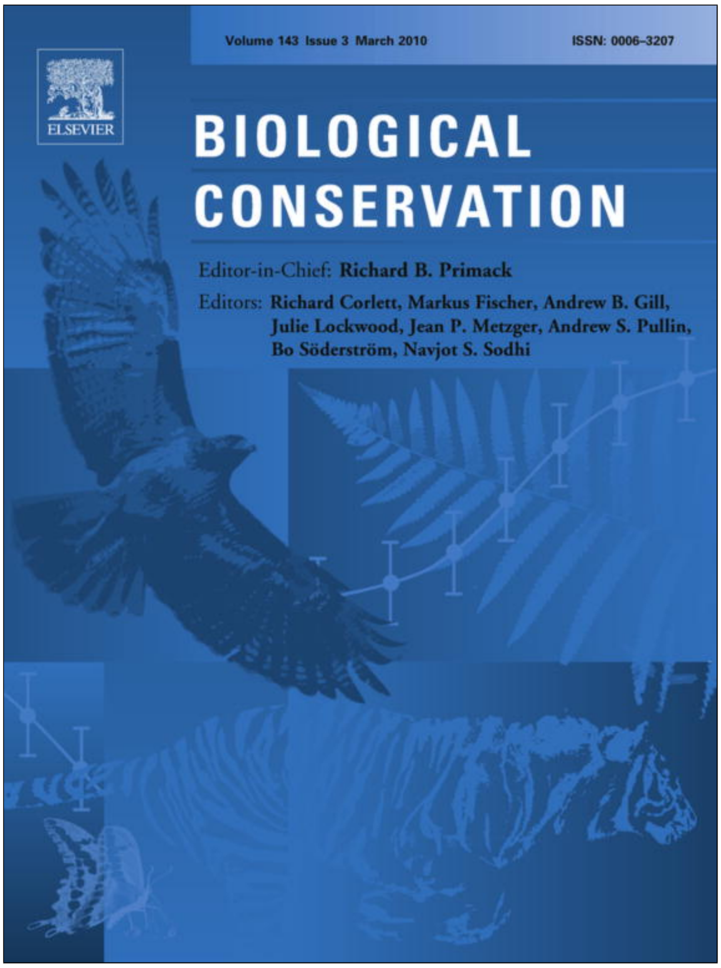
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The return of the white-tailed eagle (*Haliaeetus albicilla*) to northern Germany: Modelling the past to predict the future

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ABSTRACT

Linking age-specific vital rates to population growth through demographic matrix models can enhance our understanding of crucial population processes, vital in a conservation context. The white-tailed eagle (*Haliaeetus albicilla*) population in the Federal State of Schleswig-Holstein, Germany, has been monitored since re-colonisation in 1947 and provides a well-documented example of a recovery. We test how demographic models capture growth trajectories of a recovering population and how applicable they are in guiding population management of endangered species. From 1947 to 1974, the population was stable but the growth rate predicted by an age-structured matrix model was −6.1% per annum. The small but stable population must have been maintained by immigration. From 1975 to 2008, observed and predicted population growths were very similar (6.7% and 4% per annum respectively). Elasticity and life-stage simulation analyses identified adult and pre-breeding survival as key vital rate elements. While the prospective analyses identified survival as the key vital rate influencing population growth, the increasing reproduction rate allowed the recovery to take place; thus caution is needed when prospective modelling makes management recommendations. Nevertheless, conservation efforts should address key mortality factors such as lead poisoning and collision with wind turbines. A logistic model predicted a maximum carrying capacity of 255 pairs for the Federal State, but using the highest currently observed density (1.4 pairs per 100 km^2) and differences in habitat suitability, a more likely carrying capacity was estimated at 122 pairs. Under both scenarios, current population growth should slow soon.

1. Introduction

One of the most fundamental and oldest objectives of ecology is to understand the factors and mechanisms causing fluctuations in the population density of animals (Elton, 1927; Andrewartha and Birch, 1954; Lack, 1954; Royama, 1992; Coulson et al., 2004). The search for underlying mechanisms has recently acquired a special importance, as many populations have suffered dramatic population declines (Hunter, 2002), due to direct exploitation or persecution (Beissinger and Snyder, 1992; Casey and Myers, 1998; Ferrer et al., 2003), habitat degradation (Green and Sussman, 1990; Freedman et al., 2003) or pollution (Graveland et al., 1994; Helander et al., 2002). While the picture looks bleak overall (IUCN, 2009), there have been encouraging recoveries of endangered species (Jones et al., 1995; Corsi et al., 1999; Lalas and Bradshaw, 2003; Wegner et al., 2005; Schwartz et al., 2006). These cases provide unique opportunities to understand why populations recover so that lessons can be learned for guiding recovery actions in other species (Norris and McCulloch, 2003; Kauffman et al., 2004).

Demographic models have been used extensively to understand how changes in vital rates translate into population growth or decline (Green et al., 1996; Beissinger and Westphal, 1998; Norris and McCulloch, 2003; Whitfield et al., 2004; Katzner et al., 2006). They are powerful tools because although population dynamics can be analysed statistically using biotic and abiotic correlates (Grenfell et al., 1998; Krüger and Lindström, 2001a; Krüger et al., 2002; Coulson et al., 2004), the population trajectory is ultimately shaped by changes in birth and death rates (Krüger and Lindström, 2001b) and these have to be understood to predict future population changes and to assess the effectiveness of management action (Heppell et al., 2000). Elasticity analyses have proved to be a popular tool, which identifies those vital rate elements to which population growth responds most strongly (Benton and Grant, 1999; Caswell, 2000). While it is clear that elasticity analysis is not a panacea (Caswell, 2000; Mills et al., 2001), it nevertheless provides one vital methodological link between individuals, the life history of the species and population growth (Heppell et al., 2000). This link will be crucial if we are to gain a deeper understanding of the ultimate explanations for population growth or decline. As a recent

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further development, life-stage simulation analysis (LSA) allows for uncertainty and variability in vital rates to be incorporated and can be used to estimate the contribution of vital rates to population growth in a probabilistic framework (Wisdom et al., 2000).

The white-tailed eagle (*Haliaeetus albicilla*) is a large species (males weigh between 3100 and 5400 g, females between 3700 and 6900 g) breeding across the entire Palaearctic as well as Greenland. It is an opportunistic carnivorous species, feeding on fish, waterfowl and mammals as well as carrion. Typical of all large eagles (Thiollay, 1994; Katzner et al., 2006; Krüger and Radford, 2008), it matures late with an age at first breeding of commonly four or 5 years and a maximum lifespan of at least 36 years in the wild and 42 years in captivity (Thiollay, 1994; Struwe-Juhl, 2003). White-tailed eagle and bald eagle (*Haliaeetus leucocephalus*) populations started to decrease in the latter half of the 19th century, and most populations suffered dramatic declines in the first half of the 20th century (Thiollay, 1994; Green et al., 1996; Watts et al., 2006; Evans et al., 2009). Causes of these population crashes include direct persecution and pollution with heavy metals and especially organochlorine pesticides such as DDT which led to eggshell thinning and subsequent breeding failures (Ratcliffe, 1967; Helander et al., 2002). Since the 1980s, many populations have recovered dramatically, with population growth rates commonly exceeding 10% per annum (white-tailed sea eagle: Hauff, 1998; Kollmann et al., 2002; Evans et al., 2009; bald eagle: Dunwiddie and Kuntz, 2001; Watson et al., 2002; Jenkins and Sherrod, 2005; Saalfeld et al., 2009). As both species are charismatic flagships – they are national birds of Germany, Poland and the USA – many populations have been intensively studied over the last decades (e.g. Grier, 1982; Helander, 1985; Jacobson and Hodges, 1999; Millsap et al., 2004; Watts et al., 2006) and have been used as environmental sentinels (Helander et al., 2008).

