



## SEX-RELATED NATAL DISPERSAL OF WHITE STORKS (*CICONIA CICONIA*) IN POLAND: HOW FAR AND WHERE TO?

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**ABSTRACT.**—Distance and direction of natal dispersal were studied in a Polish White Stork (*Ciconia ciconia*) population on the basis of 25 years of banding and resighting data. Multiple regression analysis showed a significant sex-linked bias (females settled farther from the natal sites than males) and effect of banding year, in that dispersal distances were decreasing toward the end of the study period. Population indices in the hatching year and the presumed recruitment year did not help to explain the variance. The birds showed a trend toward settling southeast of the natal site, but this was significant only in individuals that settled within 50 km of the natal site. We suggest that when returning from winter sites in the southeast, young White Storks settle before they reach their presumed migratory target in the vicinity of the natal site. This is only possible if, in spite of a relatively high population density, many breeding areas and potential nesting sites remain vacant. This might also explain our failure to find density dependence in the interannual variation of dispersal distances. Received 27 April 2005, accepted 3 January 2006.

**Key words:** *Ciconia ciconia*, dispersal, dispersal direction, population ecology, sex bias, White Stork.

Натальная дисперсия *Ciconia ciconia* в Польше зависит от пола: как далеко и куда?

**РЕЗЮМЕ.**—В польской популяции *Ciconia ciconia* на основании 25-летних данных кольцевания и наблюдений за окольцованными птицами изучали расстояние и дальность натальной дисперсии. Множественный регрессионный анализ показал значимый эффект пола (самки селились дальше от места рождения, чем самцы) и года: дальность дисперсии уменьшалась к концу периода исследований. Индексы численности популяции в год рождения и предполагаемый год начала размножения не помогли объяснить вариацию. Тенденция селиться к юго-востоку от места рождения была значимой лишь у птиц, дальность дисперсии которых не превышала 50 км. Мы полагаем, что когда молодые птицы возвращаются с мест зимовок с юго-востока, они могут занимать гнезда, прежде чем достигнут предполагаемой цели миграции неподалеку от родного гнезда. Это возможно только если, несмотря на сравнительно высокую плотность гнездящейся популяции, многие гнездовые участки и потенциальные места для гнезд остаются незанятыми. Это же может быть причиной того, что мы не нашли зависимости от плотности в межгодовой вариации дальности дисперсии.

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DISPERSAL BEHAVIOR IS a fundamental feature of organisms and a major determinant of basic patterns and processes (Walters 2000). In particular, natal dispersal—movement between the places of birth and first breeding—largely governs the dynamics and genetic structure of populations (Johnson and Gaines 1990, Whitlock 2001). Natal dispersal patterns may have serious micro-evolutionary implications for avian populations (e.g., Garant et al. 2005, Postma and van Noordwijk 2005). Although numerous studies have looked at determinants of natal dispersal distance (Swingland 1983, Colbert et al. 2001), many of these used study plots too small for detection of individuals that disperse over longer distances (Hanski and Gilpin 1997, Colbert et al. 2001).

Among European birds, the White Stork (*Ciconia ciconia*) is a useful species in which to examine dispersal pattern. An easily detected, charismatic species associated with human habitation, it has been subject to long-term studies in recent decades. A significant proportion of the world's breeding population inhabits Eastern and Central Europe (Schulz 1998). Here, we concentrate on part of the important Polish White Stork population (25% of the world population). In contrast to the White Stork populations in Western Europe, the Central European ones are stable, or even increasing, in numbers, even though their survival rates vary between years (Schaub et al. 2005). In addition, it is a truly wild population, not supported by hand-reared birds, and all members of this population are long-distance migrants (Schulz 1998).

