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The demography of a newly established Osprey *Pandion haliaetus* population in France

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Using long-term mark–resighting data acquired over 27 years in continental France, we estimated demographic parameters and modelled the dynamics of a newly established population of Ospreys *Pandion haliaetus* using a life-history model. We then performed prospective and retrospective analyses to estimate the sensitivity of the population growth rate to demographic parameters, and to quantify their contribution to the observed variation in abundance. The observed population growth rate was estimated at 1.150 (from one to 38 pairs in the period 1985–2011), and the stochastic population growth rate was estimated at 1.156. The number of fledglings per nest made the largest contribution to the variance of the observed population growth rate. Breeding productivity was stable across years. In contrast, the prospective analysis indicated that the sensitivity of the population growth rate was greatest for immigration and adult survival. Our results suggest that the increase of a new and recently established breeding population of Ospreys was mainly driven by local dynamics (high productivity and high proportion of breeding individuals), with no sign of density-dependence except for juvenile survival. This probably reflects highly favourable conditions for breeding. Our results show that productivity can be a major driver in recovering raptor populations, and conservation work should aim to protect occupied nest-sites and their surrounding habitat and to maintain highly favourable foraging areas in the vicinity of breeding sites.

Keywords: demography, density-dependence, recruitment, stochastic population growth rate, vital rates.

Identifying and understanding how vital rates influence changes in population size is a central theme in ecology, and long-term studies of population dynamics are of major interest for life-history theory, population ecology, species management and conservation (Caughley 1977, Lande 1988, Tuljapurkar & Caswell 1997). In birds, population studies estimating demographic parameters and modelling population dynamics are critical steps towards understanding the processes that shape populations, and in properly guiding effective conservation and management strategies (Perrins *et al*. 1991). However, the analysis of demographic processes is no simple task and involves considerable challenges in observation and analysis for most bird species. In addition, many demographic studies have addressed declining populations (Caughley 1994), and the processes that allow a population of conservation concern to recover and to increase its breeding range and size are still little studied.

In many parts of North America and Europe, numbers of Ospreys *Pandion haliaetus* were greatly reduced by human persecution and pollution during the 19th and early 20th century (Henny 1977, Poole 1989, Schmidt 1995). Some populations, particularly in North America, suffered severe declines (up to 94%) from the 1950s to the 1970s due to the adverse effects of contaminants on productivity (Henny *et al.* 2010). During the 19th century, the Osprey bred in several regions of France, mainly in the northeast and in the south (Schweyer & Remy 1986) including Corsica (Patrimonio & Tariel 1994), but the species became

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extinct in continental France in 1968 (Müller 1989) following a prolonged period of human persecution (Thiollay & Wahl 1998).

In many regions of its range, breeding populations of Ospreys showed increases of varying magnitudes during the later half of the 20th century (Schmidt *et al.* 2001, BirdLife International 2004, Henny *et al.* 2008). Several factors appear to have contributed to these increases, including the ban on some persistent organochlorine pesticides such as DDT (Weber *et al.* 2003, Henny *et al.* 2010), re-introduction programmes (Martel 1995, Dennis & Dixon 2001), the ban on hunting in some countries (Thiollay & Wahl 1998), and the use of artificial reservoirs and artificial supports by Ospreys for feeding and nesting, respectively (Henny *et al.* 2010). In the western Palaearctic, the breeding population has largely increased since the 1970s and is currently estimated at 7600–9500 breeding pairs (Schmidt 1998, Gensbol 2005). However, the demographic causes of this increase remain poorly understood, and the demography and population dynamics of natural populations of Ospreys, and more generally of large raptors, have been relatively little studied. Although several studies have monitored breeding numbers and performances of Ospreys (e.g. Saurola 1980, Dennis 1983, Harmata *et al.* 2007, Henny *et al.* 2010), few have estimated key demographic parameters such as annual survival or recruitment using modern mark–resighting approaches (see Henny 1977, Spitzer *et al.* 1983 for standard approaches). Yet quantifying and monitoring these parameters is necessary for understanding the demographic causes of variation in population sizes, for modelling population dynamics and for conservation planning (Hernández-Matías *et al.* 2013).

Our aim was to understand the demographic processes that allowed the recovery of a small Osprey population in France studied for 27 consecutive breeding seasons. Following the first successful breeding attempt of a single pair in continental France in 1985, the population has grown steadily and has been monitored each year (Thiollay & Wahl 1998). An ongoing ringing scheme initiated in 1995 enabled us to estimate some demographic parameters through mark–resighting methods for this population (Wahl & Barbraud 2005). Using monitoring and resighting analyses, we: (1) determined age at first breeding, breeding productivity, recruitment, immigration, and juvenile and adult survival; (2) modelled the dynamics of the population using a life-history model; (3) analysed the model from a prospective and retrospective point of view by performing a sensitivity analysis (Caswell 2001); and (4) assessed evidence of density-dependence on demographic parameters.