The white-tailed eagle population monitoring programme in the Federal State of Schleswig-Holstein, Germany, is unique, however. Complete data exist since the re-colonisation started in 1947, providing an exceptional time series covering 62 years (Struwe-Juhl, 2003). Crucially, in addition to population data, individual-based data exist that permit a link between age-specific vital rates and the population level. This allows us to attribute population changes to a specific vital rate. Here, we exploit this unique opportunity and combine these data with demographic analyses using matrix models to address the following questions:

(1) Why did the population remain at a low level for 30 years after re-colonisation?
(2) What changes in vital rates have permitted exponential population growth of nearly 7% per annum since the late 1980s?
(3) To which vital rate elements is population growth most elastic, and can elasticity analysis and LSA be used to make management recommendations?
(4) Is the population viable under both environmental and demographic stochasticity?
(5) What is the likely carrying capacity of this population and when will it be reached?

2. Methods

2.1. Study area

The white-tailed sea eagle population has been studied in the Federal state of Schleswig-Holstein since the species re-colonised West Germany in 1947. The species mainly breeds around freshwater lakes in the eastern part of the state. This centre of distribution covers around 6600 km^2 or 42% of the entire area of the state and is a young moraine landscape with hills up to 168 m in height and more than 300 eutrophic lakes, fishponds and coastal brackish lagoons. Pairs used to breed only in medium sized and large (50–600 ha), undisturbed woodlands, but now some pairs are nesting in tiny forest patches and even in tree rows. During the 1990s, new breeding sites have been established close to the river Elbe and the Wadden Sea in the western part of the Federal State. For a detailed description of the study area, see Struwe-Juhl (2003).

2.2. Population monitoring

The population in Schleswig-Holstein is a particularly well-studied part of the total population of around 470 pairs in Germany in 2004 (Hauff and Mizera, 2006). Each year, known and potential nest sites are visited at least three times to collect data on territory occupancy, brood size (number of chicks per successful breeding attempt), reproduction rate (number of chicks per breeding attempt), biometrics of ringed chicks and, if apparent, causes of nest failure. Since 1977, two thirds of fledged chicks in the study area have been ringed as part of an international ringing scheme (Helander, 1985). In order to obtain age-specific vital rates, individual birds were identified and aged by their colour rings or their moulted feathers which allow reliable identification of individuals over many years (Struwe-Juhl and Schmidt, 2002; Struwe-Juhl and Grünkorn, 2007). The moult feathers allowed birds to be aged prior to becoming adults (age >4) and the variation in pigmentation pattern of tail feathers as well as the length of tail feathers and primaries can be used to identify individual adults (Struwe-Juhl and Schmidt, 2002). More precisely, the amount of dark pigmentation in the otherwise white tail feathers of white-tailed sea eagles is highly variable between individuals while intra-individual variation is small. Struwe-Juhl and Schmidt (2002) provide a series of measurements and photographs that document the reliability of this method of individual recognition. Moulted feathers were available almost continuously since 1955 for a number of nest sites and these 26 birds could therefore be aged and identified reliably. Individual identification of raptors by their moult feathers has been used in other species (Newton and Marquiss, 1982; Nielsen and Drachmann, 2003) and has been used to estimate vital rates (Krüger, 2005, 2007). However, its overall validity and usefulness has recently been questioned (Ellis, 2009).

2.3. Modelling the population

To estimate survival, the age at death of 54 ringed birds was used as well as 26 dead birds individually identified by their moult feathers, so precise lifespan was known for 80 birds from the years 1953 to 2008. We acknowledge that there is a potential bias in our estimates because finding a carcass of a dead bird might not be random with regard to age. Given the maximum age of 36 years recorded in the population (Struwe-Juhl, 2003), we were not able to model age-specific survival using mark-recapture models (Lebreton et al., 1992) due to small sample size, so we calculated age-specific survival probability directly from the distribution of age at death as $s_t = N_{t+1}/N_t$, where s denotes survival probability, N is the number of alive birds and t is the focus age class. We define age class as age +1, so fledglings were defined as the age class 1. For those age classes for which no dead birds have so far been recorded, survival rate was calculated as the mean of neighbouring age classes. To estimate survival probability for the period 1947–1974, we used information on the age class at death (first year, immature, adult) of 25 birds recovered during the period 1953–1974 from Looft and Neumann (1981). As these data only allowed us to calculate survival until adulthood for the period 1947–1974, we used the survival values for the period 1975–2008 for all subsequent adult age classes (age class >4).

For the 1947–1974 period when there were only 149 breeding attempts in total, very few (<10 cases) age-specific reproduction data were available. This was due to the unknown age of most breeders as well as the low population size (between two and nine breeding pairs). There was no linear or non-linear relationship between age of the female and reproductive output, so we used the mean reproduction rate of 0.4 chicks per breeding attempt reported in Struwe-Juhl (2003) across all ages for this period. For the period 1975–2008, age-specific reproduction rate data were available from 211 breeding attempts of 21 individual females, representing 39.7% of all breeding attempts. The values of the polynomial GLMM model with female ID as a random factor (Wald $Z = 2.142$, $p = 0.032$) were used.

$$\text{reproduction} = 1.2444 + 0.0374 \times \text{age} - 0.0011 \times \text{age}^2 \tag{1}$$

For both matrix models, reproduction rate data were multiplied by 0.5 as the model considers only females; these matrix elements are defined as fertility. We also estimated breeding probabilities as not all territorial females breed each year. The fully age-structured matrices are provided as Appendix A. Ignoring males in matrix models is common practice for monogamous species with a lifelong pair-bond (Caswell, 2001), but we acknowledge that our models do not take into account that in large eagles, males typically differ in dispersal behaviour from males (Thiollay, 1994).

We calculated the asymptotic population growth rate (λ) from a fully age-structured Leslie matrix projection model for the two periods 1947–1974 and 1975–2008. The survival rate estimates used only differed up to age class five between the two periods but age-specific fertilities differed over all age classes. Confidence limits to the asymptotic growth rate were calculated using the series approximation method described in Caswell (2001). These matrix models also provided the stable age distribution which is commonly denoted by **w**, the reproductive values, an estimate of the expected number of offspring for an average individual in a given age class (Stearns, 1992), denoted by **v**, and elasticities, which allow comparison of the relative effect on λ of different matrix components. We compared reproductive value curves to see whether differences in the number of expected offspring for a given age class between the two periods were visible across all age classes. We have used standard annotations (Caswell, 2001) and a postfledging birth-pulse approach, so there was a separate fledgling age class (age class 0), hence first year survival was a separate matrix entry and not incorporated into fertility entries (Caswell, 2001).

