

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

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Abstract

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.— The White stork *Ciconia ciconia* has been the object of several successful reintroduction programmes in the last decades. As a consequence, populations have been monitored over large spatial scales. Despite these intense efforts, very few reliable estimates of life history traits are available for this species. Such general knowledge however constitutes a prerequisite for investigating the consequences of conservation measures. Using the large-scale and long-term ringing and resighting data set of White storks in the Netherlands, we investigated the variation of survival and resighting rates with age, time and previous individual resighting history, and in a second step supplementary feeding, using capture–recapture models. Providing food did not seem to affect survival directly, but may have an indirect effect via the alteration of migratory behaviour. Large-scale population monitoring is important in obtaining precise and reliable estimates of life history traits and assessing the consequences of conservation measures on these traits, which will prove useful for managers to take adequate measures in future conservation strategies.

Key words: Age and time effects on survival, Capture–resighting models, Migrating probability, Population dynamics, Supplementary feeding, Trap–dependence.

Resumen

Empleo de análisis de datos a gran escala para evaluar rasgos de historia vital y de comportamiento: el caso de la población de cigüeñas blancas Ciconia ciconia reintroducidas en los Países Bajos.— Durante las últimas décadas, la cigüeña blanca *Ciconia ciconia* ha sido objeto de diversos y satisfactorios programas de reintroducción, lo que ha permitido controlar poblaciones a grandes escalas espaciales. Pese a la intensidad de tales esfuerzos, se dispone de muy pocas estimaciones fiables acerca de los rasgos de la historia vital de esta especie. No obstante, estos conocimientos generales constituyen un requisito previo para investigar las consecuencias de las medidas de conservación. El empleo de datos de reavistaje y de anillamiento a largo plazo y a gran escala de las cigüeñas blancas de los Países Bajos nos ha permitido investigar la variación en las tasas de supervivencia y de reavistaje según la edad, el tiempo y la historia previa de reavistajes individuales. Asimismo, en una segunda fase, hemos analizado los efectos de la alimentación suplementaria a partir de modelos de captura–recaptura. Parece que la provisión de alimentos no incidió directamente en la supervivencia, pero es posible que tuviera un efecto indirecto como consecuencia de la alteración del comportamiento migratorio. El control de la población a gran escala es fundamental para obtener estimaciones precisas y fiables de rasgos de historia vital, así como para evaluar las consecuencias de las medidas de conservación de dichos rasgos, que resultarán de especial utilidad para los gestores a la hora de emprender iniciativas apropiadas con respecto a las estrategias de conservación futuras.

Palabras clave: Efectos del tiempo y de la edad en la supervivencia, Modelos de captura–reavistaje, Probabilidad de migración, Dinámica poblacional, Alimentación suplementaria, Dependencia de las trampas.

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Introduction

Habitat degradation and loss due to human activities has led to increased extinction risks especially for rare or highly specialised species and species using several habitat types at different times of the year, such as migratory species (e.g. Senra & Alés, 1992). Conservation biology aims at helping managers to (1) assess the status of populations and identify the risk factors these populations are subject to, (2) decide which conservation measures are optimal to restore or protect endangered populations, and (3) assess the effect of such measures in a feed-back process allowing efficient measures to be taken in further conservation phases (Lebreton & Clobert, 1991; Caswell, 2001). In the last decades, many conservation actions have been undertaken, but for practical reasons, conservation programmes are often limited in space and time.

A conservation programme is often considered successful when the target population has been restored to at least the level before the decline within the duration of the programme, i.e. a short-term, numerical response. However, long-term sustainability of restored populations may not be met (Schaub et al., 2004). Conservation measures may affect population dynamics in many ways by acting on different life history or behavioural traits, and may durably change population composition (e.g. proportion of non-breeding individuals), affecting population processes such as sexual selection and intraspecific competition. A precise assessment of the success of conservation actions is an important step requiring the identification of traits affected by conservation measures (Sarrazin & Barbault, 1996; Caswell, 2001). Such assessments, however, are still scarce (Schaub et al., 2004). In particular, difficulties arise from the usually small size of the populations concerned, often preventing the computation of reliable estimates with limited confidence intervals. Large-scale, long-term population monitoring is critically needed to assess the impact of conservation actions, but is rarely compatible with financial and technical support limitations.

The conservation of the White stork *Ciconia ciconia* in Europe is one example of a large spatial scale conservation action. White stork populations strongly declined all over Europe after 1945, and became extinct or nearly extinct in many Western European countries (Bairlein, 1991). Increased mortality, due to (i) starvation on the wintering grounds, and (ii) increase of risk of collision with power lines and electrocution along the migration route, has been identified as one of the causes of population decline (Barbraud et al., 1999). Between 1950 and 1970, conservation actions were implemented at a regional or national level in several countries (Bairlein, 1991; see e.g. Schaub et al., 2004). Consequently, White stork populations have been monitored over large spatial and temporal scales, with intense efforts of ringing nestlings and identifying breeders and wintering birds (see Senra

& Alés, 1992; Tortosa et al., 1995). In the Netherlands, an intensive reintroduction programme was initiated in 1969, consisting in (i) a captive breeding programme, with the release of juveniles produced by captive pairs (until 1995), and (ii) providing nest sites (poles) and food at the release stations for non-captive, independent individuals, both during the breeding season and winter. This programme resulted in restoring the White stork population in the Netherlands up to its level before 1945 (396 breeding pairs in 2000).

An assessment of the consequences of this programme in terms of population dynamics and life history traits is now required to allow adequate further conservation measures to be taken. In particular, providing food could have altered life history traits directly and/or indirectly. Direct effects could include increased clutch size, brood size and fledgling number and body condition as well as increased juvenile and adult body condition before migration and survival (Brittingham & Temple, 1988; Hörnfeldt et al., 2000; Sasvari & Hegyi, 2001; Tortosa et al., 2002; Tortosa et al., 2003). Indirect effects could include individual behavioural changes (Bairlein, 1991), most importantly concerning foraging and migratory habits. Such changes might consist of alteration of migration route (Fiedler, 1998; Berthold et al., 2001) or wintering areas (Tortosa et al., 1995); or partial loss of the migratory habit, especially with food being provided all year round. If resident birds escape major sources of mortality linked to migration (Tortosa et al., 1995; Schaub & Pradel, 2004; Schaub et al., 2004), supplementary feeding could indirectly influence survival. Assessing the influence on survival rate of food provided at the stations, and investigating its mechanisms, thus appears of prime importance to assess the success of the reintroduction programme and predict future population dynamics under different conservation measures, and thus eventually identify further measures that are needed to keep the population size at a healthy level.

In long-lived species such as the White stork, adult survival is a key life history trait for population dynamics, and thus constitutes a preferential target for conservation measures (Lebreton, 1978; Stearns, 1992; Schaub et al., 2004). We thus focused on survival rate, and took advantage of the high ringing and resighting efforts throughout the Netherlands to perform a survival analysis at a large spatial scale. We used capture-recapture methodology to identify the factors affecting survival probability (internal factors: age, previous individual history; and environmental factors: year, food availability), and obtain reliable estimates of this life history trait according to these factors. We discuss here the technical aspects of these analyses based on long-term, large-scale data sets, and provide elements of discussion for the influence of supplementary feeding on life history traits. The biological aspects will be developed and discussed in detail elsewhere. Precise estimates of life history traits are needed to build up integrated demographic

population models allowing the assessment of the consequences of variation in life history traits on population dynamics (Caswell, 2001; Schaub & Pradel, 2004), and thus the investigation of short- and long-term population dynamics and the assessment of extinction risk under different conservation scenarios. Such integrated models constitute powerful tools to help in making optimal conservation decisions.

