

# The demography of an increasing insular Eurasian Scops Owl (*Otus scops*) population in western France

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Rapid population declines of many long-distance Afro-Palaeartic migratory bird species are ongoing across Europe but the demographic drivers are often poorly understood, thereby limiting the development of appropriate conservation actions. Using long-term population monitoring (39 years), capture–mark–recapture data and a matrix model, we estimated demographic parameters and the effect of climate variables on adult survival, and modelled the dynamics of an increasing population of Eurasian Scops Owls *Otus scops* in a landscape with agricultural abandonment in western France. The observed mean annual population growth rate was 1.055 (from 68 to 523 territorial males between 1981 and 2019). Over the study period, clutch size and hatching success were stable, but fledging success and breeding success showed slight negative trends, probably due to density-dependence. Survival varied with age, with an increase during early life and evidence for rapid senescence from 4 years old. Adult survival remained stable and was positively linked to the amount of autumn rainfall in the Sahel and to the winter North Atlantic Oscillation. Survival of younger age-classes made the largest contribution to the variance of the population growth rate, followed by clutch size, fledging success and survival of older birds. Such a long-term population increase in a landscape where intensive agriculture has decreased by 64.6% sheds some new light on the causes of the decline of European Scops Owl and other Afro-Palaeartic bird populations. We infer some of the possible causes of this large-scale decline, in particular food shortage, and discuss conservation measures that could be applicable to reverse this trend.

**Keywords:** breeding, demographic rate, density-dependence, farmland bird, *Otus scops*, population dynamics, Sahel rainfall, survival.

## INTRODUCTION

Populations of many insectivorous farmland birds have been declining by 13% across Europe over the past 25 years (Bowler *et al.* 2019), with compelling evidence for more dramatic declines since the 1960s and 1970s (Vickery *et al.* 2014). Declines of insectivores are primarily associated with agricultural intensification which has replaced traditional farming, and loss of grassland habitat and fallows (Bowler *et al.* 2019, Traba & Morales 2019), resulting in massive declines of insect biomass (Hallmann *et al.* 2017, Pilotto *et al.* 2020).

These changes have been accelerated by the Common Agricultural Policy in Western Europe since 1962 (Donald *et al.* 2001).

Long-distance Afro-Palaeartic migratory insectivores have suffered higher declines than other insectivores (Bowler *et al.* 2019) and it is suspected that climatic factors in the African wintering quarters have played a crucial role in these declines (Kanyamibwa *et al.* 1989, Zwarts *et al.* 2012, Norman & Peach 2013, Johnston *et al.* 2016, Boano *et al.* 2020). However, the population ecology of several farmland birds, and the demographic and ecological processes by which they are affected by farming practices and climate change, remain poorly known (Newton 2004, Morrison *et al.* 2016). An understanding of these

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processes is therefore urgently needed to aid in identifying and designing appropriate conservation actions to recover declining populations (Morrison *et al.* 2016). Recently, increasing research efforts have been undertaken to decipher the demographic and ecological processes affecting the population dynamics of several long-distance Afro-Palaeartic migratory insectivorous birds (Morrison *et al.* 2016, Boano *et al.* 2020, Telenský *et al.* 2020). However, our lack of knowledge and understanding still remains particularly acute for poorly known species such as owls, as most previous work has targeted passerines and waterbirds. Being mainly nocturnal, insectivorous owls feed on different and larger prey species compared with many passerines and waterbirds, and also use different breeding and foraging habitats, so that targeting this group may allow a better understanding of the mechanisms involved in insectivorous bird species decline.

The Eurasian Scops Owl *Otus scops* (hereafter referred to as Scops Owl) is a small migratory raptor that breeds in the Southern Palaeartic from Portugal to Central Asia, with a southern limit in northwest Africa (del Hoyo *et al.* 1999). The species winters mainly in sub-Saharan Africa, although southerly breeding populations in the western Palaeartic are partial migrants or sedentary (Cramp 1985, del Hoyo *et al.* 1999). There is some evidence that the species is in rapid decline over Europe, probably due to changes and intensification of agricultural practices (Bavoux *et al.* 1997, Martínez *et al.* 2007, Treggiari *et al.* 2013, Denac *et al.* 2019, Ivajnič *et al.* 2020). However, estimates of population sizes and trends for Scops Owls are scarce and imprecise (Bavoux *et al.* 1997, Barnagaud & Caupenne 2015, Herrando *et al.* 2020). Demographic data are even rarer (Bavoux *et al.* 2011, Boano & Silvano 2015) because there are very few long-term field studies, partly due to the elusive behaviour (apart from vocal activities), breeding habits with low to medium attractiveness to nestboxes, and excellent camouflage of the species. As a consequence, we have a very poor understanding of the demographic tactics of this species, and nothing is known about the effects of climate on demographic traits and population dynamics.