Alongside deterministic elasticity analysis, we used life-stage simulation analysis (Wisdom et al., 2000). A set of matrix elements was randomly selected and used to construct a fully age-structured matrix. This process was repeated 1000 times, resulting in 1000 matrix replicates with randomly varying combinations of vital rates. Population growth rate λ and elasticities were calculated for each matrix and analysed to estimate effects of each vital rate on λ and elasticities. Age-specific fertility was drawn from a log-normal distribution and age-specific survival rate from a β-probability distribution (Wisdom et al., 2000). Modelled means and variances equalled the observed data when data were pooled across all age classes and were truncated at the minimum and maximum observed in the population (0–1.5 for reproductive output and 0.25 and 0.947 for survival).

In order to introduce environmental stochasticity to estimate extinction risk, we generated an independent and identically distributed (*iid*) sequence of environments, because it is considered to be the simplest and most widely applicable model of environmental stochasticity (Caswell, 2001). At each time step, an environmental condition was drawn independently of previous conditions from a normal distribution with mean one and standard deviation of one, indicating no directional change in the environment. The environmental condition was simply a set of multiplicators which were then used randomly to affect both survival and fertility with the amount of variation generated in these vital rates being the same as observed in the population over the last 62 years (factor four between minimum and maximum for fertility, measured as annual mean reproduction rate, and factor two for survival, measured as the variation between age-specific survival estimates).

In order to estimate a potential future upper bound for this population, we used the standard continuous version of the logistic model (Roughgarden, 1998):

$$N_t = \frac{K}{1 + ((K - N_0)/N_0)e^{-rt}} \tag{2}$$

where N_t is the population size at time t, N_0 is the initial population size (one in our case), r is the growth rate of the population and K is the carrying capacity. We used the mean growth rate observed in the population between 1975 and 2008 and estimated K using least square minimization which finds that logistic growth curve which minimizes the sum of the squared distances between real population data points and the function, identical to ordinary least square non-linear regression techniques. We tested the goodness of fit of our model to the real population data using standard sum of square ratios, so $SS_{\text{Mod}}/SS_{\text{Err}} = F_{v1,v2}$ (Zar, 1999).

As a complementary and entirely independent approach, we simply assumed that the highest currently observed population density in the Federal State is close to carrying capacity. Incorporating habitat heterogeneity (ca. 58% of the State is not as suitable for white-tailed eagles due to a lack of lakes as foraging habitat) and using the highest currently observed population density in these suboptimal areas yields another estimate of a potential carrying capacity for the State. Finally, we also estimated carrying capacity by assuming that the highest currently observed population density might be close to carrying capacity and that there is no habitat heterogeneity with regard to habitat suitability. Matrix programming was done in Matlab and statistical tests in SPSS with a two-tailed significance threshold of 0.05.

3. Results

3.1. Population and reproduction dynamics

Re-colonisation of West Germany by white-tailed sea eagles started in 1947 when the first breeding pair was recorded after around 50 years of absence (Fig. 1a). After an initial increase to a maximum of eight breeding and nine territorial pairs in the late 1950s, the population remained fairly constant at this very low level until the 1980s. Since then, the population has rapidly increased to a maximum of 53 breeding and 57 territorial pairs in 2008 with an average doubling time between 1985 and 2000 of only 5.8 years.

The time series of reproduction rate and brood size showed large differences until about 1975 (Fig. 1b): during the first 30 years a very high fraction of the small number of breeding pairs failed to raise chicks. Since 1975, both brood size and reproduction rate have stabilised at a higher level. The insecticide DDT was used in Germany since the 1940s and banned in 1973, potentially explaining this very low reproduction rate of the period 1947–1974. Over the 62 years, the number of pairs and the reproduction rate were highly significantly positively correlated ($r = 0.417$, $df = 60$, $p < 0.001$). The low reproduction rate of the early years can be attributed very clearly to failed breeding attempts: while around 70% of breeding pairs failed in the beginning, this percentage decreased significantly to around 20% in the last decade (Fig. 1c, weighted regression on arcsine square

