



**White Storks (*Ciconia ciconia*) of Eastern Germany: age-dependent breeding ability, and age- and density-dependent effects on dispersal behaviour**



**White storks (*Ciconia ciconia*) of Eastern Germany:  
age-dependent breeding ability, and age- and density-  
dependent effects on dispersal behavior**

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## Abstract

Understanding the basis of dispersal behavior and nest site selection has important implications for explaining the population structure and dynamics of any given species. Individual's fitness, reproductive and competitive ability and dispersal behavior can be determined by age. Indeed, in many bird species, age- and density-dependent changes in dispersal patterns are common. Here we first examined age effects on reproductive ability and nest site selection/natal site fidelity in white storks (*Ciconia ciconia*). We asked whether both, the proportion of breeding individuals, and natal site fidelity increase with age.

White storks are soaring migratory birds breeding in large parts of Europe. Following a steep population decline, a positive trend in the population development has been observed in many regions of Europe, after the seventies of the last century. Increasing population density, especially after 1983 in the eastern sub-population in Eastern Germany allowed examining density- as well as age-dependent breeding dispersal patterns (dispersal frequency and distance). We also examined age- and density-dependency of breeding dispersal directions in given population. We asked whether and how the major migration direction in spring interacts with dispersal directions: would age and population density affect the breeding dispersal directions?

The proportion of breeding individuals in the re-sighted population decreased in old age following the increase in the first 22 years of life, probably due to senescent decay in individual's fitness. Young birds showed strong natal site fidelity, suggesting genetic components in their migratory patterns.

Young storks were dispersing more frequently than old storks in general. Significant increases in the proportion of dispersing individuals over time imply a density-dependent component in the dispersal behavior of white storks. Furthermore, a significant interaction effect was found between the age of dispersing individuals and year. Thus, old birds increasingly dispersed from their previous nest sites over time probably due to increasing competition level as a result of the population recovery.

When comparing breeding dispersal directions in young storks ( $\leq 5$  years old) with that in old storks, we found that young storks tended to disperse along their major spring migration direction, many individuals settled down along the migration route before reaching their previous breeding areas (leading to the south-eastward dispersal). Old birds also tended to disperse along the major spring migration direction; however, appeared to keep on

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migrating along the migration direction even after reaching their previous breeding areas (leading to the north-westward dispersal).

Breeding dispersal directions changed over time, with more obscured directional dispersal patterns during the second half of the observation period, when population densities were considerably higher. Here again, increase in competition seems to cause more dispersal events in storks. We discuss the potential role of age and competition for the observed age- and density-dependent patterns in dispersal behavior.



## Zusammenfassung

Das Verständnis der Mechanismen, die dem Ausbreitungsverhalten und der Wahl des Neststandorts zugrunde liegen, gibt wichtige Einsichten in Strukturen und Dynamiken von Tierpopulationen. Der Gesundheitszustand, die Produktivität und Konkurrenzfähigkeit sowie das Ausbreitungsverhalten eines Individuums können über das Alter ermittelt werden. Alters- und dichteabhängige Veränderungen in Verbreitungsmustern kommen bei vielen Vogelarten vor.

In der vorliegenden Studie untersuchten wir zunächst den Effekt des Alters auf die Reproduktivität, auf die Wahl des Neststandorts sowie auf die Geburtsorttreue des Weißstorchs (*Ciconia ciconia*). Wir fragten, ob sowohl der Anteil der brütenden Individuen als auch die Geburtsorttreue mit dem Alter zunimmt.

Weißstörche sind Zugvögel, die während der Migration zumeist segelnd die Thermik nutzen und in weiten Teilen Europas brüten. Nach einem starken Bestandsrückgang konnte in vielen Regionen Europas ab den 1970er Jahren wieder ein positiver Trend in der Populationsentwicklung beobachtet werden. Die zunehmende Populationsdichte, besonders nach 1983 in der ostziehenden Subpopulation in den fünf Bundesländern der ehemaligen DDR, erlaubte die Analyse von dichte- und altersabhängigen Präferenzen in der Richtung der Brutstandorte sowie in der Verbreitungsfrequenz und -distanz.

Wir untersuchten zudem die Alters- und Dichteabhängigkeit der Ausbreitungsrichtung einer Teilpopulation. Wir fragten, ob und wie die Hauptzugrichtung im Frühjahr mit der Verbreitungsrichtung interagiert: Beeinflussen Alter und Populationsdichte die Ausbreitungsrichtung?

Der Anteil der brütenden Individuen, die älter als 22 Jahre sind, nahm innerhalb der beobachteten Teilpopulation ab, vermutlich aufgrund einer altersbedingten Abnahme des Gesundheitszustands. Junge Vögel zeigten eine starke Geburtsorttreue, was auf eine genetische Komponente in den Zugmustern junger Störche hinweist.

Generell trat bei jungen Störchen häufiger Ausbreitungsverhalten auf als bei älteren Störchen. Eine signifikante Zunahme der Ausbreitungsdistanz von Individuen über die Zeit lässt auf eine dichteabhängige Komponente im Ausbreitungsverhalten der Weißstörche schließen.

Weiterhin wurde eine signifikante Interaktion zwischen dem Alter sich ausbreitender Individuen und dem betrachteten Jahr gefunden. Demzufolge breiteten sich alte Vögel über die Zeit über größere Distanzen aus, vermutlich um der ansteigenden Konkurrenz, bedingt durch den wachsenden Bestandsdruck, zu entgehen.

## Zusammenfassung

Junge Störche (unter fünf Jahre alt) tendieren dazu, sich auf dem Weg zu den Brutstandorten entlang der Hauptrichtung der Frühjahrsmigration zu verbreiten. Viele Individuen siedeln sich schon an, bevor sie den Neststandort des Vorjahres erreichen, was zu einer süd-östlich gerichteten Ausbreitung führt. Alte Vögel tendieren ebenso dazu, sich entlang der Hauptrichtung der Frühjahrsmigration zu verbreiten, allerdings scheinen sie über den vorjährigen Brutort hinaus zu ziehen, was zu einer nord-westlichen Ausbreitung führt. Während der zweiten Hälfte des Untersuchungszeitraums, in der die Populationsdichte deutlich anstieg, änderte sich die Ausbreitungsrichtung über die Zeit nach weniger klar definierbaren Mustern. Auch hier scheint eine Zunahme der Konkurrenz zu einem häufigeren Wechsel der Brutorte zu führen.

Abschließend diskutieren wir die potentielle Rolle von Alter und Konkurrenz in den beobachteten alters- und dichteabhängigen Mustern des Ausbreitungsverhaltens.

# Synopsis

## 1. Introduction

Dispersal behavior plays primary role in determining basic patterns and characterizing organisms (Walters 2000). Knowledge of how individuals disperse is important to the understanding of the biogeography (MacArthur and Wilson 1967), evolution and population dynamics (Greenwood 1980; Greenwood and Harvey 1982; Johnson and Gaines 1990; Forero et al. 1999; Tufto et al. 2005), and conservation biology (Bailie et al. 2000).

Birds are one of the most mobile organisms on earth and have a high potential for dispersal, especially migratory species (e.g., Helbig 1991, 1992). Selection of breeding habitats and nest-sites can have profound effects on an individual's survival and fecundity, thereby influencing the structure and growth rate of the populations (Clark et al. 2004; Citta and Lindberg 2007). Yet little is known about the mechanisms of dispersal and nest site selection, especially within avian communities (Walters 2000). It is often necessary to follow the movements made by individually marked birds over years to investigate the process of bird dispersal more in detail (Dale et al. 2004). In this thesis, we present data from a long-term study on the dispersal behavior, movement between breeding seasons, of white storks (*Ciconia ciconia*). We define natal dispersal as movements from the site of birth to that of first reproduction, and breeding dispersal as nest site shifts between successive breeding seasons made after the first time breeding/breeding attempt.

White storks are soaring migratory birds distributed throughout Europe during the breeding season (Van den Bossche et al. 2002), and a significant proportion of the total population breeds in Eastern and Central Europe (Schulz 1998). White storks are particularly suited to investigate dispersal behavior and have been subjected to long-term behavioral studies during the last decades (e.g., Chernetsov et al. 2006) because individuals are large and thus easily detectable. Moreover, the species is typically associated with human habitation (Chernetsov et al. 2006). White storks in Europe are distinguished by their differences in migration behavior into two sub-populations (Kanyamibwa et al. 1993): the western population migrates via Gibraltar and winter in Western and Northern Africa, and the eastern population migrates via the Middle East and winter in Eastern and Southern Africa (Kanyamibwa et al. 1993). Although the decrease was stronger in the western population, population size was decreased significantly in both sub-populations from the beginning to the seventies of the 20<sup>th</sup> century (Kanyamibwa et al. 1990; Senra and Ales 1992; Kanyamibwa et al. 1993; Johst et al. 2001; Hinsch 2006). White storks range in farmland/wetland (Van den

Bossche et al. 2002). Thus changes in land use such as, intensive agricultural practices and the pressure of urbanization might have led the population decline (for example, in Germany). During last century, white stork went locally extinct or nearly extinct in some regions in Europe (Schaub et al. 2004; Massemin-Challet et al. 2006); however, a positive trend in the population development has been observed recently (Van den Bossche et al. 2002). Improvements in the natural habitats such as protection and managements of stork foraging grounds might have lead to this recent population increase (Hinsch 2006). In this thesis, we focused on white storks breeding in the eastern part of Germany, which preliminary belongs to the eastern sub-population (Van den Bossche et al. 2002).

### ***1.1 Age-dependent effects on dispersal pattern and breeding ability (chapter 1)***

Age is a primary cause to determine territory change and variation in dispersal probability (Oring et al. 1983; Pärt and Gustafsson 1989; Waser 1996). Age-dependent dispersal is common among philopatric species (Harvey et al. 1984; Beletsky and Orians 1987; Badyaev and Faust 1996; Greenwood and Harvey 1982; Dale et al. 2004; Paradis et al. 1998). In bird species, first-time breeders generally disperse more often and over longer distance than experienced breeders (Greenwood and Harvey 1982; Harvey et al. 1984; Paradis et al. 1998; Hénaux et al. 2007). Individuals use abundance of conspecifics as cues to habitat quality (Stamps 1988, 2001) thereby, are attracted by conspecifics (Danchin et al. 1998; Brown et al. 2000). Dispersing from older and denser areas and choosing less dense areas may be beneficial for young inexperienced birds (Forbes and Kaiser 1994; Doligez et al. 2004) while, old experienced birds tend to choose old nest sites and nest sites with high post-breeding densities due to social attraction (Doligez et al. 2004; Chalfoun and Martin 2007; Hénaux et al. 2007). Competitive and breeding ability positively correlate with breeding experiences, which increase with age (Ollason and Dunnet 1978; Goss-Custrad et al. 1982; Wooller et al. 1990; Forslund and Pärt 1995; Sutherland 1996; Prévault et al. 2005). Old breeders are better breeders than young breeders (Richdale 1957; Coulson and White 1961; Perrins 1965; Ollason and Dunnet 1978; Harvey et al. 1979; Perrins and McCleery 1985; Wooller et al. 1990).

We tested age-dependent breeding ability in white storks by comparing the proportion of breeding individuals and age, hypothesizing the proportion of breeding individuals increases with age (chapter 1). To examine mortality effects on breeding ability, we analyzed population distribution of re-sighted birds along age, and tested the relationship between number of re-sighted birds and the proportion of breeding birds along age (chapter 1). We

tested age-dependent nest site selection (natal site fidelity) by comparing the dispersal distance between the site of birth and that of re-sighting among different age classes ( $\leq 5$  years old; 6-15 years old; and  $\geq 16$  years old) (chapter 1). We predicted that young and less competitive storks disperse for long distance, choose nest sites far from their birth sites while old and highly competitive birds choose nest sites nearby their birth sites owing to the social attraction.

## ***1.2 Density-dependent effects on dispersal behavior (chapter 2)***

Recent theoretical and experimental studies indicate that nest site density may be a cue to trigger dispersal behavior. Although individuals are often attracted by conspecifics (Danchin et al. 1998; Brown et al. 2000), individuals may avoid dense area due to high level of competition and this process may lead to density-dependent dispersal patterns (Myers and Krebs 1971; Greenwood et al. 1979; Hetmanski 2007). The average fecundity can be locally reduced at high population densities because of the increase in competition for preferred breeding and foraging sites (e.g., due to food and nest competition: Martin 1987; Newton 2004), that can render dispersal a more profitable option (Rodenhouse et al. 2003).

We re-analyzed previously published data for the population development of white storks in Eastern Germany during the last 25 years (chapter 2). The strong positive trend in the population development (see chapter 2) provided an excellent opportunity to test for density-dependent dispersal in the studied population. Dispersal behavior in many species shows an age-related component, such as longer natal dispersal (outlined above); however, breeding dispersal may be more common in young, inexperienced individuals (Dale et al. 2004). Thus, we tested whether young storks would show more breeding dispersals than older individuals (chapter 2). Specifically, we predicted that frequency of dispersal events would increase with increase in population densities, especially in young storks (chapter 2).

