x_i + h)$ .

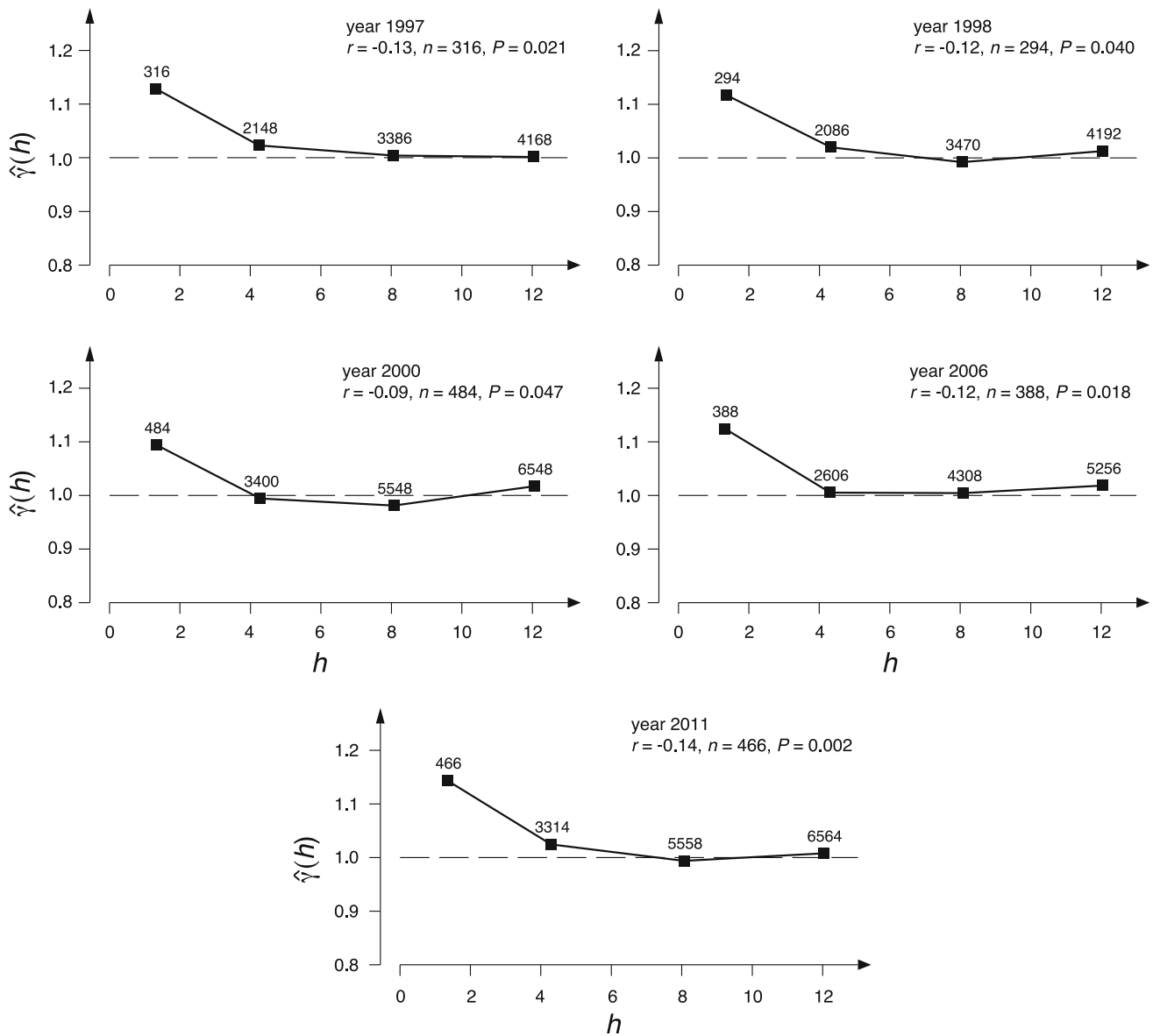
Inter-annual variation in arrival dates and spatial characteristics (pair density, nearest neighbour distance) was tested with the analysis of variance (ANOVA). Since reproductive success was zero-inflated and its distribution strongly departed from normality, we used Kruskal–Wallis test to check for inter-annual variation in this trait. Relationships between autocorrelation coefficients and arrival dates at the population level were tested with Pearson correlations. The interacting effects of arrival date and pair density on the reproductive success of white storks were analysed with multiple regression models separately for each year. The stepwise procedures of backward removal were implemented to select for significant independent variables and  $\beta$  coefficients were used to assess the character and strength of significant relationships.  $T$  test was used to compare mean arrival dates of the first quartile of the population between the groups of years when density-dependence in reproductive success was recorded and not recorded. All values were presented as mean  $\pm$  SE. Statistical analysis was performed with STATISTICA 10.0 (StatSoft, Inc 2011).