Material and methods

Species, data collection and selection for analyses

The White stork is a long-lived migratory species breeding throughout Europe. Data on ringing and live resightings of White storks in the Netherlands have been gathered and monitored by Dutch ringers. Each year, volunteers followed active nests of White storks, and wherever possible, nestlings were given individually numbered metal rings that can be read with a telescope, and parents were identified when ringed. Resightings of all other adults during the breeding season were also collected, though it is difficult to establish with certainty their breeding status.

Survival analyses were restricted to birds ringed as nestlings within the Netherlands between 1980 and 1999, using live resightings during the breeding season (April to July) for years 1981 to 2000, within the Netherlands only (less than 5% of resightings of Dutch-ringed storks during the breeding season are made outside the Netherlands). All individuals manipulated in any way were excluded from the analyses, because such manipulations may have long-term influences on survival (Sarrazin et al., 1994). We obtained 3,682 records of birds ringed as nestlings or fledglings between April and July, from 1980 to 1999. Among these birds, a total of 763 individuals have been resighted later as adults during the breeding season within the Netherlands, with a total of more than 5,700 resightings from 1981 to 2000.

Effects considered on survival and resighting probability

Age, time and cohort effects

Age, time and cohort effects, which have previously been shown to influence survival rate (Kanyamibwa et al., 1990; Kanyamibwa et al., 1993; Barbraud et al., 1999), were included in the analyses. Here, a full age effect was considered, i.e. 21 age classes were defined in the starting models. Cohort effects can arise from long-term effects during adulthood of developmental conditions shared by individuals born in the same year (Lindström, 1999; Reid et al., 2003). A cohort effect could be tested only after removal of the age x time interaction if not significant. Conversely, no sex effect was considered because too few individuals could be sexed (no sexual dimorphism or sex differences in parental

care in this species). However, survival rate has previously been found not to differ among sexes in various populations of the White stork (Kanyamibwa et al., 1993; Barbraud et al., 1999), although these studies were based on small sample sizes. The effects retained were then simplified by grouping a *posteriori* years, cohorts and age classes of similar survival and resighting estimates, and modelling age patterns with different relationships between age and survival (linear, quadratic, etc.).

Supplementary feeding

To assess the effect of providing food at the release stations, the distance from the nest to the nearest station was considered. During the nestling phase, foraging visits by parents occur mainly within 2 km from the nest (about 75% of the feeding visits by a pair), less frequently from 2 to 5 km from the nest (about 25%), and only exceptionally farther than 5 km from the nest (Dallinga & Schoenmakers, 1984; Carrascal et al., 1990; Alonso et al., 1991; see also Johst et al., 2001). Thus, the shorter the distance from the nest to the nearest station, the higher the potential influence of feeding on survival. Therefore, two different classes of distance relative to the location of the nest from the nearest release station were defined: *class 1 (close)*: breeding adults whose nest is closer than 2 km from the nearest station (feeding in majority at the station); *class 2 (distant)*: adults whose nests are farther than 2 km (rarely feeding at the station). These distance classes should reflect the percentage of feeding visits made by the parents at the stations.

Assessment of survival and resighting probabilities: capture-recapture analyses

Resighting effort during the breeding season is mainly linked to breeding activities. Because (i) a given percentage of breeding birds are missed each year, and (ii) not all birds may engage in breeding activities each year (especially in the first years of their life), resighting probability is likely to be smaller than 1. In that case, the use of capture-recapture methodology is required to get unbiased estimates of survival probability (Lebreton et al., 1992; Clobert, 1995; Martin et al., 1995). Furthermore, the class of distance to the nearest release station of an individual is susceptible to change over the course of the individual's lifetime. In this case, multi-state capture-recapture models, allowing the assessment of state-specific survival and resighting rates and transition probabilities between states (here, the distance classes), may be appropriate (Nichols et al., 1994; Nichols & Kendall, 1995).

Goodness-of-fit (GOF)

Goodness-of-fit tests were performed to ensure that the starting model (i.e. before selection) fits the data (Burnham et al., 1987; Lebreton et al., 1992). We used a modified version of Release tests (Burnham

et al., 1987) to test for trap-dependence effects (Pradel, 1993; see below). The time effect model (CJS model) was tested cohort by cohort because a strong effect of age is expected in this long-lived species with delayed maturity (see Cézilly et al., 1996). The results of these cohort-by-cohort tests were then summed over all cohorts to compute the global tests for the whole data set.

Accounting for trap-dependence

Individuals resighted at time t may not have the same probability to be resighted at time $t+1$ as individuals not resighted at time t (Burnham et al., 1987; Cam & Monnat, 2000), an effect called short-term (or immediate) "trap-dependence" (Pradel, 1993). Data were prepared for analysis of trap-dependence as described in Pradel (1993), using U-Care software (Choquet et al., 2003). Capture-resighting histories were split after each capture to allow distinction between resighting rate immediately after a resighting and after no resighting. Trap-dependence was then modelled by an artificial age-dependence structure, with two age classes (one year after the previous resighting vs. later; Pradel, 1993; see also Pugesek et al., 1995). To account for real age-dependence simultaneously, individuals were re-injected in the data after splitting their capture-resighting history into groups corresponding to their actual age. Parameters were then equalised among these groups according to year and individual's age and cohort (Appendix).

Model selection and notation

Model selection was based on the Akaike's Information Criterion corrected for effective sample size (AICc; Lebreton et al., 1992; Burnham et al., 1995). The models selected were those whose AICc value differed by less than two units from the lowest AICc model. Deviances and AICc values of the different models were calculated using software MARK (White & Burnham, 1999). All effects could not be included at once in the starting model because the number of parameters required would exceed the upper limits of our available computer memory when using MARK (~1,000). Therefore, analyses were performed in two steps: (i) first, the effects of time, age, trap-dependence and cohort on survival and resighting rates were investigated and, when appropriate, simplified *a posteriori* on the basis of parameter estimates (see above); (ii) second, this simplified model, where the number of parameters had been reduced, was used as a starting model for assessing the influence of the variables linked to conservation measures (here supplementary feeding).

Model notation has been extended from the notation defined in Lebreton et al. (1992) and in Nichols et al. (1994) for multi-state models. S_{a+1} (survival probability) is the probability that a bird of age a at time $t-1$ survives until time t (an additive effect of time and age on survival was

noted S_{a+1}). P_{a+1} (resighting probability) is the probability that a bird of age a is recaptured at time t , given that it is alive and present at time t . Subscripts c and m denote a cohort effect and an immediate trap-dependence effect on resighting rate respectively. In multi-state models, state-specific survival and resighting probabilities are noted S_{a+1xs} and P_{a+1xs} respectively. T_{a+1xsr} (transition probability) is the probability that a bird of age a in state s at time $t-1$ is in state r at time t , given that the individual has survived from time $t-1$ to time t .

Results

Simplification of time, age and cohort effects

Goodness-of-fit tests

To increase the sensitivity of the global Release test (see Horak & Lebreton, 1998), only tests for cohorts with sufficient data (i.e. at least 2 expected individuals per cell) were included. Goodness-of-fit of model S_{a+1} , P_{a+1} was strongly rejected ($\chi^2 = 308.59$, $df = 64$, $p < 0.0001$). This was due to a very high 2 CT test value ($\chi^2 = 267.64$, $df = 40$, $p < 0.0001$). Thus, resighting probability depended on previous resighting history of the individuals (trap-dependence; Burnham et al., 1987; Pradel, 1993). Here, birds resighted at time t were approximately twice as likely to be resighted again at time $t+1$ than birds not resighted at time t , i.e. a strong "trap-happiness" effect (Pradel, 1993; fig. 1). The other components of the GOF tests were not significant, except test 3 Sm, but this was due to a single cohort out of 14, i.e. close to the 1/20 expected by chance. When excluding this cohort, we obtained a non-significant 3 SR + 3 Sm + 2 Cm test ($\chi^2 = 34.16$, $df = 23$, $p = 0.063$; $\hat{c} = 1.49$). Thus trap-dependence was the major source of lack of fit. The model S_{a+1} , P_{a+1xm} fitted the data, and was used as the starting model for the model selection procedure.

