Ibis (2008), **150**, 421–424

Short communication

High turnover and moderate fidelity of White Storks *Ciconia ciconia* at a European wintering site

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Keywords: France, turnover, White Stork, wintering.

Despite considerable ringing effort, little is known about the wintering ecology of Western European populations of the White Stork *Ciconia ciconia*. A better understanding of the behaviour of White Storks in winter is important in describing the dynamics of the European breeding population, particularly as global warming induces changes in migration strategies (Ptaszyk *et al.* 2003, Fiedler *et al.* 2004).

Most European White Storks winter in Africa, where the long-term satellite tracking of two birds from Germany (Berthold *et al.* 2002, 2004) suggests they have low site fidelity, probably in response to high spatial and temporal variation in food resources. Little is known about the annual turnover of individuals at wintering sites. A small proportion of the Western European breeding population now winters in Europe. Some of these birds are adults wintering near their breeding sites (Schierer 1991, Schaub *et al.* 2004), the rest are visitors from further afield to a few Mediterranean wintering sites (Tortosa *et al.* 1995, Archaux *et al.* 2004). At one refuse tip site in southern France, the number of wintering Storks increased from 150 birds in winter 2003/2004 (Archaux *et al.* 2004), to 161 in winter 2004/2005 and 216 in January 2006. As most birds were adults, we expected a moderate annual turnover of individuals due to the high adult annual survival rate (around 0.8; Doligez *et al.* 2004, Schaub & Pradel 2004) and a high fidelity to this wintering site, which provided abundant and predictable food resources throughout the winter. In this study, we used sightings of individually ringed Storks during the winters of 2002/2003 and 2004/2005 to estimate individual turnover and site fidelity in this recently established European wintering population.

METHODS

The number of wintering Storks has been monitored annually at this site since the first wintering birds were recorded in winter 1995/96 (Archaux *et al.* 2004). During the winters of 2002/2003 and 2004/2005, an effort was made to individually identify wintering White Storks bearing rings. In 2002/2003, most of the ring resighting effort was carried out at the roosting site, at the 1.6-km^2 Reserve du Méjean, Lattes (Hérault department, southern France; 43°34′N, 3°54′E), between 1 October and 6 December. Over 14 visits, the number of birds individually identified ranged from 1 to 23, involving 48 different individuals. All ringed Storks first recorded in October were seen later that winter, suggesting that all birds we identified were wintering. The maximum count of 83 Storks was recorded on 26 November.

During winter 2004/2005, ringed individuals were searched for between 1 December and 12 January. The earliest birds returning to their breeding grounds are usually recorded by mid-January in Lattes. These visits were carried out either at the Reserve du Méjean, or at the large (0.5 km^2) rubbish tip of Montpellier, 2 km to the west, where birds foraged. Over eight visits, the number of birds individually identified ranged from 2 to 34, involving 53 different individuals. Of these, seven had been recorded during winter 2002/2003. The maximum count of 161 Storks was recorded on 5 December.

Individual turnover (T) was defined as the probability that a ringed individual selected at random in 2004/2005 was not present in 2002/2003. Apparent survival ($\varphi_{2002/03}$), the product of survival and fidelity probabilities, was defined as the probability that a ringed individual recorded in 2002/2003 was still alive and wintering at the same location in 2004/2005. To reduce the confounding effect of among-winter and among-individual variations in resighting probability on T and $\varphi_{2002/03}$, capture-mark-resighting (CMR) data were analysed with a CMR statistical model. This model, the Robust Design version of Pradel's temporal symmetry approach (Nichols & Hines 2002), uses the information of within-year sessions of resighting to estimate the probability that individuals are resighted in a given winter. Parameters documenting the between-winter dynamics of individuals are thus adjusted for, and robust to, variations in the resighting probability. In the present case of among-winter dynamics of individuals, two main sources of variation in resighting probability were expected. First, individuals carried different types of rings (i.e. metal ring, combination of colour rings without code, or plastic ring with alphanumeric code), which may have induced heterogeneity in resighting probability among individuals. Secondly, temporal variation in resighting

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Table 1. Number of Storks wintering in 2002/2003 and 2004/2005 at Lattes (southern France) by country of birth (unknown for three Storks recorded in 2002/2003).

Country	2002/2003	2004/2005
France	23	25
Germany	13	18
Switzerland	9	8
Italy	0	2

probability was expected since weather conditions, hour of day and time spent in the field varied between visits. The fitted model was then: $\varphi_{2002/03}$ $\gamma_{2004/05}$ $N_{2002/03}$(ring_type) $N_{2004/05}$(ring_type) *p*(ring_type+visit) (model notation follows Schaub *et al.* 2004), with γ the apparent seniority rate (i.e. 1 – *T*), $N_{2002/03}$ and $N_{2004/05}$ the number of ringed individuals per ring type present per winter, and *p* the resighting probabilities, which varied additively among types of ring and visits. The model was fitted with software MARK 4.3 (White & Burnham 1999). We used published survival estimates (*S*) on Western European White Stork populations to compute the fidelity probability *F* from $\varphi_{2002/03}$, with $F = \varphi_{2002/03}/S$.