METHODS

Study species

In our study area, all Osprey nest-sites were situated at the top of old (> 90 years) Scots Pine *Pinus sylvestris* trees from 22 to 30 m high, situated in mixed forests with oaks *Quercus* spp. Breeding individuals defend their nest-site (at a distance of 20–50 m, Jamieson & Seymour 1983), but not feeding territories (Poole 1989). In continental France, breeding individuals migrate mainly to West Africa to spend the winter months (Wahl 2006a,b), although some first-year birds stay in the Iberian Peninsula on their first migration (Bai & Schmidt 2012). Males and females arrive at their breeding grounds in February–March (Thiollay & Wahl 1998). Eggs (two to four) are laid during the first 2 weeks of April and fledglings leave the nest in July. Adults and juveniles start their southward migration from July to mid-August. In the study area, Ospreys mainly prey on Cyprinidae (*Chondrostoma nasus*, *Rutilus rutilus*, *Cyprinus carpio* and *Abramis brama*), the size of the prey varying between 10 and 35 cm (Thiollay & Wahl 1998, R. Libois, R. Rosoux & R. Wahl unpubl. data).

Study area

The study was carried out in the forests of Orléans (*c.* 45 000 ha; 47°43′–48°04′N, 1°52′–2°41′E) and Chambord (*c.* 5000 ha; 47°35′N, 1°32′E), central France. These forests are situated a few kilometres respectively north and south of the Loire River, and host *c.* 300 ponds up to 30 ha in area (see Thiollay & Wahl 1998 for a detailed description of the study area). Since 1985, Ospreys have nested every year in this area (Thiollay & Wahl 1998). The Orléans and Chambord forests hosted the entire breeding population of Ospreys in continental France until 2005 and more than 80% since then (Nadal & Tariel 2008).

Since the first Osprey breeding attempt in the study area, all nest-sites have been protected each year as part of a National Action Plan (Nadal & Tariel 2008). This included restricted access to the nest-sites, careful management of the forest plots with nests and a delayed waterfowl hunting season. The National Action Plan also recommended the use of artificial nests to maximize the chances of breeding successfully. From 1999 to 2004, a total of 16 artificial nests were placed in the study area within a few hundred metres of natural nests. In December 1999, strong storms swept over France and wrecked 90% of the nest trees holding natural nests as well as platform nests. All the damaged nests were replaced, including the 16 artificial nests mentioned above. No artificial nest was built after 2008 in the state forests.

Field methods

Since the first breeding attempt in 1985, the whole study area was surveyed annually by a large network of observers, which monitored the number of nest-sites occupied by breeding birds (Thiollay & Wahl 1998). Suitable nesting habitat (large forested areas with large trees) was identified on maps according to the landscape structure and searched. Searches for nests were conducted from February to July, with intense search efforts in March, April and May, when individuals spend much time displaying or are frequently observed when flying and carrying fish to potential nesting areas. Each nest-site was monitored during the breeding season and the number of chicks was recorded just before fledging at age *c.* 6 weeks (July). Observations were made from a car at 100–150 m and at *c.* 300 m away in open places.

In 1995, a mark–resighting programme was initiated (Wahl & Barbraud 2005). Chicks were ringed with a CRBPO stainless steel ring and a PVC or Darvic ring with unique alphanumeric code. The coded leg rings could be read with a telescope (60×) from a distance of up to 250 m. Since 1995, 465 chicks have been ringed. Only two individuals were observed without their PVC or Darvic ring, and for those two the stainless steel ring could be read. Consequently, we considered that tag loss was very rare and we did not take it into account in our mark–resighting analyses. Nine adults were also captured and ringed, but were not included in the analyses. Nests were checked every 1–2 days from the earliest arrivals in late February until mid-July to record arrival dates for individual birds, to identify their coded colour rings and to record laying and hatching dates in order to ring chicks at *c.* 40–45 days old. Some birds were also resighted and photographed on the migration routes and on the wintering grounds by other observers. Birds were sexed by observation of copulation, the relative size of the birds when individuals from breeding pairs were observed together, measurements of the chicks when ringed (females are on average 20% heavier and 10% larger than males; Cramp & Simmons 1980) and plumage characteristics (females have a darker plumage on the breast than males; Cramp & Simmons 1980).

Estimation of breeding parameters

We used a general linear mixed model (GLMM) with a Poisson distribution and a log link to test the effects of age and sex (explanatory variables) on the number of chicks each individual fledged (response variable). Overall, there were 91 known-age birds in the dataset, and the age of breeding adults varied from 1 to 19 years. Individual and year were fitted as random effects to control for pseudoreplication caused by repeated sampling of individuals across years, and for variation in conditions between years. We tested for linear or quadratic trends in the number of chicks fledged by an individual according to its age, which was considered a continuous variable. Analyses were performed using PROC GLIMMIX in SAS (SAS Institute Inc 2002–2003). No model selection was performed from this initial model, and we used type III test statistics (*F*- and *P*-values) for fixed effects estimated using the Satterthwaite approximation to assess the effects of explanatory variables.

To estimate age at first breeding, we applied an approach based on estimating both resighting and seniority probabilities (Pradel 1996, Hernández-Matías *et al.* 2010). The method relies on two parameters, the resighting probability (p) and the seniority probability (γ), defined as the probability that a bird that is observed as a breeder in a given year has been a breeder previously (Pradel 1996). The probability that an individual is breeding for the first time (β) is calculated as $1-\gamma$. This approach is based on reversed resighting histories, which were then examined by means of a classical survival analysis. To estimate seniority probabilities, we used date of ringing and resighting data of known-sex individuals ringed as chicks (1995–2011) for all individually marked birds according to whether a bird was seen as a breeder or not in a given year. Data were prepared following Pradel *et al.* (1997). Initially, we considered a model with time (t) and sex (s) dependence in both seniority and resighting probabilities, i.e. model ($\gamma_{s.t.}$ $p_{s.t}$). Goodness-of-fit of the initial model was performed using U-CARE 2.5 (Choquet *et al.* 2009). We then generated several models with different numbers of age-classes (1–6), with the youngest age-class corresponding to 2-year-old birds. Categorical, linear, logarithmic and the quadratic effects of age on seniority on a logit scale were considered.