## ***1.3 Breeding dispersal directions (chapter 3)***

### ***1.3.1 Age and migration directions***

In many migratory bird species, migration direction has genetic based components (Schüz 1951; Gwinner 1986; Helbig et al. 1989; Brethold 1991; Helbig 1991, 1992; Thorup et al. 2007); however, some species may also have evolutionary flexibilities of migratory adaptation (Helbig et al. 1994; Helbig 1996; Thorup et al. 2007). Young birds are guided by their innate information during the migration (Gwinner 1986; Weindler et al 1995). Dispersal

pattern in young migratory birds therefore, can be influenced by their migration routes. For example, young individuals fly congruent with their innate migration direction but may be not as far as or farther than old birds during the spring migration. By contrast, old birds likely to encounter cues triggering breeding dispersal (such as, loss of mates or nests) after they have returned to their breeding sites; hence, breeding dispersal pattern in old birds is probably not dependent on the major migration direction.

We examined age-related breeding dispersal direction patterns in white storks by comparing preferred dispersal directions among different age classes ( $\leq 5$  years old; 6–15 years old; and  $\geq 16$  years old) (chapter 3). White storks of our -study population approach to their breeding sites from south-east during spring migration. Therefore, we predicted that young storks would show south-eastern/north-western biased dispersal while, older storks would disperse less congruent with the major migratory direction.

### **1.3.2 Population density and dispersal directions**

Dispersal behavior may increase with increasing population density because of high competition for breeding sites and food (Myers and Krebs 1971; Greenwood et al. 1979; Hetmanski 2007). Following sharp population decline in the last century, population of the white stork has been developing as a result of improvements in stork habitats (outlined above). Dispersal behavior in white storks increased over time with the population increase (see chapter 2). Does the population increase affect breeding dispersal directions? Breeding dispersal behavior driven by competition due to high population density occurs after individual returned to its previous nest site from its wintering grounds. For example, there are no available vacant nest sites left nearby its previous nest site. Therefore, whether and how breeding dispersal direction patterns are indicated by migration direction can be dependent on population densities, and preferred breeding dispersal direction(s) is/are probably less congruent with the migration direction at high population densities. We tested this idea by comparing directional patterns in breeding dispersals between two periods of times, directory after the population recovery started (1980–1992), and later (1993–2006), when the population densities were higher (chapter3).

### **1.4 White stork ringing data**

We have analyzed data of ringed white storks that were provided by *Hiddensee Bird ringing Centre (Vogelwarte Hiddensee)*. The original data-set contains ringing and re-sighting information of a total number of  $n=5,868$  individually ringed (re-sighted  $n=14,252$ ) white

storks that were ringed at their nest as nestlings in 49°21'–54°30'N, 10°10'E–30°11'E, between 1964 and 2006, re-sighted in 34°14'S–56°38'N, 24°30'E–77°41'E, between 1965 and 2006. In this thesis, we focused on white storks that were ringed and re-sighted in Eastern Germany (50°39'–54°09'N, 10°10'–15°01'E).

The analyses of age-dependent effects on dispersal patterns and breeding ability (chapter 1) are based on a total of  $n=4,104$  individually ringed individuals that were ringed between 1964 and 2006 and re-sighted between 1965 and 2006 (re-sighted  $n= 9,793$ ), including  $n=2,722$  breeding individuals (re-sighted  $n= 4,414$ ).

The analyses of age- and density-dependent breeding dispersal patterns (chapter 2) are based on a total of  $n= 1,230$  individually ringed breeding individuals that were re-sighted in successive breeding seasons between 1980 and 2006 (re-sighted  $n=2,698$ ). (Data before 1980 were excluded from the analyses because ringing and monitoring activities were less regular in the preceding years, while ringing and monitoring were conducted in a systematic fashion after 1980.)

The analyses of age- and population density-dependent dispersal directions (chapter 3) are based on total of  $n=178$  individually ringed individuals that were re-sighted as breeding birds between 1980 and 2006 (re-sighted  $n=196$ ) and dispersing between successive breeding seasons. Data before 1980 were excluded from the analyses (outlined above).

## **2. Thesis objectives and organization**

This thesis consists of three main chapters that are written as independent manuscripts. Each chapter is followed by short text sections. The objectives of the thesis are:

- (i) to investigate impacts of the age on reproductive ability and natal site fidelity in white storks (*Ciconia ciconia*) (chapter 1)
- (ii) to investigate age- and density-impacts on the breeding dispersal behavior in white storks (*Ciconia ciconia*) (chapter 2)
- (iii) to investigate age- and density-dependent effects on changes in the breeding dispersal directions in white storks (*Ciconia ciconia*) (chapter 3)

Although each of the three chapters presents significant contributions to ecological research, this approach results inevitably in a certain repetitions in the manuscripts, especially the introduction, and method sections. All chapters (slightly different versions) are previewed

for submission to scientific journals with supports from co-authors: Prof. Dr. D. Wallschläger, my supervisor; Dr. U. Köppen; and Dr. M. Plath (chapter 2 and 3). On account of the idea of publishing each chapter, this thesis is written in the first person plural.

### **3. Key results**

#### **3.1 Age-dependent reproductive ability and natal site fidelity in the white stork (*Ciconia ciconia*) (chapter 1)**

In the first part of this chapter, we analyzed age-specific reproductive ability of white storks breed in Eastern Germany. Unexpectedly, we found early sexual maturity (at first few years of age) in some individuals. Number of the re-sighted individuals along the age was normally distributed. Neither ‘age’ nor ‘number of re-sighted birds’ had a significant effect on the proportion of breeding birds. A significant quadratic relationship was found between age and the proportion of breeding individuals.

In the second part of this chapter, we tested age-specific nest site selection (natal site fidelity) in the given population. Regardless of age, most of the white storks selected nest sites within 19 km from their natal sites. Young storks showed stronger natal site fidelity than old storks. (Young birds tended to settle within 9 km from their natal sites more than between 10 and 19 km, while old storks tended to settle between 10 and 19 km more than within 9 km from their natal sites.) Mean distances between new nest sites and natal sites did not differ significantly among the age classes.

#### **3.2 Age-and density- dependent effects on breeding dispersal in white stork (*Ciconia ciconia*) (chapter 2)**

In the first part of this chapter, we analyzed the population development of white storks in Eastern Germany (we re-analyzed published census count data of breeding pair of white storks in Eastern Germany between 1983 and 2006). Although large fluctuations in population size were observed after 1987 [population decreases due to adverse weather condition (wet and cold throughout the breeding seasons) in 1988, 1991, 2005 and 2006], population density of the breeding storks increased significantly during the last 25 years.

In the second part of this chapter, we examined age-and density-related breeding dispersal distance and frequency of given population. Young storks disperse more often in general – but not for longer distance – than old storks. The proportion of dispersing individuals increased over time accompanied with the density increase. A significant interaction effect was found between the age of dispersing individuals and year, suggesting



old storks increased frequency of dispersal behavior over time. Neither age nor year had a statistically significant effect on dispersal distance.

### ***3.3 Dispersal patterns in the white stork (*Ciconia ciconia*): age-and density-dependent changes in dispersal directions (chapter 3)***

We tested whether age and density affect the breeding dispersal directions of white storks breed in Eastern Germany. We found that both young and old storks tended to disperse along the major migration direction when they are returning from Africa in spring. But interestingly, we found different dispersal direction preferences between young birds and old birds. Many young birds chose nest sites along the migration route, but before reaching their previous breeding sites (leading to showed south-east-biased dispersal). By contrast, old birds kept migrating along the migration route even after reaching their previous breeding sites (leading to showed north-west-biased dispersal).

Breeding dispersal directions changed over time. One cohort of birds preferred south-east direction while other cohort preferred north-west direction in the first half of the observation period. By contrast, less clear-cut dispersal direction preferences were observed during the second half of the observation period.

## **4. Discussion**

Sexual maturity of white storks is suggested as 4-5 years of age in previous studies (e.g., Schimkat 2007); however, we found some individuals showing breeding attempts at the first years of life (chapter 1). Individual's fitness and survival rate, as well as population dynamics of migratory birds are highly dependent on the environmental variation (e.g., food availability) in their wintering areas (Schaub et al. 2005; Barbraud et al. 1999). Environmental condition such as food availability during wintering may influence the maturity of white storks. Therefore, in order to understand the mechanism of the early maturity of white storks, it is important to conduct further observation on the environmental condition at the wintering area in relation to the fitness of individuals.

Reproductive performance positively correlates with breeding experiences that increase with age in many animals (Clutton-Brook 1988; Newton 1989; Weimerskirch 1992; Reid et al. 2003; Mauck et al. 2004; Frederic et al. 2007). Breeding success in bird species increases with age (Ollason and Dunnet 1978; Wooller et al. 1990; Pr eault et al. 2005). Thus, increase in the proportion of breeding birds over first 22 years of life in the studied population is supported by previous studies (chapter 1). However, the proportion of breeding white storks

decreased in old age. In many vertebras mortality increases at old age (Reznic et al. 1990; Ricklefs et al. 2003; Remeš 2006). For example, in little penguin (*Eudyptula minor*), survival rate decreases in old age (Sidhu et al. 2007). Decline in reproductive ability and the cost of reproduction at old age is common in many long-lived animals (Clutton-Brock 1988; Sæther 1990; Bennett and Owens 2002). Breeding success and reproductive performance decline in old birds as an expression of senescence (Newton 1988; Velando et al. 2006; Kim et al. 2007; Berman et al. 2009). Increase in mortality seems to play a role in observed decline in the number of old re-sighted white storks; however, number of re-sighted storks did not affect the proportion of breeding storks. Therefore, independent of the mortality, likewise in many other long-lived animals, senescent decay in the fitness and breeding ability is likely to lead to the decline in the proportion of breeding individuals in aging storks.

In many bird species, young and inexperienced breeders disperse over longer distance than old and experienced breeders (Greenwood and Harvey 1982; Harvey et al. 1984; Paradis et al. 1998; Hénaux et al. 2007) Thus, we predicted that young storks settle far away from their natal sites. Furthermore, old storks settle nearby their natal sites due to social attraction and site familiarities. Contrary to our prediction, we found higher natal site fidelity in young storks than in old storks (chapter 1). Factors affecting the nest site selection may be age-specific. Migration direction and distance of young migratory birds are guided by innate information (Gwinner 1986; Weindler et al. 1995). Returning to natal sites is beneficial for young birds because of familiarity within potential breeding sites (Greenwood 1980; Pärt 1995), mating advantages (Pärt 1994), and less attacks by resident adults (Van der Jeugd 2001). Environmental influence or behavioral learning tradition leads to dispersal behavior (Helbig 1992). Distribution and breeding success of white storks are local physiographic condition dependent (Johst et al. 2001; Kuźniak 2006). Genetic biased migration system and advantages in philopatric may play important roles in nest site selection in young storks while, environmental conditions and possibly inbreeding avoidance may be more important in old storks. Dispersal is a common option for animals to reduce the occurrence of inbreeding (Greenwood 1980; Pusey 1987; Gandon 1999; Szulkin and Shelton 2007; Jamieson et al. 2009). Moreover, experienced birds return to the breeding area and occupy the best place earlier than young breeders (Brooke 1979; Lundberg et al. 1981; Goss-Custrad et al. 1984; Newton 2004; Hénaux et al. 2007). Thus, to expect high breeding success, experienced storks probably occupy attractive nest sites that are apart from their natal sites first, possibly to avoid inbreeding, but not too far so that individuals can have a benefit from their site familiarities.

Age-related differences in dispersal behavior have been reported for many bird species (Greenwood et al. 1979; Greenwood and Harvey 1982; Doligez et al. 2004). In our study, young breeders dispersed more often – but not for longer distance – than old storks (chapter 2). Breeding dispersals are often driven by breeding failure and mate loss (Greenwood and Harvey 1982; Nager et al. 1996; Waser 1996; Wiklund 1996; Forero et al. 1999). Increase in mortality at old age (Reznick et al. 1990; Ricklefs et al. 2003; Remeš 2006; Sidhu et al. 2007) possibly leads to high mate loss rate in old birds. Young and less experienced birds have lower breeding success than experienced old birds (Richdale 1957; Coulson and White 1961; Perrins 1965; Ollason and Dunner 1978; Harvey et al. 1979; Perrins and McCleery 1985; Wooler et al. 1990). Thus, mate loss probably leads to breeding dispersal in older storks while breeding failure plays an important role in breeding dispersal of younger and less experienced birds.

Older and experienced birds prefer old colonies and patches with high post-breeding density due to the social attraction; conversely, young birds choose patches with lower post-breeding densities because of the expected lower level of competition (Doligez et al. 2004; Chalfoun and Martin 2007; Hénaux et al. 2007). Thus, we predicted that increase in population densities would increase breeding dispersal behavior, especially in young individuals.