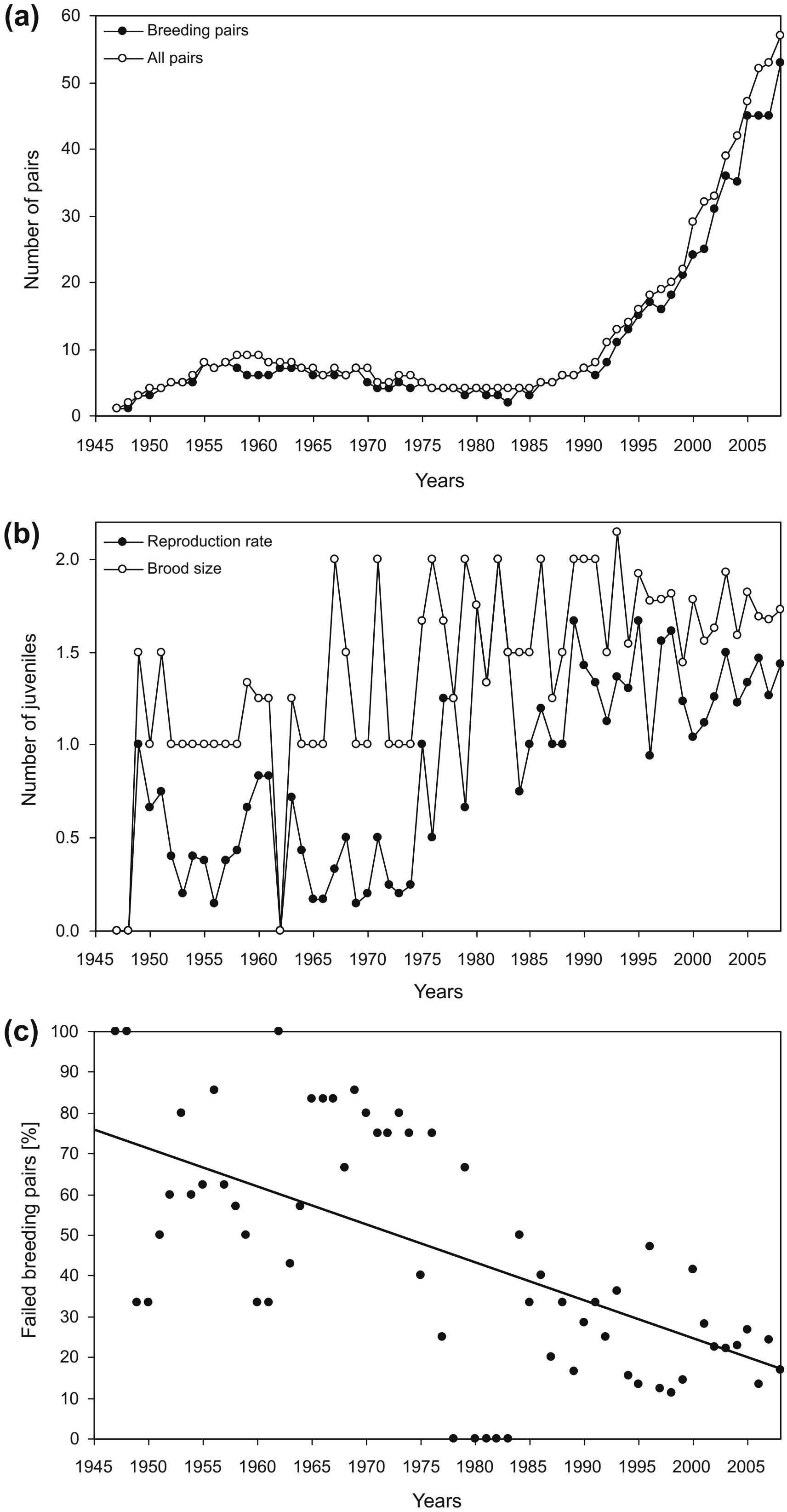

Fig. 1. Time series of the white-tailed sea eagle population (a) and reproduction rate (number of fledged chicks per breeding pair) and brood size (b) in Schleswig-Holstein from 1947 to 2006. Relationship between time and the percentage of failed breeding pairs (c). The relationship was fitted using weighted regression because sample sizes varied substantially between years.

root transformed data: $F_{1,60} = 49.3$, $p < 0.001$). This high level of breeding failure from 1947 to 1974 also explains why there was no relationship between age of the female and reproductive output for this period.

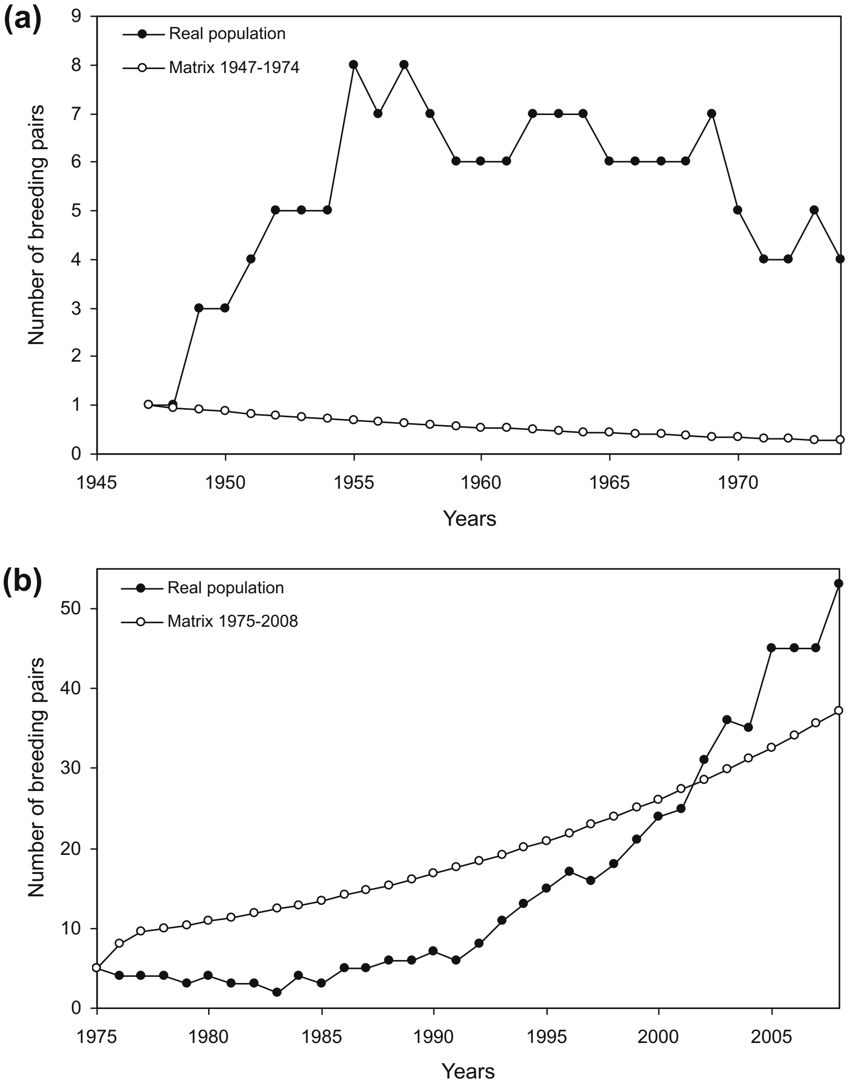

Fig. 2. Comparison of observed population dynamics and growth predicted by a deterministic matrix model for the period 1947–74 (a) and for the period 1975–2008 (b).

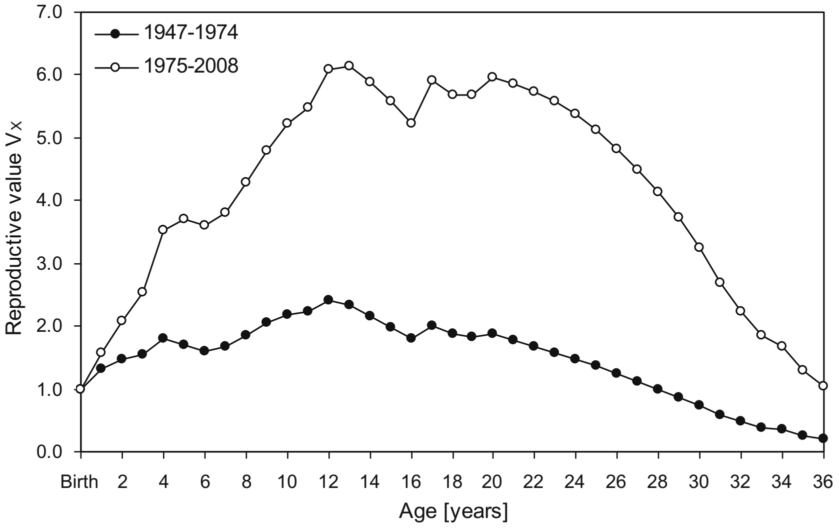

Fig. 3. Reproductive values (number of female offspring an average female eagle of a given age class is expected to have over the rest of her life) for the period 1947–1974 and 1975–2008 as calculated by the deterministic matrix models.

3.2. Modelling the past

The asymptotic growth rate λ of the matrix model for the period 1947–1974 was 0.941 which translates into an annual growth rate of −6.1%. The 95% confidence interval of λ ranged from 0.8933 to 0.988 and does not encompass the observed growth rate of the population ($\lambda = 1.017$, $r = 1.7\%$ per annum with a s.e. of ±2.9%). The projected growth rate was significantly different from one ($Z = 2.446$, $p < 0.02$) and differences between projected and real population growth rates were highly significant ($Z = 3.145$, $p < 0.002$). The matrix does not capture the trend observed in the real population (Fig. 2a): according to the matrix, re-colonisation should have been short-lived, a stable population over 30 years being very unlikely under this model.