## Results

Reproductive success of storks varied from 0 to 6 chicks per pair, being 3 fledglings the mode [Fig. S1 in Electronic Supplementary Material (ESM)]. Reproductive success showed significant between-year variation (Kruskal–Wallis:  $H_{17,3352} = 231.3$ ,  $P < 0.001$ ), ranging from  $1.40 \pm 0.10$  to  $2.69 \pm 0.10$  fledglings per pair (Fig. S2 in ESM). Significant annual variation was also found in arrival dates of storks at their breeding territories (ANOVA:  $F_{11,1343} = 14.31$ ,  $P < 0.001$ ; Fig. S3 in ESM). At the population level, arrival dates of early breeders expressed with the first quartile values of all arrival dates ranged from 23 March to 01 April (Fig. S4 in ESM). Much greater inter-annual variation was recorded in the timing of arrival of late breeders, expressed with the third quartile value of all arrival dates (29 March–19 April; Fig. S4 in ESM). Arrivals at first and third quartiles were positively correlated ( $r_p = 0.66$ ,  $n = 12$ ,  $P = 0.020$ ). There were no significant trends in the population size of storks over the course of the study period ( $r_p = 0.23$ ,  $n = 18$ ,  $P = 0.35$ ; see also Fig. S5 in ESM).

The hypothesis of a clumped distribution was refuted because no significant positive autocorrelations in stork productivity in a lag of 2 km was found (Fig. S6 in ESM). In contrast, significant negative autocorrelations in reproductive success were recorded in five out of 18 years (Fig. 2), indicating that pairs with high reproductive success neighbored with pairs of low success (Fig. S7 in ESM). In all other years, reproductive success was randomly distributed within the population (Fig. S7 in ESM). We found that spatial distribution of productivity was affected by the time at which early breeders arrived at their breeding territories, as indicated by significant negative relationship between autocorrelation coefficients and the first quartile value of arrival dates ( $r_p = -0.58$ ,  $n = 12$ ,  $P = 0.045$ ; Fig. 3). In the years of delayed arrival there was a tendency for the reproductive success to be negatively autocorrelated within the population (satellite pattern of distribution). By contrast, in the years when storks arrived early, their reproductive success tended to be more randomly distributed over the study area. Spatial distribution of productivity was not affected by the timing of arrival of late breeders as the autocorrelation coefficients did not correlate significantly with the third quartile value of all arrival dates ( $r_p = -0.38$ ,  $n = 12$ ,  $P = 0.22$ ).

There were significant between-year differences in the density of breeding pairs within the studied population (ANOVA:  $F_{17,3334} = 1.84$ ,  $P = 0.018$ ; range from  $1.91 \pm 0.15$  to  $2.49 \pm 0.13$  breeding pairs/2 km radius), although no significant variation was recorded in the nearest neighbour distance (ANOVA:  $F_{17,3334} = 1.30$ ,  $P = 0.19$ ; range from  $1.24 \pm 0.05$  to  $1.47 \pm 0.07$  km). In



**Fig. 2** Standardized variograms for reproductive success of white storks in the years with significant negative autocorrelations (satellite pattern of distribution) over the first lag ( $h = 2$  km). Semivariances  $\hat{\gamma}(h)$  are shown in four chosen lags, with values  $>1$  indicating a

four out of 12 study years for which data on arrival dates were collected, we found negative density-dependence in reproductive success. In all these cases, the effects of pair density acted differently on early- and late-arriving individuals as revealed by significant density/arrival-date interactions (year 2000:  $F_{1,102} = 5.98$ ,  $P = 0.016$ ; year 2001:  $F_{1,100} = 4.54$ ,  $P = 0.036$ ; year 2003:  $F_{1,119} = 6.68$ ,  $P = 0.011$ ; year 2006:  $F_{1,110} = 13.16$ ,  $P < 0.001$ ). Beta coefficients of all four interaction terms were negative (year 2000:  $\beta = -0.011 \pm 0.005$ ; year 2001:  $\beta = -0.009 \pm 0.004$ ; year 2003:  $\beta = -0.002 \pm 0.001$ ; year 2006:  $\beta = -0.210 \pm 0.006$ ), indicating that late-arriving breeding pairs incurred greater fitness costs (or derived