Population size of white storks in Eastern Germany increased significantly during last 25 years (Fig. 1; see chapter 2). Proportion of dispersing individuals also increased over time as predicted (chapter 2). Increasing population densities followed by increases in foraging and nest site competition possibly affected dispersal behavior in our study population. However, we found a significant interaction effect between age and year. Therefore, even though still less than younger individuals, contrary to our prediction, older birds were dispersing relatively more during the study period. Aging individuals are probably more affected by nest competition because of decline in their competitive abilities (e.g., Clutton-Brock 1988; Stearns 1992; Jones et al. 2000; Kim et al. 2007). In blue-footed boobies (*Sula nebouxii*), breeding success and competitive abilities in old birds decrease (Velando et al. 2006), with increase in breeding dispersal (Kim et al. 2007). Nesting birds have stronger site-fidelity than mate-fidelity (Hénaux et al. 2007) therefore; young birds may compete with and replace old resident individuals on nests and thus, old birds may be forced to search for new nests.

Age-dependent dispersal behavior is common in several bird species (Greenwood and Harvey 1982; Verhulst et al. 1997; Serrano and Tella 2003). Inexperienced young storks are faithful to their natal site (chapter 1); however, breeding failure may lead to dispersals in

young storks (chapter 2). Young storks, probably the first time breeders, thus, may select nest sites nearby their natal areas, but those that fail to breed change their nest sites in following year. In our study, we found that young storks dispersed more in a south-eastern direction, while old birds dispersed more in a north-western direction (chapter 3). Eastern population white storks approach their nest sites from Eastern and Southern Africa during spring migration (Chernetsov et al. 2006). Thus, the southeast-biased dispersal in young storks implies that, some young storks, probably those that failed to breed in previous year, migrate toward their previous nests but find vacant nest sites during their spring migration (Sokolov et al. 1984; Morton et al. 1991) and settle in these areas (Chernetsov et al. 2006) instead of flying back to their previous nests. Population increases in available vacant breeding site in south-eastern regions, such as Saxony and South-West Poland (Profus and Chromik 2001; Herschmann 2001; Chernetsove et al. 2006) can be explained by the above- mentioned age-specific dispersal behavior.

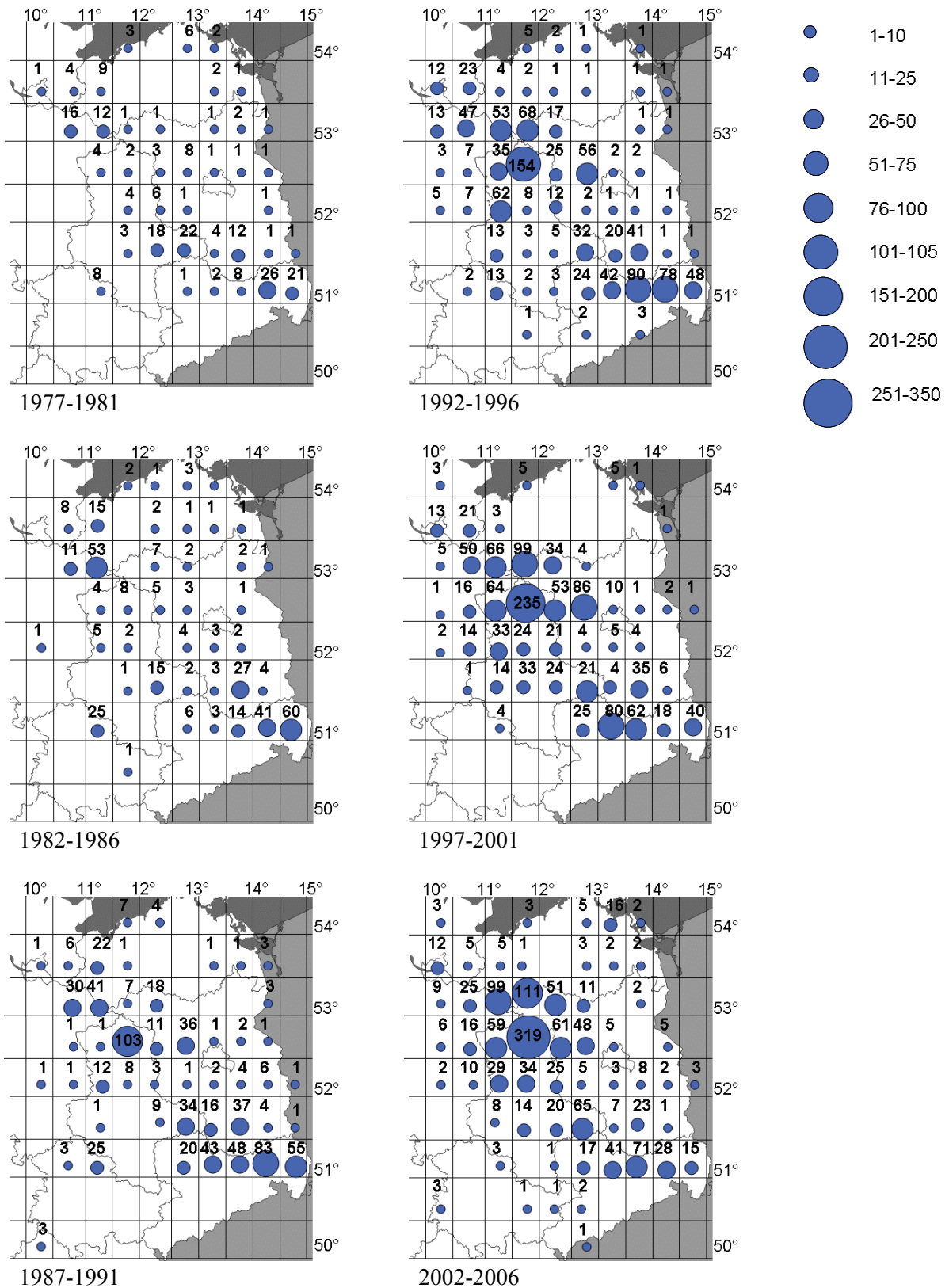
North-west-biased dispersal in old storks, which congruent with the major spring migration direction indicates that old birds also have some genetic components in the migration direction. Some adults may migrate toward their previous nests but continue flying in the same direction if they fail to breed. Breeding dispersal in old birds is driven by mate loss and also can be by breeding failure in the previous year (Greenwood and Hardy 1982; Nager et al. 1996; Waser 1996; Wiklund 1996; Forero et al. 1999). If breeding failure in the previous year is a determinant of breeding dispersal in old storks, those birds failed to breed in the previous year fly toward their previous nests, but might not stop at their previous nest sites owing to their experience in the previous year and keep on migrating in the same direction during spring migration. Breeding success of white storks is strongly dependent on agricultural land use in a given area (Johst et al. 2001). Hence, dispersal behavior in storks can be also affected by changes in agricultural land use.

We found changes in the distribution patterns of breeding dispersal direction over time. While there were two major breeding dispersal direction during the first period (south-east-biased and north-west-biased dispersal), distribution pattern of breeding dispersal direction during the second observation period was more obscure. The south-east-biased breeding dispersal is probably because of the vacant available breeding area in south-eastern regions (outlined above) and the north-west-biased breeding dispersal could be explained by improvements of the foraging areas in the north-western regions such as Hamburg started in the 1970s (Hinsch 2006). We argue the influence of the increase in competition as a result of population increase here. Population density of white storks in Eastern Germany has been

## Synopsis – Discussion

increasing during last decades (Van den Bossche et al. 2002; Hinsch 2006; Itonaga et al. submitted). Competition for preferred breeding and foraging sites increases at high population densities, so average fecundity can be locally reduced (Martin 1987; Doligez et al. 2004; Newton 2004; Mallord et al. 2007). Increase in population densities may be associated with high levels of dispersal (Myers and Krebs 1971; Doligez et al. 2004). In the case of breeding dispersal owing to increase in competition, individuals encounter to those cues that trigger dispersal behavior after they return to their previous breeding sites. This kind of dispersal may be less clear-cut directional dispersal because this happens after the spring migration.

# Synopsis – Discussion



**Fig.1: Population development of white storks in Eastern Germany.**

Number of re-sighted breeding white storks between 1977 and 2006 (only ringed individuals).

## **5. Overall conclusions**

- (i) Some individuals showed breeding attempts in the first few years of life suggesting, strong impact of environmental condition in wintering area on individual's fitness. However, further research needs to be conducted to explain the mechanism of this early maturity.
- (ii) The proportion of breeding white storks increased with age over first 22 years of life; however, decreased in old age probably due to senescent decay.
- (iii) White storks were likely to be faithful to their natal site in general; however, natal site fidelity is stronger in young birds. Age-specific natal site fidelity indicates age-dependent factors for nest site selection.
- (iv) Young storks disperse more often in general but not for longer distance. Changing nests within neighborhood of their natal sites in subsequent years is therefore, probably common in young inexperienced storks. Observed age-dependent dispersal behavior suggests that factors leading to breeding dispersal are probably age dependent.
- (v) Increase in dispersal behavior (especially in the old individuals) accompanied the recent population increase of white storks in Eastern Germany, suggesting that breeding dispersal behavior in this species is density-dependent. Strong density effects on old birds suggests competitive ability decline in old birds as an expression of senescent decay. Indeed, breeding ability decreased in old age probably due to senescent decline in fitness of aging storks.
- (vi) In our study population, breeding dispersal directions were age-dependent. Breeding failure seems to bring dispersal not only in young storks but also in old storks; however, cues for nest site selection are probably age-specific in white storks. Young storks are probably attracted to vacant new areas where they can avoid high competition while environmental condition and experience play important roles in old storks.
- (vii) More storks leave their previous breeding sites over time owing to the high competition as a result of recent population increase. Dispersal direction in this

case is less predictive from the migration route since dispersal driven by high competition happens after individuals have reached its breeding site.

- (viii) Observed age- and density-dependent dispersal patterns suggest, age-specific cues triggering dispersal behavior, and competition effects on dispersal event. We propose that breeding failure leads to dispersals in young birds while, dispersals in old storks are driven more by mate loss. Competition plays an important role in dispersal behavior in white storks; however, impact of competition seems to be age-dependent.
- (ix) This thesis enhances our knowledge of dispersal behavior as a primary cue to understand the population structure and population dynamics of animals, and contributes developing underpinning mechanisms of dispersal behavior in bird species more in detail.
- (x) Logistic growth in the studied population indicates that our study population is about to reach its carrying capacity. Therefore, it will be interesting to observe: if frequency of dispersal behavior also reaches the maximum, and whether and how the dispersal direction changes in the near future.

## **6. Declaration of my own contribution to the presented manuscripts**

I designed the experiments, performed the statistical analysis on the data, and wrote the major part of the manuscripts by myself, using relevant literature for all three studies. While conducting the research, I was provided the data from *Hiddensee Bird ringing Centre (Vogelwarte Hiddensee)*, and advised by Prof. Dr. D. Wallschläger, Dr. U. Köppen, and Dr. M. Plath (in chapter 2 and 3), who contributed to advanced drafts and final stage of the manuscript as co-authors.



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## Chapter 1:

### Age-dependent reproductive ability and natal site fidelity in the white stork (*Ciconia ciconia*)



Nest information boards in Rühstädt

# Age-dependent reproductive ability and natal site fidelity in the white stork (*Ciconia ciconia*)<sup>1</sup>

## 1. Abstract

Age is an important factor to determine individual's fitness, reproductive and competition ability, as well as dispersal behavior. Here we examine, age-related differences in reproductive ability and nest site selection in white storks (*Ciconia ciconia*), soaring migratory birds breed in Europe. We tested whether: 1) the proportion of breeding birds increase with the age, 2) age affects the nest site selection (natal area fidelity) using long-term bird ringing data provided by *Hiddensee Bird Ringing Centre (Vogelwarte Hiddensee)*. The proportion of breeding birds increased over the first 22 years of life, then decreased in old age, suggesting senescent decay in individual's fitness. We found age-related nest site selection differences. Young birds showed stronger natal site fidelity than old birds. We discuss potential factors for observed age-related differences in nest site selection in white storks.

**Keywords:** Age-dependent, Breeding ability, Nest site selection, Natal site fidelity, White stork, *Ciconia ciconia*

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## **2. Introduction**

Dispersal behavior is a fundamental feature of organisms, and a major determinant of basic patterns and process characterizing organisms (Walters 2000). Understanding patterns of dispersal in vertebrates is important from biogeography (MacArthur and Wilson 1967), evolutionary and population dynamics (Tufto et al. 2005), behavioral ecology (Greenwood 1980), and conservation biology (Baillie et al. 2000).