RESULTS

Details on the country of birth and age of the Storks identified in 2002/2003 and in 2004/2005 are given in Table 1 and Figure 1, respectively. The birds wintering in 2004/2005 originated from eastern France, Germany, Switzerland and Italy in the same proportion as birds wintering in 2002/2003 (although two Storks from Italy and one from northern Germany were observed in 2004/2005 only; exact Wilcoxon rank sum test, $W = 7$, $df = 4$, $P = 0.89$). Similarly, the age structure of the wintering population did not significantly differ between 2002/2003 and 2004/2005 (Fig. 1; Wilcoxon rank sum test, $z = 0.35$, $P = 0.73$).

When heterogeneity of resighting rates among individuals was modelled as a function of ring type, as defined in the Robust Design model, the resighting probability differed significantly among types of rings ($\chi^2_2 = 14.83$, $P < 0.001$). On average, the resighting probability per visit was 0.124 (range: 0.017–0.429) for metal rings, 0.087 (0.011–0.322) for combinations of colour rings without code and 0.203 (0.034–0.608) for plastic rings with code.

The probability that an individual resighted in 2004/2005 was also present in 2002/2003 was 0.145 ± 0.051 (0.071–0.274). This corresponded to a turnover *T* of 0.855 ± 0.051 (0.726–0.929) over 2 years, or 0.620 ± 0.066 (0.484–0.739) if estimated on an annual basis.

The probability that an individual resighted in 2002/2003 was still alive and present at the wintering site in 2004/2005, φ, was 0.235 ± 0.084 (0.109–0.435), or a rate of 0.484 ± 0.087 (0.322–0.651) if estimated on an annual basis. Assuming a mean annual survival of 0.8, an average value of *S* for Western European White Storks older than 1 year (Barbraud *et al.* 1999, Doligez *et al.* 2004, Schaub & Pradel 2004), the yearly fidelity rate to the wintering site is $F \sim 0.605 \pm 0.109$ (0.403–0.814).

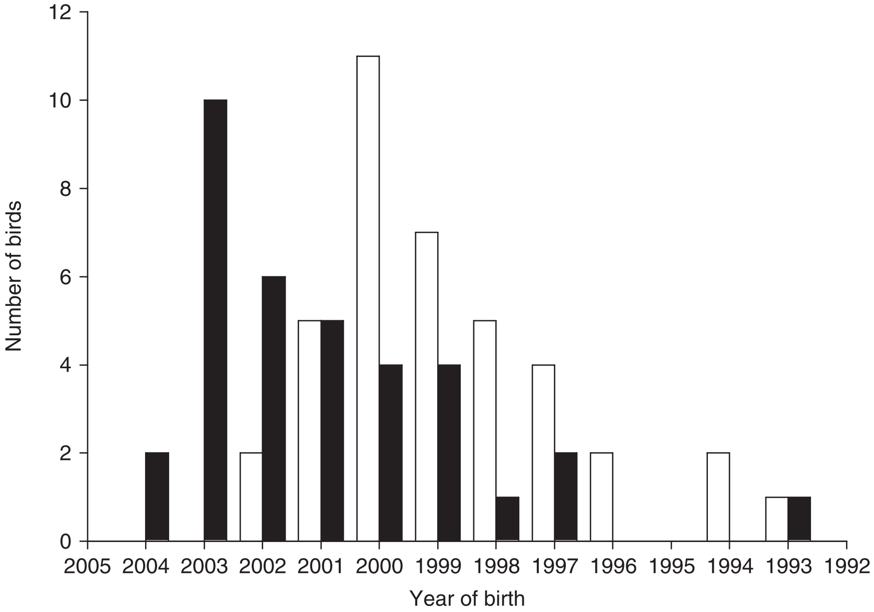

Figure 1. Year of birth for the 39 and 35 known-age White Storks wintering respectively in 2002/2003 (white bars) and 2004/2005 (black bars) at Lattes, southern France.

DISCUSSION

Although the number of wintering birds almost doubled between the winters of 2002/2003 and 2004/2005, only 15% of the birds wintering in 2004/2005 had been recorded in 2002/2003. To our knowledge, this is the first estimate of individual turnover at a wintering site for the White Stork. This high turnover of individuals results primarily from a rapid increase in the number of wintering Storks. Additionally, low fidelity to the wintering area and/or short-distance changes of wintering sites within the wintering area probably contributed to a high turnover. The latter interpretation seems unlikely for three reasons. First, no other regular roost and foraging place is known in the vicinity of the study area. Secondly, there are few other sites in southern France where Storks regularly winter: 45 km to the east (ornithological reserve of Pont de Gau, Bouches du Rhône), $N_{2006/07} = 2$ Storks; 80 km to the east (rubbish dump of Entressen, Bouches du Rhône), $N_{2003/04} = 32$ Storks (Merle & Chapalain 2005) and 95 km to the south-west (zoological park of Sigean, Aude), $N_{2006/07} = 11$ Storks (F. Barréda pers. comm.). Thirdly, exchanges among these wintering sites have so far been extremely rare: one bird was recorded at Lattes in winter 2004/2005 and at the rubbish tip of Entressen in winter 2006/2007 (data provided by the National Museum of Natural History of Paris). Thus, short-distance movements within Mediterranean France, of Storks from one winter to the next are unlikely to explain the high between-winter individual turnover rate.