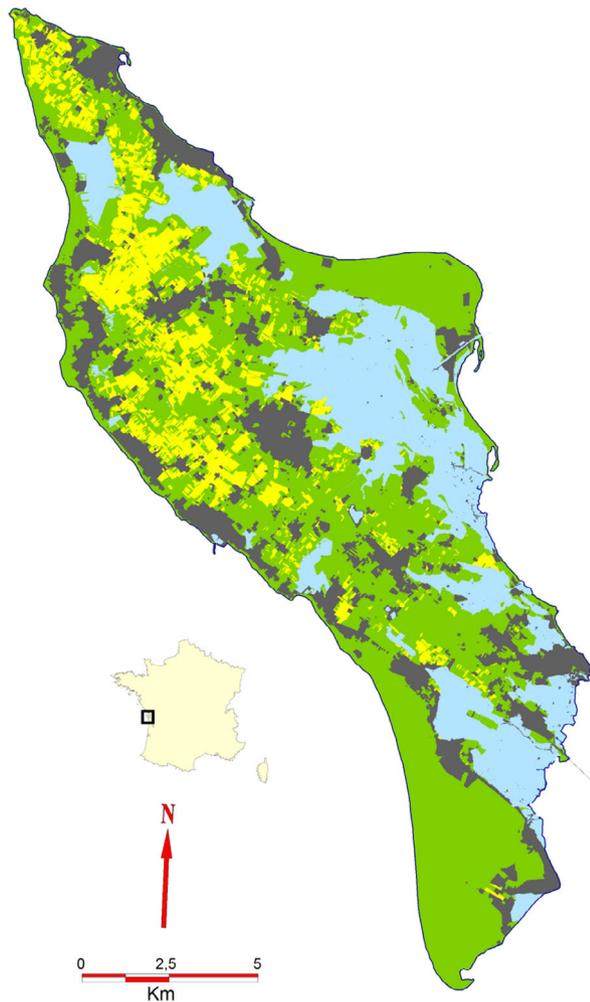
Our aim here was to understand the demographic and environmental processes that drive the dynamics of a migratory Scops Owl population breeding in a region where, contrary to the overall

trend, intensive agricultural practices have decreased. Scops Owls have been studied on Oléron Island, western France, since 1981, and there is strong evidence that the population has increased over the last four decades (Bavoux *et al.* 2011, 2012). Using monitoring data combined with a capture–mark–recapture scheme we: (1) determined the population trend over 39 years; (2) estimated age at first breeding, breeding parameters (clutch size, brood size, hatching success, fledging success, breeding success) and age-specific survival; (3) assessed evidence of density-dependence on demographic parameters; (4) assessed the effects of climate covariates on adult survival; (5) modelled the dynamics of the population; and (6) analysed a matrix population model from a prospective and retrospective point of view by performing sensitivity analyses (Caswell 2001).

## METHODS

### Study area

The study area was Oléron Island (45°48'N to 46°03'N, 1°25'W to 1°11'W, 174.4 km<sup>2</sup>, <https://www.insee.fr/fr/statistiques/1405599?geo=EPCI-241700624>) located in the central part of the French Atlantic coast (Fig. 1). This island is 30 km long, 10 km at the widest, and with an average altitude of 10 m. The climate is oceanic with annual rainfall of  $\approx$  750 mm, a mean annual temperature of 13 °C (mean minimum 7.4 °C in February, mean maximum 19.6 °C in August), and a high number of hours of sunshine (> 2250 h/year on average). The habitat of Oléron Island was described for the period 2006–2008 by Bavoux *et al.* (2012) and consists of a mosaic of urbanization (26% of the island area), wetlands with fresh and saltwater (23%), woodland and wooded areas (22%; half dominated by Maritime Pine *Pinus pinaster* sometimes associated with Evergreen Oak *Quercus ilex*, half being dominated by *Quercus* sp. including Common Oak *Quercus robur*), cropland (19%), of which vineyards constitute a quarter of the cultivated area, wasteland and dunes (10%). Between 1968 and 2017, the number of habitations increased by a factor of 3.1 and the resident human population density increased from 90.3 to 127.3 individuals/km<sup>2</sup> (INSEE 2020). During summer months (July–August) the resident human population density



**Figure 1.** Location of the study area, Oléron Island, France. Green areas show woodland, grassland and fallowland; yellow areas show cultivated land; dark grey areas show urbanized land; blue areas show wetlands. The extent of habitat areas corresponds to the year 2006 with updates from fieldwork in 2008.

increases by a factor of 10–15 due to mass tourism (Bavoux *et al.* 2012).

To characterize the changes in agricultural surfaces we used the AGRESTE database (<https://agreste.agriculture.gouv.fr/agreste-web>). This database (based on farmers' statements) is composed of land use expressed in hectares for each French municipality, distinguishing different types of crops and non-agricultural areas. The years available were 1970, 1979, 1988, 2000 and 2010. The AGRESTE database distinguishes several categories of agricultural land use, which were grouped into three classes: arable surfaces (mainly cereals),

surfaces with perennial cover (mainly fodder and orchards) and vineyards. For each class we summed the surface areas of land for the eight municipalities of Oléron Island.

