ELSEVIER

Is the reintroduced white stork (*Ciconia ciconia*) population in Switzerland self-sustainable?

Michael Schaub [a,b,c,*], Roger Pradel [a], Jean-Dominique Lebreton [a]

[a] *Centre d'Ecologie Fonctionelle et Evolutive, CNRS, BP 5051, 1919 Route de Mende F-34293 Montpellier Cedex 5, France*
[b] *Zoologisches Institut – Conservation Biology, Universität Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland*
[c] *Schweizerische Vogelwarte, CH-6204 Sempach, Switzerland*

Abstract

The migratory white stork (*Ciconia ciconia*) became extinct in Switzerland in 1950. A reintroduction project with intensive management (translocation, prevention of migration, artificial feeding) started in 1948, and 175 pairs were breeding in 2000. For the period 1973–2000 we estimated annual survival rates and fledging success to estimate the population growth rate by a stochastic matrix projection model. Compared to other populations, adult survival rate (0.86, with 95% CI: 0.81–0.89) was very high and little variable over time, juvenile survival (0.37, CI: 0.31–0.43) was comparable to other populations whereas the average fledging success was low (1.65) but strongly variable over time. The population growth rate was positive, indicating that the population is self-sustainable at the moment. The growth of the white stork population was largely favoured by the high adult survival which more than compensates for the low fledging success. The population growth rate is particularly sensitive to changes in adult survival, but it would be very difficult to improve this further with management. However, maintenance of the high adult survival is crucial and an improvement in fledging success seems important for the long-term persistence of the white stork population in Switzerland. Fledging success depends on habitat quality, and thus restoration of breeding habitats should be the main management activity in the near future.
© 2003 Elsevier Ltd. All rights reserved.

Keywords: Elasticity; Environmental stochasticity; Matrix population model; Survival rate; Reproductive success

1. Introduction

A measure of success of a reintroduction programme is the establishment of a self-sustaining population (Scott and Carperter, 1987) of naturally behaving individuals. A population is self-sustaining if its long-term growth rate is not negative and if the probability of persistence despite given environmental or demographic stochasticity is high. Natural behaviour of individuals may be defined as behaviour that was shown previously in the extinct population. At some point, the success of the reintroduction programme should be evaluated in order to adjust future management activities. Such analyses for reintroduced species are still scarce (Scott

and Carperter, 1987; Sarrazin and Barbrault, 1996) although they are also useful for future projects.

The migratory white stork (*Ciconia ciconia*) became extinct in Switzerland in 1950. A reintroduction project started in 1948, and in 1960 the first free-flying pair reproduced (Bloesch, 1980). The main reintroduction activities included continuous releases of white storks reared in captivity and artificial feeding of free-flying individuals. In addition, nestlings of free-flying pairs were either taken into captivity and released after maturity, or their wing feathers were clipped. Both treatments resulted in preventing the first migration and hence enhancing survival expectation.

According to their pre-breeding history and manipulations in early life, the present population consists of two different types of white storks: (1) white storks from releases either of captive or of freely born, but temporarily captive or wing-feather-clipped, individuals

---

(hereafter, 'manipulated'), and (2) individuals that were born in the wild and had never been in captivity (hereafter, 'non-manipulated'). Manipulated white storks usually do not migrate any more, and so do not behave naturally. The number of free-flying (manipulated and non-manipulated) reproducing white storks increased from 15 breeding pairs in 1970 to 175 in 2000. Because there are now a large number of free-flying white storks, management as defined above has almost completely stopped, and the proportion of non-manipulated white storks is increasing.

We focus on the question: would the population of non-manipulated white storks in Switzerland be self-sustainable, even if the number of the manipulated white storks becomes zero? Self-sustainability can be assessed by extinction probabilities or by population growth rate. Extinction probabilities have recently been criticised by several authors (Ludwig, 1999; Fieberg and Ellner, 2000), mainly because their confidence intervals are usually very large, which reduces the reliability of interpretations. As the extinction probability is a positive function of the population growth rate (Lande and Orzack, 1988), we estimate here this growth rate to evaluate whether the population is self-sustaining. We argue that the population is likely to be self-sustaining if its growth rate is significantly larger than zero. In addition, we performed a perturbation analysis in order to find out to which vital rate the population growth rate is most sensitive. Finally, we discuss possible options for the future management of the white stork population in Switzerland.

2. Population trend and the history of reintroduction in Switzerland

White storks live in open, farmed lowlands, feed mainly on invertebrates, including a large amount of lumbricidae, and small vertebrates (Moritzi et al., 2001) and often breed in close vicinity of humans in a wide area in Europe and Northern Africa (Cramp, 1977). White storks from western Europe migrate in a narrow flyway across Iberia and via the Strait of Gibraltar to winter either in flood plains of large rivers just south of the Sahara desert in Western Africa or, in recent years, on the Iberian peninsula (Bairlein, 1981; Tortosa et al., 1995). At the beginning of the 20th century the white stork was widely distributed in Switzerland. Probably because of the destruction of marshes and intensification of farming in the breeding area, increased hunting pressure along the migration pathways and rainfall variation in the wintering quarters, the population started to decline. In 1900, 140 breeding pairs were known, these declined to 16 in 1930 and the last breeding pair was observed in 1949 (Glutz von Blotzheim, 1962).
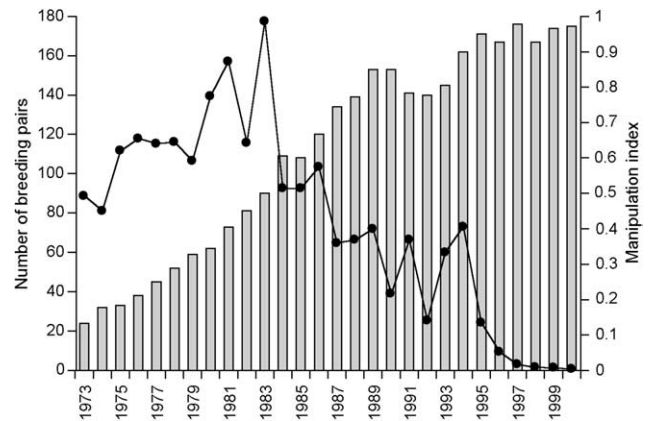

Fig. 1. Annual numbers of free nesting white storks in Switzerland (columns) and an index of annual management intensity of young white storks (line). The management index is the quotient of the number of manipulated (held temporarily in captivity, translocated or wing-feather-clipped) nestlings and the total number of fledged nestlings.