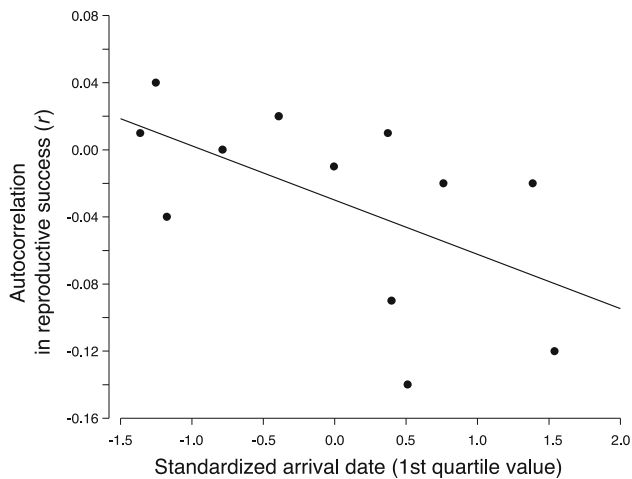
negative autocorrelation and values  $<1$  a positive autocorrelation. Dashed lines indicate standardized total variance. Numbers of pair comparisons are given in each case above the symbol

lower fitness benefits) while breeding in high densities comparatively to the early-arriving conspecifics (Fig. 4). Negative density-dependence in stork productivity tended to occur in the years of delayed population arrival at breeding grounds, which was demonstrated at a nearly significant statistical level ( $t = 2.09$ ,  $df = 10$ ,  $P = 0.063$ ).

### Discussion

In this study, we found that the timing of arrival to the breeding grounds determined the spatial pattern of reproductive success within a population of white storks. In



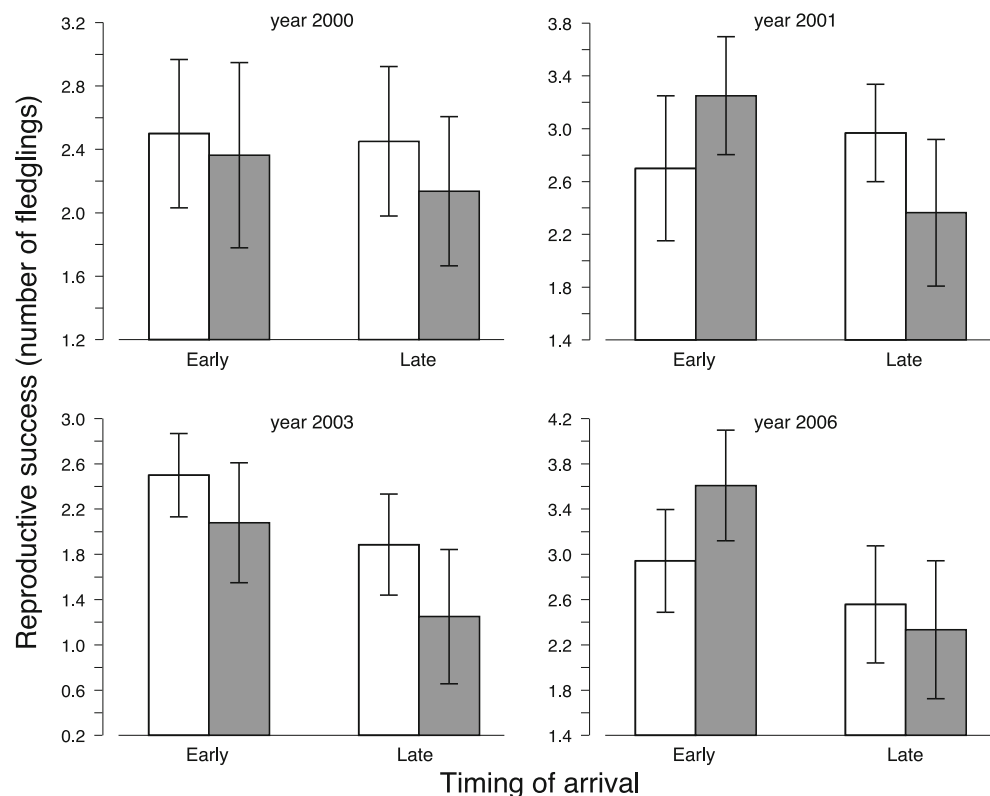


**Fig. 3** Relationship between the spatial distribution of reproductive success (coefficients of autocorrelation calculated with Pearson product-moment correlations) and timing of arrival of white storks to their breeding territories in 2000–2011, central Poland. Standardized first quartile value of arrival dates is assumed to express the time of year at which the first storks were able to return to the breeding territories (arrival of early-breeders)