### Study species

The Scops Owl is a small (60–135 g), insectivorous, trans-Saharan migrant nocturnal raptor that breeds in open and semi-open woodland habitats of the middle–lower latitudes of the Palaearctic and in northwest Africa (del Hoyo *et al.* 1999). Scops Owls are present on Oléron Island from mid-March to September, where they mainly use forest habitats dominated by deciduous and mixed woodlands (79.7% of singing males, Bavoux *et al.* 2012), with urbanized areas and equipped camping areas being less preferred (10.8% and 5.9%, respectively). Vocal territorial activities start when males arrive on the breeding sites and decrease during the chick-rearing period. Nesting occurs in tree cavities, holes in buildings or walls, old nests of other species such as Eurasian Magpie *Pica pica*, Common Crow *Corvus corone* and Woodpigeon *Columba palumbus* as well as vegetation structures such as witches' broom (Costa 2001, Bavoux *et al.* 2011, Grieco 2018). Each pair produces only one clutch per year. On Oléron, laying (normally three to five eggs) occurs from mid-May to mid-June and eggs are incubated for 24–25 days. Hatching occurs from late May to early August. Chicks leave the nest 20–25 days after hatching (G. Burneleau & C. Bavoux unpubl. data) and are fed by parents during the following 2–3 weeks. Chicks are fed almost exclusively (> 89% by frequency) with insects, mainly Orthoptera (52%, with 33% being Great Green Bush-cricket *Tettigonia viridissima*), Lepidoptera (31%, mostly Noctuidae and Arctiidae) and Phasmatodea or stick insects (15%) (Bavoux *et al.* 1993). Scops Owls winter in Africa between 15°N and 5°S, mainly in wooded savannas with tall grass and dense bush. One bird ringed on Oléron Island was recovered (27 January 1987) on the Ivory Coast near Vavoua (7°22'30"N, 6°28'37"W).

### Field methods

Scops Owl territorial males were monitored on the entire island through 16 annual surveys from 1981 to 2019 (1981, 1985, 1987–1988, 1996, 1998, 2000–2007, 2012 and 2019). Surveys were

performed by the same observers (C. Bavoux, G. Burneleau & L. Mimaud) using a standardized protocol detailed in Bavoux *et al.* (2011). Briefly, the entire island was covered by a network of 185 point counts (Supporting Information Fig. S1). Point counts were spread over Oléron Island in areas where the species was present or assumed to be present, and were the same from year to year. Point counts were surveyed between the end of May and early June (laying period) for 4 h after sunset and when meteorological conditions were favourable (no precipitation, no or little wind). At each point count, a tape-recorded male hoot was played for 1 min, followed by a period of 2 min during which all males that responded to playback within a 500-m-radius circle were recorded and positioned on a 1:25 000 IGN (Institut Géographique National) map using the BDORTHO IGN information geographical system. As only 54% of the island surface area was covered during each annual survey, the proportion of hooting males for the entire island was extrapolated using ordinary kriging (see Bavoux *et al.* 2011 for further details). The probability to detect a male that responded to playback was estimated in 2008 from a sub-sample of 30 point counts (randomly selected from the total number of point counts) using a removal capture–recapture model (Bavoux *et al.* 2011). Extrapolated numbers of males that responded to playback on the entire island were corrected using this detection probability ( $0.808 \pm 0.014$ ), assuming a constant detection probability for all years, in order to obtain the total number of territorial males on the island while taking into account the uncertainty in detection probability. From the extrapolated number of territorial males, we estimated the average annual population growth rate over the entire study period using the relationship  $(N_{2019}/N_{1981})^{(1/38)}$ , where  $N_{1981}$  is the number of males in 1981 and  $N_{2019}$  is the number of males in 2019.

During 1984–1990 and 2000–2008, Scops Owls were ringed as part of a capture–mark–recapture programme initiated by G. Burneleau and C. Bavoux (Bavoux *et al.* 2011) under a licence administered by the Centre de Recherche sur la Biologie des Populations d'Oiseaux, Muséum National d'Histoire Naturelle, Paris, France. Between 1984 and 1990, 89–129 nestboxes were set up on Oléron Island (Supporting Information Fig. S2). Each year all newly adult individuals and fledglings captured in nestboxes

were ringed with a metal ring. Individuals previously ringed were captured, identified and their breeding status (breeding, non-breeding) assessed. Adult individuals were sexed according to the presence of a brood patch, as only females incubate eggs (Cramp 1985). In nestboxes occupied by breeding individuals we recorded clutch size, the number of chicks hatched and the number of chicks just before fledging. To do so, an average of 6.3 (sd = 5.0) visits per nestboxes per year were made from laying and until the fledglings left the nest. The same capture–mark–recapture protocol was conducted between 2000 and 2008 with a sample of 60–103 nestboxes. Nestboxes were set up at the beginning of the study where singing males were detected. The storm 'Martin' devastated many nestboxes at the end of 1999. New nestboxes were set up in 2000 and 2001 in the same areas as those monitored in 1984–1990 (Fig. S2).