One year before extinction, a reintroduction programme started (for details see Bloesch, 1980; Boettcher-Streim, 1986). For several years, nestlings mainly from Algeria were imported and released after fledging. Owing to the very low return rate of these birds, the practice was changed. Most young white storks were then kept in captivity until they were mature at the age of 4 years. Such white storks have been breeding near the sites of release since 1960.

An unintentional effect of this treatment was that most white storks completely lost their migratory habit and became resident. Initially there was one station (Altreu) where the white storks were held in captivity and released, but later more and more satellite-stations joined the project (23 in 1992). To ensure that the white storks bred in the vicinity of these stations and that they survived in winter, they were regularly fed at the stations. Consequently, the number of free-flying breeding pairs rapidly increased in the last 30 years (Fig. 1), on average at an annual rate of $\mu = 0.085$ ($\mu = \log(n_{2000}/n_{1973})/29$). Since 1971 an increasing proportion of the young white storks have fledged naturally. These individuals migrate in a similar way as other west-migrating populations (Jenni et al., 1991), and thus can be regarded as behaving naturally. Today, most of the free-flying white storks are not handled any more (Fig. 1), and the frequency and extent of artificial feeding have also decreased.

3. Methods

3.1. The structure of the white stork population

The non-manipulated white storks are not independent of the manipulated part of the population. We have

to decide first, which part of this population should be analysed to answer our main question about the self-sustainability of the present population.

Young white storks reared by manipulated parents enter into the non-manipulated part of the population if they have not been handled in any way except for ringing. In contrast, young white storks reared by non-manipulated parents add to the manipulated part if they have been taken temporarily into captivity or if they have been prevented from migrating by the clipping of wing feathers. As soon as these management activities stop, the number of young white storks from non-manipulated parents entering the manipulated part will drop to zero immediately. Conversely, the appearance of non-manipulated young white storks from manipulated parents may continue until the manipulated parents have died or stop reproducing. As direct management has already largely stopped, we assume the non-manipulated part of the population to be influenced by the manipulated compartment only through the appearance of non-manipulated young.

Now, a constant number of 'immigrants' into a population each year has no effect on the growth rate of that population ($\log \lambda$) if it is already larger than zero without the immigrants and if there is no density-dependent regulation: regardless of the number of immigrants, in the long run, the population will increase at the rate of $\log \lambda$. On the other hand, if the population is decreasing, the population size will stabilise at a level slightly lower than the amount of immigrants (Pulliam, 1988). Therefore, it is sufficient to consider $\log \lambda$ of the non-manipulated part to decide whether in the long run the population will be self-sustaining; hence, for our considerations, we can neglect the contribution of the manipulated parents.

3.2. Matrix model and estimation of the population growth rate

The deterministic growth rate is consistently larger than the stochastic growth rate, which includes environmental and/or demographic stochasticity (Dennis et al., 1991; Caswell, 2001). Significant covariation among vital rates or density-dependent compensation in vital rates generally decreases the population growth rate as well (Lebreton and Gonzalez-Davila, 1993; Caswell, 2001). In order to judge the self-sustainability it is better to get a conservative estimate of the population growth rate. When estimating the population growth rate, we therefore take into account the environmental stochasticity, the covariation among vital rates and, if significant, density dependence. We did not consider demographic stochasticity because the studied population was sufficiently large to make its effect on the population growth rate negligible (Lande, 1993; Caswell, 2001).

We estimated the stochastic population growth rate by simulation using an age-classified Leslie-matrix. Leslie-matrix population models have very favourable properties. For example the asymptotic time-invariant population growth rate as well as the stable age distribution and age-specific reproductive rates are simply calculated from this matrix (Caswell, 2001). Because white storks start to breed in the third or fourth year of life (Zink, 1967) we defined a matrix model with four age classes, and considered a pre-breeding census and a projection interval of one year:

$$A_i = \begin{bmatrix} 0 & 0 & \frac{1}{2}m_3 f_i S_i^j & \frac{1}{2}m_4 f_i S_i^j \\ S_i^{ad} & 0 & 0 & 0 \\ 0 & S_i^{ad} & 0 & 0 \\ 0 & 0 & S_i^{ad} & S_i^{ad} \end{bmatrix}, \tag{1}$$

where f_i is the average number of fledglings per breeding female in year i, S_i^{ad} is the adult survival rate during year i, S_i^j is the first year survival rate during year i, m_3 is the proportion of storks that start to breed already in their third year of life, and m_4 is the proportion of reproducing storks older than 3 years. Lebreton (1978) estimated m_3 in an Alsace white stork population ($m_3 = 0.475$). We used the same value, because we could not estimate m_3 for the Swiss population due to the sparseness of the recapture data. We assume that all adults in the breeding population attempted to reproduce each year (i.e., $m_4 = 1$).

To create the A_i, we selected randomly one of the 28 study years with probability 1/28 and filled the matrix with the fecundity and survival estimates of this year. By doing so, we retained the possible correlation structure among all vital rates within years. We started the simulation with a population vector n_0 of size $N_0 = 1$. This vector was then left-multiplied 11,000 times with A_i. After discarding the first 1000 steps to eliminate transient dynamics, the stochastic population growth rate was estimated according to Cohen et al. (1983) and Caswell (2001) as:

$$\log \hat{\lambda}_s = \frac{1}{10,000} \sum_{i=1001}^{11,000} \log \left(\frac{N_{i+1}}{N_i} \right). \tag{2}$$

Elasticities to lower level parameters in A_i were calculated from the average projection matrix A, because differences between stochastic and deterministic elasticities are usually negligible (Benton and Grant, 1996; Caswell, 2001). All these calculations were performed with MATLAB (Anon., 1992).