Natal dispersal in birds is generally sex-biased, with females settling farther from their natal sites than males (Greenwood 1980, Sokolov 1997). However, good empirical data on natal dispersal patterns are still needed (Colbert et al. 2001; but see Dale et al. 2005). In the present study, we aimed to identify determinants of natal dispersal distance in a White Stork population breeding in southern Poland. The study was done on a regional rather than local scale, so that birds settling >100 km from the natal nest still had a fairly high detection probability. Therefore, the study was not limited to birds that remain in the close vicinity of their natal site (e.g., one to several kilometers). The birds included in the study were proven to be breeding and linked to a particular nest, which is a clear advantage compared with random recoveries from the breeding

period. We tested sex, hatching year, number of siblings, age at resighting, and population indices in the hatching year and in the year of presumed recruitment.

#### METHODS

Field work was conducted in the breeding seasons 1980–2004 in southern Poland, between the towns of Ostrow Wielkopolski and Katowice, an area that has breeding densities typical of White Storks in Poland (near Ostrow Wielkopolski: ~9 breeding pairs per 100 km<sup>2</sup> [Dolata 2003, P. T. Dolata unpubl. data]; in Upper Silesia: ~6 pairs per 100 km<sup>2</sup>, but rising to 20 pairs per 100 km<sup>2</sup> locally in river valleys in the region of Silesia [Profus 1991, Profus and Chromik 2001, P. Profus unpubl. data]). The study area covered ~7,000 km<sup>2</sup>. White Storks in the area built nests mainly on trees, electricity poles, and the roofs of buildings.

As an index of population size, we used data collected from part of the study area (~1,700 km<sup>2</sup> in extent), where the size of the local population was established by standard methods, as used in the International Census of White Storks (Creutz 1985, Schulz 1998).

During the breeding seasons, we tried to band the chicks in all available nests; therefore, data on brood size were collected as well. All adult White Storks breeding in the study area were checked for bands (observations by telescope and binoculars). Additionally, we asked all farmers whether White Stork nests were located in their farm buildings and whether storks with leg-bands were present. Every effort was made to read bands on all marked individuals breeding in the study area.

Seventy-three White Storks were included in the analysis. These birds were hatched in 1977–2000 and resighted in 1980–2004. Only the first resighting was included, so that each individual was included only once. Breeding dispersal is a very rare event in the White Stork, and both cases in our sample refer to distances <10 km. Of the birds included in the study, 63 individuals were banded and resighted in Poland, 2 were emigrants from the region (resighted or recovered in Austria and Germany), and 8 were immigrants to the region (banded in Austria, Germany, or Czech Republic and resighted in western Poland). Of the 73 birds, sex was determined from observations of breeding behavior in 44 individuals (25 males, 19 females). In 59 cases,

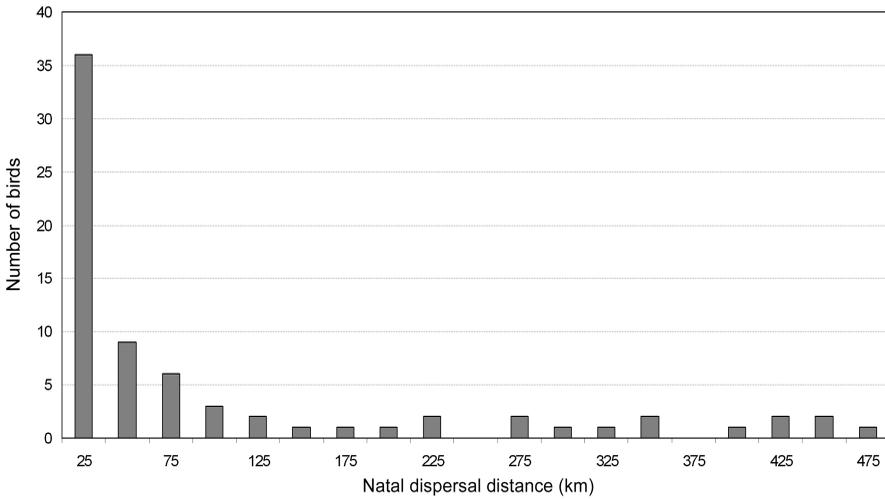


FIG. 1. Frequency distribution of dispersal distances in all White Storks pooled ( $n = 73$ ).

we knew the number of chicks raised in the brood from which our birds originated. No birds included in the study were siblings.