## Statistical analysis

### *Estimating breeding parameters*

We estimated clutch size (number of eggs per nest), hatch size (number of eggs hatched per nest), brood size (number of fledglings per nest), hatching success (number of eggs hatched per egg laid counted at nests), fledging success (number of chicks fledged per egg laid counted at nest) and breeding success (number of chicks fledged per egg counted at nests). We excluded all observations with incomplete egg counts and nests with more than six eggs ( $n = 3$ ) based on maximum clutch size reported in the literature (del Hoyo *et al.* 1999), assuming these resulted from two females that laid in the same nest. To test for year-to-year differences in clutch size, hatch size and brood size we used generalized linear models (GLMs) by treating year as a fixed factor covariate with a Gaussian distribution or with a Poisson distribution and log-link (Zuur *et al.* 2009). We checked for over-dispersion using a quasi-Poisson or a Gaussian model; none was detected. To test for temporal trends, year was treated as a fixed-effect continuous covariate. To test for year-to-year differences in hatching success, fledging success and breeding success, we used GLMs by treating year as a fixed-factor covariate with binomial distribution and identity-link. To test for temporal trends, year was treated as a fixed-effect continuous covariate. We initially attempted to use

generalized linear mixed models with nest-site as a random effect but the data were too sparse to run such models and many nests were sampled only once (Supporting Information Fig. S3). We used the R package *stats* to fit GLMs (R Development Core Team 2019).

#### *Estimating age-specific survival probabilities*

Ringed and recapture data of individuals ringed as chicks were coded for all individually marked birds according to whether a bird was seen or not seen in a given year. The mark–recapture analysis was based on a dataset involving 701 marked birds of known age over the 1984–1990 and 2000–2008 periods. Chicks were not sexed. We considered an initial model with age dependence in both apparent survival probability  $\phi$  and recapture probability  $p$ . Because the sample size of recaptured chicks was limited, the number of age-classes was reduced to four (model  $\phi_{a4}$ ,  $p_{a4}$  where ‘a’ denotes age). To test for variation in survival and recapture probabilities, we fitted models in order of decreasing complexity by reducing the number of age-classes. We modelled the recapture probability first, and then the survival probability. Once we obtained the best model structure for  $p$ , we also fitted models where survival was modelled as a Gompertz, Weibull, logarithmic and linear function of age. The goodness-of-fit of the Cormack–Jolly–Seber model was assessed using U-Care (Choquet *et al.* 2009). Model selection was based on the adjusted Akaike’s information criterion (AICc). When two models had similar support ( $\Delta\text{AICc} < 2$ ), we used model averaging to estimate survival parameters accounting for uncertainty in model selection (Burnham & Anderson 2002). Survival estimates were obtained from these data using the program MARK 9.0 (White & Burnham 1999).

#### *Estimating winter climate effects on adult survival*

To model the effect of climate outside the nesting period on adult survival, we considered observations of individuals marked as adults for the two periods (1984–1990 and 2000–2008) to build capture histories. The mark–recapture analysis was based on a dataset involving 302 marked adults (177 females and 125 males). We considered an initial model with sex and time dependence in both apparent survival probability  $\phi$  and recapture probability  $p$ . To test for variation in survival and recapture probabilities, we fitted models in order

of decreasing complexity. We modelled the recapture probability first, and then the survival probability. The goodness-of-fit of the Cormack–Jolly–Seber model was assessed using U-Care (Choquet *et al.* 2009). Model selection was based on AICc. Survival estimates were obtained from these data using the program E-SURGE. To investigate the relationships between adult survival rates of Scops Owls and climate conditions, three large-scale climatic variables were considered: Sahel rainfall, North Atlantic Oscillation (NAO) and El Niño–Southern Oscillation (see Supporting Information S1). We performed an analysis of deviance (ANO-DEV, Grosbois *et al.* (2008)) to test for the effect of these covariates on survival (see Supporting Information S1).

#### *Density-dependence*

We used the stochastic Gompertz population model to make an inference on density-dependence. The Gompertz model was fitted on the total number of territorial males issued for the point counts and corrected by the detection factor (see Supporting Information S2). By log-transforming the number of territorial males in year  $t$  ( $N_t$ ) and putting  $x_t = \ln(N_t)$ , this model was defined as:

$$x_{t+1} = r + (1 - b)x_t + \varepsilon_t$$

where  $1 - b$  is the lag 1 autocorrelation of the log-transformed number of territorial males,  $r$  is the growth rate for  $N = 1$  territorial male,  $b$  is a measure of the strength of density-dependence, and  $\varepsilon_t$  is the normally distributed process error with mean zero and standard deviation  $\tau$  (Lebreton & Gimenez 2013). When  $b = 0$  the process is density-independent. Uncertainty in the numbers of territorial males was modelled with a log-normal distribution so that the log-transformed number of breeding pairs estimate in year  $t$  was given by  $y_t = x_t + \eta_t$ , where  $\eta_t$  is observation error with mean zero and standard deviation  $\sigma$ .