Model selection

Resighting probability models were simplified first to keep greater power for survival modelling (Lebreton et al., 1992). Additive effects of age, time, trap-dependence and cohort on resighting probability were retained in the final model (table 1). Similarly, an additive effect of age and time on survival probability was retained, i.e. temporal variation of survival probability was parallel among age classes. No cohort effect could be detected on survival probability (table 1). Additional attempts to reduce resighting probability with the simplified survival model were unsuccessful (table 1). The final model retained at this stage was thus S_{a+1} , $P_{a+1+c+m}$, with a total of 97 parameters. No other model could compete with this model, as differences in AICc values were

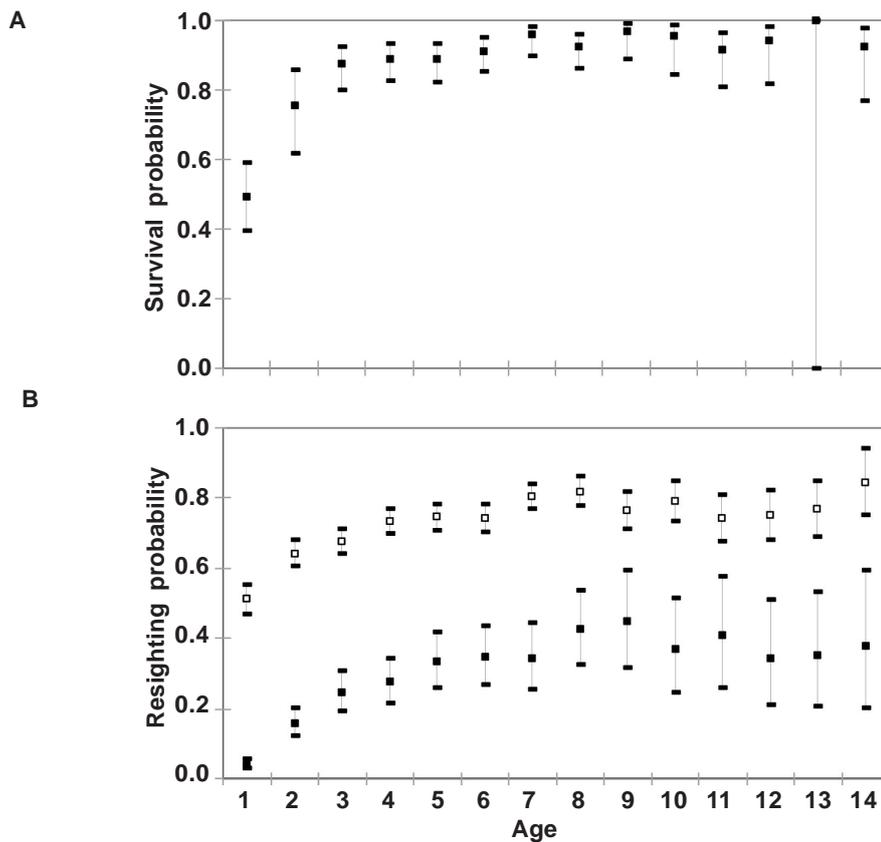


Fig. 1. Variation in survival and resighting probabilities with age: survival (A) and resighting (B) probability estimates (\pm SE) for year 1994 (medium survival and resighting rate–year, see fig. 2) are shown as examples (birds aged up to 14 years because only birds born after 1980 were included). Survival and resighting probabilities increase gradually with age up to 8 years, when they stabilise. This increase is modelled appropriately by a quadratic relationship for survival (A) and an inverse quadratic relationship for resighting (B), on a logit scale (see table 2). Because age and time effects were additive (see table 1), the age-specific patterns of variation in other years are parallel to those shown in the examples here. In B, trap-dependence on resighting rate is also illustrated: black squares, birds not resighted in the previous year; open squares, birds resighted in the previous year. (Survival and resighting estimates were obtained from model S_{a+t}, P_{a+t+m} .)

Fig. 1. Variación según la edad en las probabilidades de supervivencia y de reavistaje: estimaciones de probabilidad (\pm EE) de supervivencia (A) y de reavistaje (B) para el año 1994 (supervivencia media y tasa de reavistaje–año, fig. 2) a modo de ejemplos (aves de más de 14 años de edad, dado que sólo se incluyeron aves nacidas después de 1980). Las probabilidades de supervivencia y de reavistaje aumentan gradualmente con la edad, hasta alcanzar los 8 años, que es cuando se estabilizan. Este aumento se modela adecuadamente mediante una relación cuadrática para la supervivencia (A) y una relación cuadrática inversa para el reavistaje (B), en una escala logit (ver tabla 2). Dado que los efectos de la edad y del tiempo fueron aditivos (tabla 1), las pautas de variación por edades en otros años son análogas a las indicadas en los ejemplos que se detallan aquí. En B, también se ilustra la dependencia de las trampas en la tasa de reavistaje: cuadros negros, aves no reavistadas el año anterior; cuadros blancos, aves reavistadas el año anterior. (Las estimaciones de supervivencia y de reavistaje se obtuvieron a partir del modelo S_{a+t}, P_{a+t+m} .)

always much larger than 2 (table 1). When only breeding birds were included in the analysis (i.e. excluding birds of unknown breeding status), the same final model was selected (results not detailed here).

A posteriori characterisation of the effects retained To simplify further the model selected, effects of age, time and cohort on survival and resighting probabilities were characterised explicitly (table 2). Both sur-

Table 1. Steps of the simplification of the starting model S_{axt}, P_{axtxm} to model $S_{a+t}, P_{a+t+c+m}$. Model notation according to Lebreton et al. (1992): Np. Number of identifiable parameters; T. Time; A. Age; TD. Trap-dependence; *Indicates the model selected in each step. The deviance value given here is the relative deviance from the saturated model (deviance of the saturated model: 3,332.87).

Tabla 1. Fases de la simplificación del modelo de inicio S_{axt}, P_{axtxm} al modelo $S_{a+t}, P_{a+t+c+m}$. Las anotaciones sobre el modelo se basan en Lebreton et al. (1992): Np. Número de parámetros identificables; T. Tiempo; A. Edad; TD. Dependencia de las trampas; * Indica el modelo seleccionado en cada fase. El valor de desviación indicado corresponde a la desviación relativa con respecto al modelo saturado (desviación del modelo saturado: 3.332,87).