3.3. Data sampling and estimation of the vital rates

Prior to 1973, the number of non-manipulated white storks was very low. Therefore we restricted our analysis to the period 1973–2000.

3.3.1. Fledging success

The number of breeding pairs and the number of fledged juveniles per breeding pair (defined as having laid at least one egg) were recorded every year by members of 'Storch Schweiz'. Because the reproducing pairs breed usually close to the stork stations, they could easily be surveyed by the local managers, and hence only very few breeding attempts and fates of broods remained undetected or unknown. We estimated the fledging success in a given year as the ratio of the total number of fledged white storks to the number of breeding pairs. We tested for density-dependence by regressing annual fledging success on the annual number of breeding pairs. We could not estimate separately the fledging success of the manipulated and the non-manipulated individuals because too few ring resightings have been made. We assume, therefore, that the fledging success of the two groups is identical.

3.3.2. Survival rates

Recoveries and resightings at the breeding grounds of ringed, non-manipulated storks were used to estimate survival rates. Each year more than 90% of all storks born in Switzerland were ringed in the nest at the age of about 5–7 weeks. Resightings were conducted by different members of 'Storch Schweiz', but with temporally and spatially varying effort. Ring recoveries were obtained from the Swiss ringing centre (Swiss Ornithological Institute, Sempach).

From 1973 to 2000, 3592 non-manipulated nestlings and 11 adults were ringed in Switzerland. The mean date of nestling ringing was 15 June, and the annual survival rates were therefore estimated from mid June to mid June. Of these ringed storks, 106 have been resighted at least once at their subsequent breeding sites. We included all recaptures conducted at one of the breeding sites in Switzerland between 1 March and 31 August. The mean date of these recaptures was 14 June, fitting very well with the mean date of ringing. Because white storks mostly do not breed until they are 3 years old (Zink, 1967; Biber et al., 2003), we excluded all resightings of younger storks to reduce heterogeneity in resighting probabilities. Up to the 14 June 2001, 475 ringed storks were recovered dead.

We performed a combined analysis of the resighting and recovery data (Burnham, 1993; Catchpole et al., 1998; White and Burnham, 1999). In this analysis, four different parameter types are estimated: S, the probability that a marked stork survives from one year to the next (survival probability); F, the probability that a surviving marked stork remains in the study area (site fidelity probability); p, the probability to see a living, marked and not emigrated stork (resighting probability); and r, the probability that a marked, dead white stork is found and its ring is reported (recovery probability).

It is well known that the survival rate of white storks during their first year of life is lower than thereafter (Lebreton, 1978; Schaub and Pradel, in press; Doligez et al., in press) and that fidelity to the breeding sites is very high, once storks have started to breed (Zink, 1967). When modelling survival (S) and fidelity (F) rates we therefore always included an age effect that lasts one year after birth. As the main mortality causes may differ between first year and adult storks, the recovery rate (r) might be age-dependent as well. Since only resightings of adult storks were included, the probability (p) is not modelled as age-dependent. Because of the long study period and possible changes in observation effort through time, we also initially considered time dependence for all parameter types. The maximal model from which we intended to start model selection was denoted as $\{S_{a2*t}, p_t, r_{a2*t}, F_{a2*t}\}$, where subscript $a2$ refers to 2 age classes, t to time-dependence and $*$ to an interaction.

There exists no established goodness-of-fit (GOF) test for this model. Therefore we conducted separate GOF tests for the recovery data, using a parametric bootstrap procedure with MARK (White and Burnham, 1999) and for the resighting data using U-CARE (Choquet et al., 2001). The bootstrap GOF test for model $\{S_{a2}, r_{a2}\}$ was significant ($P = 0.022$, 1000 runs), perhaps due to a slight overdispersion ($\hat{c} = 1.156$). The GOF test for the resighting data was not significant (model $\{S_t, p_t\}$, $\chi^2_{62} = 79.16$; $P = 0.07$). However, the subtest 3Sm, which is particularly sensitive to the failure of the assumption of recapture rate homogeneity among individuals, was highly significant (3Sm: $\chi^2_9 = 45.61$; $P < 0.01$). In fact, the resighting effort differed among stations. We therefore divided the data into two parts, one containing all storks that were ringed and resighted in the largest colony Altreu (47.18°N, 7.45°E), and one with all other stork colonies. Neither the overall GOF of the model with colony-specific (denoted as c) survival and resighting rates (model $\{S_{t*c}, p_{t*c}\}$, $\chi^2_{73} = 28.60$; $P > 0.99$), nor test 3Sm alone ($\chi^2_8 = 4.25$; $P = 0.84$) was significant. The most general model that we consider most appropriate to fit the data was then $\{S_{a2*t}, p_{t*c}, r_{a2*t}, F_{a2*t}\}$.

Model selection and parameter estimation were performed using program MARK (White and Burnham, 1999). We used the Akaike's information criterion modified for small sample size (AICc) (Burnham and Anderson, 1998) for model selection.

We formulated a set of 135 biologically meaningful models. The survival and fidelity rates were always assumed to be age-dependent, but not always time-dependent ($S_{a2*t}, S_{a2+t}, S_{a2}$; $F_{a2*t}, F_{a2+t}, F_{a2}$; subscript + refers to additivity of two effects). For the resighting rate we always retained the time dependent structure, because the resighting effort varied over time. In some models we included a colony effect on the resighting

probability, in others not (p_{t*c}, p_{t+c}, p_t). Five model structures were considered for the recovery rate ($r_{a2*t}, r_{a2+t}, r_t, r_{a2}, r_.$; subscript. refers to constancy). The 135 models were obtained by combining all these structures.