Estimation of survival

Ringing and resighting data of individuals ringed as chicks were coded for all individually marked birds according to whether a bird was seen or not in a given year. The mark–resighting analysis was based on a dataset involving 455 marked birds of known age, 222 females and 233 males, over the 1995–2011 period. Estimates were obtained from these data using program MARK (White & Burnham 1999). We considered an initial model with time (*t*) and age (*a*) dependence separately for each sex (*s*) in both apparent survival probability Φ and resighting probability *p*, i.e. model $\Phi_{s.a.t}$ $p_{s.a.t}$ (Lebreton *et al.* 1992). Because the sample size was limited, this model could not be fitted and we reduced the number of age-classes to five (model $\Phi_{s.a5.t}$ $p_{s.a5.t}$). To test for variation in survival and resighting probabilities, we fitted models in order of decreasing complexity starting with model $\Phi_{s.a5.t}$ $p_{s.a5.t}$. We first modelled the resighting probabilities and then the survival probabilities. Because the structure of our starting model included an age effect and thus differed from the standard Cormack–Jolly–Seber (CJS) model, we used a bootstrap procedure for goodness-of-fit testing implemented in the program MARK with 1000 bootstrapped samples.

All models for estimation of survival and recruitment were fitted using the program MARK and model selection was based on the Akaike's information criterion (AICc) (Burnham & Anderson 2002). When two models had similar support (ΔAICc < 2), we used Akaike weights to give quantitative information on the likelihood of each model, given the data. Variance and confidence intervals for time-varying parameters were estimated using the delta method from the values estimated for each year (Seber 1982).

Density-dependence

Because density-dependence was shown to affect demographic parameters in a recovering Osprey population (Bretagnolle *et al.* 2008), we tested for its effects on population size, productivity and survival. We used the Gompertz population model to analyse the strength of density-dependence on population size (Royama 1992). The model is defined as: $N_{t+1} = N_t e^{(a - b \ln N_t)}$, where N_t is the number of breeding pairs in year *t*, *a* is an intercept and *b* is a measure of the strength of density-dependence. When $b = 0$, the process is density-independent, and on a log scale is a Gaussian random walk with drift given by *a*. The Gompertz model becomes linear on a log scale, denoting $x_t = \ln(N_t)$ and $r = \ln(\lambda)$: $x_{t+1} = r + (1 - b)x_t$. To measure the strength of density-dependence on demographic traits (number of fledglings per nest and survival), we used models in which each trait was modelled as a linear function of N_t. For the number of fledged chicks per nest, the number of pairs was entered as an additional explanatory variable in the GLMM model described above. For survival, we used a linear logistic relationship of survival with N_t: $logit(\Phi) = c + d\ N_t$, where *c* is an intercept and *d* is a measure of the strength of density-dependence. We fitted this equation in a mark–resighting model where N_t was entered as a covariate of survival. To assess the impact of N_t on survival, we used an ANODEV test (Grosbois *et al.* 2008).

Population modelling

To study the dynamics of the population, we built female-only, age-classified prebreeding census matrix population models (Caswell 2001). These models consisted of four age-classes. Model parameters were first-year (juvenile) survival, adult survival from age 2 and older, and the proportion of breeders from each age-class. The proportion of breeders was taken from the estimates of the seniority analysis (see above). As breeding starts at age 2, this parameter was fixed to 0 at age 1. Fecundity was modelled as the average number of chick fledged by an individual and was not age-dependent (see Results), assuming a sex ratio of 1 : 1. Field observations revealed the presence of immigrants in the study population based on ring resightings (see Results); therefore, we took into account the immigration rate in our matrix models. The number of immigrants was estimated as the number of individuals present that had been ringed in other populations, and we calculated the average proportion of immigrants from 1995 to 2011 as the number of immigrants observed in a given year divided by the number of breeders of the same year. As immigration rate was estimated using ringed individuals only, it was probably underestimated. We thus performed simulations by increasing the immigration rate by 10%, 20% and 30% to test whether the modelled population growth rate was a better fit with the observed one.

We first built a deterministic matrix model with no stochasticity, which included the mean values of the demographic rates. From this matrix analysis, we estimated the deterministic growth rate (λ), the stable age distribution and the sensitivities of λ to variations in demographic rates θ ($\partial\lambda/\partial\theta$) (Caswell 2001). We then estimated the contribution of temporal variations of each demographic parameter θ to the variability of λ using the first-order Taylor expansion: $V(\lambda) = s(\theta)^2\text{var}(\theta)$, where s($\theta$) is the sensitivity of λ to parameter θ, and we assumed that vital rates varied independently (Caswell 2001). The sensitivity analyses correspond to prospective analyses, and the contribution of the observed variance in vital rates on the variance of the population growth rate corresponds to retrospective analyses.