Model	Np	Deviance	AICc	Effect tested
First step, simplifying resighting probability (effects on resighting probability)				
S_{axt}, P_{axtxm}	592	5,384.35	10,036.11	Starting model
$S_{axt}, P_{(axt)+m}$	401	5,634.91	9,829.52	Additive effect of TD
* S_{axt}, P_{a+t+m}	249	5,921.36	9,774.67	Additive effects of A, T and TD
S_{axt}, P_{axm}	249	6,021.42	9,874.73	No T effect
S_{axt}, P_{txm}	248	7,003.65	10,854.78	No A effect
S_{axt}, P_{axt}	400	5,942.05	10,134.35	No TD
S_{axt}, P_{a+m}	231	6061.95	9,876.07	No T effect, additive A and TD effects
S_{axt}, P_{t+m}	230	7,072.13	10,884.08	No A effect, additive T and TD effects
S_{axt}, P_{a+t}	248	6,251.79	10,102.91	No TD, additive effects of A and T
S_{axt}, P_a	230	6,433.52	10,245.48	A effect only
S_{axt}, P_t	229	7,177.83	10,987.61	T effect only
S_{axt}, P_m	212	7,416.03	11,189.07	TD effect only
$S_{axt}, P_{.}$	211	7,567.42	11,338.30	Constant resighting probability
Second step, simplifying survival probability (effects on survival probability)				
S_{axt}, P_{a+t+m}	249	5,921.36	9,774.67	Starting model
* S_{a+t}, P_{a+t+m}	78	6,087.32	9,578.34	Additive effects of A and T
S_a, P_{a+t+m}	60	6,157.79	9,611.93	No T effect
S_t, P_{a+t+m}	59	6,362.27	9,814.37	No A effect
$S_{.}, P_{a+t+m}$	41	6,419.84	9,835.31	Constant survival probability
Third step, checking for effects on resighting probability (effects on resighting probability)				
* S_{a+t}, P_{a+t+m}	78	6,087.32	9,578.34	Starting model
S_{a+t}, P_{a+t}	77	6,428.87	9,917.84	No TD
S_{a+t}, P_{a+m}	60	6,239.43	9,693.58	No T effect
S_{a+t}, P_{t+m}	59	7,217.07	10,669.17	No A effect
S_{a+t}, P_a	59	6,622.48	10,074.59	No T effect nor TD
S_{a+t}, P_t	58	7,334.87	10,784.93	No A effect nor TD
S_{a+t}, P_m	41	7,577.01	10,992.48	No A nor T effects
$S_{a+t}, P_{.}$	40	7,763.45	11,176.88	Constant resighting probability
Fourth step, testing for cohort effect (effects on survival S and resighting probability P)				
$S_{a+t+c}, P_{a+t+m+c}$	116	6,016.51	9,586.15	Additive cohort effect on S and P
S_{a+t+c}, P_{a+t+m}	97	6,068.91	9,599.11	Additive cohort effect on S
* $S_{a+t}, P_{a+t+m+c}$	97	6,037.40	9,567.60	Additive cohort effect on P
S_{a+t}, P_{a+t+m}	78	6,087.32	9,578.34	No cohort effect

Table 2. *A posteriori* characterisation of age, time and cohort effects on survival and resighting probabilities in the previously selected model $S_{a+t}, P_{a+t+c+m}$: Np. Number of identifiable parameters. Simplification of the effects: A². Quadratic relationship with age on a logit scale (survival probability); 1/A². Inverse quadratic relationship with age on a logit scale (resighting probability); t3. Separation of survival probability in three time periods: 1981 to 1987, 1988 to 1995, and 1996 to 2000 (see fig. 2A); t3. Separation of resighting probability in three categories of years: low resighting probability (1985 and 1987), high resighting probability (1992, 1995 and 1999), and medium resighting probability (other years) (see fig. 2B); c3. Separation of resighting probability in three types of cohort: low resighting rate-cohorts, high resighting rate-cohorts, and the 1982 cohort (with a very high resighting rate, see text). (Deviance and AICc values for the final simplified model $S_{A^2(\delta)+t3}, P_{1/A^2(\delta)+t^3+c3+m}$ are given.)

Tabla 2. *Caracterización a posteriori* de los efectos de la edad, el tiempo y las cohortes en las probabilidades de supervivencia y de reavistaje en el modelo previamente seleccionado $S_{a+t}, P_{a+t+c+m}$: Np. Número de parámetros identificables. Simplificación de los efectos: A²: Relación cuadrática con la edad en una escala logit (probabilidad de supervivencia); 1/A²: Relación cuadrática inversa con la edad en una escala logit (probabilidad de reavistaje); t3. Separación de la probabilidad de supervivencia en tres períodos de tiempo: de 1981 a 1987; de 1988 a 1995; y de 1996 a 2000 (fig. 2A); t3. Separación de la probabilidad de reavistaje en tres categorías de años: probabilidad de reavistaje baja (1985 y 1987), probabilidad de reavistaje alta (1992, 1995 y 1999), y probabilidad de reavistaje media (otros años) (fig. 2B); c3. Separación de la probabilidad de reavistaje en tres tipos de cohortes: cohortes con una tasa de reavistaje baja, cohortes con una tasa de reavistaje alta, y la cohorte de 1982 (con una tasa de reavistaje muy elevada; ver el texto). Se indican los valores de desviación y de AICc para el modelo final simplificado $S_{A^2(\delta)+t3}, P_{1/A^2(\delta)+t^3+c3+m}$.

Effect simplified	Survival	Resighting	Deviance	Np	AICc
Starting selected model	S_{a+t}	$P_{a+t+c+m}$	6,037.40	97	9,567.60
Age effect on survival	$S_{A^2(\delta)+t}$	$P_{a+t+c+m}$	6,057.79	80	9,552.92
Time effect on survival	S_{a+t3}	$P_{a+t+c+m}$	6,059.98	81	9,557.17
Age effect on resighting	S_{a+t}	$P_{1/A^2(\delta)+t+c+m}$	6,050.49	79	9,543.57
Time effect on resighting	S_{a+t}	P_{a+t^3+c+m}	6,053.34	81	9,550.53
Cohort effect on resighting	S_{a+t}	$P_{a+t+c3+m}$	6,052.99	80	9,548.12
Final simplified model	$S_{A^2(\delta)+t3}$	$P_{1/A^2(\delta)+t^3+c3+m}$	6,139.76	12	9,496.68

vival and recapture probabilities increased with age up to a plateau (fig. 1). Age-dependence could *a posteriori* be modelled with a quadratic relationship on a logit scale for survival probability, and with an inverse quadratic relationship on a logit scale for resighting probability (table 2). This difference indicates that the increase of resighting probability with age is steeper than the increase of survival probability. Both survival and resighting probabilities reached a plateau at age 8 (stabilisation at age 6: AICc = 9,503.09; age 7: AICc = 9,498.23; age 8: AICc = 9,496.68; age 9: AICc = 9,496.26; age 10: AICc = 9,496.13).

Time-dependence of survival probability could be modelled by considering three periods (1981 to 1987, 1988 to 1995, and 1996 to 2000; table 2, fig. 2A). The first period corresponded to high survival rates but low sample sizes, as reflected by large confidence intervals. Survival decreased during the second period, and again during the third one (fig. 2A).

The break in 1995–1996 corresponded to the end of the captive breeding phase of the reintroduction. A linear decline in survival probability over the 21 years of the period was tested and rejected, but other ways of modelling survival probability could also have been retained. In particular, time-dependence of survival probability could most likely be modelled parsimoniously using external meteorological variables, both during the breeding season and the winter season (Kanyambwa et al., 1993; Barbraud et al., 1999). The separation in three time periods performed here is not claimed to be the most parsimonious nor best fitting the data. Resighting probability was rather constant over the 20 years, except in years 1985 and 1987 when it was particularly low, and in years 1992, 1995, and 1999 when it was particularly high (fig. 2B). Grouping years in these three categories (low-, medium- and high-resighting rates) appropriately modelled time-dependence of resighting rate (table 2). Similarly, the

cohort effect on resighting probability could be modelled by considering three types of cohort: (i) high resighting probability-cohorts (1980, 1985, 1987, 1988, 1990, and 1993 to 1999), (ii) low resighting probability-cohorts (1981, 1983, 1984, 1986, 1989, 1991, 1992), and (iii) the 1982 cohort, with an exceptionally high resighting probability (table 2). The origin of these differences between cohorts in resighting probabilities is not clear.

This *a posteriori* characterisation of age, time and cohort effects on survival and resighting probabilities thus decreased the final number of parameters to be estimated down to 12. The final model for this first step was noted $S_{A^2(8)+t^3}$, $P_{1/A^2(8)+t^3+c3+m}$ (table 2).