Once a parsimonious model was obtained, we investigated possible density-dependence in the survival rate by modelling them as a logit-linear function of the logarithm of the number of breeding pairs.

Among the non-manipulated white storks there are birds that winter in Switzerland, probably attracted by manipulated conspecifics. Because they are fed in winter, they are expected to have higher survival than migrants. The proportion of the residents is likely to decrease when winter feeding is stopped, which is a management option. For the assessment of self-sustainability it was therefore important to estimate the survival rate of the migratory segment of the population. But as potential migrating white storks cannot be distinguished from potential residents at the time of ringing, we were not able to estimate directly the survival rate of the migrants. However, we know the overall survival rate from the analyses described above. If we know the survival rate of the white storks wintering in Switzerland and their proportion among all non-manipulated white storks, we can get a rough estimate of the survival rate of the migrating white storks.

At one satellite-station (Möhlin; 47.55°N, 7.83°E) resightings were obtained also during winter, from 1987 to 2000. The year in which the storks were seen for the first time in winter was considered as the year of ringing. A hundred-and-twenty free-flying (but not exclusively non-manipulated) individuals were observed in at least one winter. Out of these, 47 were one year old, and 73 older. Forty storks were resighted in at least one later winter, and 16 were found dead. We analysed these data with the same model which simultaneously handles resightings and recoveries of dead birds as described before. We intended in this way to obtain a rough estimate of the survival rate of wintering storks and therefore did not consider models in which the survival rate varied over time.

As the first age class refers here to the age between 0.5 and 1.5 years, and as mortality just after fledging is probably high, we suspect that there might be no further age differences once the young reached full independence. We thus considered two models for survival: S_{a2} and $S_.$. The effort of resighting varied between years and we therefore only considered the time-dependent model for this parameter (p_t). As in the previous analysis, we suspected the reporting and the site fidelity rates to be age- and/or time-dependent ($r_{a2*t}, r_{a2+t}, r_{a2}, r_t, r_.$; $F_{a2*t}, F_{a2+t}, F_{a2}$). We combined all these structures to obtain a set of 30 candidate models. We assessed the goodness-of-fit to the resighting data only with U-CARE (Choquet et al., 2001), separately for white storks first seen as

juveniles and those first seen as adults. Neither of these tests was significant (juveniles: $\chi^2_{18} = 6.61$, $P = 0.99$; adults: $\chi^2_{16} = 13.70, P = 0.62$). We concluded that a more complicated model which accounted for age differences in survival would be suitable. We did not test the GOF of the recovery data separately because they were too few.

3.4. The survival rate scenarios considered

We considered two values for the mean adult survival rate. First, we used the average survival rate estimate based on the overall sample, and secondly we used the same estimate corrected for the presence of residents as explained above. Furthermore, if we found that survival was constant over time, we would nevertheless consider a scenario with time-dependent survival rates. If the temporal variation were small it might not be detected in the model selection process. As temporal variation in survival reduces the population growth rate compared to when survival is assumed constant over time, the potentially false finding of constant survival may result in an overly optimistic estimate of the population growth rate. We prevent this by considering a scenario with time-dependent survival. We used the shrinkage estimators of the time-dependent survival rates, as they contain only true temporal variation that is separated from sampling variation (Burnham and White, 2002). In summary, we considered up to four scenarios to estimate the population growth rate, (i) with time-invariant survival rates of all non-manipulated storks, (ii) with time-invariant survival rates corrected for residents, (iii) with time-varying survival rates of all non-manipulated storks, and (iv) with time-varying survival rates corrected for residents.

4. Results

4.1. Fledging success

During the 28 years, 3123 breeding attempts were recorded and 4759 storks fledged. The average mean annual fledging success was 1.649 (min: 0.743, max: 2.625, $n = 28$), with strong temporal variation (Fig. 2). Mean annual fledging success slightly decreased with increasing population size ($b = -0.0034$ (S.E. 0.0018); $F_{1,26} = 3.74$, $P = 0.064$). However, because the trend was weak and non-significant, we did not consider density-dependent regulation for population modelling.

4.2. Survival rates of non-manipulated storks

The preferred model was characterised by: (i) time-dependent recovery rates (average 0.145, range 0–0.267); (ii) age-dependent fidelity rates [(juveniles 0.380 (95%
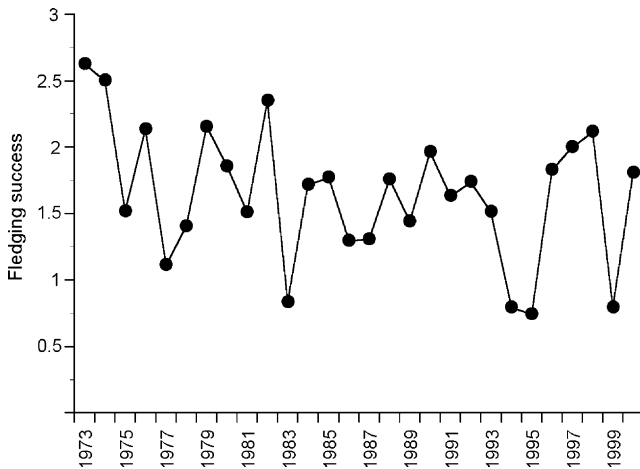
Fig. 2. Fledging success (average number of fledgings per breeding pair) of white storks in Switzerland from 1973 to 2000.
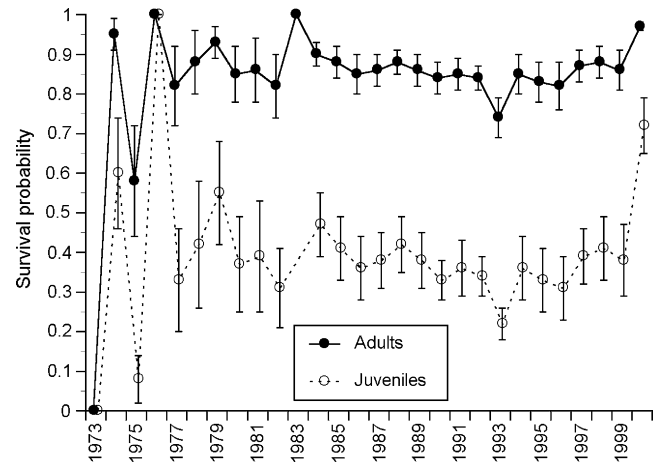