years when the first storks returned late to their breeding territories, there was a negative spatial autocorrelation of breeding success, which means that pairs with a high reproductive success neighbored with pairs of low

success. Such a pattern could most possibly arise due to intensified competition for food resources during the period of chick rearing in years when early breeders arrived late. Aggressive territorial behaviour of storks is often confined to the closest vicinity of their nests, preventing them from being overtaken by conspecific intruders (Denac 2006). However, storks not always act with aggression towards their neighbours. High tolerance of storks for other breeding pairs may lead, at least locally, to the formation of dense breeding aggregations that in some cases may even function as colonies (Vergara and Aguirre 2006), which is especially common in the Western European populations (Jovani and Tella 2007). Colonial breeding of storks could be maintained through evolution, as feeding areas of neighbouring pairs are spatially separated from their nesting locations. In consequence, white storks are often forced to make long foraging trips that usually take up to 5 km (Johst et al. 2001; Moritzi et al. 2001), but occasionally could be even longer (Alonso et al. 1994). For the same reason, neighbouring breeding pairs frequently share the same foraging areas. Although foraging in flocks has been reported in some populations of white stork (Carrascal et al. 1990), most of birds often exhibit aggressive behaviours at feeding grounds. Under such circumstances, individuals from high-quality pairs are likely to actively expel subordinate neighbours from the good-quality

**Fig. 4** Reproductive success of early- and late-arriving white storks with respect to the breeding densities in four different years (indicated on the plots), central Poland. For the purpose of presentation, birds were classified as arriving early or late in the season, and as breeding in low (white area) or high (grey area) densities. Both classifications were made on the basis of median values of arrival dates and nesting densities (pairs/2 km radius), respectively. All values presented as mean  $\pm$  1.96  $\times$  SE. The scales of the vertical axis label differ



patches of foraging habitat, a mechanism that could be classified as a classic interference competition (Case and Gilpin 1974). Occurrence of aggressive behaviours at feeding territories were confirmed by direct observations in the studied population (Podlaszczuk 2012). Alternatively, if high-quality pair tolerates the presence of subordinates within their foraging area, an exploitation competition may occur, resulting in reduced availability of food resources for low-quality birds after their extensive exploitation by the higher-quality individuals. Under the limitation of food supplies, both these mechanisms of competition should lead to the appearance of negative autocorrelation in the breeding success of neighbouring pairs that was revealed in this study.

We can identify several potential causes of why low-quality storks could decide to nest in the close vicinity of high-quality conspecifics. Firstly, this kind of satellite pattern may arise due to the limitation of suitable nesting sites and foraging areas. Most of white storks from Central European populations prefer to nest on specific anthropogenic structures (Tryjanowski et al. 2009), which may be limited in availability, especially in the proximity of favourable foraging grounds such as wetlands or river valleys. Thus, assuming that early-arriving birds settle in the best territories that are randomly distributed over the breeding area, later-arriving individuals would have to accept less attractive territories and fit in the despotic distribution of early breeders. Secondly, nest building is very costly in terms of time and energy for white storks (Vergara et al. 2010), so it could be more advantageous for newly recruited, inexperienced birds to occupy an old nest in the neighbourhood of a high-quality pair, instead of building a new one in a previously unoccupied area. Finally, it cannot be excluded that first-time breeders use reproductive success of more experienced conspecifics as a public information on the quality of habitat patches, which has been reported for a number of other avian species (Doligez et al. 2002). Under such circumstances, young inexperienced storks could be attracted to settle close to the high-quality pairs which raise, on average, more fledglings than pairs of lower quality.

There are a few non-exclusive mechanisms that could explain how higher intensity of intra-specific competition is found in those years preceded by a later arrival at the breeding grounds of the high quality individuals. Firstly, delayed return of storks is most frequently caused by harsh weather conditions along the migration route or at breeding grounds just prior to the arrival of birds (Ptaszyk et al. 2003). Unfavourable late-winter or early-spring conditions may affect prey densities of white stork. Winter plays a crucial role in shaping population dynamics of small vertebrates across the northern regions (Hanson and Henttonen 1988). Such environmental events as formation of ice on

the ground have been reported to exert detrimental effects on the survival of rodents (Aars and Ims 2002), an important diet component of white stork (Antczak et al. 2002). In consequence, late arrival of storks at breeding grounds may coincide with low prey abundance throughout the entire reproductive period, under which circumstances the intensity of intra-specific competition is likely to increase and high-quality pairs may try to monopolize most of available resources at the expense of their low-quality neighbours.