Influence of distance to the nearest release station

75.0% of birds (2,760 out of 3,682) where ringed in nests located less than 2 km away from the nearest release station (distance class 1). This can be explained by a breeding activity quasi-exclusively located at the release stations during the first 8 years (until 1987), combined with high numbers of nest poles provided for the breeding birds close to the stations.

Assessing variable status: dynamic vs. fixed over individuals' lifetime

We first assessed whether the distance class changed over time for a given individual in our data set. 40.6% of resighted birds (264 out of 651) changed class of distance either between hatching and first breeding attempt and/or between several breeding attempts. Thus, the influence of class of distance to the nearest release station on survival rate and resighting probability had to be investigated using a multi-state approach.

Further simplifications of the starting model

Further simplifications of the starting model were needed and made before investigating the influence of the distance class. Because variation in survival and resighting probabilities with age stabilised at age 8, capture-recapture histories were still split to account for trap-dependence, but after splitting, individuals were re-injected in a single group when aged 8 years or more. This left us with eight age groups instead of 21. Furthermore, the cohort effect was eliminated from this multi-state analysis, because the number of parameters required to parameter the PIMs in MARK would otherwise again exceed the limit. Because the cohort effect was only additive, we assumed that eliminating it should not strongly affect model selection. With no cohort effect, 402 parameters were needed.

Survival and distance to the nearest release station

The starting model was $S_{(A^2(8)+t^3) \times s}$, $P_{(1/A^2(8)+t^3+m) \times s}$, $T_{a(8) \times t \times s}$ with two states (*close* and *distant*, i.e. two

classes of distance), thus two transitions possible from each state (i.e. one transition estimated per state, $T_{\text{close to distant}}$ and $T_{\text{distant to close}}$, with $T_{\text{close to close}} = 1 - T_{\text{close to distant}}$ and $T_{\text{distant to distant}} = 1 - T_{\text{distant to close}}$). Again, transition and resighting probabilities were simplified first to keep greater power for survival modelling. An additive effect of age, time and class of distance was retained on transition probabilities (table 3). Individuals were more likely to move and breed closer to the stations than the reverse. Storks were less likely to change class of distance with increasing age, and this variation was successfully modelled by an inverse relationship on a logit scale (table 3). Finally, transitions were particularly low (close to zero) in years 1984 and 1985, and particularly high in year 1997. Separating years in these three categories (low-, medium- and high-transition rates) appropriately modelled time-dependence of transition rate (table 3). With this simplified modelling of transition probability, an effect of class of distance was retained on resighting probability, in interaction with trap-dependence alone or trap-dependence and age (table 3; effects not detailed here). Finally, when simplifying survival probability, the models with (i) no effect of the class of distance and (ii) an additive effect of the class of distance to age and time effects on survival competed, the second being slightly less supported (AICc difference between both models: 1.81; table 3). This suggests that the class of distance only has at best a slight direct effect on survival, survival rates being lower for birds seen far from the stations (class 2, *distant*) than birds seen close (class 1, *close*) (results not detailed here).

Discussion

Our study was a first step in understanding the consequences of conservation measures on the White stork population biology and dynamics in the Netherlands through the identification of the factors responsible for the patterns of variation of survival and resighting probabilities. We focused on survival probability as the major life-history trait determining population dynamics in this long-lived species (Lebreton, 1978; Stearns, 1992; Schaub et al., 2004). We discuss below advantages and technical aspects of using large-scale data sets to test for the effect of many factors (age, time, previous history, etc) on survival and resighting probabilities. The biological implications of these effects, and the assessment of conservation measures (here, direct and indirect influences of providing food on survival), need further investigation, and will be discussed elsewhere.

Estimates of survival rates with capture-resighting analyses and their variation according to different factors (age, density, meteorological variables) have previously been given for several European populations of White storks (Kanyamibwa et al., 1990; Kanyamibwa et al., 1993; Barbraud et al., 1999; Schaub et al., 2004). Except for the Swiss

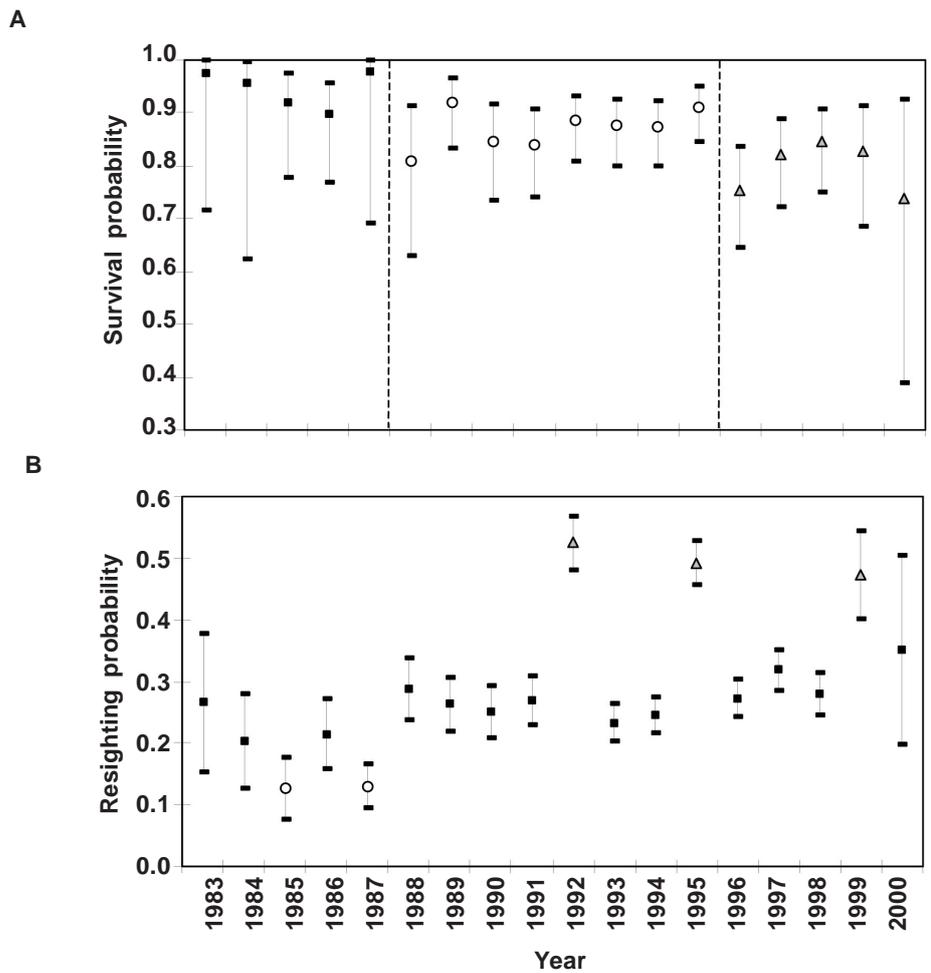


Fig. 2. Variation in survival and resighting probabilities with time. Third-year survival (A) and resighting (B) probability estimates are shown as examples (years 1983 to 2000 because only birds born after 1980 were included). For survival, three time periods were defined: 1981 to 1987 (high survival probabilities with high confidence intervals, black squares); 1988 to 1995 (medium survival probabilities, open circles); and 1996 to 2000 (low survival probabilities, grey triangles) (see text and table 2). For resighting, three categories of years were defined: low resighting rate years (1985 and 1987, open circles); high resighting rate years (1992, 1995 and 1999, grey triangles); and medium resighting rate years (other years, black squares) (see text and table 2). Temporal variation of survival and resighting probabilities for other age-classes again parallel those shown here because age and time effects were additive (see table 1). (Estimates were obtained from model S_{a+t}, P_{a+t+m} .)