Multiple regression analysis was used to identify variables that significantly predicted dispersal-distance variation. We used both forward and backward stepwise analyses to check on the robustness of model selection. All tests were two-tailed. Dispersal directions were analyzed using the methods of circular statistics (Batschelet 1981). The Moore modification of the Rayleigh test was used to test for the randomness of dispersal directions, weighting the angles by dispersal distances (Zar 1999).

RESULTS

*Dispersal distance and factors that govern it.*—The minimum dispersal distance of White Storks included in our analysis was 0.4 km and the maximum 463 km (mean  $\pm$  SD:  $94 \pm 132.2$  km), the median was 26 km, and the first and third quartiles were  $-10$  and  $113$  km, respectively ( $n = 73$ ; Fig. 1). The mean and maximum values are probably underestimates, because the reporting probability of birds that were banded in the study area and settled outside its boundaries was smaller than that of birds that remained in the area.

Only two White Storks showed a nonzero breeding dispersal, both for a distance  $\leq 10$  km. Almost all the birds in our sample, once settled, returned to the same breeding area throughout their lives.

We built a multiple regression model with log-transformed dispersal distance as a dependent variable and hatching year, age at first resighting, and sex and number of chicks in the natal nest as predictors. Only hatching year and sex were significant predictors, and the same model was selected when doing forward and backward elimination. Because number of siblings was an insignificant predictor, and because it was not known for every nest, we increased our sample size by building a model without including this variable (Table 1).

Females bred significantly farther from their natal sites than males (Fig. 2). The sex-related difference was also significant when tested by the Mann-Whitney  $U$ -test ( $z = 3.34$ ,  $P = 0.001$ ). Median dispersal distance was 15 km in males ( $n = 25$ ), and 177 km in females ( $n = 19$ ). Dispersal distance was significantly shorter in birds hatched after the median date (1994) than

TABLE 1. Results of multiple regression analysis of dispersal distance on hatching year, sex, and age at first resighting. Dispersal distance was log-transformed before analysis. Age variable was excluded from the model.

Variable	$\beta \pm SE$	$t$	$P$
Year	$-0.3588 \pm 0.1254$	$-2.86$	$0.0066$
Sex	$-0.4346 \pm 0.1254$	$-3.47$	$0.0013$
$R^2 = 0.392$			$<0.0001$
$F = 13.195^a$ SE of estimate: $0.6379$			

<sup>a</sup>  $df = 2$  and  $41$ .

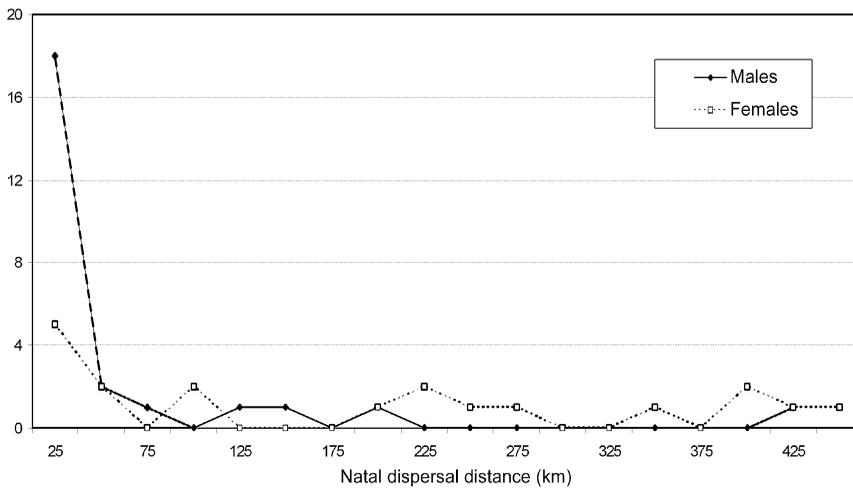


FIG. 2. Frequency distribution of dispersal distances in male ( $n = 25$ ) and female ( $n = 19$ ) White Storks. The difference between sexes is significant (Mann-Whitney  $U$ -test,  $z = 3.44$ ,  $P = 0.0006$ ).