Crypsis of population dispersal in bird species have been studied over decades. Age is an important factor for variation in dispersal probability (Pärt and Gustafsson 1989; Waser 1996). Age-specific dispersal is widely reported among philopatric species (Harvey et al. 1984; Beletsky and Orians 1987; Badyaev and Faust 1996; Greenwood and Harvey 1982; Dale et al. 2004; Paradis et al. 1998). The primary causes determining territory change is age (Oring et al. 1983). Young individuals generally disperse more often and for longer distances than experienced breeders (Hénaux et al. 2007). Competitive ability increases with age and experience of individuals (Goss-Custard et al. 1982; Forslund and Pärt 1995). Choosing nearby empty patches by dispersing from older and denser patches can be an attractive strategy for inexperienced breeders (Forbes and Kaiser 1994; Doligez et al. 2004) while experienced breeders prefer the oldest patches and patches with high post-breeding densities that likely to be good integrative indicators of future success (Doligez et al. 2004; Chalfoun and Martin 2007; Hénaux et al. 2007). Birds use abundance of conspecifics as cues to habitat qualities (Stamps 1988, 2001). Movements made by individually marked birds over years might be necessary to understand the process of dispersals (Dale et al. 2004). Reproductive ability of animals can be determined by age (Clutton-Brook 1988; Newton 1989; Weimerskirch 1992; Reid et al. 2003; Mauck et al. 2004; Frederic et al. 2007). Breeding success increases with age in many bird species (Ollason and Dunnet 1978; Wooller et al. 1990; Sutherland 1996; Préault et al. 2005). In this paper, we present long-term study data on the age-dependent reproductive ability as well as nest site selection (natal site fidelity) of white storks (*Ciconia ciconia*) in Eastern Germany. White storks, European regional birds (Latus and Kujawa 2005), are an useful species in which to investigate dispersal models due to their easily detected, charismatic characteristics and association with human habitations, and they have been subjected to long-term studies in recent decades (Chernetsov et al. 2006). White storks in Europe are classified by their migration behavior and distribution differences into two sub-populations (Kanyamibwa et al. 1993): the western population, breeds in south-west Europe and migrates to Central-west/Northern Africa for wintering, and the eastern sub-population, breeds in north-east Europe and migrants to Central-east/Southern Africa for



wintering. In the present study, we focused on white storks breeding in Eastern Germany, which preliminary belongs to the eastern sub-population (Van den Bossche et al. 2002).

In the first part of our study, we tested if age has an effect on reproductive performance of white storks. In general, experienced old breeders are better breeders than inexperienced young breeders (Richdale 1957; Coulson and White 1961; Perrins 1965; Ollason and Dunnet 1978; Harvey et al. 1979; Perrins and McCleery 1985; Wooler et al. 1990). Thus, we predicted that the proportion of breeding birds increases with age.

We tested age related natal site fidelity by comparing the distance between natal sites and re-sighting nest sites among different age classes. We predicted that young storks settle in new nest sites far from their natal sites, while old birds settle in nest sites close to their natal sites that are probably old areas with high post-breeding success.

### **3. Methods**

#### **3.1 Census counts**

We analyzed data of ringed white storks that were provided by the *Hiddensee Bird Ringing Centre (Vogelwarte Hiddensee)*. Nestlings were ringed individually at their nests in Eastern Germany (50°39'–54°09' N, 10°10'–15°01' E) between 1964 and 2006 with rings that have different ID numbers on, and the re-sighting data were recorded every breeding season (between March and August) in Eastern Germany over 40 years (1965–2006) by volunteer workers. Our analyses are based on a total of  $n=4,104$  individually ringed and re-sighted individuals (re-sighting  $n=9,793$ ), including  $n=2,722$  breeding individuals (re-sighting  $n=4,414$ ). The data-set consists two parts: ringing data contains information of ringing date, geographical coordinates of the nests, and re-sighting data contains information of re-sighting dates, geographical coordinates of the re-sighting points, distance between the ringed location (nest) and re-sighting locations, and breeding status of individuals at re-sightings.

#### **3.2 Statistical analysis**

We calculated the proportion of the breeding birds by dividing the number of breeding individuals by the number of re-sighted birds for each age (1–29 years old). We expected impact of mortality on the number of the re-sighted individuals and also on the reproductive ability. Thus, we first applied Kolmogorov-Smirnov test (SPSS16.0) to test the population distribution of number of re-sighted bird along the age then, used multiple regression with 'proportion of breeding individuals' as dependent variable, 'age' and 'number of re-sighted

birds' as independent variables (SPSS16.0) to test whether age and number of re-sighted birds affect the proportion of breeding individuals. There were no linear relationship between age and the proportion of breeding birds (see below) therefore, we used a curve fitting procedure (as implemented in SPSS16.0) to examine the relationship between the proportion of breeding individuals (dependent variable) and age (independent variable).

To test for differences in dispersal distances among age classes, we split the data-set into three different age classes:  $\leq 5$  years old; 6-15 years old; and  $\geq 16$  years old. We also split the data-set into twenty one different distance classes (distance between the natal area and re-sighting area): 0–9 km; 10–19 km; 20–29 km; 30–39 km; 40–49 km; 50–59 km; 60–69 km; 70–79 km; 80–89 km; 90–99 km; 100–109 km; 110–119 km; 120–129 km; 130–139 km; 140–149 km; 150–159 km; 160–169 km; 170–179 km; 180–189 km; 190–199 km; and more than 200 km. We compared dispersal distances among the age classes using Chi-square tests. Mean distances between natal sites and re-sighting sites for each age classes, and STDV of the mean distances was calculated.

## **4. Results**

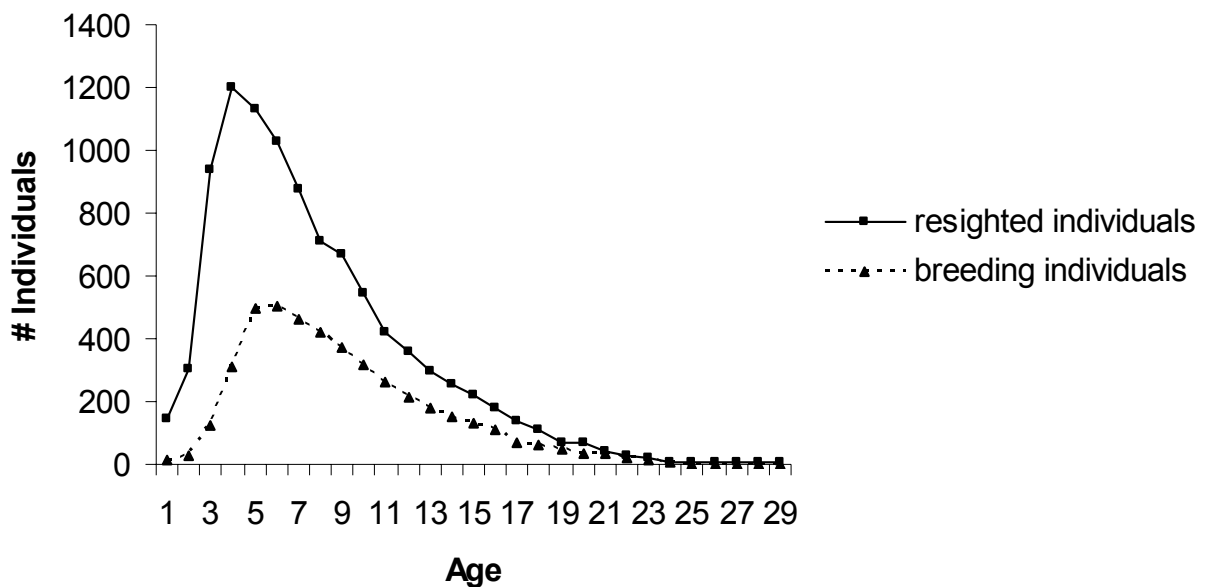
### **4.1 Age-dependent reproductive ability**

The youngest breeding birds were one year old (14 individuals, 0.32% of the total breeding birds, 9.46% of the re-sighted one year old birds) and the oldest breeding birds were 29 years old (two individuals, 0.05% of the total breeding birds, 33.33% of the re-sighted 29 years old birds) in the studied population (Fig.1). The proportion of breeding birds was as maximum at the age of 22 (24 individuals, 11.44% of the total breeding birds, 85.71% of the re-sighted 22 years old birds; Fig. 1). The number of re-sighted birds along the age was normally distributed (*Kolmogorov-Smirnov-Z*=1.03, *P*=0.24; Fig 2). In the analysis of factors affecting the proportion of breeding individuals (multiple regression  $R^2=0.329$ ) neither 'age' ( $B=0.913$ ,  $SE=0.724$ ,  $\beta=0.374$ ,  $t=1.261$ ,  $P=0.219$ ) nor 'number of re-sighted birds' ( $B=0.03$ ,  $SE=0.16$ ,  $\beta=0.060$ ,  $t=0.203$ ,  $P=0.840$ ) had a statistically significant effect on the proportion of breeding birds. Significant quadratic relationship was found between age and the proportion of breeding birds ( $F_{1,27}=29.69$ ,  $P<0.0001$ ,  $n=29$ ,  $R^2=0.70$ ; Fig.2).

### **4.2 Dispersal behavior**

We detected significant differences in distance classes among age classes ( $\chi^2=132.22$ ,  $df=40$ ,  $P<0.001$ ; Fig 3). Indeed, age classes differed in the relative frequency of birds that preferred

one of the two major distance classes: in the youngest age classes, 19.88% of birds were re-sighted within 9 km from their natal sites, while 13.01% of the birds were re-sighted between 10 and 19 km from their natal sites (Fig.3). In the second age class, 12.69% of the birds were re-sighted within 9 km from their natal sites, while 14.84% of the birds were re-sighted between 10 and 19 km from their natal sites (Fig. 3). In the oldest age group, only 10.00% of the birds were re-sighted within 9 km from their natal sites, while 21.43% of the birds were re-sighted between 10 and 19 km from their natal sites (Fig. 3). Significant fluctuations were not observed in the mean distance between natal sites and new nest sites among different age classes (Mean distance for the: first age class =74.20 km; second age class = 65.35 km; third age class =71.02 km, STDV=4.48 km). [Foraging trips in white storks are up to radius of approximately 5 km around the nests (Sackl 1985; Böhning-Gaese 1990; Struwe and Thomsen 1991; Lakeberg 1993; Johst et al. 2001) therefore, we did not consider STDV of 4.48 km as a significant fluctuation.]



**Fig.1:** The number of re-sighted individuals and breeding individuals along the age.

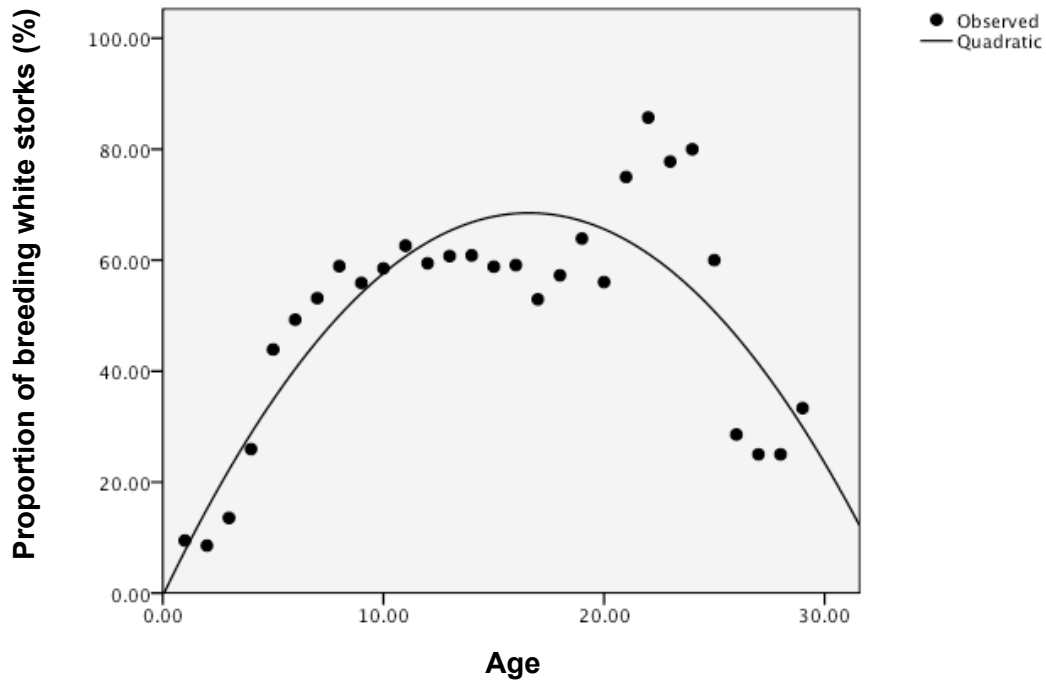


Fig. 2: Proportion of breeding storks along the age.