The asymptotic growth rate λ of the matrix model for the period 1975–2008 was 1.040 which translates into an annual growth rate of 4%. The 95% confidence interval of λ ranged from 0.976 to 1.103 and encompasses the observed growth rate of the population over this period ($\lambda = 1.069$, $r = 6.7\%$ per annum with a s.e. of ±1.9%). The projected growth rate was not different from one ($Z = 1.219$, p = ns) and was not significantly different from the observed growth rate ($Z = 0.849$, p = ns). In contrast to the model for the period 1947–1974, the projected growth rate captures the real population trend over the last 30 years well (Fig. 2b).

The differences between the two models are large with regard to projected growth rates (−6.1% per annum compared to +4% per annum) and the two growth rates are significantly different ($Z = 3.488$, $p < 0.001$). The relationship of reproductive value with age highlights the difference in reproduction at all ages that underlies the different projections (Fig. 3). While reproductive value peaks at around 2.4 female offspring at age twelve for the 1947–1974 period, peak reproductive value is just over six female offspring at age thirteen for the 1975–2008 period. Reproductive values from a matrix model provide the expected contribution of each age to long-term population growth (Caswell, 2001). Differences in the height of the two reproductive value curves highlight the large differences in overall fertility between the two periods, where an average female aged 12 is expected to have only two female offspring in the rest of her life for the 1947–1974 period, but ca. six female offspring for the 1975–2008 period. These differences are due to an average reproduction rate of only 0.4 juveniles per breeding attempt for the period 1947–1974 but 1.4 juveniles per breeding attempt for the period 1975–2008.

A comparison of the overall age structure in the two periods (Table 1) further emphasises the magnitude of differences brought about by the lower fertility during 1947–1974. The stable age distribution shows very large differences. Because of the low fertility, only 12.9% of females were modelled to be chicks for the 1947–1974 matrix, about half the proportion in the period 1975–2008 (23%). In general, the age distribution of the 1947–1974 matrix is shifted towards older ages compared to 1975–2008: from age class 13 onwards the corresponding proportions were at least twice as high for the 1947–1974 matrix. While 2.8% of females should be at least 30 years of age in the 1947–1974 period, the corresponding figure is 0.1% in the 1975–2008 period. These results emphasise that the 1947–1974 population was deprived of fledglings and immature birds and hence had an excess of older birds. Despite these large differences in stable age structure between the two periods, population growth is similarly elastic to changes in fertility and survival for both periods. As commonly observed in very long-lived, iteroparous species, population growth was much more elastic to changes in survival than to changes in fertility (Table 1). All fertilities contributed only 6.9% to population growth for the 1947–1974 period and this rose to only 10.2% for the 1975–2008 period. The single vital rate element to which population growth was most elastic to was pre-breeding survival. Those four age classes had a combined elasticity of 28.8% for the 1947–1974 period and 41.2% for the 1975–2008 period. Overall, however, adult survival was most important, contributing 64.3% to population growth for the 1947–1974 period and 48.6% for the 1975–2008 period.

Table 1
Asymptotic growth rate λ and r, damping ratio $\rho(\lambda/\lambda_2)$, convergence time ($1/\log(p)$) and generation time T ($\log(R_0)/\log(\lambda)$), the stable age distribution **w** and elasticities for the two matrices. Damping ratio and convergence time indicate how quickly a matrix model converges to the stable age distribution and exhibits a constant growth rate, while the generation time T describes how many years a population needs to grow by a factor of R_0 (Caswell, 2001).

	Matrix 1947–1974			Matrix 1975–2008		
	Growth rate λ: 0.9408 ($r = -0.0610$) Damping ratio: 1.132 Convergence time: 18.571 years Generation time: 11.964 years			Growth rate λ: 1.040 ($r = 0.0392$) Damping ratio: 1.234 Convergence time: 10.951 years Generation time: 13.667 years		
Age class	Stable age distribution	Elasticity fertility	Elasticity survival	Stable age distribution	Elasticity fertility	Elasticity survival
1	0.129	0.000	0.072	0.230	0.000	0.103
2	0.093	0.000	0.072	0.163	0.000	0.103
3	0.080	0.000	0.072	0.125	0.000	0.103
4	0.074	0.000	0.072	0.103	0.000	0.103
5	0.061	0.007	0.065	0.075	0.014	0.089
6	0.058	0.007	0.058	0.064	0.017	0.072
7	0.055	0.006	0.052	0.054	0.014	0.058
8	0.047	0.005	0.047	0.041	0.012	0.045
9	0.038	0.004	0.042	0.028	0.009	0.037
10	0.031	0.004	0.039	0.021	0.006	0.030
11	0.027	0.003	0.036	0.016	0.005	0.026
12	0.024	0.003	0.033	0.013	0.004	0.022
13	0.021	0.002	0.030	0.010	0.003	0.019
14	0.020	0.002	0.028	0.009	0.003	0.016
15	0.020	0.002	0.026	0.008	0.002	0.014
16	0.020	0.002	0.023	0.007	0.002	0.011
17	0.019	0.002	0.021	0.006	0.002	0.009
18	0.017	0.002	0.019	0.005	0.001	0.008
19	0.016	0.002	0.017	0.004	0.001	0.006
20	0.015	0.002	0.016	0.004	0.001	0.005
21	0.013	0.002	0.014	0.003	0.001	0.004
22	0.013	0.001	0.013	0.002	0.001	0.004
23	0.012	0.001	0.011	0.002	0.001	0.003
24	0.012	0.001	0.010	0.002	0.001	0.002
25	0.011	0.001	0.009	0.002	0.000	0.002
26	0.011	0.001	0.007	0.001	0.000	0.002
27	0.010	0.001	0.006	0.001	0.000	0.001
28	0.009	0.001	0.005	0.001	0.000	0.001
29	0.009	0.001	0.004	0.001	0.000	0.001
30	0.008	0.001	0.003	0.001	0.000	0.000
31	0.008	0.001	0.002	0.001	0.000	0.000
32	0.007	0.001	0.002	0.001	0.000	0.000
33	0.006	0.001	0.001	0.000	0.000	0.000
34	0.004	0.000	0.001	0.000	0.000	0.000
35	0.002	0.000	0.000	0.000	0.000	0.000
36	0.001	0.000	0.000	0.000	0.000	0.000
37	0.000	0.000	0.000	0.000	0.000	0.000

Results of the LSA analysis both confirmed and slightly changed those of the deterministic elasticity analysis. Pre-breeding survival had the highest elasticity per age class, but adult survival elasticities were most important when summed over all age classes (Fig. 4a). While the rank order of elasticities did not change for pre-breeding survival, it increasingly frequently did so from age class eight onwards. Variance in population growth was also explained mostly by pre-breeding survival (Fig. 4b). Together, these four matrix elements explained 55% of variation in population growth. Reproductive output matrix elements only explained 13.5% of the variation in population growth, but this was over three percentage points higher than in the standard elasticity analysis, confirming that variability of a vital rate also influences its scope to affect population growth.

3.3. Predicting the future

Incorporating a level of environmental stochasticity comparable to the fluctuations in vital rates observed over the last 62 years and across the 37 age classes into the matrix model for the period 1975–2008 produced a population trajectory that exhibited slow growth. The average stochastic population growth rate was 1.5% per annum, so environmental stochasticity reduced the growth rate by 2.4% points. Despite this environmental stochasticity, there would be a 0% modelled extinction risk over the next 100 years (due to the annual non-stochastic growth rate of 3.9% per annum). The modelled extinction risk under demographic stochasticity would also be essentially zero.