before it ( $n_{\text{after}} = 25$ ,  $n_{\text{before}} = 33$ , Mann-Whitney  $U$ -test:  $z = 3.05$ ,  $P = 0.002$ ).

To look for potential effects of density dependence on dispersal distances, we tested the effects of two potential indices in our model as independent variables: total number of chicks produced by White Stork pairs in a plot representative of the study area in the year of hatching, and an index of population density in the year of hatching +3 years. Most Polish White Storks return to their breeding areas at this age (Kania 1985), and it was also the youngest resighting age in our sample. However, neither index was included in the model as a significant predictor.

*Dispersal direction.*—Directions of dispersal were significantly nonrandom (Fig. 3; Moore modification of Rayleigh test:  $R' = 1.153$ ,  $n = 70$ ,  $P < 0.025$ ). Mean direction was  $149^\circ$  (Rayleigh test, with distances neglected:  $r = 0.32$ ,  $P < 0.001$ ,  $n = 70$ ). Birds showed a tendency toward settling southeast of their natal sites. However, if only birds dispersing distances  $>50$  km are included, the directional bias is no longer significant (Moore modification of Rayleigh test,  $R' = 0.692$ ,  $P > 0.10$ ; mean direction  $129^\circ$ ,  $r = 0.21$ ,  $P = 0.286$ ,  $n = 28$ ). Among birds that settled within 50 km of their natal nests, directional bias was significant in males ( $R' = 1.170$ ,  $P < 0.01$ ; mean direction  $184^\circ$ ,  $r = 0.51$ ,  $P = 0.011$ ,  $n = 17$ ) but not in females ( $R' = 0.441$ ,  $P > 0.50$ ; mean direction  $152^\circ$ ,  $r = 0.25$ ,  $P = 0.667$ ,  $n = 7$ ). However, it

should be noted that the sample size of females was very small.

DISCUSSION

Frequency distribution of natal dispersal distances generally agreed with the values

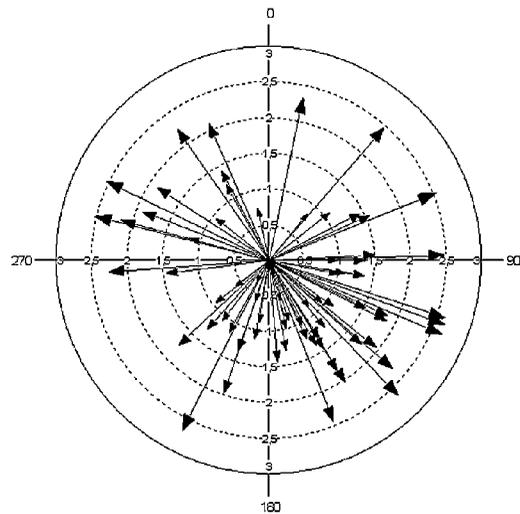


FIG. 3. Directions and distances of natal dispersal of White Storks. Distances (km) are log-transformed for a better visual effect. Directions are spatially nonrandom (Moore modification of Rayleigh test,  $R' = 1.153$ ,  $P < 0.025$ ).

reported from northern Germany (Meybohm and Dahms 1975) and former East Prussia (Hornberger 1954). It is well established that the size of the census area is crucial in estimating dispersal distances, and that estimates based on the data from too small an area may be seriously biased (Hanski and Gilpin 1997, Colbert et al. 2001). However, although we may have underestimated the range of White Stork dispersal, it is unlikely that factors causing bias in our estimates (i.e., low reporting probability from outside the main study area) operated differently in different years or were sex-related. The White Stork is a familiar species that breeds nearly exclusively in human settlements, at least in the study region. It is unlikely that any bird in the study bred in natural, unmonitored habitat. Therefore, reporting probability was relatively high and spatially uniform across our study region. Thus, we may safely assume that the results of multiple regression analysis were not distorted and that female White Storks indeed dispersed farther than males, a pattern common to birds as opposed to mammals (for reviews, see Greenwood 1980, Clarke et al. 1997, Sokolov 1997).