More probably, the variation in turnover not explained by population increase resulted from both mortality of a proportion of the wintering birds, and from a moderate wintering-area fidelity of the survivors. Indeed, assuming a yearly survival rate of 0.8, reported in several Western European populations (Barbraud *et al.* 1999, Doligez *et al.* 2004, Schaub *et al.* 2004), only 64% of the Storks wintering in 2002/2003 were presumably alive during winter 2004/2005. Thus, only *c.* 60% of the birds surviving from one winter to the next one would have been faithful to the wintering site. This value corresponds to medium level of fidelity to winter site for waterbirds (e.g. Robertson & Cooke 1999, Frederiksen *et al.* 2002, range: 0.35–0.9). This rate certainly varies between winters, due to density dependence, feeding or climatic conditions. However, the smooth increase in the number of wintering Storks in Lattes since 1995 (Archaux *et al.* 2004) may suggest limited yearly fluctuations in the fidelity rate. This rate is lower than the White Stork nest-site fidelity of around 80% reported from western France (Barbraud *et al.* 1999) and central Spain (Vergara *et al.* 2006). This moderate winter site fidelity suggests that the choice of the wintering area is plastic, with around 40% of the birds changing wintering area between winters. Berthold *et al.* (2002, 2004) reported year-round movements of two radio-tracked White Storks over 5 or 6 years. These birds wintered successively at sites in Chad, Sudan and South Africa, hundreds of kilometres apart. In contrast, most birds wintering at the Mediterranean wintering site remained there for the whole winter (non-significant test for open population; Archaux *et al.* 2004). Constant food provisioning by the local rubbish dump is likely to explain this low intra-winter mobility compared to African wintering sites.

The few faithful birds returning to this northern wintering site may have attracted and favoured the settlement of migrant Storks that otherwise would have continued their migration southwards. This attraction seems weak for first-winter birds as they were under-represented among wintering Storks (around 6% in 2002/2003 and 2004/2005) compared to their numerical importance among migrating Storks in autumn in the area (55%; Archaux *et al.* 2004). This suggests that first-winter birds rely essentially on their innate migratory program to reach their wintering grounds, whereas older birds may have more flexible migration strategies (Chernetsov *et al.* 2004). Although Storks faithful to the Lattes wintering site only represent a small proportion of the wintering birds, they may have played a major role in the subsequent establishment of new wintering birds, thus contributing to the rapid increase of this northern wintering population. These potentially strong roles of migration flexibility and attraction by conspecifics in the rapid evolution of wintering strategies would support a major role for phenotypic, behavioural plasticity in the adaptive response of migrant species to climate warming (Pulido & Berthold 2004). Beside phenotypic plasticity, natural selection may also play a role in the rapid evolution of new wintering strategies. If wintering close to breeding grounds induces assortative mating among early-arriving individuals, then divergent migratory strategies could evolve rather rapidly (Bearhop *et al.* 2005). This divergent evolution would be reinforced if wintering close to breeding grounds insures a better reproductive success. In Spain and Poland, birds returning early to their breeding grounds have larger clutches, produce more chicks, have higher breeding success (in Poland) and are older than birds returning later in the season (in Spain) (Tryjanowski *et al.* 2004, Vergara *et al.* 2007). Nevertheless, it remains to be demonstrated that the arrival date on the breeding grounds depends on the distance to the wintering site (as birds wintering further away may start migrating earlier) and that Storks tend to winter closer to their breeding grounds from year to year. Finally, our 2-year study did not allow us to assess the between-year change in the fidelity rate, nor the respective importance of temporary and permanent emigration rates (the latter being not discernible from the mortality rate). These two issues need more than two primary sessions of capture-resighting to be addressed. Future studies will have to tackle this dynamics of movements among wintering areas.

We are grateful to P. Mayet, C. Faucon, G. Zapata and S. Merle for providing us with census data, to the Montpellier district for letting us search for ringed Storks at the rubbish dump of Lattes and to C. Barbraud, M. Schaub and P. Donald for their helpful comments on the manuscript. We also thank the National Ringing Centres in France (Muséum National d'Histoire Naturelle), Switzerland and Germany (Radolfzell, Heligoland) for providing us with ringing data.

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Received 26 June 2007;
revision accepted 17 December 2007.