A final question remains to be addressed and that is the most likely carrying capacity or stable population size for the white-tailed sea eagle in Schleswig-Holstein. As a first approach, the logistic model with the lowest least square provided a highly significant fit to the observed population data since 1947 ($F_{3,58} = 172.7$, $p < 0.001$, Fig. 5). The curve predicts a carrying capacity of 255 pairs and lower growth rates during the increase phase than currently observed.

If we use the highest population density currently observed in optimal areas of the species in Schleswig-Holstein (1.4 pairs per 100 km^2) and incorporate habitat heterogeneity (ca. 58% of the state is not as suitable for white-tailed eagles) and currently observed maximum densities for these less suitable areas (0.3 pairs per 100 km^2) we estimate a lower bound carrying capacity of 122 breeding pairs. However, in some parts of their range, white-tailed eagles do not breed near water, so using the 1.4 pairs per 100 km^2 throughout the Federal State yields a carrying capacity of 224 pairs.

4. Discussion

Linking long-term population trajectories directly to their demographic mechanisms, changes in age-specific birth and death rates, provides a deep insight into the processes influencing population growth (Heppell et al., 2000; Krüger and Lindström, 2001b;

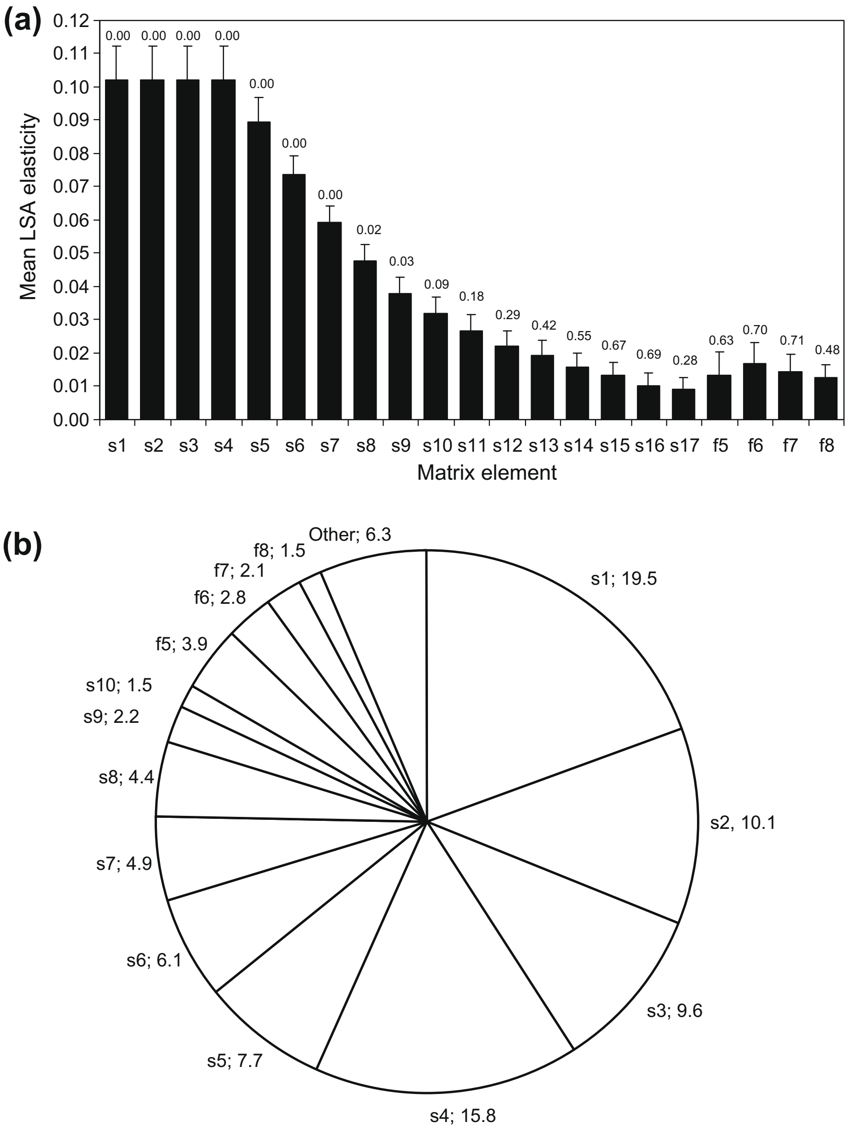

Fig. 4. Elasticities of vital rate matrix elements using life-stage simulation analysis (a). Survival rates are denoted by (*s*) and fertility by (*f*) with numbers referring to the age classes of Table 1. Mean elasticities and standard deviations for the 21 most important matrix elements are shown from the simulation with means and standard deviations being the same as in the observed data. Numbers above the bars indicate the proportion of times out of 1000 randomly generated matrix replicates that a particular matrix element had an elasticity whose rank order differed from that of the mean matrix of Table 1. Variance in population growth rate explained by stochastically varying matrix elements (b).

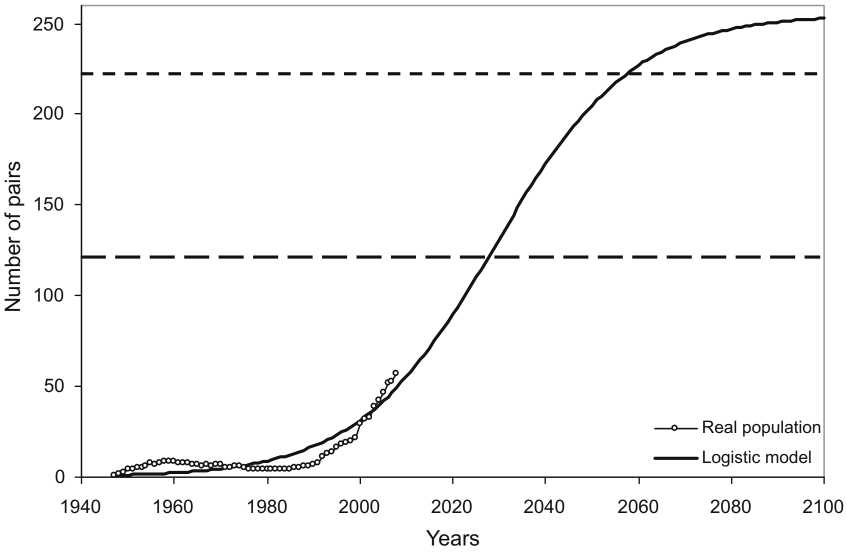

Fig. 5. Carrying capacity model using the observed growth rate and an initial population size of one pair. The bold dashed line shows an estimate of maximum population size based on current observed maximum densities in the two major habitat types of the Federal State, the thin dashed line shows an estimate of maximum population size without habitat heterogeneity.

Nicoll et al., 2003; Carrete et al., 2006; Krüger, 2007). Here, we used this paradigm and matrix models to address questions about the past and future of a flagship species of great conservation concern in Europe.