Fig. 2. Variación según el tiempo en las probabilidades de supervivencia y de reavistaje. La supervivencia durante el tercer año (A) y las estimaciones de probabilidad de reavistaje (B) se indican a modo de ejemplo (de 1983 a 2000, dado que sólo se incluyeron aves nacidas después de 1980). Para la supervivencia, se definieron tres períodos de tiempo: de 1981 a 1987 (probabilidades de supervivencia altas, con intervalos de confianza elevados, cuadros negros); de 1988 a 1995 (probabilidades de supervivencia medias, círculos blancos); y de 1996 a 2000 (probabilidades de supervivencia bajas, triángulos grises) (ver texto y tabla 2). Para el reavistaje, se definieron tres categorías de años: años con una tasa de reavistaje baja (1985 y 1987, círculos blancos); años con una tasa de reavistaje alta (1992, 1995 y 1999, triángulos grises); y años con una tasa de reavistaje media (otros años, cuadros negros) (ver texto y tabla 2). La variación temporal de las probabilidades de supervivencia y de reavistaje para otras clases de edad es análoga, una vez más, a las indicadas aquí, debido a que los efectos de la edad y del tiempo fueron aditivos (ver tabla 1). (Las estimaciones se obtuvieron a partir del modelo S_{a+t}, P_{a+t+m} .)

Table 3. Steps of the simplification of the multi-state model $S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)xtxs}$ testing for an effect of the class of distance to the nearest release station (state s) on survival and resighting probabilities: Np. Number of identifiable parameters. * Indicates the model selected in each step. When simplifying resighting and survival probabilities before *a posteriori* characterising transition probability, the same models were selected for survival and resighting probabilities.

Tabla 3. Fases de la simplificación del modelo multiestado $S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)xtxs}$ para comprobar un efecto de la clase de distancia con respecto a la estación de liberación más próxima (estado s) sobre las probabilidades de supervivencia y de reavistaje: Np. Número de parámetros identificables; * Indica los modelos seleccionados en cada fase. Cuando se simplificaron las probabilidades de reavistaje y de supervivencia antes de llevar a cabo una probabilidad de transición a posteriori mediante técnicas de caracterización, se seleccionaron los mismos modelos para las probabilidades de supervivencia y de reavistaje.

Model	Np	Deviance	AICc
First step, simplifying transition probability			
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)xtxs}$	284	5,318.16	9,390.9
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{(a(\theta)+t)xs}$	74	5,468.83	9,091.8
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)xt+s}$	153	5,406.71	9,191.6
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)xs+t}$	55	5,500.93	9,085.0
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)+txs}$	67	5,471.78	9,080.4
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)xt}$	152	5,469.43	9,255.3
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)xs}$	36	5,561.09	9,108.5
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, T_{txs}	60	5,523.17	9,117.4
* $S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)+t+s}$	48	5,508.73	9,078.5
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)+t}$	47	5,589.25	9,157.0
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)+s}$	29	5,565.61	9,096.8
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, T_{t+s}	41	5,565.43	9,121.0
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)}$	28	5,626.34	9,155.5
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, T_t	40	5,617.33	9,170.8
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, T_s	22	5,614.50	9,131.6
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, T_{\cdot}	21	5,667.53	9,182.6
Second step, <i>a posteriori</i> characterisation of transition probability			
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)+t+s}$	48	5,508.73	9,078.5
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{a(\theta)+t^3+s}$	31	5,522.37	9,057.6
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{1/A(\theta)+t+s}$	42	5,509.81	9,067.4
* $S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{1/A(\theta)+t^3+s}$	25	5,523.08	9,046.2
Third step, simplifying resighting probability			
$S_{(A^2(\theta)+t^3)xs}$, $P_{(1/A^2(\theta)+t^3+m)xs}$, $T_{1/A(\theta)+t^3+s}$	25	5,523.08	9,046.2
$S_{(A^2(\theta)+t^3)xs}$, $P_{1/A^2(\theta)xs+t^3xs+m}$, $T_{1/A(\theta)+t^3+s}$	24	5,528.05	9,049.2
* $S_{(A^2(\theta)+t^3)xs}$, $P_{1/A^2(\theta)xs+t^3+mxs}$, $T_{1/A(\theta)+t^3+s}$	23	5,524.34	9,043.4
$S_{(A^2(\theta)+t^3)xs}$, $P_{1/A^2(\theta)+t^3xs+mxs}$, $T_{1/A(\theta)+t^3+s}$	24	5,523.46	9,044.6
$S_{(A^2(\theta)+t^3)xs}$, $P_{1/A^2(\theta)xs+t^3+m}$, $T_{1/A(\theta)+t^3+s}$	22	5,529.35	9,046.4
$S_{(A^2(\theta)+t^3)xs}$, $P_{1/A^2(\theta)+t^3xs+m}$, $T_{1/A(\theta)+t^3+s}$	23	5,528.11	9,047.2
* $S_{(A^2(\theta)+t^3)xs}$, $P_{1/A^2(\theta)+t^3+mxs}$, $T_{1/A(\theta)+t^3+s}$	22	5,524.66	9,041.7
$S_{(A^2(\theta)+t^3)xs}$, $P_{1/A^2(\theta)+t^3+m+s}$, $T_{1/A(\theta)+t^3+s}$	21	5,529.39	9,044.5
$S_{(A^2(\theta)+t^3)xs}$, $P_{1/A^2(\theta)+t^3+m}$, $T_{1/A(\theta)+t^3+s}$	20	5,547.03	9,060.1

Table 3. (Cont.)

Model	Np	Deviance	AICc
Fourth step, simplifying survival probability			
$S_{(A^2(\delta)+t^3)xs'}$ $P_{1/A^2(\delta)+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	22	5,524.66	9,041.7
$S_{A^2(\delta)xs+t^3}$ $P_{1/A^2(\delta)+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	20	5,525.76	9,038.8
$S_{A^2(\delta)+t^3xs'}$ $P_{1/A^2(\delta)+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	20	5,525.00	9,038.1
* $S_{A^2(\delta)+t^3+s'}$ $P_{1/A^2(\delta)+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	18	5,525.91	9,034.9
* $S_{A^2(\delta)+t^3}$ $P_{1/A^2(\delta)+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	17	5,526.12	9,033.1
$S_{(A^2(\delta)+t^3)xs'}$ $P_{1/A^2(\delta)xs+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	23	5,524.34	9,043.4
$S_{A^2(\delta)xs+t^3}$ $P_{1/A^2(\delta)xs+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	21	5,525.40	9,040.5
$S_{A^2(\delta)+t^3xs'}$ $P_{1/A^2(\delta)xs+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	21	5,524.78	9,039.8
$S_{A^2(\delta)+t^3+s'}$ $P_{1/A^2(\delta)xs+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	19	5,525.64	9,036.7
* $S_{A^2(\delta)+t^3}$ $P_{1/A^2(\delta)xs+t^3+mxs'}$ $T_{1/A(\delta)+t^3+s}$	18	5,525.88	9,034.9

population, which also used large samples (more than 3,500 individual recovery histories over 28 years; Schaub et al., 2004), previous studies obtained much smaller adult survival estimates (0.65 to 0.78), despite higher resighting rates (0.85 to 0.95). The difference in survival between these studies and ours likely arises from the much smaller sample sizes on which the former were based, combined with differences in wintering conditions between years 1970's (droughts in Africa) and 1990's (increasing number of storks wintering in Spain), or different conservation measures in different populations. The large-scale and long-term monitoring of the White stork population in the Netherlands, in relation with the reintroduction programme, allowed the gathering of a very large and high quality resighting data set. Ringing and resighting efforts have been high over the whole study period. As a consequence, we were able to model fine patterns of variation in survival and resighting probabilities with age and time, detect small effects of these factors and obtain precise estimates of these parameters.