Fig. 3. Shrunken survival rates of adult and juvenile non-manipulated white storks in Switzerland, estimated by the best model with temporal variation in survival rates ($S_{a2+t}, p_{t+c}, r_., F_{a2}$). Vertical lines show the shrunken standard errors.

Table 1
Selection of the seven best models describing survival probability (S), resighting probability (p), recovery rate (r) and fidelity probability (F) of white storks in Switzerland, 1973–1999

Model	Deviance	np	ΔAICc	Akaike weight
$S_{a2}, p_{t+c}, r_t, F_{a2}$	736.7	50	0.00	0.52
S_{a2}, p_t, r_t, F_{a2}	739.2	49	0.41	0.42
$S_{a2+t}, p_{t+c}, r_., F_{a2}$	743.4	50	6.72	0.02
$S_{a2+t}, p_t, r_., F_{a2}$	746.3	49	7.51	0.01
$S_{a2}, p_{t+c}, r_., F_{a2}$	800.4	23	8.59	0.01
$S_{a2+t}, p_{t+c}, r_{a2}, F_{a2}$	743.4	51	8.74	0.01
$S_{a2}, p_{t+c}, r_{a2+t}, F_{a2}$	743.6	51	8.98	0.01

The model subscripts refer to age (*a2*), time (*t*), and colony effects (*c*), and to constancy (.). The number of estimated parameters is given by (*np*), and the small-sample size adjusted Akaike's information criterion differences by (*ΔAICc*).

Table 2
Selection of the seven best models describing survival probability (S), resighting probability (p), recovery rate (r) and fidelity probability (F) of wintering white storks in Möhlin

Model	Deviance	np	ΔAICc	Akaike weight
$S_., p_t, r_., F_{a2+t}$	332.0	28	0.00	0.51
$S_{a2}, p_t, r_., F_{a2+t}$	331.1	29	1.68	0.22
$S_., p_t, r_{a2}, F_{a2+t}$	331.7	29	2.24	0.17
$S_{a2}, p_t, r_{a2}, F_{a2+t}$	330.8	30	4.01	0.07
$S_., p_t, r_., F_{a2}$	369.1	16	7.82	0.01
$S_{a2}, p_t, r_., F_{a2}$	368.6	17	9.62	0.00
$S_., p_t, r_{a2}, F_{a2}$	368.9	17	9.62	0.00

The model subscripts refer to age (*a2*) and time effects (*t*), and to constancy (.). The number of estimated parameters is given by (*np*), and the small-sample size adjusted Akaike's information criterion differences by (*ΔAICc*).

confidence interval 0.233–0.554), adults 0.849 (95% CI: 0.740–0.917)]; (iii) time- and colony-dependent resighting rates and (iv) age-dependent survival rates (Table 1). The estimated first year survival rate was 0.369 (95% CI: 0.314–0.426), and the adult survival was 0.856 (95% CI: 0.810–0.893). There was no evidence of density-dependent compensation in survival rates ($\{S_{a2 *\ln (\# \text{ breeding pairs})}, p_{t+c}, r_t, F_{a2}\}$: ΔAICc = 3.49). The best model with temporal variation in the survival rates ($\{S_{a2+t}, p_{t+c}, r_., F_{a2}\}$) was clearly worse than the best model, indicating that temporal variation was not important. Nevertheless, in order to get a conservative estimate of the stochastic population growth rate, we used the shrunken estimates from the latter model for the population projections (Fig. 3).

4.3. Survival rates of resident storks

Model selection favoured a model with a survival rate that was equal for both age classes (Table 2). The sur-

vival estimate for adults was higher (0.885, 95% CI: 0.794–0.939) than the corresponding estimate in the previous analysis of the mixture of residents and migrants. The next best model with less than half the weight of the best one differed in that the survival rate was age dependent, but otherwise had the same structure.

4.4. Adult survival rate of migrating storks

The proportion of white storks born in Möhlin and still alive in winter that were observed alive or were found dead during winter (months November, December, January, February) in Switzerland, in the Alsace or in Germany is a lower limit estimate of the proportion of residents. In all, 192 free-flying storks were born in

Möhlin between 1987 and 2000, of which an estimated 122 were still alive at the end of December of the year of birth (assuming a first year survival rate of 0.37). Twenty-one of them were seen or recovered in Switzerland during winter, thus a minimal estimate for the proportion of residents is 0.172. Note that this number of storks seen in winter is considerably lower than the number for the estimate of the survival rates of residents (120). This is because, in the former case, only non-manipulated storks are included, whereas in the latter case all storks are considered. If 17.2% of the non-manipulated storks are residents and if this estimate is typical for the whole of Switzerland, then the annual survival rate of migratory adult storks would be 0.850 (= $(0.856 - 0.172 * 0.885)/(1 - 0.172)$), not very much lower than estimated for all non-manipulated white storks (0.856).

4.5. Stochastic population growth rate and perturbation analysis

The estimates of the shrunken survival probabilities before the year 1984 were rather imprecise and some were even at the boundary (Fig. 3), which was probably caused by the low sample size at that time. To reduce the influence of the uncertainty of these estimates on the population growth rates, we only considered the last 17 years (1984–2000) for the scenarios including environmental stochasticity in survival rates. The stochastic population growth rate was the highest when there was no temporal variation in the survival rates and when the adult survival rate was not adjusted for the birds wintering in Switzerland (Table 3). The mean stochastic population growth rate and its 95% confidence limits were larger than zero in all scenarios.