Then, to attempt to identify the demographic parameters involved in density-dependent processes, we used the output obtained from the Gompertz model for the total number of territorial males as a covariate of adult survival and breeding parameters (clutch size, hatching success, fledging success and breeding success) using the same statistical approaches as described above (*Estimating*

breeding parameters and Estimating winter climate effects on adult survival).

### Population modelling

We constructed a female-only, pre-breeding, age-structured stochastic matrix population model with four age-classes (Caswell 2001). Between each age-class from fledging to age-class 4 and older, birds survived with age-specific annual survival probability  $\phi_1$ ,  $\phi_2$ ,  $\phi_3$ ,  $\phi_4$ . We used survival estimates from the selected capture–recapture models where survival varied as a function of age. Fertility ( $F$ ) was estimated as  $\phi_0 \times CS \times HS \times FS \times P \times 0.5$ , where  $\phi_0$  is juvenile survival,  $CS$  is mean clutch size,  $HS$  is hatching success,  $FS$  is fledging success,  $P$  is the proportion of breeders, and assuming a 50 : 50 sex ratio. We assumed that parameters  $CS$ ,  $HS$  and  $FS$  did not vary with age. Reproduction begins at age 1 as recorded from field data of marked birds and from the literature (del Hoyo *et al.* 1999). To estimate age-specific breeding proportions at age 1 ( $P_1$ ) and older ( $P_{2+}$ ), we used a multistate model (Pradel & Lebreton 1999). Individuals marked as chicks were either observed in the breeder state or not observed. Two states were specified: a breeder state when an individual was detected as a breeder and a non-breeder state when an individual was detected as a non-breeder (chicks, or initial state, being always non-breeders). The method relies on three parameters, the survival probability ( $\phi$ ), recapture probability ( $p$ ) and transition probability ( $\psi$ ), defined as the probability that a bird was breeding for the first time. The recapture probability of individuals marked as chicks was fixed at 0 (unobservable state). Once in the state breeder, individuals were assumed to stay in this state for the remainder of their life, such that transition from breeder to non-breeder was impossible (see Supporting Information S3 and Table S1). Environmental stochasticity was then incorporated in the matrix model by sampling the yearly values of survival, hatching success and fledging success from a beta distribution, and the yearly values of clutch size from a log-normal distribution (Morris & Doak 2002), whose mean and process variance were set equal to those previously estimated. Process variance of  $\phi_0$ ,  $\phi_1$ ,  $\phi_2$ ,  $\phi_3$ ,  $\phi_4$  and clutch size, hatching success and fledging success were estimated following Gould and Nichols (1998). For  $\phi_1$ ,  $\phi_2$ ,  $\phi_3$  and  $\phi_4$  we used the adult file, assuming equal variances for all parameters, and a model where adult

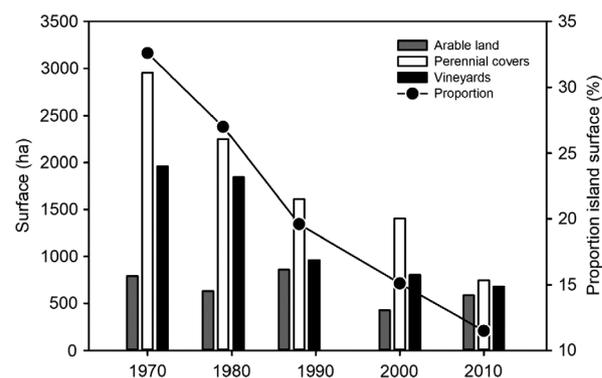
survival was time-dependent and capture probability was constant. For  $\phi_0$  we used the chick file and a model where juvenile survival was time-dependent, survival of individuals older than 2 was constant, and capture probability was constant.

From the matrix model, we estimated the population growth rate  $\lambda$ , the stable age distribution, and the sensitivities and elasticities of  $\lambda$  to variations in demographic rates  $\theta$  ( $\partial\lambda/\partial\theta$ ) (Caswell 2001). We then estimated the contribution of temporal variations of each demographic parameter  $\theta$  to the variability of  $\lambda$  using the first-order Taylor expansion:  $V(\lambda) = s(\theta)^2\text{var}(\theta)$ , where  $s(\theta)$  is the sensitivity of  $\lambda$  to parameter  $\theta$ , and we assumed that vital rates varied independently (Caswell 2001). The sensitivity analysis corresponds to prospective analyses, and the contribution of the observed variation in vital rates on the variance of  $\lambda$  corresponds to retrospective analyses. The stochastic matrix population model was analysed by Monte Carlo simulations (1000 iterations) using the software ULM (Legendre & Clobert 1995).