In particular, our study is probably one of the first to include a full age- and trap-dependence simultaneously (see Pugesek et al., 1995; Frederiksen & Bregnballe, 2000). Age dependent survival was modelled in previous studies using a two-pseudo age class structure (first year after initial resighting vs. later; Kanyamibwa et al., 1990), which did not account for fine age variation in survival rate, and probably also resulted in underestimated adult survival rates (see also Tavecchia et al., 2001). A progressive increase of survival prospects early in life, as found here, has been shown in several long-lived species (Frederiksen & Bregnballe, 2000; Tavecchia et al., 2001), thus strongly encouraging complex modelling of age-

specific survival rate, using large data sets to provide sufficient power (see also Pugesek et al., 1995; Harris et al., 1997). Such an increase might be widespread among long-lived species, although it has only rarely been detected because the age structure modelled was too simple (Hafner et al., 1998; Prévot-Julliard et al., 1998; Forero et al., 2001; but see Bauchau et al., 1998).

However, the use of large data sets collected at large spatial scales also imposes constraints and limitations, because their analysis involves (i) a large set of candidate models, and (ii) complex models with many parameters, as the influence of more factors are investigated. Here, we faced the problem of the upper limit of the number of parameters based on our available computer memory when using MARK (1,000). Because of this limit, we had to adopt a strategy to simplify the models investigated to reduce parameter number (see e.g. Pugesek et al., 1995), and chose a two-step procedure mixing *a priori* and *a posteriori* effects: (i) simplifying age and time modelling of survival and resighting probabilities, and (ii) using the *a posteriori* simplified model in a multi-state model to investigate the effect of the class of distance. We could not define a starting model including all effects of interest simultaneously in MARK. Moreover, we also reduced the number of models to be compared by simplifying resighting (and transition) probability before survival probability (i.e. we did not explore the whole model space). While this approach renders analyses tractable in MARK, it does not guaranty that the best model is retained. *A posteriori* modelling should normally be used to create new hypotheses to be tested with another data set, in an *a priori* way. Here we mixed both approaches, which decreases the strength of evidence for the selected model. A theoretical assessment of the influence of

different strategies used to simplify model selection procedures on the model retained would be helpful to ensure that results are robust. It may turn out that, in the case of complex models on large data sets, MARK may not be the appropriate capture–recapture analysis software to perform model selection.

The simplifying strategies could be based on *a priori* knowledge of the species biology and results of previous studies. For instance, a trap–happiness when individuals are identified without physical capture, as for the White stork, may be due to higher resighting probability of breeders compared to non-breeders, associated with delayed maturity (Lebreton, 1978; Kanyamibwa & Lebreton, 1992). In this case, trap–dependence may be modelled using two states, breeder and non-breeder, with state–specific resighting probabilities. Here, such a two–state approach again could not have been performed using MARK because of our limits in parameter numbers. However, Release tests on the data set restricted to resighting histories after the first resighting as a breeder indicated that trap–happiness occurred within adults. Furthermore, trap–happiness was retained when resightings of birds of unknown status, probably mostly non-breeders, were excluded from the data, a result differing from other studies (Lebreton et al., 1992; Cézilly et al., 1996). Thus, resighting heterogeneity was observed among breeders. Trap–happiness may rather be due to spatial heterogeneity in resighting effort associated with high philopatry (Prévot–Julliard et al., 1998). Birds may be expected to have a higher resighting rate when breeding close to the stations than far, because of time constraints in resighting effort. Further analyses including geographical estimates of resighting effort are required to investigate this mechanism of trap–dependence.

Our detailed modelling of survival and resighting probabilities allowed us to start investigating the consequences of conservation measures, here supplementary feeding, on these traits. Providing food did not seem to strongly affect survival rate directly, but may affect it indirectly (see Schaub & Pradel, 2004; Schaub et al., 2004). The influence of supplementary feeding on the probability of migrating, and survival differences between residents and migrants is still in need of investigation. Eventually, a complete understanding of the White stork population dynamics in the Netherlands will also require the detailed characterisation of recruitment (Clobert et al., 1994; Pradel, 1996), reproductive success and dispersal, and of their variation with age, time (Pradel et al., 1997), breeding density (Barbraud et al., 1999), and supplementary feeding (Moritzi et al., 2001; Tortosa et al., 2002; Tryjanowski & Kuzniak, 2002). It will then become possible to build an integrated population model, incorporating the estimates obtained. Such a model would allow us to understand the mechanisms of population dynamics (see Thomson & Cotton, 2000) and thus to predict the consequences of future conservation actions for the White stork in the Netherlands.

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References

- Alonso, J. C., Alonso, J. A. & Carrascal, L. M., 1991. Habitat selection by foraging White storks, *Ciconia ciconia*, during the breeding season. *Can. J. Zool.*, 69: 1957–1962.
- Barbraud, C., Barbraud, J.–C. & Barbraud, M., 1999. Population dynamics of the White stork *Ciconia ciconia* in Western France. *Ibis*, 141: 469–479.
- Bairlein, F., 1991. Population studies of White storks (*Ciconia ciconia*) in Europe. In: *Bird Population Studies. Relevance to Conservation and Management*: 207–229 (G. J. M. Hirons, Eds.). Oxford Univ. Press, Oxford.
- Bauchau, V., Horn, H. & Overdijk, O., 1998. Survival of Spoonbills on Wadden Sea islands. *J. Avian Biol.*, 29: 177–182.
- Berthold, P., van den Bossche, W., Fiedler, W., Kaatz, C., Kaatz, M., Leshem, Y., Nowak, E. & Querner, U., 2001. Detection of a new important staging and wintering area of the White stork *Ciconia ciconia* by satellite tracking. *Ibis*, 143: 450–455.
- Brittingham, M. & Temple, S. A., 1988. Impacts of supplemental feeding on survival rates of black–capped chickadees. *Ecology*, 69: 581–589.
- Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. & Pollock, K. H., 1987. *Design and Analysis Methods for Fish Survival Experiments Based on Release–Recapture*. American Fisheries Society Monographs n°5, Bethesda, Maryland.
- Burnham, K. P., White, G. C. & Anderson, D. R., 1995. Model selection strategy in the analysis of capture–recapture data. *Biometrics*, 51: 888–898.