We then focused on a stochastic matrix model to estimate the stochastic growth rate λ_{stoch}. First, we estimated the process variance of the vital rates estimated from the mark–resighting and GLMM models following White (2000) and Morris and Doak (2002). The process variance was estimated from the mean over all replicates (i.e. years). Environmental stochasticity was then incorporated in the matrix model by sampling the yearly values of survival and reproductive rates, respectively, from a beta distribution and a lognormal distribution (Morris & Doak 2002), whose mean and process variance were set equal to those previously estimated. Demographic stochasticity in survival and reproductive rates were incorporated, respectively, by sampling the number of individuals in each age-class from a binomial distribution and by sampling the number of fledglings produced in a Poisson distribution (Akçakaya 1991).

To compare the deterministic and stochastic models' predictions with the observed population dynamics, we calculated the observed growth rate as $\lambda_{obs} = (N_t/N_0)^{(1/t)}$ (Caughley 1977). The stochastic matrix population model was analysed by Monte Carlo simulations (1000 iterations) using the package popbio (Stubben *et al.* 2007) implemented in program R (R Development Core Team 2011). Initial stage abundances corresponded to the stable age distribution based on the number of breeders actually observed in 1985. All values are reported ± 1 se unless otherwise stated.

RESULTS

Breeding population size

The number of breeding pairs observed in continental France has gradually increased since 1985, reaching a maximum of 38 breeding pairs in 2011 (Fig. 1). Based on these numbers, the observed population growth rate was equal to 1.150.

Breeding parameters

From the 465 individuals ringed as fledglings, 103 were re-sighted at least once in the study area, giving a return rate of 22.2%. The average observed ages at first breeding were 4.28 ± 2.04 (mode = 3 years, *n* = 48, range 2–11 years) for females and 4.64 ± 1.58 (mode = 4 years, *n* = 45, range 2–8 years) for males. Most individuals (85.9%) were observed breeding for the first time between 3 and 6 years of age (Fig. 2).

For the seniority analyses, the initial model was accepted (χ^2_{13} = 1.32, *P* = 0.999). All the best models considered that the resighting probability was constant over time (estimates ranging from 0.879 to 0.895 and 95% confidence interval (CI) limits ranging from 0.811 to 0.936), and the best and second-best models considered four age-classes (Table 1). The first and second models respec-

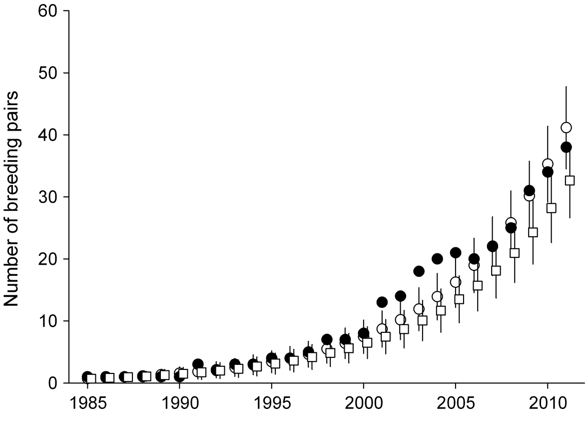

Figure 1. Number of breeding pairs of Osprey in continental France observed (black dots), modelled using a stochastic matrix population model with a 0.048 annual immigration rate (white squares) and with a 0.058 annual immigration rate (white dots). Error bars indicate ± se.

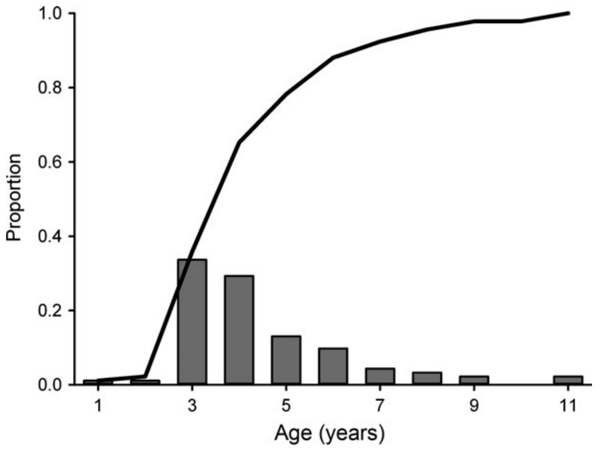

Figure 2. Observed age at first breeding of Ospreys in continental France: proportion (bars) and cumulative proportion (solid line) of age at first breeding.

tively suggested linear and logarithmic effects of the age effect on seniority probability, with an evidence ratio of 1.4 for the model with a linear effect. Both models yielded very similar parameter estimates. The probability of first reproduction (β) was estimated at 0.986 and 0.938 for 2-year-old individuals, 0.913 and 0.866 for 3-year-old individuals, 0.617 and 0.659 for 4-year-old individuals, respectively, and at 0.198 and 0.197 for 5-year-old or older individuals (Fig. 3). There was no evidence of a sex effect.

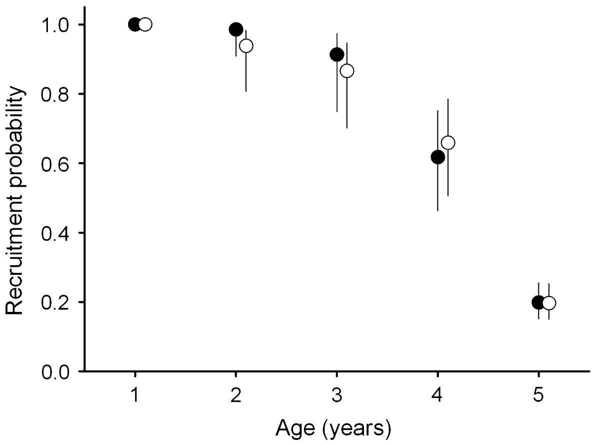

Figure 3. Probability of recruitment of Ospreys in continental France by age-class under a model with a linear age effect (filled circles) and a logarithmic age effect (empty circles), considering four age-classes. Error bars indicate 95% CI. Recruitment probability for 1-year-olds was fixed at one because this age-class was not considered in the models.