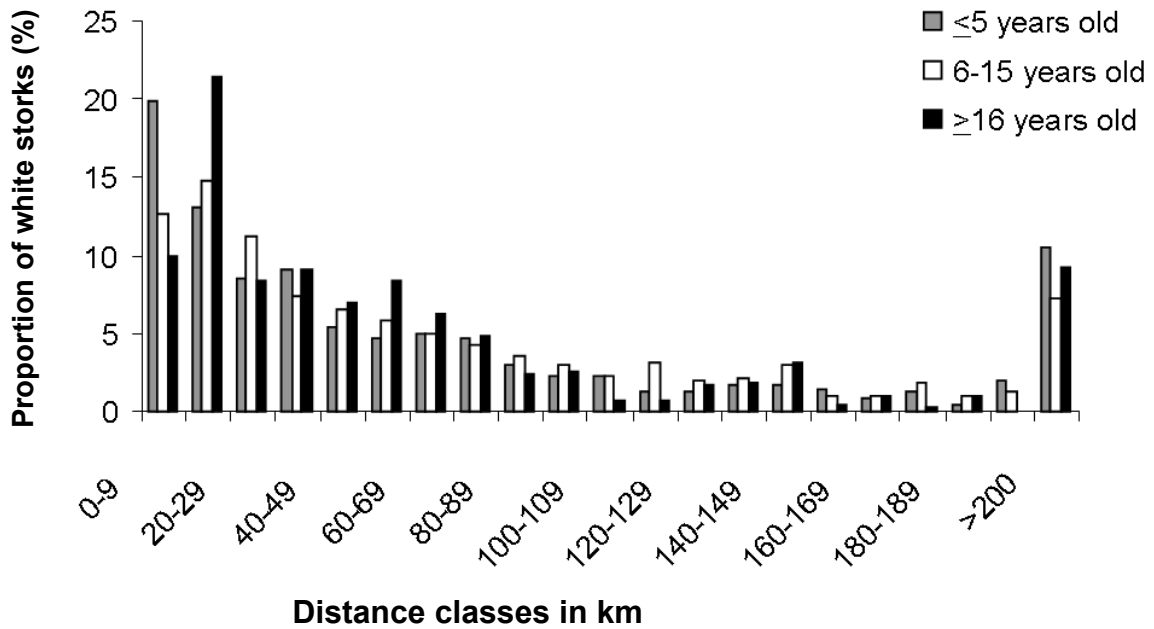


Fig. 3: Proportion of white storks per distance classes for each age classes

## **5. Discussion**

### **5.1 Age-dependent reproductive ability**

Although majority of white storks are sexually matured between 4 and 5 years old (Schimkat 2007), some individuals showed breeding attempts in the first few years of age. The environmental variation experienced by migratory bird species in their wintering areas has significant consequences on individuals' fitness and population dynamics (Schaub et al. 2005). Survival rate of young white storks increases with the amount of rainfall in the Sahelian wintering area (Barbraud et al. 1999). Environmental conditions include of the food availability at the wintering area may have strong influence on maturity in white storks. It will be extremely interesting to observe the relationship between fitness in the early matured birds and environmental condition at their wintering ground.

Reproductive performance increases with age in many vertebrates (Clutton-Brook 1988; Newton 1989; Weimerskirch 1992; Reid et al. 2003; Mauck et al. 2004; Frederic et al. 2007). Age-specific breeding success is common in many bird species (Richdale 1957; Coulson and White 1961; Perrins 1965; Harvey et al. 1979; Perrins and McCleery 1985; Wooller et al. 1990; Forslund and Pärt 1995). For example, in the fulmar (*Fulmarus glacialis*), breeding success positively correlates with breeding experiences, which increases with age (Ollason and Dunnet 1978). In short-tailed shearwaters (*Puffinus tenuirostris*), reproductive performance increases with age and breeding experiences (Wooller et al. 1990). In black birds (*Turdus merula*), fledglings success is higher in old males than in young males (Préault et al. 2005). In our present study, the proportion of breeding birds increased over first 22 years of life. Likewise in many other bird species, white storks increase their breeding ability with their age and experiences; however, the proportion of breeding birds decreased in old age. Age-specific mortality is common in many vertebras (Reznick et al. 1990; Ricklefs et al. 2003; Remeš 2006). Survival of little penguin (*Eudyptula minor*) declines gradually in old age (Sidhu et al. 2007). Force of natural selection declines with adult age (Charlesworth 1994). In many long-lived animals, reproductive performance and the cost of reproduction decrease as they age (Clutton-Brock 1988; Sæther 1990; Bennett and Owens 2002). For example, in sparrowhawks (*Accipiter nisus*), reproductive success increases with age during the first reproductive years to reach a plateau at middle age followed by decline in old age as an expression of senescence (Newton 1988). In blue-footed boobies (*Sula nebouxii*), breeding success decreases in older birds with decreases in competitive abilities probably due to senescent decline in their physical condition (Velando et al. 2006; Kim et al. 2007). Reproductive senescence occurs in aging southern fulmar (*Flumarus glacialoides*) (Berman et

al. 2009). Decrease in number of re-sighted storks after the first four years of life suggests high mortality in middle-age and old storks; however, number of re-sighted storks did not affect the proportion of breeding storks in our study population. Therefore, likewise in many other long-lived animals, declining breeding ability in aging white storks seems to be as an expression of senescent decay.

## 5.2 Dispersal behaviour

Age-related dispersal behavior differences are common among bird species (Greenwood and Harvey 1982; Verhulst et al. 1997; Serrano and Tella 2003), Young breeders more likely to disperse for long distances (Greenwood and Harvey 1982; Harvey 1984; Paradis et al. 1998). In European duck species: northern shovellers (*Anas clypeata* L); common pochards (*Aythya farina*); and tufted ducks (*Aythya fuligula*), for example natal dispersal distances are greater than breeding dispersal distances (Blums et al. 2003). First-time breeders tend to disperse for longer distance than experienced breeders in great cormorants (*Phalacrocorax carbo sinensis*) (Hénaux et al. 2007), and shags (*Phalacrocorax aristorelis*) (Aebischer 1995). Based on the aforementioned studies, we predicted that young storks settle far away from their natal sites. Moreover, old and highly competitive storks settle near their natal sites owing to conspecific attraction.

Majority of the birds were re-sighted not far away (within 19 km) from their natal area like in previous studies (Chernetsov et al. 2006; Kania 2006). In general, white storks are probably faithful to their natal areas. Contrary to our prediction, young storks settled nearby their natal sites, while old storks settled partly away from their natal sites. Migration direction and distance in many species have a genetic basis and modified by physiological and environmental factors (Gwinner and Wiltschko 1978; Moore 1984; Berthold 1986; Helbig 1992; Akesson 1993; Alerstam 1997; Bruderer and Liechiti 1998; Nievergelt et al. 1999). Young migratory birds are guided by innate information on the migratory distance and direction (Gwinner 1986; Weindler et al. 1995). The directional dispersal differences in white stork individuals have genetic basis (Schüz 1951). Probably, genetic components and tradition influence on the nest site selections in young storks. Many species of birds and mammals are philopatric (Greenwood 1980) because of high familiarity with food sources and refuges from predators (Greenwood and Harvey 1982). Young lesser kestrels (*Falco naumanni*) try to settle within their natal areas (Serrano et al. 2003) because by returning to their natal sites, individuals can have benefit from familiarity within potential breeding sites (Greenwood 1980 and Pärt 1995), from mating advantages (Pärt 1994), and also less attacks by resident adults

(van der Jeugd 2001). On the other hand, nest site selection in old storks seems to be influenced by different factors such as, avoidance of inbreeding and environmental conditions. Dispersal as an option to avoid inbreeding is common in many animals (Greenwood 1980; Pusey 1987; Gandon 1999; Szulkin and Shelton 2007; Jamieson et al. 2009). Dispersal behavior is likely to arise from environmental influences or behavioral learning traditions (Helbig 1992). Distribution of white stork pairs is depending on local physiographic conditions (Kuźniak 2006). Wet areas close to food sources are preferred by white storks (Rubucha and Jerzak 2006). Experienced birds return to the breeding area earlier than first-time breeders during the spring migration (Hénaux et al. 2007). Birds occupy the best place first when they arrive in their breeding area in spring or wintering area in autumn so that late arrivals are relegated to poor places (Brooke 1979; Lundberg et al. 1981; Goss-Custrad et al 1984; Newton 2004). Experienced storks probably occupy nests in attractive areas that are far enough to avoid inbreeding, but not too far from their natal areas first, so that individuals can take an advantage of their site familiarities and expect high breeding success.

In conclusion, number of breeding white storks increased with age first, then decreased probably due to senescent decay in their fitness. Although white storks are faithful to their natal sites in general, nest site fidelity is stronger in the young birds. Different factors are likely affecting nest site selections in young birds and old birds. To understand mechanisms of nest site selections more in detail, it will be interesting to research on age-dependent breeding dispersal behavior (subsequent movement between nest sites after first reproduction).

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## Introduction to the following chapter

In the previous chapter, we tested the impact of age on breeding ability and nest site selection (natal site fidelity) in white storks. Our results showed age-dependent reproductive ability and nest site selection in the given species. Stronger natal site fidelity in young birds than in old birds suggests nest site changes in old birds (after first time breeding attempts: breeding dispersal). Breeding dispersal is maybe therefore, common in white storks like in some other bird species (Newton 2000<sup>2</sup>; Lang et al. 2002<sup>3</sup>; Dale et al. 2004<sup>4</sup>).

Density is also one of the primary cues triggering dispersal behavior (Mayers and Krebs 1971<sup>5</sup>; Doligez et al. 2004<sup>6</sup>). Previously reported population recovery in white storks after a steep population decline (Kanyamibwa et al. 1990<sup>7</sup>, 1993<sup>8</sup>; Senra and Ales 1992<sup>9</sup>; Johst et al. 2001<sup>10</sup>; van den Bossche et al. 2002<sup>11</sup>; Hinsch 2006<sup>12</sup>) allowed us an excellent opportunity to analyze the impact of density increases on dispersal behavior.

We subject to test age- as well as density-dependent breeding dispersal patterns of white storks in the following chapter.

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## Chapter 2:

### Age- and density-dependent effects on breeding dispersal in white stork (*Ciconia ciconia*)



# Age- and density-dependent effects on breeding dispersal in white stork (*Ciconia ciconia*)<sup>13</sup>

## 1. Abstract

The white stork (*Ciconia ciconia*) is a migratory bird breeding in large parts of Europe. Following a steep population decline, a recovery of white stork populations has been observed in many regions of Europe after the seventies of the last century. Increasing population densities in the Eastern German sub-population (with a marked increase in numbers of breeding pairs especially after 1983) allowed examining density- as well as age-dependent breeding dispersal patterns. Generally, young storks were dispersing more frequently than older storks. The proportion of dispersing individuals increased significantly over time, suggesting a density-dependent component in the dispersal behavior of white storks. Moreover, a significant interaction effect was observed between the age of dispersing individuals and year: over time also older individuals increasingly dispersed from their previous nest site. We discuss the potential role of competition for the observed density-dependent patterns in dispersal behavior.

**Keywords:** White stork, *Ciconia ciconia*, Population dynamics, Age-dependent dispersal, Density-dependent dispersal

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## **2. Introduction**

Dispersal behavior plays a critical role for the geographical distribution as well as the population structure of a given species (Greenwood. 1980; Greenwood and Harvey 1982; Johnson and Gaines 1990; Walters 2000). Thus, examining dispersal patterns is important both from an evolutionary perspective and to understand the dynamics of populations at a regional scale (Tufto et al. 2005). Numerous studies evaluated the importance of natal dispersal in birds (Greenwood and Harvey 1982; Verhulst et al. 1997; Serrano et al. 2003; Martin et al. 2008), but in many species also adult individuals may disperse *after* their first nesting period (Newton 2000; et al. 2002; Dale et al. 2004).

Breeding habitat and nest-site selection can have a profound effect on an individual's survival and fecundity, thereby influencing the structure and growth rate of populations (Clark et al. 2004; Citta and Lindberg 2007). Recent theoretical and experimental studies indicate that individuals may cue on the nest site density in their dispersal behavior. Individuals are often attracted by conspecifics (Danchin et al. 1998; Brown et al. 2000); on the other hand, individuals may avoid areas with high individual densities due to increased competition. This may lead to density-dependent dispersal patterns (Myers and Krebs 1971; Greenwood et al. 1979; Hetmanski 2007).

To investigate the process of density-dependent breeding dispersal in more detail, it is often necessary to follow the movements made by individually marked birds over years (Dale et al. 2004). In the present paper, we present data from a long-term study on age- and density-dependent breeding dispersal in white storks (*Ciconia ciconia*). We define breeding dispersal as shifts in home range centroids between successive breeding seasons. White storks are distributed throughout Europe during the breeding season (Van den Bossche et al. 2002), and a significant proportion of the total population breeds in Eastern and Central Europe (Schulz 1998). White storks are particularly suited to investigate dispersal behavior because individuals are large and thus easily detectable. Moreover, the species typically nests on rooftops, i.e., within rural human settlements, and it has been subjected to long-term studies during the last decades (e.g., Chernetsov et al. 2006).