## RESULTS

### Changes in agricultural practices

Between 1970 and 2010, the proportion of the Oléron Island surface area occupied by intensive agriculture decreased from 32.6% to 11.5%, representing a 64.6% decrease from 5704 to 2017 ha (Fig. 2). This was mainly due to major decreases



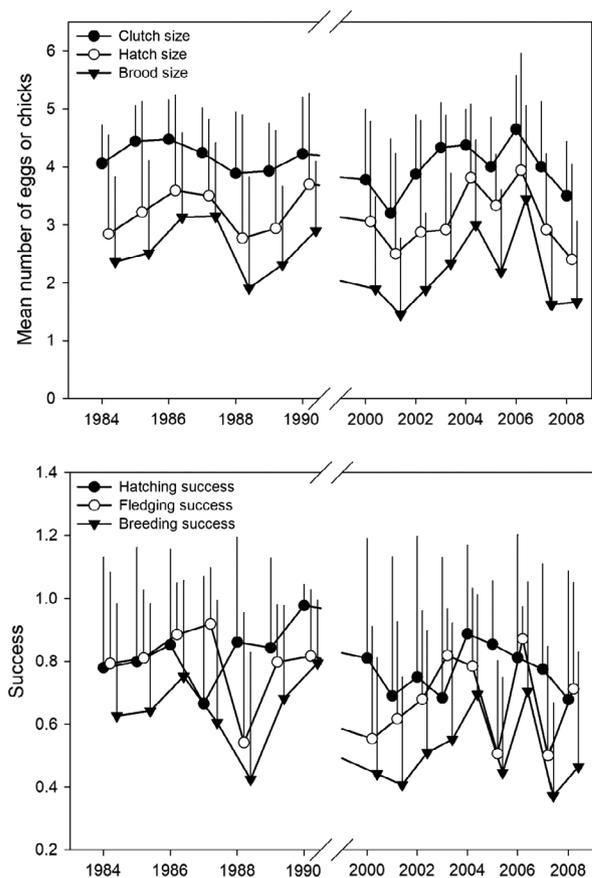
**Figure 2.** Changes in cultivated surface areas at Oléron Island, France, between 1970 and 2010. Histograms represent surface areas for three categories of agricultural land use, and filled circles represent the cultivated proportion of the entire Oléron Island area. Data from <https://agreste.agriculture.gouv.fr/agreste-web/>

in perennial cover (mainly intensive fodder-producing areas) and vineyards, and to a lesser extent to arable surfaces. Areas not used for agriculture were mainly replaced by urbanized areas, with a 31.8% increase of the human population between 1982 and 2017 (INSEE 2020 <https://statistiques-locales.insee.fr/#c=home>), and by areas occupied by forests, shrubs and wasteland (Supporting Information Fig. S4).

### Breeding parameters

The average proportion of nestboxes occupied by breeding Scops Owls was 20.4% (sd = 6.5%, min = 8.3%, max = 32.3%, Supporting Information Fig. S5). Overall mean clutch size, hatch size, brood size, hatching success, fledging success and breeding success are shown in Table 1. There was no evidence of year-to-year variation or temporal trend in hatch size (all  $P > 0.068$ ; Table 1, Fig. 3). Clutch size varied between years (with low clutch sizes in 2001) and showed a negative temporal trend ( $\beta = -0.015 \pm 0.006$ ,  $P = 0.022$ ; Fig. 3). The number of fledged chicks per nest varied between years (with low numbers of fledged chicks in 2001 and 2006), with evidence of a negative temporal trend ( $\beta = -0.009 \pm 0.004$ ,  $P = 0.029$ ; Fig. 3). There was no evidence of year-to-year variation in hatching success (all  $P > 0.187$ ) or of a temporal trend (Table 1, Fig. 3), but fledging and breeding success varied between years (with low fledging success in 1988, 2000, 2005 and 2007 and low breeding success in 2001 and 2007), with negative temporal trends ( $\beta = -0.008 \pm 0.002$ ,  $P < 0.001$  and  $\beta = -0.007 \pm 0.002$ ,  $P = 0.005$ , respectively; Fig. 3).

The average observed age at first breeding was  $1.9 \pm 0.9$  years (mode = 1, range 1–4 years). Most



**Figure 3.** Breeding parameters of Scops Owls at Oléron Island, France, measured during two monitoring periods: 1984–1990 and 2000–2008. Error bars are  $\pm$  sd.

individuals (79%) were observed as breeders at 1 or 2 years of age. The probability to access first reproduction was estimated at  $0.816 \pm 0.235$  for 1-year-olds and at 1 for 2-year-olds (Supporting Information Table S1).

**Table 1.** Breeding parameters of Scops Owl at Oléron Island (1984–2008). For each parameter we give the mean  $\pm$  sd and sample sizes in parentheses.  $P_{\text{trend}}$  indicates the  $P$ -value of a generalized linear model testing for temporal trends (see Methods).