During the period 1985–2011, Ospreys produced an average of 1.89 ± 1.09 fledglings per nest per year (mode = 2, range 0–4, $n = 368$). Breeding productivity was relatively stable between years (Fig. 4a), and when tested as a fixed effect, year was not significant ($F_{14,261.4} = 1.27$, $P = 0.22$). The number of fledglings produced varied non-linearly according to age (Table 2), increasing from age 1 to about age 6 and

Table 1. Modelling resighting (p) and seniority (γ) probabilities for Ospreys (1995–2011) in continental France. For each model, we present the model description, the effect tested, deviance (Dev), number of estimable parameters (np), AICc and ΔAICc (see Methods), and Akaike weights (w_i). Model notation indicates age effect (a), time effect (t), sex effect (s), linear effect of age effect (lin), quadratic effect of age effect ($quad$), and logarithmic effect of age effect (ln). The number of age-classes considered is reported after the age effect.

Model	Effect	Dev	np	AICc	ΔAICc	w_i
$\gamma_{lin(a4)}p$	Linear effect of age	308.6	4	387.7	0	0.301
$\gamma_{\ln(a4)}p$	Logarithmic effect of age	309.3	4	388.4	0.7	0.212
$\gamma_{a4}p$	Four age-classes	308.6	5	389.7	2.0	0.111
$\gamma_{quad(a4)}p$	Quadratic effect of age	308.6	5	389.7	2.0	0.111
$\gamma_{quad(a5)}p$	Quadratic effect of age	309.4	5	390.5	2.8	0.074
$\gamma_{s.lin(a4)}p$	Sex effect and linear effect of age	305.6	7	390.9	3.2	0.061
$\gamma_{a5}p$	Five age-classes	308.3	6	391.5	3.8	0.045
$\gamma_{s.\ln(a4)}p$	Sex effect and logarithmic effect of age	306.6	7	391.9	4.2	0.037
$\gamma_{a6}p$	Six age-classes	306.8	7	392.1	4.4	0.033
$\gamma_{lin(a5)}p$	Linear effect of age	314.8	4	393.8	6.1	0.014
$\gamma_{\ln(a5)}p$	Logarithmic effect of age	319.6	4	398.5	10.8	0.001
$\gamma_{a3}p$	Three age-classes	322.7	4	401.7	14.0	0.001
$\gamma_{a2}p$	Two age-classes	348.9	3	425.8	38.1	0.001
γp	No time dependence	356.1	2	431.1	43.4	0.000
$\gamma_t p_t$	No sex dependence	319.2	31	460.7	73.0	0.000
$\gamma_{s.t}p_{s.t}$	–	295.2	62	529.4	141.7	0.000

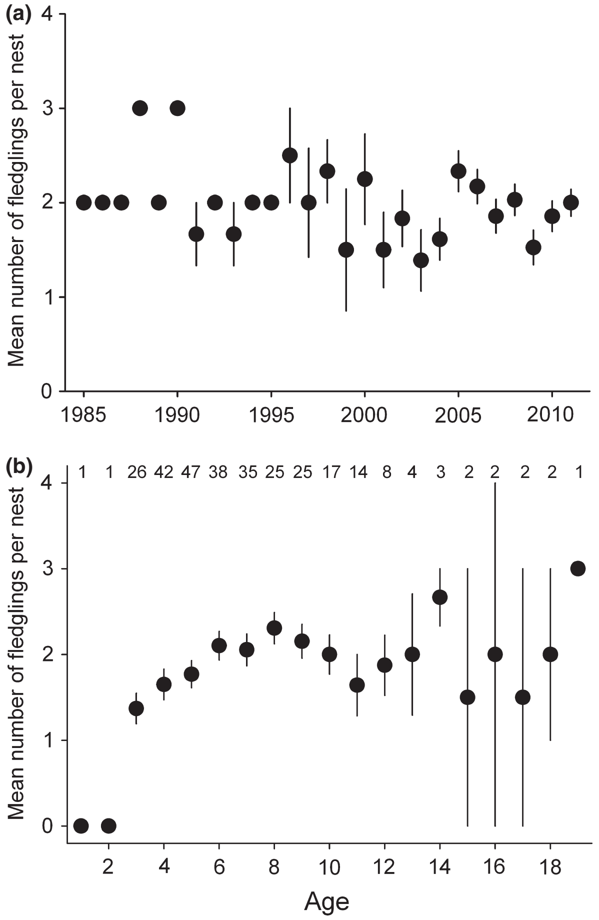

Figure 4. Mean number of fledglings per nest for breeding Ospreys (1985–2011) in continental France. Error bars indicate ± 1 se. (a) as a function of years. (b) as a function of age. Values indicate sample sizes.

Table 2. Results of the mixed model testing for the effects of age, sex and number of breeding pairs (*N*) on the number of fledglings per nest of Ospreys in central France between 1996 and 2011. Test statistics (*F* and *P* values) are type III, and df for fixed effects were estimated using the Satterthwaite approximation. Goodness-of-fit: χ^2/df = 0.56. Variance components plus their se are shown for random effects.