We present elasticities from the first scenario only, as the differences between the different scenarios turned out to be marginal. Population growth rate was by far the most sensitive to changes in adult survival rate (Table 4). For example a proportional change in adult survival rate resulted in approximately a seven times larger change in population growth rate than the same proportional change in juvenile survival rate, in fledging success or in the proportion of breeding adults. The population growth rate was almost unaffected by the

Table 4
Lower level elasticities of the population growth rate to variation in vital rates

Vital rate	Elasticity
Juvenile survival (S_j)	0.124
Adult survival (S_{ad})	0.876
Fledging success (f)	0.124
Probability to start breeding at age 3 (m_3)	0.012
Proportion of breeding adults (m_4)	0.112

The elasticities were calculated based on a matrix model using the survival rates from scenario one and the average fledging success.

proportion of white storks starting to breed at the age of 3 years (Table 4).

5. Discussion

5.1. Demography and population growth

Our analysis shows that the stochastic population growth rate of the reintroduced white storks is positive, and that the population can be considered to be self-sustaining. The first two scenarios, where no temporal variation in the survival rates was considered, were slightly too optimistic, because there was certainly some, but perhaps small, temporal variation in survival rates. Furthermore, the proportion of breeding adults was assumed to be 1, which was certainly a slight overestimate. Moreover, the proportion of non-manipulated birds that winter in Switzerland might have been higher than estimated here; in consequence, the average survival rate of the migrants is likely to be slightly lower than estimated. In contrast, the last two scenarios were rather pessimistic, because they include too much variation in the survival rates. However, even with the overestimated variation, the average population growth rate was still larger than zero. We conclude that the probability of extinction of the white stork population in Switzerland is nearly zero over the short term (~25 years).

The comparison of the observed population growth rate (based on the census data) and the expected one (based on the stochastic matrix projection model) is only reasonable for the most recent years where the

Table 3
Stochastic population growth rates ($\log \widehat{\lambda}_s$) with 95% confidence intervals in parentheses estimated under different scenarios

Scenario	Stochastic population growth rate
Survival rate constant, no correction for residents	0.0406 (0.0395–0.0417)
Survival rate constant corrected for the presence of residents	0.0351 (0.0340–0.0362)
Survival rate time dependent, no correction for residents	0.0386 (0.0365–0.0409)
Survival rate time dependent corrected for the presence of residents	0.0313 (0.0290–0.0336)

The estimate was obtained by 11,000 bootstrap simulations, of which the first 1000 have been discarded.

management activity was low, and hence the observed population growth reflects more or less natural conditions. Considering the last 10 years, the observed population growth rate was lower ($\mu = \log(n_{1990}/n_{2000})/10 = 0.013$) than the expected one (scenario four, only last 10 years considered; $\log \lambda_s = 0.027$). There are several possible reasons for this discrepancy. First, and most likely in our opinion, the observed population growth rate was lower due to dispersal, which was not considered in our model. Ring recoveries and resightings show that a number of Swiss storks have settled abroad, most frequently in the Alsace (France) and Baden-Württemberg (Germany). Second, environmental variation and/or density-dependent regulation could have changed the breeding probabilities (m_3, m_4) which were considered constant in our model. Third, the proportion of wintering white stork in Switzerland may be underestimated, which in turn would overestimate the survival rates of migratory white storks. Fourth, the growth rate estimated with the census data may be biased, because not all breeding pairs were found each year. It is possible that the proportion of undetected pairs increased as the population increased, resulting in an underestimate of the growth rate.

The population growth rate was by far the most sensitive to changes in the adult survival rate and about as sensitive to changes in the other vital rates considered. This means that a relatively small change in the adult survival rate to <0.82 would be sufficient for the population to start to decline. Relatively larger changes in the other vital rates could be tolerated by the population until it would start to decline.

Similarly high estimates of adult survival are reported for white storks from the Netherlands, which were reintroduced in a similar way as those in Switzerland (Doligez et al., in press). In contrast, lower estimates of adult survival were found in populations that were not created by reintroduction (Germany and Alsace: between 0.58 and 0.75 [Kanyamibwa et al., 1993]; western France: between 0.74 and 0.78 [Barbraud et al., 1999]). A main source of variation in the adult survival rate is the amount of rainfall in the wintering quarters (Sahel); in dry periods survival is reduced (Kanyamibwa et al., 1990, 1993; Barbraud et al., 1999). During the period considered here, rainfall in the Sahel was relatively low in the 1970s and increased slightly thereafter. In recent years, an increasing number of white storks including Swiss ones have wintered in southern Spain (Tortosa et al., 1995). These storks avoid the potentially dangerous crossing of the Sahara desert and profit from high food availability on irrigated fields and on rubbish tips in Spain. Furthermore, kills due to power line collisions have slightly decreased in recent years (Schaub and Pradel, in press). All these factors may have enhanced survival.

First year survival rate of Swiss storks was within the range of other sites (Baden-Württemberg: 0.26–0.40 [Bairlein and Zink, 1979]; Alsace: 0.39–0.48 [Lebreton, 1978]). Since this parameter is difficult to estimate, the sources of its variation have not been studied yet.