Parameter	Estimate (n)	Range	$P_{\text{trend}}$
Clutch size	4.06 $\pm$ 0.95 (266)	1–6	0.022
Hatch size	3.15 $\pm$ 1.72 (275)	0–6	0.622
Brood size	2.40 $\pm$ 1.55 (294)	0–5	0.029
Hatching success	0.79 $\pm$ 0.36 (266)	0–1	0.617
Fledging success	0.73 $\pm$ 0.28 (227)	0–1	<0.001
Breeding success	0.58 $\pm$ 0.36 (266)	0–1	0.005

### Age-specific survival

From the 702 individuals ringed as chicks, only 14 were recaptured at least once in the monitored nestboxes, giving a return rate of 2%. The goodness-of-fit test of the Cormack–Jolly–Seber model was significant ( $\chi^2 = 31.1$ ,  $df = 12$ ,  $P = 0.002$ ). This was mainly due to test 3.SR ( $\chi^2 = 30.6$ ,  $df = 7$ ,  $P < 0.001$ ) and to transient individuals (z-statistic for transient = 4.02,  $P < 0.001$ ). As age was explicitly taken into account in our initial model ( $\phi_{a4}$ ,  $p_{a4}$ ), this model fitted the data ( $\chi^2 = 0.998$ ,  $df = 5$ ,  $P = 0.963$ ).

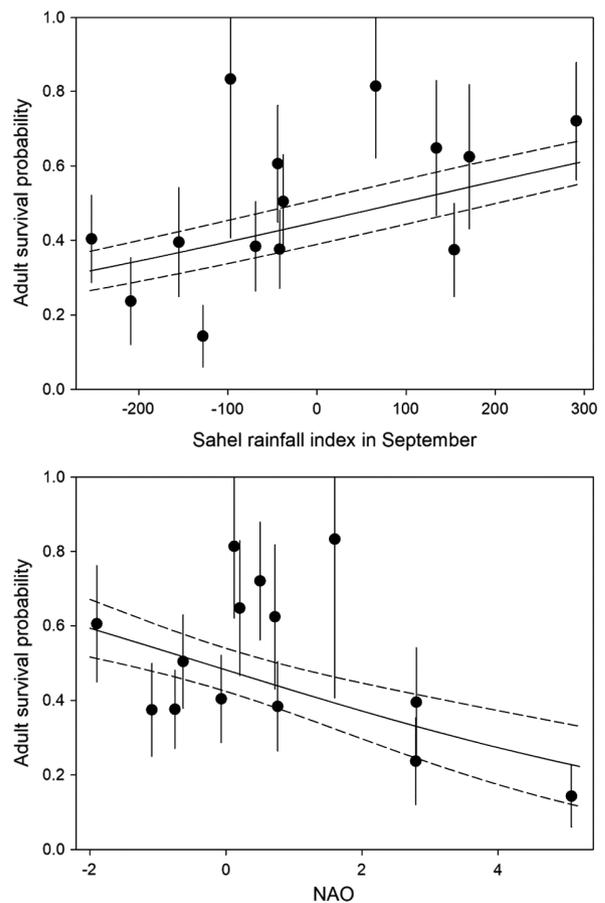
Modelling the recapture probability indicated that it was best modelled as constant across ages (Supporting Information Table S2), and was  $0.395 \pm 0.101$ . There was substantial model uncertainty regarding survival (Table S2). As a model where survival was a function of four age-classes ( $\phi_{a4}$ ,  $p_{a1}$ ) had a much lower deviance than other models, we used this model structure to perform model averaging (Anderson & Burnham 2002, Arnold 2010). Model-averaged apparent survival estimates indicated that survival increased from  $0.052 \pm 0.019$  during the first year, to  $0.536 \pm 0.184$  during the second year and to  $0.734 \pm 0.190$  during the third year, and declined to  $0.580 \pm 0.150$  for individuals older than 4 years.

### Climate effects on adult survival

The goodness-of-fit tests of the Cormack–Jolly–Seber model to estimate adult survival indicated that models fitted the data satisfactorily ( $\chi^2 = 22.4$ ,  $df = 45$ ,  $P = 0.998$ ). Model selection provided evidence that recapture probabilities did not differ between years, periods or sexes, and was  $0.405 \pm 0.053$  (Supporting Information Table S3). There was also evidence that survival probabilities did not differ between sexes and periods. ANODEV tests provided statistical support for the effect of two covariates on adult survival (Table S3): the Sahel rainfall index in September was positively related to survival ( $\beta = 0.358 \pm 0.165$ ; 95% confidence interval (95% CI) 0.036–0.681;  $r^2 = 35\%$ ; Fig. 4), and the winter NAO index was negatively related to survival ( $\beta = -0.467 \pm 0.192$ ; 95% CI  $-0.843$  to  $-0.091$ ;  $r^2 = 42\%$ ; Fig. 4).