Effect	df$_n$	df$_d$	*F*	*P*	Estimate	se
Fixed effects						
Age	1	307	6.98	0.009	0.113	0.043
Age^2	1	304.2	4.62	0.032	−0.005	0.002
Sex	1	64.1	0.00	0.978	0.002	0.086
N	1	19.9	0.04	0.846	−0.001	0.005
Random effects						
Individual					0.0564	0.0254
Year					0.0053	0.0071
Residual variance					0.5562	0.0532

remaining stable at older ages (Fig. 4b). The effect of sex on the number of fledglings produced was not significant (Table 2). The random effect for individual identity and year respectively accounted for 9.1% (z = 2.22, P = 0.01) and 0.9% (z = 0.74, P = 0.23) of the total variance in breeding success (estimated as the respective ratios of the variance of the random effects for individual identity and year to the total residual variance).

Survival

The bootstrap GOF test indicated that our initial model fitted the data satisfactorily (P = 0.09). Modelling the resighting probability indicated that it was best modelled as age- but not time-dependent, and that resighting probability did not differ between sexes (Table 3). Resighting probability was best modelled as a function of five age-classes and increased with age from 0.115 ± 0.028 (95% CI = 0.070–0.183) at age 1 to 0.856 ± 0.025 (0.799–0.899) at age 5 and older. Survival was best modelled as a function of two age-classes. Survival during the first year was time-dependent and varied between years. Average survival for first-year birds was estimated at 0.495 ± 0.043 (95% CI = 0.149–0.713). Survival of individuals from age 2 was estimated at 0.875 ± 0.017 (0.837–0.905). The oldest bird in the breeding population was 19 years old.

Immigration and emigration

Between 1995 and 2011, 16 birds were recruited to the study population, all of which had been ringed as fledglings in Germany. The average immigration rate was 0.048 ± 0.022. Of the 465 fledglings ringed in the study area, none was found breeding in another country. However, 11 (seven females and four males) were found breeding in France outside the study area at a maximum distance of *c.* 170 km from their birthplace.

Density-dependence

There was no evidence of density-dependence on the number of breeding pairs (b = 0.025 ± 0.042; 95% CI = −0.063 to 0.112; z-test = 0.595, P (one-tailed) = 0.276), and on the number of fledged chicks per nest (Table 2). There was some evidence of an effect of density on juvenile survival (ANODEV: $F_{1,14}$ = 4.68, P = 0.048), which

Table 3. Modelling resighting (*p*) and survival (Φ) probabilities for Ospreys (1995–2011) in continental France. For each model, we give model description, the effect tested, deviance (Dev), number of estimable parameters (np), AICc and ΔAICc (see Methods), and Akaike weights (w_i). Model notation indicates age effect (*a*), time effect (*t*) and sex effect (*s*). The number of age-classes considered is reported after the age effect.

Model	Effect	Dev	np	AICc	ΔAICc	w_i
Modelling *p*						
$\Phi_{s.a5.t}\ p_{s.a5.t}$	–	353.5	266	1803.9	518.5	0.000
$\Phi_{s.a5.t}\ p_{s.a5}$	No time dependence	499.9	150	1495.5	210.1	0.000
$\Phi_{s.a5.t}\ p_{a5}$	No sex dependence	509.4	145	1489.3	203.9	0.000
$\Phi_{s.a5.t}\ p_{a4}$	Four age-classes	516.5	144	1493.4	208.0	0.000
Modelling Φ						
$\Phi_{s.a4.t}\ p_{a5}$	Four age-classes	533.8	121	1442.3	156.9	0.000
$\Phi_{s.a3.t}\ p_{a5}$	Three age-classes	541.7	95	1378.7	93.3	0.000
$\Phi_{s.a2.t}\ p_{a5}$	Two age-classes	555.6	67	1321.9	36.5	0.000
$\Phi_{s.t}\ p_{a5}$	One age class	652.0	37	1348.8	63.4	0.000
$\Phi_{a2.t}\ p_{a5}$	No sex dependence	595.3	36	1289.9	4.5	0.095
$\Phi_{a2}\ p_{a5}$	No time dependence	671.5	7	1304.5	19.1	0.000
$\Phi_{a1.t,a2}\ p_{a5}$	No time dependence for age 2	621.2	22	1285.4	0.0	0.904
$\Phi_{a1,a2.t}\ p_{a5}$	No time dependence for age 1	638.3	21	1300.4	15.0	0.000

was negatively related to the number of breeding pairs ($d = -0.084 \pm 0.022$; 95% CI −0.127 to −0.042; Fig. 5). Adult survival was not density-dependent (ANODEV: $F_{1,13} = 2.77$, $P = 0.120$).

Population dynamics

The deterministic population growth rate was 1.159, and the generation time was 9.6. Prospective analyses indicated that the population growth rate showed the highest sensitivity to immigration and adult survival, followed by changes in first-year survival rate, the proportion of breeders at age 4 and older, the number of fledglings per nest and the proportion of breeders at younger ages (Table 4). By contrast, retrospective analyses suggested that the number of fledglings per nest made the largest contribution to variance of the population growth rate (Table 4), followed by the proportion of breeders at age 4 and older. Survival during the first year and immigration made intermediate contributions. Adult survival and the proportion of breeders at younger ages made the smallest contributions.