Fledging success during the study period (1.65 fledglings/breeding pair) was significantly lower than before extinction (2.3; Moritzi et al., 2001; Biber et al., 2003). It was also low compared to the rapidly growing population in western France (3.2 fledging/breeding pair; Barbraud et al., 1999), but within the range of populations in the Alsace (1.44), in Baden-Württemberg (1.64) and in the Netherlands (1.39) in about the same period (Bairlein, 1991). A significant part of the variation in fledging success between years in Swiss storks was caused by weather during breeding: fledging success was increased when temperature was high and the amount of precipitation low (Moritzi et al., 2001). Fledging success also depends on habitat quality and farming practice: it is higher where the amount of grassland is high (Schneider, 1988) and where the grassland is mown sequentially (Johst et al., 2001). We found a marginally significant tendency in the fledging success to decrease either over time or with increasing density. As the number of breeding pairs and time were very strongly correlated ($r = 0.976$), these two effects could not be separated. This aspect needs further investigation. If the declining breeding success is density-dependent it is of no conservation concern, since it would recover at lower density. Density-dependent breeding success was found in a French population (Barbraud et al., 1999). However, if the observed decline should turn out to be a trend over time, e.g. due to decreasing habitat quality, this would threaten the population.

Based on the possible and observed variation in the vital rates and the sensitivity analysis we can speculate about the demographic reasons for the extinction and the recovery. The reproductive success decreased in the period when the population declined (Bairlein, 1991), suggesting that a drop in reproductive success was in part responsible for the extinction. However, the reproductive success at the time just before extinction was still significantly higher than now (Moritzi et al., 2001), pointing towards additional mechanisms for the population decline. Bairlein (1991) showed that the period of population decline in Central Europe paralleled a decline in Sahelian rainfall. Knowing that survival is linked with Sahelian rainfall and that population growth is very sensitive to changes in adult survival, it is likely that a drop in adult survival was another factor responsible for the extinction. The recovery of the Swiss population was initiated by releases and intensive management, but was much facilitated by an increased adult survival. The ongoing destruction of the breeding habitats (decreasing amount of meadows) is probably the main reason for the low fledging success nowadays.

However, the high adult survival more than compensates for the negative effect of the reduced fledging success.

5.2. Proposals for future management

The actual population size of 175 free-flying breeding pairs should be enough as a founder population (Griffith et al., 1989). Further releases and management practices like translocations or prevention of migration by wing feather clipping would probably not enhance substantially the probability of success. Resources for management should be directed to actions that increase the vital rates or reduce their variations.

Because of its high elasticity, adult survival rate is potentially the most rewarding parameter on which to focus management. However, as pointed out, it is already very high and not very variable – and hence it would be difficult to improve any further. To maintain this high survival rate, actions that have negative impact on it should be avoided (i.e. habitat destruction in breeding and wintering areas, power line collisions, hunting). Schaub and Lebreton (in press) showed that mortality induced by power lines is almost completely additive to the remaining mortality, hence reducing power line mortality would directly increase survival.

Because the population growth rate is little sensitive to changes in the reproductive parameters, only substantial increases would enhance the probability of persistence of the Swiss white stork population. Nevertheless, we think that the enhancement of reproductive success through habitat restoration (see e.g. Schneider, 1988; Senra and Alés, 1992; Carrascal et al., 1993; Johst et al., 2001) should become a principal aim in the management of the population. Several reasons lead to this claim. First, compared to the survival rates, fledging success was very variable, and has thus a much greater potential to be changed by management. Although the population growth rate is not particularly sensitive to changes in fledging success, it is probably more easily enhanced or maintained high when management is focused on enhancing fledging success rather than survival rates (Ehrlén and van Groenendael, 1998). Second, the probability that the high adult survival rate would decline seems more likely than to increase. High adult survival was the result of the reintroduction management through providing food and thereby increasing residency of Dutch white storks (Doligez et al., in press). If food provisioning in particular during winter were to decrease, it can be expected that the proportion of migrating white storks would increase and consequently the average survival rate would decrease. It is likely that similar relationships are valid also for Swiss storks. To buffer against a possible decline, the fledging success must either improve or its variation over time reduce. Finally, the success of a species reintroduction pro-

gramme is usually much more likely when the factors that caused the population extinction have been eliminated (Griffith et al., 1989). One major reason was the destruction of breeding habitats – and habitat restoration for white storks has remained marginal up to now in Switzerland.

Acknowledgements

References

Anonymous, 1992. MATLAB reference guide. MathWorks, Natick, MA.

Bairlein, F., 1981. Analyse der Ringfunde von Weissstörchen (*Ciconia ciconia*) aus Mitteleuropa westlich der Zugscheide: Zug, Winterquartier, Sommerverbreitung vor der Brutreife. Vogelwarte 31, 33–44.

Bairlein, F., 1991. Population studies of white storks *Ciconia ciconia* in Europe, with reference to the western population. In: Perrins, C., Lebreton, J.-D., Hirons, R. (Eds.), Bird Population Studies: Relevance to Conservation and Management. Oxford University Press, Oxford, pp. 207–229.

Bairlein, F., Zink, G., 1979. Der Bestand des Weissstorchs *Ciconia ciconia* in Südwestdeutschland: eine Analyse der Bestandsentwicklung. Journal für Ornithologie 120, 1–11.

Barbraud, C., Barbraud, J.-C., Barbraud, M., 1999. Population dynamics of the white stork *Ciconia ciconia* in western France. Ibis 141, 469–479.

Benton, T.G., Grant, A., 1996. How to keep fit in the real world: elasticity analyses and selection pressures on life histories in a variable environment. American Naturalist 147, 115–139.

Biber, O., Moritzi, M., Spaar, R., 2003. Der Weissstorch *Ciconia ciconia* in der Schweiz – Bestandsentwicklung, Altersaufbau und Bruterfolg im 20. Jahrhundert. Der Ornithologische Beobachter 100, 17–32.

Bloesch, M., 1980. Drei Jahrzehnte Schweizer Storchenansiedlungsversuch *Ciconia ciconia* in Altreu, 1948–1979. Der Ornithologische Beobachter 77, 167–194.

Boettcher-Streim, W., 1986. Der Wiederansiedlungsversuch des Weissstorches in Altreu/Schweiz. Beiheft zu der Veröffentlichung für Naturschutz und Landschaftspflege Baden-Württemberg 43, 315–388.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: A Practical Information Theoretic Approach. Springer, New York.