There is a major difference in the migration behavior between the two sub-populations of white storks in Europe (Kanyamibwa et al. 1993): the western population migrates via Gibraltar and winter in Central-west/Northern Africa, and the eastern population migrates via the Middle East and winter in Central-east/Southern Africa (Kanyamibwa et al. 1993). A sharp population decline was observed in both sub-populations from the beginning to the seventies of the 20<sup>th</sup> century, even though the decrease was stronger in the western population

(Kanyamibwa et al. 1990; Senra and Ales 1992; Kanyamibwa et al. 1993; Johst et al. 2001; Hinsch 2006). In most parts of its range the white stork is a farmland/wetland species (Van den Bossche et al. 2002), and the population decrease (for example, in Germany) can be attributed primarily to changes in land use, intensified agricultural practices and the extension of human settlements. White stork went locally extinct or nearly extinct in some regions in Europe during the last century (Schaub et al. 2004; Massemin-Challet et al. 2006); however, a positive trend in the population development has been observed recently (Van den Bossche et al. 2002). This recent increase is probably driven by the improvement of the natural habitats such as the protection and management of stork foraging grounds (Hinsch 2006).

In this study we focused on white storks breeding in the eastern part of Germany, which belong to the eastern European sub-population (Van den Bossche et al. 2002). In the first part of our study we re-analyzed previously published data on the population increase during the past 25 years. The strong increase of population densities (see below) provided an excellent opportunity to test for density-dependent dispersal patterns in the examined population. At high population densities, competition for preferred breeding and foraging sites increases, so average fecundity can be locally reduced (e.g., due to food and nest competition: Martin 1987; Newton 2004), which can render dispersal a more profitable option (Rodenhouse et al. 2003). Dispersal behavior tends to show an age-related component in many species [i.e., young individuals are more likely to disperse from their natal area (Greenwood and Harvey 1982; Harvey et al. 1984; Paradis et al. 1998)], but also breeding dispersal may be more common in young, inexperienced individuals (Dale et al. 2004). Therefore, we tested whether young storks would exhibit more breeding dispersal than older individuals.

Specifically, we predicted that the relative frequency of dispersal events would increase with increasing population density. Young storks should disperse more than old storks and this effect might be even more pronounced at high population densities.

### **3. Methods**

#### **3.1 Census counts**

For the analysis of the population development, we reanalyzed census count data of white stork breeding pairs in the federal states: Berlin; Brandenburg; Mecklenburg-Vorpommern; Saxony; and Saxony Anhalt between 1983 and 2006 (Berlin 1983–1988, Mecklenburg-Vorpommern 1993–1995 and Saxony Anhalt 1983–1990: Kaatz and Kaatz 1996; Brandenburg 1983–1995 and Berlin 1989–1995: Ludwig 2001; Saxony 1983–1995:



Herschmann 2001; Mecklenburg-Vorpommern 1983–1992: Zöllick 1996; Saxony Anhalt 1991–1995: Kaatz and Kaatz 2001; Berlin, Brandenburg, Mecklenburg-Vorpommern, Saxony, and Saxony Anhalt 1996–2000: Kaatz 2001; Berlin, Brandenburg, Mecklenburg-Vorpommern, Saxony, and Saxony Anhalt 2001–2006: Kaatz 2008).

For the analysis of breeding dispersal behavior, we used data of ringed white storks that were provided by the *Hiddensee Bird Ringing Centre (Vogelwarte Hiddensee)*. Our analysis is based on breeding dispersal only, so data considered here starting during the second breeding year of each individual. White stork nestlings were individually ringed at their nests in Eastern Germany (50°39'–54°09'N, 10°10'–15°01'E) between 1964 and 2006. Re-sighting data were collected over 40 years (1965–2005) in eastern Germany by volunteer workers. The re-sighting data were all collected during the breeding season (between March and August), and calculations of home range centroids are based on data from breeding individuals only. We excluded the data before 1980 from the analysis because ringing and monitoring activities were less regular in the preceding years, while ringing and monitoring was conducted in a systematic fashion after 1980. Our analyses are based on a total of  $n=1,230$  (re-sighting  $n=2,698$ ) individually ringed breeding individuals. There were some regional differences in the ringing and monitoring activities; however, considering the large sample size on which our study is based, the impact of these differences seems negligible.

Individual birds were re-sighted, on average (mean $\pm$ SD),  $1.45\pm 1.07$  times per breeding season (range: 1–21). Each time a bird was sighted, geographic coordinates were noted. Geographic coordinates of nest sites were also noted; where nest sites were unknown, home range centers were calculated for each individual as the numerical means of all X- and Y-coordinates for a given breeding season. Dispersal distances were calculated from the distance of the home range centers between two successive years. For the statistical analyses, only those data were included where individuals were re-sighted in successive years.

### **3.2 Statistical analyses**

We used a curve fitting procedure (as implemented in SPSS 12.0) to examine the relationship between numbers of white stork breeding pairs (dependent variable) and year (independent variable).

For the statistical analyses, breeding dispersal was conservatively defined as an individual shifting its home range center by more than 10 km. Foraging trips in white storks generally do not exceed a radius of approximately 5 km around the nest (Sackl 1985; Böhning-Gaese 1990; Struwe and Thomsen 1991; Lakeberg 1993). We compared the

proportion of dispersing individuals using a logistic regression while including ‘breeding dispersal’ (yes or no) as dependent variable and ‘age’, ‘year’, and the interaction term of ‘age by year’ as independent variables. A significant interaction effect would indicate that age-classes responded differently to increasing population densities. For the comparison of dispersal distances, we used multiple regression analysis, with ‘dispersal distance’ as a dependent variable, and ‘age’ and ‘year’ as covariates. For this analysis, we included only those individuals that did show breeding dispersal (non-zero analysis).

## **4. Results**

### **4.1 Population dynamics**

While the population size grew in an almost linear fashion between 1983 and 1987, larger fluctuations in population size were observed after 1987—still, the number of breeding pairs increased steadily. Due to these fluctuations, a curve fitting procedure found two models (exponential or logistic growth) to be equally likely (both  $F_{1, 22}=22.00$ ,  $P<0.0001$ ,  $n=24$ ,  $R^2=0.49$ ; Fig. 1), while a purely linear relationship was less likely ( $R^2=0.46$ ).

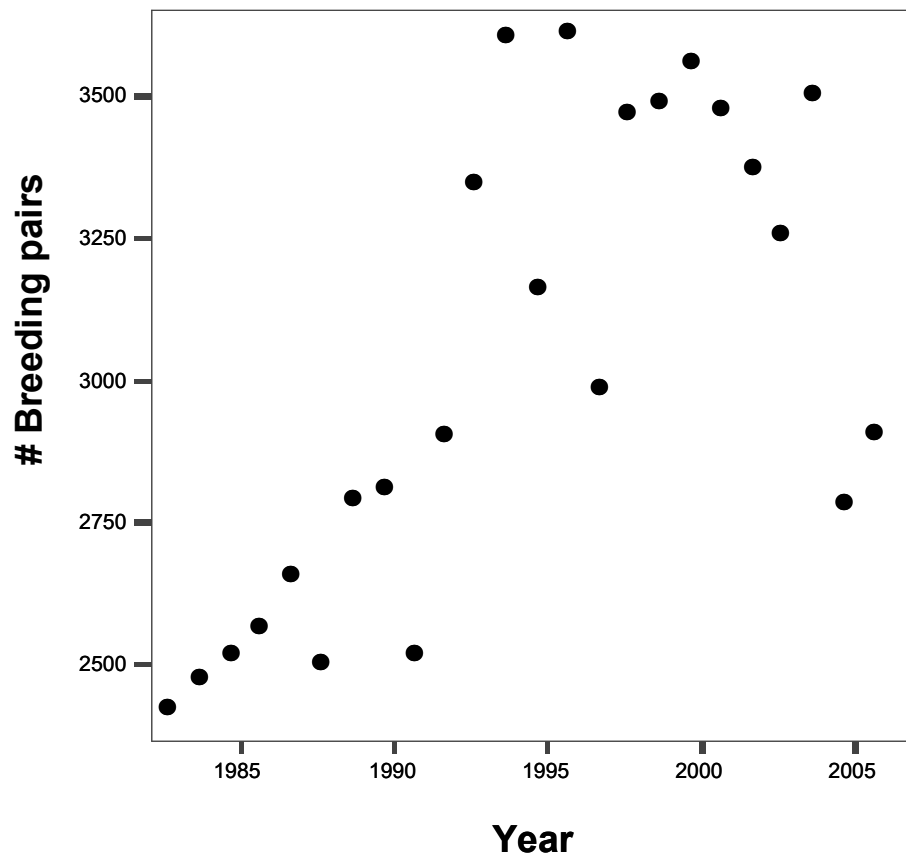
### **4.2 Dispersal behavior**

#### **4.2.1 Proportion of dispersing white storks**

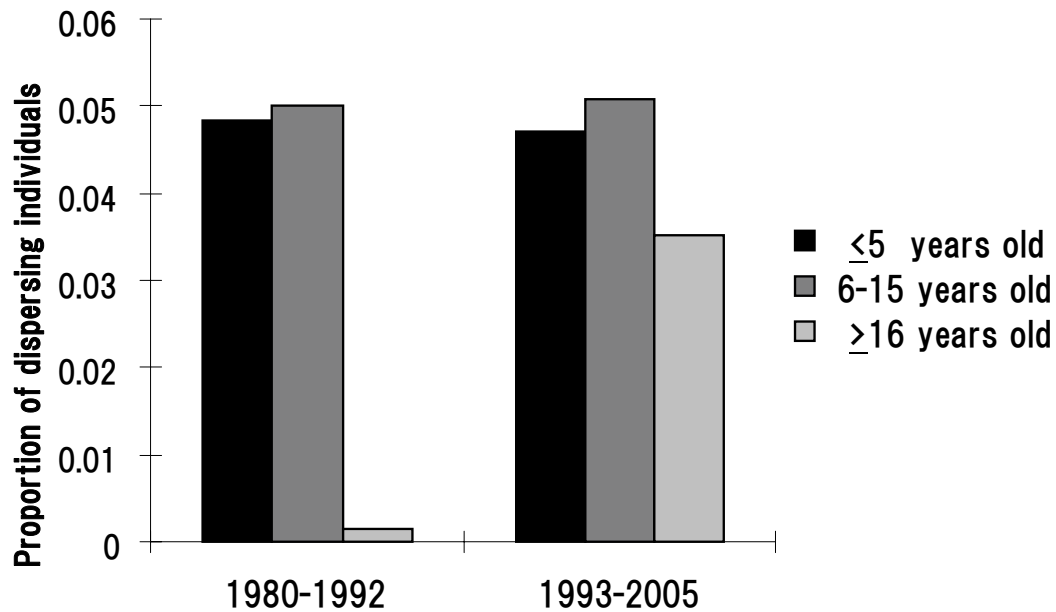
In a logistic regression (Nagelkerke  $R^2=0.011$ ), we found both ‘age’ ( $B=21.994$ ,  $SE=7.938$ ,  $Wald=7.676$ ,  $df=1$ ,  $P=0.006$ ) and ‘year’ ( $B=0.124$ ,  $SE=0.044$ ,  $Wald=8.147$ ,  $df=1$ ,  $P=0.004$ ) to affect the proportion of dispersing storks. However, also a significant interaction effect was detected ( $B=-0.011$ ,  $SE=0.004$ ,  $Wald=7.669$ ,  $df=1$ ,  $P=0.006$ ), reflecting that also older storks increasingly showed breeding dispersal during the course of our study (Figure 2).

#### **4.2.2 Dispersal distances**

In the analysis of dispersal distances in the subset of dispersing individuals (multiple regression;  $R^2=0.001$ ), neither ‘age’ ( $B=-1.076$ ,  $SE=2.682$ ,  $\beta=-0.008$ ,  $t=-0.401$ ,  $P=0.688$ ) nor ‘year’ ( $B=2.418$ ,  $SE=1.875$ ,  $\beta=0.025$ ,  $t=1.290$ ,  $P=0.197$ ) had a statistically significant effect. Similar results were obtained when we calculated several generalized linear models (GLM) instead, in which we included ‘year’ (covariate), ‘age’ (categorical factor) and the interaction of ‘age by year’. We ran several different models with different coding of age classes, still, none of the effects considered were statistically significant (results not shown).



**Fig. 1:** Annual census count data of breeding white storks between 1983 and 2006 showing the increase of the white stork population in Eastern Germany.



**Fig. 2:** Proportion of storks that were dispersing between two successive breeding periods. Breeding dispersal was defined as spatial shifts in home range centers for more than 10 km. For display purpose, the data-set was split by year (first and second half of the observation period) and age (three age classes:  $\leq 5$  years, 6–15 years and  $\geq 16$  years of age).