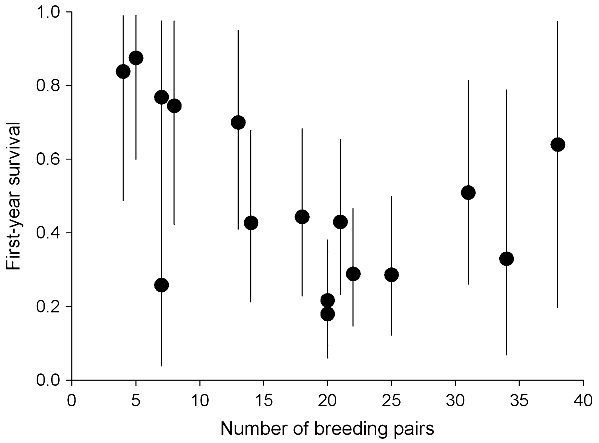

Figure 5. Relationship between probability of first-year survival and breeding population size of Ospreys (1995–2011). Error bars indicate 95% CI.

The stochastic population growth rate was 1.156 (95% CI = 1.154–1.158). The model predictions fitted relatively well with the observed counts of breeding pairs, although predicted numbers were slightly underestimated (Fig. 1). A stochastic population model where the immigration rate was increased by *c.* 20% (0.058 instead of 0.048) yielded a perfect fit with the observed data (Fig. 1).

DISCUSSION

The rate of increase of this newly established Osprey population was similar to those found in other increasing or recovering Osprey populations and is coherent with the overall increase of the species in the Western Palaearctic since the early 1970s (Schmidt 1998). For example, the rate of initial population increase was 15% in Corsica before the occurrence of density-dependence (Thibault & Bretagnolle 2001) and 13% in Scotland

Table 4. Demographic parameter mean value, sensitivity and elasticity of population growth rate in demographic parameters, and their contribution to variance of the population growth rate (λ) for the Osprey from 1985 to 2011. Sensitivities, elasticities and contributions to variance were calculated on the basis of a deterministic model.

Parameter	Mean (se)	Sensitivity	Elasticity	Contribution to variance of λ
Juvenile survival	0.487 (0.066)	0.3359	0.1411	0.000491
Adult survival	0.875 (0.005)	0.9075	0.7178	0.000021
Fecundity	1.890 (1.018)	0.0865	0.1411	0.008955
Immigration	0.048 (0.022)	0.9502	0.0393	0.000437
Breeding proportion age 2	0.014 (0.001)	0.0587	0.0040	0.000000
Breeding proportion age 3	0.296 (0.060)	0.0464	0.0157	0.000008
Breeding proportion age 4	0.950 (0.012)	0.1757	0.1214	0.001105

(Dennis 1995). An important finding in our analyses is the difference in the results of prospective and retrospective analyses. From a prospective point of view and as predicted by life-history theory for long-lived species with reduced fecundity, deferred breeding and high adult survival rates (Sæther & Bakke 2000), the sensitivity of population growth rate to adult survival was high, and the adult survival variability was weak. The sensitivity of population growth rate to immigration was similar to that of adult survival, but its elasticity was *c.* 18 times lower. Thus, for example, a 5% proportional change in adult survival and immigration rate would result in a relatively larger change in population growth rate for survival than for immigration. Juvenile survival, fecundity and the breeding proportions at age 4 and older had different sensitivities but similar elasticities, suggesting that a 5% proportional change in these parameters would result in similar changes in population growth rate. However, the high sensitivity of population growth rate to juvenile survival suggests that this parameter is of critical importance for the population persistence. By contrast, the retrospective analysis of the projection population matrix parameters demonstrated that productivity (number of fledglings per pair) played a critical role in the increase of the population. Its contribution was about eight times larger than the contribution of the proportion of breeding individuals of age 4 and older, which was the parameter that had the greatest influence on the population growth rate after productivity. Immigration and juvenile survival substantially contributed to the increase of the population, although *c.* 20 and *c.* 18 times less than productivity, respectively, whereas adult survival contributed *c.* 434 times less than productivity.

Because we studied a small population, our dataset was inherently limited. As a consequence, productivity showed large variance because of the effect of demographic stochasticity, and survival showed small variance because of low statistical power to detect between-year variations. Therefore, we cannot exclude the possibility that the difference between contributions to variance of λ by survival and productivity was inflated due to these limitations in the data.

The probability of recruiting as a breeder increased with age, as found for other species (e.g. Pradel *et al.* 1997, Hernández-Matías *et al.* 2010). Most Ospreys recruit between their 3rd and 5th year of life, with very low probability of recruitment before the 3rd year. A relatively high proportion of individuals recruited among 5-year-olds and in older age-classes. We do not believe this was due to late-recruiting individuals that may have bred unnoticed for several years at the same site at which they were eventually detected, as our probability of detecting a marked bird was high. Late-recruiting individuals could have bred elsewhere before they were observed breeding in the study area, although breeding dispersal is rare in this species (Schmidt *et al.* 2006). An alternative explanation is that part of this Osprey population recruits at older ages. Indeed, floaters (non-territorial adult individuals) appear to be relatively common in Osprey populations (Mougeot *et al.* 2002, Bretagnolle *et al.* 2008, Englund & Greene 2008) and their number may have increased as the population grew.