Burnham, K.P., 1993. A theory for combined analysis of ring recovery and recapture data. In: Lebreton, J.-D., North, P.M. (Eds.), Marked Individuals in the Study of Bird Population. Birkhäuser, Basel, pp. 199–213.

Burnham, K.P., White, G.C., 2002. Evaluation of some random effects methodology applicable to bird ringing data. Journal of Applied Statistics 29, 245–264.

Carrascal, L.M., Bautista, L.M., Lázaro, E., 1993. Geographical variation in the density of the white stork *Ciconia ciconia* in Spain: influence of habitat structure and climate. Biological Conservation 65, 83–87.

Cramp, S., 1977. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palaearctic. Oxford University Press, Oxford.

Caswell, H., 2001. Matrix Population Models. Construction, Analysis and Interpretation. Sinauer, Sunderland, MA.

Catchpole, E.A., Freeman, S.N., Morgan, B.T.J., Harris, M.P., 1998. Integrated recovery/recapture data analysis. Biometrics 54, 33–46.

Choquet, R., Reboulet, A.-M., Pradel, R., Lebreton, J.-D., 2001. U-CARE (Utilities – capture-recapture) user's guide. Typoscript. CEFE/CNRS, Montpellier.

Cohen, J.E., Christensen, S.W., Goodyear, C.P., 1983. A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac river. Canadian Journal of Fisheries and Aquatic Sciences 40, 2170–2183.

Dennis, B., Munholland, P.L., Scott, J.M., 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 61, 115–143.

Doligez, B., Thomson, D.L., van Noordwijk, A.J., in press. Using large-scale data analysis to assess life history and behavioural traits: the case of the reintroduced white stork *Ciconia ciconia* population in the Netherlands. Animal Biodiversity and Conservation.

Ehrlén, J., van Groenendael, J., 1998. Direct perturbation analysis for better conservation. Conservation Biology 12, 470–474.

Fieberg, J., Ellner, S.P., 2000. When is it meaningful to estimate an extinction probability? Ecology 81, 2040–2047.

Glutz von Blotzheim, U.N., 1962. Die Brutvögel der Schweiz. Aargauer Tagblatt, Aarau.

Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C., 1989. Translocation as a species conservation tool: status and strategy. Science 245, 477–480.

Jenni, L., Boettcher-Streim, W., Leuenberger, M., Wiprächtiger, E., Bloesch, M., 1991. Zugverhalten von Weissstörchen *Ciconia ciconia* des Wiederansiedlungsversuchs in der Schweiz im Vergleich mit jenem der West- und der Maghreb-Population. Der Ornithologische Beobachter 88, 287–319.

Johst, K., Brandl, R., Pfeifer, R., 2001. Foraging in a patchy and dynamic landscape: human land use and the white stork. Ecological Applications 11, 60–69.

Kanyamibwa, S., Bairlein, F., Schierer, A., 1993. Comparison of survival rates between populations of the white stork *Ciconia ciconia* in Central Europe. Ornis Scandinavica 24, 297–302.

Kanyamibwa, S., Schierer, A., Pradel, R., Lebreton, J.-D., 1990. Changes in adult annual survival rates in a western European population of the White Stork *Ciconia ciconia*. Ibis 132, 27–35.

Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142, 911–927.

Lande, R., Orzack, S.H., 1988. Extinction patterns of age-structured populations in a fluctuating environment. Proceedings of the National Academy of Sciences USA 85, 7418–7421.

Lebreton, J.-D., Gonzalez-Davila, G., 1993. An introduction to models of subdivided populations. Journal of Biological Systems 1, 389–423.

Lebreton, J.-D., 1978. Un modèle probabiliste de la dynamique des populations de cigogne blanche (*Ciconia ciconia* L.) en Europe occidentale. In: Legay, J.M., Tomassone, R. (Eds.), Biométrie et Ecologie, vol. 1. Société Française de Biométrie, Paris, pp. 227–343.

Ludwig, D., 1999. Is it meaningful to estimate a probability of extinction? Ecology 80, 298–310.

Moritzi, M., Maumary, L., Schmid, D., Steiner, Y., Vallotton, L., Spaar, R., Biber, O., 2001. Time budget, habitat use and breeding success of white storks *Ciconia ciconia* under variable foraging conditions during the breeding season in Switzerland. Ardea 89, 457–470.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. American Naturalist 132, 625–661.

Sarrazin, F., Barbrault, R., 1996. Reintroduction: challenges and lessons for basic ecology. Trends in Ecology and Evolution 11, 474–478.

Schaub, M., Pradel, R., in press. Assessing the relative importance of different sources of mortality from recoveries of marked animals. Ecology.

Schaub, M., Lebreton, J.-D., in press. Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. Animal Biodiversity and Conservation.

Schneider, M., 1988. Periodisch überschwemmtes Dauergrünland ermöglicht optimalen Bruterfolg des Weissstorchs (*Ciconia ciconia*) in der Save-Stromaue (Kroatien/Jugoslawien). Vogelwarte 34, 164–173.

Scott, J.M., Carperter, J.W., 1987. Release of captive-reared or translated endangered birds: what do we need to know? Auk 104, 544–545.

Senra, A., Alés, E.E., 1992. The decline of the white stork *Ciconia ciconia* population of western Andalusia between 1976 and 1988: causes and proposals for conservation. Biological Conservation 61, 51–57.

Tortosa, F.S., Mañez, M., Barcell, M., 1995. Wintering white storks (*Ciconia ciconia*) in south west Spain in the years 1991 and 1992. Vogelwarte 38, 41–45.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Suppl.), 120–139.

Zink, G., 1967. Populationsdynamik des Weissen Storchs, *Ciconia ciconia*, in Mitteleuropa. In: Proceedings International Ornithological Congress XIV, pp. 191–215.