4.1. Why did the population remain at a low level for 30 years after re-colonisation?

After successful re-colonisation, the population remained stable. The matrix projection for this period predicts a rapidly declining population. Two alternative explanations can be used to reconcile model and reality. First, parameters explicitly in the model could be wrong and second, the model captures the intrinsic population growth rate but the population was kept stable by net immigration (assumed to be zero in the model) from other areas. Given that all breeding attempts were closely monitored, it is unlikely that the low estimate for fertility is inaccurate. While our survival estimates for this early period are based on few data (juvenile and immature survival) or on the 1975–2008 data (adult survival), we consider it extremely unlikely that the large difference between model and reality is due to this parameter uncertainty. Juvenile and immature survival were estimated to be higher for the 1947–1974 period (48% of chicks reach age class 5) then for the 1975–2008 period (38% of chicks reach age class 5). All adult survival probabilities would have to be, on average, 11% higher than our 1975–2008 estimates for the 1947–1974 population matrix to have a stable trajectory, with many survival probabilities very close to 1.0. Given that such high adult survival (0.98 on average) is unlikely and has not been reported from other studies (Helander, 2003; Evans et al., 2009), we believe that the population must have been kept alive by immigration from other areas such as East Germany and Poland. These two areas have indeed repeatedly supplied Schleswig-Holstein with white-tailed eagles that have subsequently bred, evidenced by sightings of colour-ringed birds (Köppen, 2006; Struwe-Juhl and Grünkorn, 2007). Schleswig-Holstein was formerly at the western limit of the population and sink characteristics, balanced by immigration from the east, were likely. While we cannot exclude the possibility of density-dependent processes resulting in very high survival rates at the initial low population density, we believe this to be unlikely as even today there are no signs of density-dependent processes affecting survival or reproduction. Today, population expansion has reached neighbouring countries Denmark and, most recently, the Netherlands with our studied sub-population no longer at the edge of distribution.

4.2. What changes in vital rates have permitted exponential population growth of nearly 7% per annum since the late 1980s?

Since the late 1970s, significantly higher reproduction rates have been observed and since 1985, the population has increased rapidly due to these higher reproduction rates across all age classes. Similar increases have been observed in other populations of this species and the closely related bald eagle (Jacobson and Hodges, 1999; Watson et al., 2002; Jenkins and Sherrod, 2005; Watts et al., 2006; Evans et al., 2009). As DDT was banned in the USA from 1973 as well, the similarities point out towards the large effect the ban had on population trajectories in both species.

The increase in our population is captured reasonably well by our matrix model for this period, making it highly likely that the observed increase in reproduction was sufficient to turn this population from a sink into a source population. Indeed there is clear evidence from sightings of colour-ringed birds that the re-colonisation of Denmark in 1995 and the Netherlands in 2006 was facilitated by emigrating individuals from Schleswig-Holstein (Kollmann et al., 2002; Roder and Bijlsma, 2006; Struwe-Juhl and Grünkorn, 2007). Given the differences between the matrix models for the two periods, the interpretation of differences in model population trajectories is straightforward. The low reproduction rate for the period 1947–1974, due to pesticides (Struwe-Juhl, 2003; Scharenberg and Struwe-Juhl, 2006), was further reduced stochastically by human disturbance at nest sites (Kollmann et al., 2002). This meant that even females in their prime years did not necessarily achieve a high reproductive success. This made population recovery impossible and necessitated immigration to keep the population alive. Thanks to the ban of DDT in West Germany in 1972 (Kollmann et al., 2002), and intensive nest-guarding and related management measures, reproduction rates have substantially increased since the late 1970s. With a time lag due to the high age at first reproduction of the species, the population started to increase. Our matrix model strongly suggests that this regional increase in reproduction is a sufficient explanation for the remarkable comeback observed over the last 30 years and highlights the fact that reproduction, despite having low elasticities (see below), heavily influenced the population trajectory (see also Gaillard et al., 2000). However, as we cannot completely exclude the possibility of changes in survival rate between the two study periods, survival could have contributed to the population increase, too.

4.3. To which vital rate elements is population growth most elastic to and can elasticity analysis and LSA be used to make management recommendations?

An important lesson from our study is that one has to be very careful in using elasticity analyses to guide management decisions in long-lived species. Had we completed our elasticity and LSA analyses 60 years ago, we would have recommended efforts to increase survival rates, yet the crucial change in vital rates that allowed this population to recover was the increase in reproduction rate (see also Katzner et al., 2007 for a similar conclusion). Long-lived species almost invariably show high elasticities for survival (Sæther and Bakke, 2000; Evans et al., 2009) and that can be misleading. Nevertheless, some caution is needed at this point again as we cannot strictly rule out changes in survival rate between the periods 1947–1974 and 1975–2008 due to data limitations.

Nevertheless, given that the 1975–2008 matrix model captures the population trend so well, attention should be paid to both the deterministic elasticity analysis as well as the life-stage simulation analysis. While elasticity analyses are far from being a holy grail in population management (Hiraldo et al., 1996; Mills et al., 2001; Norris and McCulloch, 2003), we believe that tentative conclusions can be drawn, especially as the LSA analysis confirmed many points made by the deterministic elasticity analysis. First, population growth is much more elastic to a change in survival than a change in fertility, despite the fact that a substantial increase in fertility brought about the population increase. This is not surprising for such a long-lived, iteroparous organism (Heppell et al., 2000; Cuthbert et al., 2004; Katzner et al., 2006; Evans et al., 2009). Second, population growth was also very elastic to changes in pre-breeding survival. This is in agreement with other empirical studies (Arcese et al., 1992; Gaillard et al., 2000; Reid et al., 2004), whereas others emphasised that pre-breeding survival is not such an important factor influencing the growth rate of long-lived organisms (Pfister, 1998; Sæther and Bakke, 2000; Katzner et al., 2006). However, adult survival was still the most important component once elasticities are summed across all age classes. Standard elasticities must sometimes be interpreted with some caution due to covariation between vital rates or density-dependent constraints (van Tienderen, 1995; Grant and Benton, 2000; Reid et al., 2004). The structure of covariation between vital rate elements is unknown for this population. However, as the LSA analysis confirmed the importance of pre-breeding survival under a vast range of parameter settings, we feel that pre-breeding survival deserves closer attention in a conservation context.

Translating the results of an elasticity analysis into conservation recommendations merits caution, because a vital rate element with a high elasticity might show limited variation or because there is limited scope to boost this vital rate element through conservation action (Hiraldo et al., 1996; Norris and McCulloch, 2003). In our case, however, there are simple but profound management implications. It is known that immature white-tailed eagles are especially reliant on scavenging during the winter (Cramp and Simmons, 1980) and it is also known that the species and other raptors are very much affected by lead poisoning through lead bullets left in carcasses (Scheuhammer and Norris, 1996; Kenntner et al., 2001; Fisher et al., 2006), so efforts should be made to address the lead poisoning problem (Watson et al., 2009). In addition, white-tailed eagles and other large raptors suffer mortality from collision with wind turbines in wind farms (Fielding et al., 2006) and this is a more frequent cause of death in Schleswig-Holstein than lead poisoning (Struwe-Juhl, unpublished data). There is considerable room for improvement of these vital rate elements, as currently only 38% of fledged chicks are estimated to survive to breeding age (we estimated mean annual survival rate to be 0.78 for juveniles before reaching maturity at the age of 4 years; thereafter mean annual survival was 0.87 for adults for the period 1975–2008). This percentage is in good agreement with the 34% of fledged chicks recruiting in a re-introduced Scottish population (Evans et al., 2009). The estimate of 0.87 for adult survival is at the lower end of other estimates for this species and the bald eagle (Helander, 2003; Evans et al., 2009) and might indicate both a bias due to the small sample and/or lower survival due to lead poisoning and accidents. Further research should also address the habitat use and large movements of immature sea eagles (Millsap et al., 2004) to identify additional mortality risks.