Average productivity was among the highest recorded for the species, which on average produces 1.44 fledglings per nest per year (range of average values: 0.90–2.01, Supporting Information Table S1). This high productivity suggests that food resources are particularly abundant in the study area and that the negative effects of anthropogenic activities often reported for the species, either direct such as human disturbance or indirect such as contaminants (Henny *et al.* 2010), are minimal. Most nests are closely monitored throughout the breeding season and several public awareness initiatives have been undertaken since 1999 as part of a National Action Plan (Nadal & Tariel 2008). Tissue concentrations of pesticides, PCBs (polychlorinated biphenyls) and heavy metals among Ospreys collected in France are low and suggest no threats from contamination (Lemarchand *et al.* 2012). Diet studies in the study area indicate that Ospreys feed on 20 freshwater fish species, mainly Cyprinids, which are abundant in the River Loire and the surrounding dense network of permanent water bodies within the study area (Thiollay & Wahl 1998). In addition, although the population has been increasing, we did not detect any negative effect of density on productivity, suggesting that the carrying capacity has not yet been reached. Nest density in the study area is *c.* 3–4 nests/100 km^2, still lower than nest density in Corsica (*c.* 5–6 nests/100 km^2) where density-dependence in productivity has been detected (Bretagnolle *et al.* 2008). The high proportion of breeding individuals in the population is also consistent with the absence of density-dependence (Bretagnolle *et al.* 2008).

Annual adult survival rates (*c.* 0.875) were relatively high compared with previous estimates: Sweden, 0.81 (Ryttman 1994) and 0.72–0.86 (Eriksson & Wallin 1994); East Coast USA, 0.85–0.90 (Spitzer *et al.* 1983) and 0.804–0.838 (Henny & Wight 1969). This suggests favourable conditions on the breeding grounds but also along the migration route and in wintering areas. First-year survival (*c.* 0.487) was similar or slightly lower than estimates in other populations: Sweden, 0.65 (Ryttman 1994) and 0.53 (Eriksson & Wallin 1994); East Coast USA, 0.427–0.485 (Henny & Wight 1969). This relatively low value of first-year survival may be related partly to a negative effect of density. Although we were not able to identify the mechanism through which density impacted first-year survival, it is unlikely that it was caused by resource depletion as found in other raptor species such as the Mauritius Kestrel *Falco punctatus* (Nicoll *et al.* 2003, Nevoux *et al.* 2011), given the high productivity in the population. Behavioural interference is a more likely mechanism, as shown in an Osprey population in Corsica (Bretagnolle *et al.* 2008), and may apply to territory establishment (Mougeot *et al.* 2002). As our survival estimates may be confounded by permanent emigration, it could be that some young individuals were forced to emigrate from the study area when density increased and competition for nest-sites and territories became more intense.

Our results showed that the population increase was due mainly to local-born individuals that recruited later as breeders and not to immigration. The Osprey is gregarious and there is a strong conspecific attraction in this raptor, which could explain the presence of immigrant individuals recruiting in the population as observed in other species (e.g. Oro & Pradel 2000). Although immigration contributed to the increase in the breeding population, the current population would not suffer from a lack of immigrants. Indeed the stochastic population growth rate estimated with an immigration rate fixed to zero is 1.109 ± 0.002, indicating that without immigration the breeding population would increase by 10.9% annually, all else being equal. This result is of general interest to understand the mechanisms that allow the recovery of previously declined populations. Although several recovering raptor populations such as the Golden Eagle *Aquila chrysaetos* in the Alps (Fasce *et al.* 2011), the Griffon Vulture *Gyps fulvus* in central France (Sarrazin & Legendre 2000), the White-tailed Eagle *Haliaeetus albicilla* in northern Germany (Krüger *et al.* 2010), the Bearded Vulture *Gypaetus barbatus* in northern Spain (Oro *et al.* 2008) and the Red Kite *Milvus milvus* in the UK (Smart *et al.* 2010) are closely monitored, few studies have quantified the contributions of vital rates to the growth of these populations. Using retrospective analyses, Krüger *et al.* (2010) showed that the increase in natural White-tailed Eagle populations was mainly explained by pre-breeding survival (55%) and that reproductive output only explained 13.5% of the variation in population growth. Evidence for density-dependence on productivity and proportion of breeders was found in the Golden Eagle (Fasce *et al.* 2011) and in the Bearded Vulture (Carrete *et al.* 2006, Oro *et al.* 2008), but these studies did not perform or report retrospective analyses. Compared with these studies, our results show that productivity can be a major driver in recovering raptor populations and that density-dependence may also affect survival parameters.

In conclusion, our findings stress the importance of studying the demographic processes in newly settled and growing populations. Much attention has been focused on demographic analyses of declining populations, which in many circumstances helped to identify the causes of decline and to propose conservation actions. However, causes of decline may differ from causes of increase in some populations, and our understanding of the demographic processes that allow a species to recover or to settle and increase its population remains inadequate. Our results suggest that the high productivity and recruitment probability contribute significantly to the growth of the population. This suggests that conservation work should aim, in addition to maintaining high juvenile and adult survival, to protect occupied nest-sites, their surrounding habitat and to maintain highly favourable foraging areas in the vicinity of breeding sites. As natal dispersal from our study site is likely to increase in future years, conservation actions must aim at maintaining or increasing searches and monitoring of new breeding nuclei at a national scale. At a broader perspective, our results suggest that re-introduction programmes for this species, and possibly other raptor species, should aim to maximize the productivity of re-introduced individuals and the attractiveness of the re-introduction areas to potential recruits.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Osprey mean productivity at several localities.