## 5. Discussion

In our present study, between 0.16 and 5.08% of white storks dispersed from their previous nest sites (depending on age classes and year; Figure 2), so most individuals showed high breeding site-fidelity. Breeding dispersal is generally lower than natal dispersal in most birds (Greenwood and Harvey 1982; Serrano and Tella 2003; Hénaux et al. 2007). In razorbills (*Alca torda*), for example, only 3.0% of breeding individuals changed their territory (Lavers et al. 2007). Also in lesser kestrel (*Falco naumanni*), only a small fraction of individuals (3.6%) showed breeding dispersal (Serrano and Tella 2003), while at least 23.4% of breeding males in the ortolan bunting (*Emberiza hortolana*) dispersed (Dale et al. 2004), and in the black kite (*Milvus migrans*), 29.2% of individuals showed breeding dispersal (Forero et al. 1999).

### 5.1 Age-dependent effects

Age-related differences in breeding dispersal behavior are common in several bird species (Greenwood and Harvey 1982; Verhulst et al. 1997; Serrano and Tella 2003). First-time

breeders typically tend to disperse more and for longer distances than older, more experienced breeders (Paradis et al. 1998; Hénaux et al. 2007). In our study, young (less experienced) breeders indeed dispersed more often—but not for longer distances—than older storks.

One general explanation for dispersal behavior is the avoidance of inbreeding, which is mainly achieved by the movement of young (sub-adult) birds away from their natal area before individuals breed for the first time (i.e., natal dispersal: Greenwood and Harvey 1982). Breeding dispersal, by contrast, seems to be affected by other factors/ underlies different constraints, such as breeding failure and loss of the mate (Greenwood and Harvey 1982; Nager et al. 1996; Waser 1996; Wiklund 1996; Forero et al. 1999). While mate loss probably plays an important role especially in the breeding dispersal of older storks, breeding failure leading to breeding dispersal may be more common in younger, less experienced birds, which have lower breeding success (Richdale 1957; Coulson and White 1961; Perrins 1965; Harvey et al. 1979; Perrins and McCleery 1985; Wooller et al. 1990). Also in the fulmar (*Fulmarus glacialis*), for example, breeding success appears to be positively correlated with breeding experience, which increases with age (Ollason and Dunnet 1978).

## **5.2 Density-dependent effects**

Colonizing a nearby empty or less densely packed colony while dispersing from older and denser colonies can be an attractive strategy for inexperienced (i.e., younger) breeders in colonial seabirds (Forbes and Kaiser 1994). Young great tit (*Parus major*) males disperse more in years with a high population density (Greenwood et al. 1979). On the other hand, experienced breeders prefer the oldest colonies owing to social attraction in Brewer's sparrow (*Spizella breweri*) and great cormorant (*Phalacrocorax carbo sinensis*) (Chalfoun and Martin 2007; Hénaux et al. 2007). Older and, therefore, more experienced collared flycatchers (*Ficedula albicollis*) choose patches with a high post-breeding density; conversely, subordinate yearlings choose patches with lower post-breeding densities due to the expected lower level of competition (Doligez et al. 2004). Based on the aforementioned studies, we predicted that increasing densities (and thus, increased competition for nest sites and food) would lead to more breeding dispersal over time—especially in younger individuals.

During the last 25 years, a significant increase was found in the population size (number of breeding pairs) of white storks in Eastern Germany (Figure 1). As predicted, the proportion of dispersers also increased over time. We propose that the dispersal behavior in our study population of white stork was indeed affected by increasing population densities, which led to increased competition for foraging and nest sites.

However, a significant interaction effect between age and year was found. Contrary to our prediction, older individuals were dispersing relatively more during the course of the study (albeit still less than younger individuals). It is tempting to speculate here that aging individuals were more affected by competition for nests because of decreasing competitive abilities (e.g., Clutton-Brock 1988; Stearns 1992; Jones et al. 2000; Kim et al. 2007). Nesting birds (e.g., great cormorants) show site-fidelity rather than mate-fidelity (Hénaux et al. 2007), so young intruding individuals may compete with—and finally replace—an older, resident individual on a nest. Consequently, old birds may be more forced to search for new nesting opportunities under high competition. In blue-footed boobies (*Sula nebouxii*), breeding success clearly decreases in older birds with decreased competitive abilities (Velando et al. 2006), while at the same time breeding dispersal increases progressively with age (Kim et al. 2007).

In summary, the recent population increase of white storks in Eastern Germany was accompanied by a general increase in dispersal behavior (especially in older individuals), suggesting that breeding dispersal behavior is density-dependent. The population size appears to increase less during the past 10 years (Figure 1), still, due to pronounced fluctuations in numbers of breeding pairs during the past years, logistic growth and exponential growth were—statistically—equally likely. Assuming that logistic growth is the biologically more realistic scenario, we argue that the studied population is about to reach its carrying capacity. Hence, it will be especially interesting to observe whether the frequency of dispersing individuals also reaches a maximum in the nearer future.

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## Introduction to the following chapter

In the previous chapter, we tested age- and density-dependent breeding dispersal patterns in white storks. We found that age affected breeding dispersal patterns in the given species.

Causes leading to dispersal behavior are thus, probably age-dependent.

Migration direction of young birds have genetic basis (Schüz 1951<sup>14</sup>; Gwinner 1986<sup>15</sup>; Heidg et al. 1994<sup>16</sup>; Berthold 1991<sup>17</sup>; Heidg 1991<sup>18</sup>, 1992<sup>19</sup>; Pulido and Berthold 2003<sup>20</sup>). Dispersal patterns in young birds can be influenced by their migration routes. By contrast, since causes leading to breeding dispersal behavior are age-dependent, old birds may show different dispersal patterns.

We also found density-dependent breeding dispersal patterns in the previous chapter. Breeding dispersal events increased with increase in the population density. Does increasing density also affect the dispersal directions?

We ask whether/how age and density affect the breeding dispersal directions of white storks in the following chapter.

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## Chapter 3:

### Breeding dispersal patterns in the white stork (*Ciconia ciconia*): age- and density-dependent changes in dispersal directions



Stork chicks at their nest in Rühstädt

# Breeding dispersal patterns in the white stork (*Ciconia ciconia*): age- and density-dependent changes in dispersal directions<sup>21</sup>

## 1. Abstract

Age- and density-dependent changes in dispersal patterns are common in many bird species. Here, we examined age- and density-dependency of breeding dispersal directions in the white stork (*Ciconia ciconia*), a migratory bird breeding in large parts of Europe. We asked whether and how the direction of the major spring/autumn migration route (from south-east to north-west) affects breeding dispersal directions. When comparing breeding dispersal directions in young individuals ( $\leq 5$  years old) with breeding dispersal directions in more experienced older individuals, we found that young storks tended to disperse along the major migration direction, in a way that many individuals settled down along the migration route before reaching their previous breeding area (leading to a preferential south-eastward dispersal). Old birds also tended to follow the major migration route, but appear to keep on migrating in a north-western direction during breeding dispersal. Our study population has recovered only recently (after the 1970ies) following a steep population decline. This allowed contrasting phases with different population densities. Breeding dispersal directions changed over time, with less clear-cut directional dispersal patterns during the second observation period, when population densities were higher. Increased competition seems to bring about that more storks leave their previous breeding sites, and this process may happen only after an individual has reached its breeding site, so migration directions are less predictive of dispersal at high population densities.

**Keywords:** Bird migration, Competition, Density-dependence, Long-distance migration, Dispersal behavior

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## **2. Introduction**

### **2.1 Dispersal and migration directions in birds**

Understanding dispersal behavior is vital to the understanding of the population structure and -dynamics of any given animal species (Greenwood 1980; Greenwood and Harvey 1982; Johnson and Gaines 1990; Forero et al. 1999). Obviously, birds are among the most mobile organisms on earth and have a high potential for dispersal, especially migrating species (e.g., Helbig 1991, 1992). Migration directions in many bird species have been shown to have a strong underlying genetic basis (Schüz 1951; Gwinner 1986; Helbig et al. 1989; Berthold 1991; Helbig 1991, 1992; Pulido and Berthold 2003), and pronounced variation can be found among populations, but sometimes also among individuals within populations (Helbig et al. 1994; Helbig 1996; Thorup et al. 2007). While dispersal in young non-migrating animals simply means that adolescent/sub-adult individuals move away from their natal area so as to occupy a vacant territory elsewhere (Greenwood and Harvey 1982; Paradis et al. 1998; Hénaux et al. 2007), dispersal patterns in young migratory species can be influenced by their migration routes. For example, one means by which young birds may disperse can be to just not fly as far as (or, alternatively, farther than) old birds when returning from their wintering grounds. By contrast, breeding dispersal in old birds is predicted to show a different pattern. Old individuals encounter cues triggering breeding dispersal (like the loss of a nest or breeding partner) after they have returned to their breeding site; hence, breeding dispersal of old birds is unlikely to be dependent on the direction of the major migration route.

In this paper, we present data from a long-term study on the breeding dispersal behavior (movements between breeding seasons) of white storks (*Ciconia ciconia*). White storks are soaring migratory birds in Europe, and a significant proportion of the total population breeds in Eastern and Central Europe (Schultz 1998). White storks are typically associated with human habitation (Chernetsov et al. 2006). Moreover, individuals are large and, thus, easily detectable, so the species is particularly suited to investigate dispersal behavior and has been subjected to long-term behavioral studies during the last decades (e.g., Chernetsov et al. 2006). Most importantly, white storks in Europe are distinguished by their divergent migration behavior in two sub-populations (Kanyambwa et al. 1993): the western population migrates via Gibraltar and winters in Western and Northern Africa, and the eastern population migrates via the Middle East and winters in Eastern and Southern Africa (Kanyambwa et al. 1993; Schaub et al. 2005). In the present study, we examined breeding dispersal directions in the eastern population. The distinctive migration behavior of this

population provided us with specific predictions about the preferred dispersal directions: When comparing different age-classes, young storks should preferentially disperse along a south-eastern/north-western axis. By contrast, older storks might show a different (breeding) dispersal pattern with no clear-cut directionality.

## **2.2 Population density and dispersal directions**

Breeding habitat and nest-site selection strongly affects an individual's survival and fecundity (Clark et al. 2004; Citta and Lindberg 2007), and increased competition for breeding sites due to high population densities may lead to increased dispersal (Myers and Krebs 1971; Greenwood et al. 1979; Hetmanski 2007; Itonaga et al. submitted). In white stork, changes in land use, intensified agricultural practices, and the extension of human settlements caused a sharp population decline in both sub-populations from the beginning to the seventies of the 20<sup>th</sup> century (Kanyamibwa et al. 1990; Bairlein 1991; Senra and Ales 1992; Johst et al. 2001; Hinsch 2006). Following a more recent improvement of stork habitats, such as the protection and management of breeding and foraging grounds (Hinsch 2006), a positive trend in the population development has been observed after the seventies of the 20<sup>th</sup> century (Schulz 1999; Van den Bossche et al. 2002; Itonaga et al. submitted). Consequently, population densities have been increasing steadily, which has indeed led to more dispersal over time (Itonaga et al. submitted). Do increased population densities affect breeding dispersal directions? Competition due to high population densities is a factor that leads an individual to disperse *after* it has returned from its wintering grounds (e.g., because there are no unoccupied nest sites left close to its previous breeding site). Therefore, whether and how breeding dispersal directions are dictated by migration directions may be dependent on population densities, and the major breeding dispersal direction(s) of a given population may be less congruent with its migration direction at high population densities. We tested this idea by comparing patterns of breeding dispersal distributions between two periods of time, directly after the onset of the population recovery, and later, when densities were considerably higher (see Itonaga et al. submitted).

## **3. Methods**

### **3.1 Census counts**

We analyzed data obtained from ringed white storks that were provided by the *Hiddensee Bird Ringing Centre (Vogelwarte Hiddensee)*. Nestlings were ringed individually at their

nests in Eastern Germany (50°39'–54°09'N, 10°10'–15°01'E) starting in 1964, and re-sighting data for adult individuals were recorded every year during the breeding season (between March and August) over 40 years (1965–2005) by volunteer workers in Eastern Germany. Ringing and monitoring were conducted in a more systematic fashion after 1980, so our current analysis is based on monitoring data obtained after 1980.

Breeding individuals were re-sighted, on average (mean±SD), 1.45±1.07 times per breeding season (range: 1–21). Geographical coordinates were noted each time a bird was sighted. For each individual, home range centers were calculated as the numerical means of the X- and Y-coordinates for a given year. Breeding dispersal distances were calculated from the distance of the home range centers between two successive years. Dispersal was conservatively defined as spatial shifts in home range centers that were >10 km. This decision was made because white stork home ranges cover, on average, a radius of 5 km (Johst et al. 2001; Sackl 1985; Böhning-Gaese 1990; Struwe and Thomsen 1991; Lakeberg 1993). Breeding dispersal directions were calculated from the resulting vectors between the home range centers of two successive years. For the statistical analysis, only those data were included where individuals were re-sighted in two successive years. A total of  $n=178$  (re-sighting  $n=196$ ) individually ringed breeding individuals that were dispersing between two successive breeding seasons could be analyzed in this study.

### **3.2 Statistical analysis**

To test for differences in breeding dispersal directions among age classes, the data-set was split into three different age groups:  $\leq 5$  years old, 6–15 years old, and  $\geq 16$  years old. To test if the almost linear increase in population densities after the seventies of the 20<sup>th</sup> century has an impact on breeding dispersal directions, we split the data-set by year into two periods: 1980–1992 and 1993–2006.