4.4. Is the population viable under both environmental and demographic stochasticity?

The stochastic growth rate is a more realistic estimate of long-term population growth than the asymptotic growth rate because it takes temporal variation in vital rates into account (Tuljapurkar, 1990). For our white-tailed eagle population, stochasticity reduced the growth rate from 3.9% to 1.5% per annum and modelled extinction risk over the next 100 years was zero under both environmental and demographic stochasticity, so it seems that the population is reasonably buffered against environmental stochasticity in the long-term future. The difference between asymptotic and stochastic growth rate is more marked than those reported for red deer *Cervus elaphus* (Benton et al., 1995) or choughs *Pyrrhocorax pyrrhocorax* (Reid et al., 2004) which share high adult survival rates with the white-tailed sea eagle. Part of the explanation is that the 62 years of reproduction rates encompass most likely higher than natural variation due to those early years with a very low reproduction rate and this higher level of variation translates into lower stochastic population growth.

4.5. What is the likely carrying capacity of this population and when will it be reached?

With the population growing, the question arises when the carrying capacity is likely to be reached. At the moment, there are the first signs of density-dependent effects: the frequency of territorial intrusion and territorial fighting has significantly increased in recent years (Struwe-Juhl and Grünkorn, 2007), but so far there are no signs of density dependence in vital rates. Such density-dependent effects on vital rates have recently been nicely documented in the recovery of a bearded vulture (*Gypaetus barbatus*) population in Spain (Carrete et al., 2006). In contrast, even higher annual growth rates have been reported for other white-tailed eagle populations (Helander et al., 2003; Evans et al., 2009). Ferrer et al. (2003) have used the percentage of immature breeders as an early warning signal for a population decline in the Spanish imperial eagle (*Aquila adalberti*), but the young age at first breeding observed in our population is a sign that the population is nowhere near carrying capacity with plenty of vacant territories (see also Evans et al., 2009). We have tried to estimate where the maximum final carrying capacity is most likely to be with two different models.

Our logistic model predicts a carrying capacity of 255 pairs for the state of Schleswig-Holstein. This estimate should be viewed as a maximum carrying capacity because it does not incorporate any degree of habitat heterogeneity. Our other approaches, with our without differences in habitat suitability, produced lower bound carrying capacities of 122 and 224 pairs. While all these approaches should be regarded as speculative, they predict that the observed population growth should slow down over the next decade.

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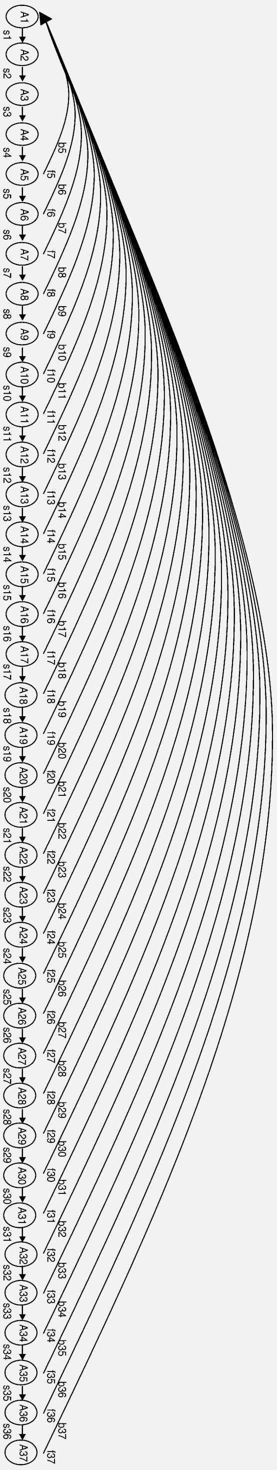
Appendix A

Schematic diagram of the fully age-structured matrix for the white-tailed sea eagle population of Schleswig-Holstein with matrix entries used. Survival entries were estimated from the age of death of 80 birds and fertility entries were either means (1947–1974) or the estimated age-specific values of a polynomial general linear mixed model.

Age Class	Survival rate (*s*)		Fertility (*f*)		Breeding probability (*b*)	
	47–74	75–08	47–74	75–08	47–74	75–08
1	0.720	0.741				
2	0.889	0.800				
3	0.875	0.857				
4	0.857	0.750				
5	0.889	0.889	0.2	0.685	0.620	0.620
6	0.875	0.875	0.2	0.698	0.880	0.880
7	0.786	0.786	0.2	0.710	0.880	0.880
8	0.727	0.727	0.2	0.720	0.970	0.970
9	0.750	0.750	0.2	0.730	0.970	0.970
10	0.792	0.792	0.2	0.738	0.970	0.970
11	0.833	0.833	0.2	0.746	0.970	0.970
12	0.808	0.808	0.2	0.752	0.970	0.970
13	0.905	0.905	0.2	0.757	0.970	0.970
14	0.947	0.947	0.2	0.761	0.970	0.970
15	0.946	0.946	0.2	0.764	0.970	0.970
16	0.944	0.944	0.2	0.766	0.970	0.970
17	0.767	0.767	0.2	0.767	0.970	0.970
18	0.923	0.923	0.2	0.767	0.970	0.970
19	0.878	0.878	0.2	0.765	0.970	0.970
20	0.833	0.833	0.2	0.763	0.970	0.970
21	0.900	0.900	0.2	0.759	0.970	0.970
22	0.895	0.895	0.2	0.755	0.970	0.970
23	0.895	0.895	0.2	0.749	0.970	0.970
24	0.895	0.895	0.2	0.742	0.970	0.970
25	0.895	0.895	0.2	0.734	0.970	0.970
26	0.895	0.895	0.2	0.725	0.970	0.970
27	0.889	0.889	0.2	0.715	0.970	0.970
28	0.882	0.882	0.2	0.703	0.970	0.970
29	0.875	0.875	0.2	0.691	0.970	0.970
30	0.866	0.866	0.2	0.677	0.970	0.970
31	0.857	0.857	0.2	0.663	0.970	0.970
32	0.762	0.762	0.2	0.647	0.970	0.970
33	0.667	0.667	0.2	0.630	0.970	0.970
34	0.500	0.500	0.2	0.612	0.970	0.970
35	0.500	0.500	0.2	0.593	0.970	0.970
36	0.250	0.250	0.2	0.573	0.970	0.970
37	0.000	0.000	0.2	0.552	0.970	0.970



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