The trend toward shorter dispersal distances in the latter part of the study period is more difficult to put into context. Population indices (total fecundity of the White Stork population in the hatching year or population density index in the presumed recruitment year) did not help explain the variance. Certainly this does not rule out the existence of a density-dependent mechanism that would control dispersal distance. Even though we failed to show this mechanism with the data available to us, some form of such mechanism may exist.

The fact that age at first resighting did not help to predict dispersal distance emphasizes that breeding dispersal is a rare event in the studied White Stork population, which occurs over relatively short distances. This is also shown directly by our data (only two cases of breeding dispersal, both short range).

Dispersal of White Storks in the study area was spatially nonrandom. The birds preferred to settle southeast of their natal site. It is necessary to emphasize that this trend was significant in birds that remained within 50 km of their natal site (Moore modification of Rayleigh test,  $R' = 1.253$ ,  $P < 0.01$ ; mean direction  $156^\circ$ ,  $r = 0.40$ ,  $P < 0.001$ ,  $n = 42$ ), but not in those that dispersed over

longer distances. Therefore, this trend was not a result of some birds settling far to the southeast. Polish White Storks belong to the population that migrates each fall to Africa, to the southeast, through the Bosphorus, Levant, and Egypt, as revealed by banding recovery analysis (Kania 1985) and satellite tracking (Berthold et al. 1997, 2001, 2002; Van den Bossche et al. 2002). In spring, they approach their migration target from the southeast. It can be expected that the dispersal direction biased toward the southeast is at least partly attributable to birds finding good breeding habitats and nest sites when approaching the imprinted migratory target (Sokolov et al. 1984, Morton et al. 1991), and settling in these areas.

Our results might have been distorted in the northwestern part of the study area (or farther northwest of it) if there had been a program for the banding (without subsequent resighting) of the White Storks. In that case, more birds would have been found moving from the northwest to the southeast than vice versa. In reality, effort spent banding and resighting was uniformly distributed spatially; therefore, we believe that spatially biased natal dispersal found in this study is not an artifact.

Spatially biased dispersal has been reported to occur in several warbler species and in Pied Flycatchers (*Ficedula hypoleuca*) on a narrow spit on the southeastern Baltic coast (Sokolov 1997). However, data from an enlarged study plot in the same area showed that Pied Flycatcher dispersal was not spatially biased in either sex (Sokolov et al. 2004). We believe that the southeast-biased dispersal in our White Stork population suggests that even though this population is large and increasing (Profus and Chromik 2001), it is still not in equilibrium so that nest sites and breeding habitats are readily available. This population still has a potential for further growth. This could also be a reason behind our failure to find density dependence in the natal dispersal distance. Alternative possible factors constraining the birds to settle south of their place of origin (e.g., climatic conditions becoming more severe) are at odds with the fact that the average ambient temperature in the study area was increasing during the study periods and with the increase in population size (Ptaszyk et al. 2003; Tryjanowski et al. 2004, 2005).

Natal dispersal in the White Stork was not spatially biased in the 1960s and early 1970s in a then-declining north German population

(Meybohm and Dahms 1975). However, from the former East Prussia, before World War II, an easterly—and especially northeasterly—bias in dispersal direction was reported (Hornberger 1954). The latter population lived under high density, so the first-time breeders had to look for vacant breeding possibilities, which they mainly found in the east, causing an eastward range expansion (Ringleben 1950).

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