For each sub-set of data, we tested for deviations from random circular distribution patterns of dispersal vectors using Rao's spacing test (Batschelet 1981; Mardia and Jupp 2000). For a comparison among age classes or between time periods, frequency distributions of breeding dispersal directions were lumped into 45° categories for each sub-set of data. We compared distribution patterns using Chi-square tests. For each sub-set of data, we tested for a correlation between breeding dispersal directions and breeding dispersal distances by calculating the Circular-linear correlation coefficient (Mardia and Jupp 2000).



## 4. Results

### 4.1 Age-dependent effects

When we split the data-set according to age classes, the circular distribution patterns of breeding dispersal directions differed significantly from random in all three age classes (Fig. 1). We detected a significant difference in breeding dispersal directions among age classes ( $\chi^2=47.24$ ,  $df=14$ ,  $P<0.01$ ). Due to the small sample size in the oldest age class, we recalculated the Chi-square test while combining the two older age classes; still, a significant difference between age classes was detected ( $\chi^2=24.51$ ,  $df=7$ ,  $P<0.001$ ).

Indeed, age classes differed in the relative frequencies of birds that preferred one of the two major breeding dispersal directions: in the youngest age class, 36.0% of birds dispersed at directions between 90° and 135° (i.e., along the predicted south-eastern/north-western axis), while only 14.7% of birds preferred dispersal directions between 270° and 315° (Fig. 1a). In the second age class, 17.3% of birds preferred directions between 90° and 135°, and 25.5% of birds dispersed at directions between 270° and 315° (Fig. 1b). There was more variance in breeding dispersal directions in the second age class (Fig. 1b). In the third age class, 36.4% of birds preferred directions between 90° and 135°, and 54.5% dispersed at directions between 270° and 315° (Fig. 1c); the latter result; however, must be interpreted with caution due to very low sample size ( $n=11$ ).

Breeding dispersal directions were not correlated with breeding dispersal distance in all cases (Circular-linear correlation coefficient, first age class:  $r=0.098$ ,  $P=0.50$ ,  $n=75$ , second age class:  $r=0.16$ ,  $P=0.075$ ,  $n=110$ , third age class:  $r=0.18$ ,  $P=0.78$ ,  $n=11$ ).

### 4.2 Density-dependent effects

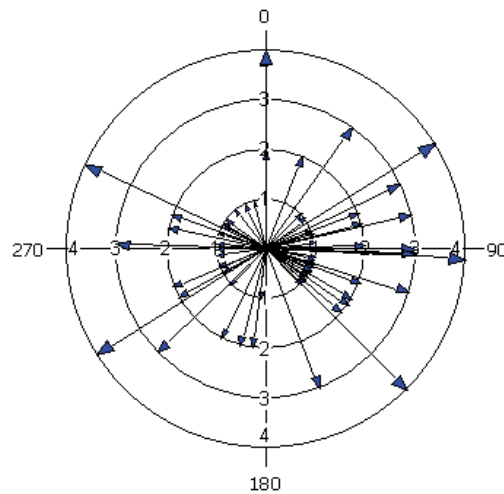
When we split the data-set into two periods, a non-random circular distribution pattern of breeding dispersal directions was found during the first half of the study period (1980–1992; Fig. 2a). The distribution pattern of breeding dispersal direction during the second period (1993–2006) did not significantly differ from a random distribution (Fig. 2b).

The distribution patterns of breeding dispersal directions were significantly different between the first and the second half of the study period ( $\chi^2=14.36$ ,  $df=7$ ,  $P<0.05$ ). As predicted from our previous analysis, during the first period, one cohort of birds dispersed preferentially at directions between 90° and 135° (25.0% of birds) while another cohort preferred directions between 270° and 315° (30.0% of birds; Fig. 2a). During the second period, relatively more storks preferred directions between 90° and 135° (25.6% of birds)

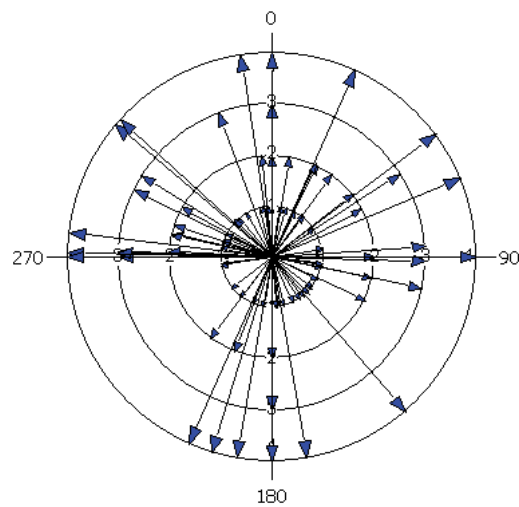
while the relative frequency of dispersers that preferred directions between 270° and 315° remained more or less constant (21.8% of birds; Fig. 2b). However, variance in breeding dispersal directions was generally much higher during the second period.

Breeding dispersal directions were not correlated with breeding dispersal distance in both cases (Circular-linear correlation coefficient, 1980–1992:  $r=0.11$ ,  $P=0.66$ ,  $n=40$ ; 1993–2006:  $r=0.12$ ,  $P=0.13$ ,  $n=156$ ).

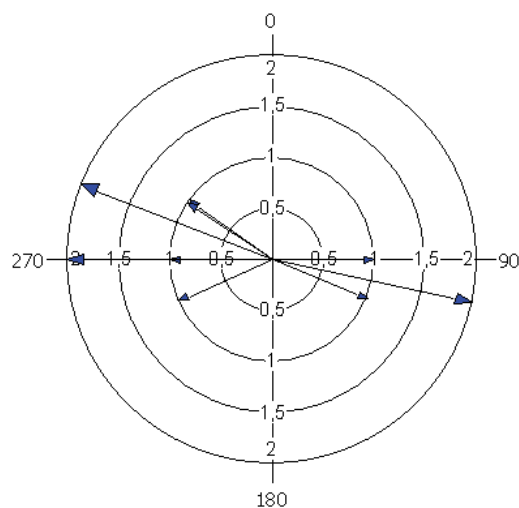
1a



1b

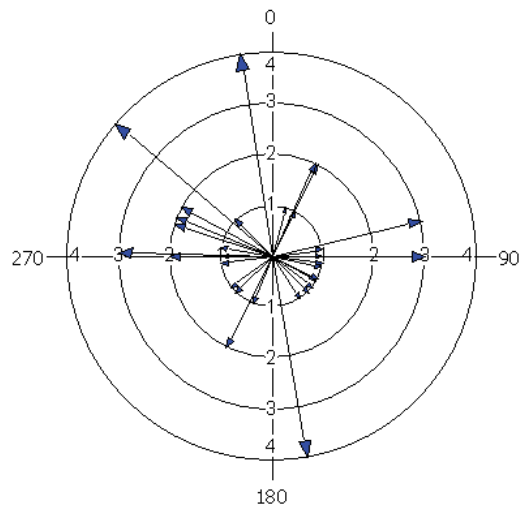


1c

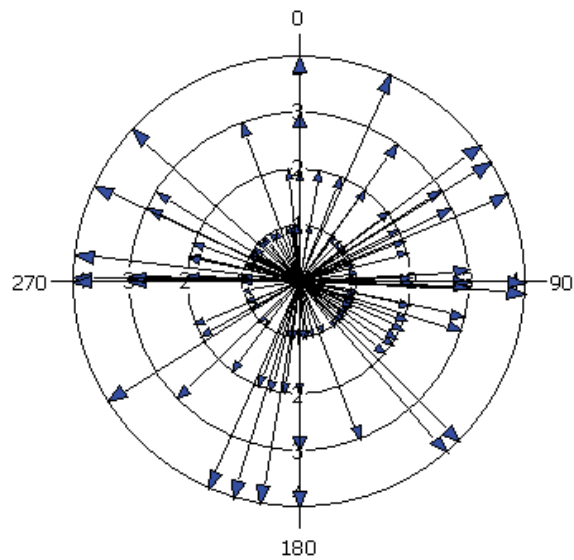


**Fig. 1:** Direction and distance of dispersal of white storks among the three age classes: (a)  $\leq 5$  years old (Rao's Spacing Test:  $r=0.24$ ,  $P<0.01$ ,  $U=160.20$ ,  $n=75$ , mean angle= $107.00^\circ$ ), (b) 6–15 years old (Rao's Spacing test:  $r=0.045$ ,  $P<0.01$ ,  $U=169.91$ ,  $n=110$ , mean angle= $27.00^\circ$ ), (c)  $\geq 16$  years old (Rao's Spacing test:  $r=0.24$ ,  $P<0.01$ ,  $U=213.55$ ,  $n=11$ , mean angle= $304.00^\circ$ ). The length of vectors represents dispersal distance. The data-set was split by distance for display purpose (distance class: 1=10–24.99 km, 2=25–49.99 km, 3=50–99.99 km, 4=100 km–).

2a



2b



**Fig. 2:** Direction and distance of dispersal of white storks during the two periods: **(a)** 1980–1992 (Rao’s spacing test:  $r=0.016$ ,  $P<0.01$ ,  $U=166.00$ ,  $n=40$ , mean angle= $140.50^\circ$ ), **(b)** 1993–2006 (Rao’s spacing test:  $r=0.085$ ,  $0.10>P>0.05$ ,  $U=165.69$ ,  $n=156$ , mean angle= $102.00^\circ$ ). The length of vectors represents dispersal distance. The data-set was split by distance for display purpose (see legend to Figure 1).

## **5. Discussion**

Age-related differences in dispersal behavior have been reported for several bird species (Greenwood et al. 1979; Greenwood and Harvey 1982; Doligez et al. 2004). We found young storks to disperse more in a south-eastern direction, while old bird breeding dispersal was more in a north-western direction. In spring, white storks of the eastern population approach their nest sites from Eastern and South-eastern Africa (Chernetsov et al. 2006). Inexperienced young storks are faithful to their natal areas (Chernetsov et al. 2006). Young storks thus, may select nest sites nearby their natal areas probably for their first time breeding attempts, but those individuals fail to breed change the nest sites in following year. Breeding failure may lead to dispersals in young storks (Itonaga et al. submitted). The south-east-biased dispersal in young storks, therefore, suggests that some young birds found suitable breeding habitats and nest sites during their returning from the wintering grounds (Sokolov et al. 1984; Morton et al. 1991) and settled in these areas (Chernetsov et al. 2006) instead of flying the complete route. The described south-eastward range expansion of the population can, therefore, be explained partly by the above-mentioned age-specific dispersal behavior along with the availability of vacant breeding sites in south-eastern regions, such as Saxony and South–West Poland (Profus and Chromik 2001; Herschmann 2001; Chernetsov et al. 2006).

Unexpectedly, we found a north-west-biased dispersal in the second age-class, which is also congruent with the major migration direction in spring. Hence, also old birds appear to be influenced to some degree by their (innate) migratory direction during breeding dispersal. One possibility would be that some old birds fly toward their previous breeding sites but then continue migrating in the same direction if they fail to breed. Breeding dispersal in older birds is thought to be driven by factors like loss of the partner, but also by breeding failure in the previous year (Greenwood and Harvey 1982; Nager et al. 1996; Waser 1996; Wiklund 1996; Forero et al. 1999). If the previous breeding success (or, in this case: failure) indeed is a determinant of breeding dispersal in old storks also, then this might provide another explanation for why dispersal directions were—to some extent—congruent with the major migration direction. Those old individuals that were already “preoccupied” not to return to their previous nest sites might not stop at their previous nest sites when returning in spring but keep on migrating in the same direction. Breeding success/failure of white storks is strongly affected by agricultural practices and the type of land use in a given area (Johst et al. 2001). Hence, local changes in agricultural land use could have a strong influence on storks’ dispersal behavior.

Distribution patterns of breeding dispersal directions also changed over time. While the two major breeding dispersal directions were discernible during the first period (for reasons outlined above), the distribution pattern of breeding dispersal directions became more obscured during the second period. We argue that increased food- and nest site-competition as a result of higher population densities plays a major role here. Population densities in white stork have indeed been increasing steadily during the past decades (Van den Bossche et al. 2002; Hinsch 2006; Itonaga et al. submitted ). Competition for preferred breeding and foraging site is positively correlated with population densities, and the average fecundity of bird populations can be locally reduced at high densities (Martin 1987; Doligez et al. 2004; Newton 2004; Mallord et al. 2007), so increased population densities can be accompanied by increased levels of dispersal (Myers and Krebs 1971; Doligez et al. 2004; Itonaga et al. submitted). In the case of breeding dispersal due to increased competition, individuals will inevitably first return to their previous breeding sites and will only then encounter those cues that trigger dispersal behavior. Since this happens after the spring migration, this kind of breeding dispersal may be less congruent with the major migratory direction.

### **6. Acknowledgements**

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