Even if prey abundance remains unaffected by the late-winter/early-spring conditions, its peak availability may not match with the peak of food requirements of the entire stork population when the arrival at breeding grounds is substantially delayed. For many predatory avian species from northern regions, availability of food resources is known to initially increase in spring, but at some point the pattern reverses and food abundance starts to decline as the season further progresses (Safina and Burger 1985; Visser et al. 1998). In migratory birds, the timing of arrival at breeding grounds and initiation of reproduction is evolutionarily selected to maximize fitness benefits resulting from synchronization of the chick rearing and high food availability periods, a phenomenon recognized as a match/mismatch hypothesis (Visser et al. 2004; Durant et al. 2007). When the most energy expensive part of breeding phenology does not correspond to the peak food availability, an intra-specific competition for food resources should increase, which could primarily result in poor reproductive output of low-quality stork pairs. Some evidence that white storks adjust the timing of egg laying to match nestling period with the period of high vole availability has been recently presented for Central-European populations (Hušek et al. 2013).

Another mechanism that may be, at least to some extent, responsible for the intensification of intra-specific competition in the years of late arrival is associated with changes in photoperiod along stork breeding season. The reproductive cycle of white stork is relatively long, taking over 3 months from initiation of egg laying to the fledging of chicks (Hancock et al. 1992). Furthermore, offspring remain dependent on the parental food delivery relatively long after leaving the nest. This means that the parental care of white storks may well extend into July or even August, a period when daylength starts to shorten considerably in northern latitudes, which reduces the time available for foraging. In fact, it has been reported that towards the end of the breeding season delivery rates of adult storks may be limited by the time of daylight and storks may continue foraging after sunset in order to fulfil energetic needs of their offspring (Podlaszczuk 2012). Storks may become time-limited at the end of chick rearing period also because of the spatial changes in food availability within

their territories. It was demonstrated that foraging distance of white stork increases over the course of the season, as the food gradually depletes in the close vicinity of nests due to its over-exploitation by nest owners (Alonso et al. 1991). In conclusion, providing that the timing of arrival correlates with laying dates as was demonstrated in other stork populations (Tryjanowski et al. 2004; Vergara et al. 2007), delayed arrival at breeding grounds may be associated with raising offspring under less favourable photoperiod. Such changes are expected to bring negative fitness consequences by causing serious time-limitations of foraging by stork parents and, possibly, by increasing the intensity of interference competition between neighbouring pairs.

Apart from inter-annual relationships, we also found intra-seasonal interactions between the spatial pattern of reproductive success and individual arrival dates. In four out of 12 years of study, we found that late-arriving storks were more disadvantaged (or less advantaged) while nesting in high densities comparatively to early-arriving birds. Early-arriving individuals are usually of higher phenotypic quality and, thus, are expected to occupy patches of habitat favourable in terms of food availability. Since attractive habitats are likely to cause high nesting densities (Beshkarev et al. 1994), rich foraging areas are frequently associated with intensified intra-specific competition. As late-arriving storks of low quality are likely to be out-competed by high-quality neighbours, the optimal reproductive strategy for late-arriving birds could be to settle in less favourable habitat where nesting densities are lower. Reduced breeding success in high breeding densities has been reported in other European populations of white stork (Barbraud et al. 1999). Density-dependent patterns of reproductive success of white storks in Slovenia were suggested to arise due to the intra-specific exploitation competition, which is consistent with our results (Denac 2006). This hypothesis was also supported by food supplementation experiments which demonstrated that, at least in some populations, reproductive success of white storks is limited by the food availability during the breeding season (Djerdali et al. 2008). Similarly, it was found that stork pairs occupying territories with unlimited anthropogenic food supplies and negligible intra-specific competition (e.g., near rubbish dumps) had higher reproductive success in comparison to pairs that exploited natural food resources, even if their territories were of good quality (Tortosa et al. 2002; Massemmin-Challet et al. 2006). We also found a tendency for the negative density-dependent effects to occur during the years of delayed population arrival at breeding grounds, which further supports the link between the phenology of spring migration and spatial patterns of productivity within the populations of white stork.

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