- Cam, E. & Monnat, J.-Y., 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *J. Anim. Ecol.*, 69: 380–394.
- Carrascal, L. M., Alonso, J. C. & Alonso, J. A., 1990. Aggregation size and foraging behaviour of White storks *Ciconia ciconia* during the breeding season. *Ardea*, 78: 399–404.
- Caswell, H., 2001. *Matrix Population Models*. Sinauer Associates, Sunderland.
- Cézilly, F., Viallefont, A., Boy, V. & Johnson, A. R., 1996. Annual variation in survival and breeding probability in greater flamingo. *Ecology*, 77: 1143–1150.
- Choquet, R., Reboulet, A.-M., Pradel, R., Gimenez, O. & Lebreton, J.-D., 2003. U-Care user's guide, Version 2.0 Mimeographed document, CEFE/CNRS Montpellier. <ftp://ftp.cefe.cnrs-mop.fr/Soft-CR>.
- Clobert, J., 1995. Capture–recapture and evolutionary ecology: a difficult wedding? *J. Applied Stat.*, 22: 989–1008.
- Clobert, J., Lebreton, J.-D., Allaine, D. & Gaillard, J. M., 1994. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrates populations: II. Longitudinal models. *Biometrics*, 50: 375–387.
- Dallinga, H. & Schoenmakers, M., 1984. Populatieveranderingen bij de ooievaar *Ciconia ciconia* in de periode 1850–1975 (Population changes of the White stork *Ciconia ciconia* during the period 1850–1975). Rijksuniversiteit Groningen, Groningen, The Netherlands.
- Fiedler, W., 1998. Joint VogelWarte Radolfzell–Euring migration project: a large-scale ringing recovery analysis of the migration of European bird species. *EURING Newsletter*, 2: 31–35.
- Forero, M. G., Tella, J. L. & Oro, D., 2001. Annual survival rates of adult Red-necked nightjars *Caprimulgus ruficollis*. *Ibis*, 143: 273–277.
- Frederiksen, M. & Bregnballe, T., 2000. Evidence for density-dependent survival in adult cormorants from a combined analysis of recoveries and resightings. *J. Anim. Ecol.*, 69: 737–752.
- Hafner, H., Kayser, Y., Boy, V., Fasola, M., Julliard, A.-C., Pradel, R. & Cézilly, F., 1998. Local survival, natal dispersal, and recruitment in Little egrets *Egretta garzetta*. *J. Avian Biol.*, 29: 216–227.
- Harris, M. P., Freeman, S. N., Wanless, S., Morgan, B. J. T. & Wernham, C. V., 1997. Factors influencing the survival of Puffins *Fratercula arctica* at a North Sea colony over a 20-year period. *J. Avian Biol.*, 28: 287–295.
- Horak, P. & Lebreton, J.-D., 1998. Survival of adult Great tits *Parus major* in relation to sex and habitat; a comparison of urban and rural populations. *Ibis*, 140: 205–209.
- Hörnfeldt, B., Hipkiss, T., Fridolfsson, A.-K., Eklund, U. & Ellegren, H., 2000. Sex ratio and fledging success of supplementary-fed Tengmalm's owl broods. *Mol. Ecol.*, 9: 187–192.
- Johst, K., Brandl, R. & Pfeifer, R., 2001. Foraging in a patchy and dynamic landscape: human land use and the White stork. *Ecol. Appl.*, 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. & Lebreton, J.-D., 1992. Variation des effectifs de cigogne blanche et facteurs du milieu: un modèle démographique. In: *Les Cigognes d'Europe: 259–264* (J.-L. Mériaux, A. Schierer, C. Tombal & J.-C. Tombal, Eds.) Colloque International, Metz 1991, Inst. Européen d'Ecologie.
- 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.
- Lebreton, J.-D., 1978. Un modèle probabiliste de la dynamique des populations de Cigogne blanche *Ciconia ciconia* L. en Europe occidentale. In: *Biométrie et Ecologie: 277–343* (R. Tomassone, Eds.) Société Française de Biométrie, Paris.
- Lebreton, J.-D., Burnham, K., Clobert, J. & Anderson, D. R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.*, 62: 67–118.
- Lebreton, J.-D. & Clobert, J., 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling. In: *Bird Population Studies: Relevance to Conservation and Management: 105–125* (G. J. M. Hirons, Eds.) Oxford University Press, Oxford.
- Lindström, J., 1999. Early development and fitness in birds and mammals. *TREE*, 14: 343–348.
- Martin, T. E., Clobert, J. & Anderson, D. R., 1995. Return rates in studies of life history evolution: are biases large? *J. Applied Stat.*, 22: 863–875.
- Moritz, M., Maumary, L., Schmid, D., Steiner, I., 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.
- Nichols, J. D., Hines, J. E., Pollock, K. H., Hinz, R. L. & Link, W. A., 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. *Ecology*, 75: 2052–2065.
- Nichols, J. D. & Kendall, W. L., 1995. The use of multi-state capture–recapture models to address questions in evolutionary ecology. *J. Applied Stat.*, 22: 835–846.
- Pradel, R., 1993. Flexibility in survival analysis from recapture data: handling trap-dependence. In: *Marked Individuals in the Study of Bird Populations: 29–37* (P. M. North, Eds.) Birkhäuser Verlag, Basel/Switzerland.
- 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics*, 52: 703–709.
- Pradel, R., Johnson, A. R., Viallefont, A., Nager, R. G. & Cézilly, F., 1997. Local recruitment in the

- Greater flamingo: a new approach using capture–mark–recapture data. *Ecology*, 78: 1431–1445.
- Prévot–Julliard, A.–C., Lebreton, J.–D. & Pradel, R., 1998. Re–evaluation of adult survival of Black–headed gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *Auk*, 115: 85–95.
- Pugesek, B. H., Nations, C., Diem, K. L. & Pradel, R., 1995. Mark–resighting analysis of a California gull population. *J. Applied Stat.*, 22: 625–639.
- Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I. & Monaghan, P., 2003. Environmental variability, life–history covariation and cohort effects in the red–billed chough *Pyrrhocorax pyrrhocorax*. *J. Anim. Ecol.*, 72: 36–46.
- Sarrazin, F., Bagnolini, C., Pinna, J.–L., Danchin, E. & Clobert, J., 1994. High survival estimates of Griffon vultures (*Gyps fulvus fulvus*) in a reintroduced population. *Auk*, 111: 853–862.
- Sarrazin, F. & Barbault, R., 1996. Reintroduction: challenges and lessons for basic ecology. *TREE*, 11: 474–478.
- Sasvari, L. & Hegyi, Z., 2001. Condition–dependent parental effort and reproductive performance in the White stork *Ciconia ciconia*. *Ardea*, 89: 281–291.
- Schaub, M. & Pradel, R., 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. *Ecology*, 85: 930–938.
- Schaub, M., Pradel, R. & Lebreton, J.–D., 2004. Is the reintroduced White stork (*Ciconia ciconia*) population in Switzerland self–sustainable? *Biol. Cons.*, 119: 105–114.
- 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. *Biol. Cons.*, 61: 51–57.
- Stearns, S. C., 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Tavecchia, G., Pradel, R., Boy, V., Johnson, A. R. & Cézilly, F., 2001. Sex– and age–related variation in survival and cost of first reproduction in greater flamingos. *Ecology*, 82: 165–174.
- Thomson, D. L. & Cotton, P. A., 2000. Understanding the decline of the British population of Song thrushes *Turdus philomelos*. In: *Ecology and Conservation of Lowland Farmland Birds*: 151–155 (J. A. Vickery, Eds.). British Ornithologists Union, Tring.
- Tortosa, F. S., Caballero, J. M. & Reyes–Lopez, J., 2002. Effect of rubbish dumps on breeding success in the White stork in Southern Spain. *Waterbirds*, 25: 39–43.
- Tortosa, F. S., Manéz, M. & Barcell, M., 1995. Wintering White storks (*Ciconia ciconia*) in South West Spain in the years 1991 and 1992. *Die Vogelwarte*, 38: 41–45.
- Tortosa, F. S., Perez, L. & Hillstrom, L., 2003. Effect of food abundance on laying date and clutch size in the White stork *Ciconia ciconia*. *Bird Study*, 50: 112–115.
- Tryjanowski, P. & Kuzniak, S., 2002. Population size and productivity of the White stork *Ciconia ciconia* in relation to Common vole *Microtus arvalis* density. *Ardea*, 90: 213–217.
- White, G. C. & Burnham, K. P., 1999. Program MARK: estimation from population of marked animals. *Bird Study*, 46, supplement: 120–138.
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Appendix. (Cont.)

Second group (birds released after a resighting at age 2)

X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
21	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
	21	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
		21	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
			21	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
				21	3	4	5	6	7	8	9	10	11	12	13	14	15	16	

....

Fourth group (birds released after a resighting at age 4)

X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
			23	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
				23	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
					23	5	6	7	8	9	10	11	12	13	14	15	16	17	18

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Parameters 21 and 23 here are set different from parameters 2 and 4 respectively to account for trap-dependence, and X is set to 0.

In the analysis including class of distance as a state variable, a set of PIMs is defined for each state.