### Density-dependence

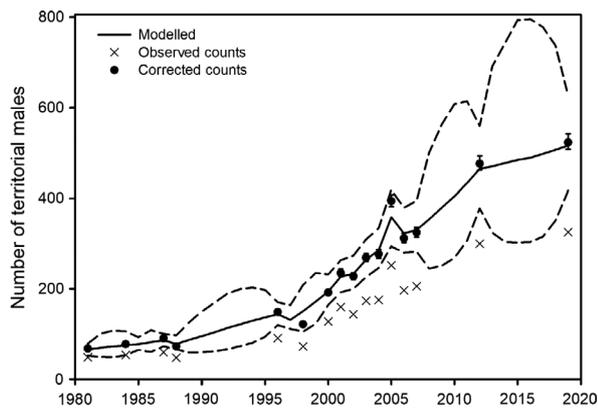
The Gompertz state-space model estimated numbers of territorial males that were close to the corrected observed counts (Fig. 5) and suggested strong evidence for density-dependence in abundance of Scops Owls (Supporting Information Table S4). There was no effect of the number of territorial males on adult survival (ANODEV:  $F_{1,12} = 1.162$ ,  $P = 0.302$ ), clutch size ( $P = 0.085$ ) or hatching success ( $P = 0.637$ ). However, there was a negative relationship with fledging success ( $\beta = -0.00059 \pm 0.00017$ ,  $P < 0.001$ ) and breeding success ( $\beta = -0.00053 \pm 0.0002$ ,  $P = 0.009$ ; Supporting Information Fig. S6).



**Figure 4.** Relationships between adult survival of Scops Owls breeding at Oléron Island, France, Sahel rainfall index in September, and North Atlantic Oscillation (NAO) in December, January, February and March. Filled circles indicate survival as a function of year. Plain line indicates the modelled relationships. Dashed lines indicate 95% confidence intervals. Error bars are  $\pm$  se.

### Population dynamics

The observed population growth rate over the period 1981–2019 was 1.055, indicating that the number of territorial males increased at a rate of 5.5% per year. The stochastic population growth rate predicted by the matrix population model was 0.647. The discrepancy between observed and modelled population growth rate was probably due to juvenile survival, which was particularly low (0.052). A juvenile survival probability of 0.482 was needed for the stochastic growth rate ( $1.055 \pm 0.002$ ) to correspond to the observed growth rate. Prospective analyses indicated that the population growth rate showed the highest elasticity to juvenile survival, clutch size, hatching



**Figure 5.** Population dynamics of Scops Owls at Oléron Island, France, between 1981 and 2019. Observed counts of territorial males are indicated by crosses. Filled circles indicate counts corrected for detection probability and spatial heterogeneity (see Bavoux *et al.* 2011). Plain line indicates abundance estimates based on a Gompertz model including an effect of density-dependence. Dashed lines indicate 95% confidence intervals of the Gompertz model. Error bars indicate 95% CI of the counts.

success and fledging success, followed by the proportion of breeders older than age 2, survival at older age-classes and the proportion of breeders at age 1 (Table 2). Retrospective analyses suggested that juvenile survival made the largest contribution to variance of the population growth rate (Table 2), followed by fledging success. Clutch size, survival at age 1, survival at age 4 and older, and fledging success had intermediate contributions. Other parameters made the smallest contributions. The reproductive value was 0.24 for the first, third and fourth age-classes and was 0.27 for the second age-class. Generation time was estimated at 2.4 years.

## DISCUSSION

Our study provides detailed information on the demographic parameters, fitness parameters, population dynamics and effects of climate variability on survival of the Scops Owl using one of the most complete datasets available. Results indicate a long-term increase of the population on Oléron Island. From a demographic point of view, this increase seemed mainly to be due to high survival during the first 2 years of life and to high clutch size, and to a lesser extent to high adult survival or fledging success. Density-dependence was detected in this increasing population, with a slight

**Table 2.** Demographic parameter mean value, sensitivity and elasticity of population growth rate in demographic parameters, and their contribution to variance of the population growth rate for Scops Owls on Oléron Island between 1984 and 2008. Numbers in parentheses indicate process variance.  $\phi_i$  indicates survival of juveniles and age-classes 1–4, CS indicates clutch size, HS indicates hatching success, FS indicates fledging success, and Pbi indicates accession to first reproduction at age 1 and 2.

Parameter	Estimate	Sensitivity	Elasticity	Contribution
$\phi_0$	0.482 (0.331)	1.046	0.514	0.119872
$\phi_1$	0.536 (0.044)	0.466	0.211	0.000420
$\phi_2$	0.734 (0.044)	0.211	0.172	0.000086
$\phi_3$	0.580 (0.044)	0.129	0.083	0.000032
$\phi_4$	0.580 (0.044)	0.231	0.149	0.000103
CS	4.060 (0.282)	0.126	0.541	0.001263
HS	0.790 (0.001)	0.621	0.514	< 0.000001
FS	0.730 (0.120)	0.704	0.535	0.007137
Pb1	0.816	0.198	0.137	–
Pb2	1.000	0.335	0.390	–

negative effect on fledging and breeding success. The results showed that climate conditions in the overwintering area of Scops Owls affected yearly survival, with rainy conditions in the Sahel zone and in northwest Africa during autumn and winter favouring survival.

## Demographic tactic of the Scops Owl

Scops Owls present a demographic tactic typical of highly reproductive species on the slow–fast gradient of life-histories (Gaillard *et al.* 1989, Saether & Bakke 2000). The oldest known bird from our database was 5 years old, and the oldest age recorded in the wild for Scops Owls is 6 years and 10 months from the Euring database. Generation time was low, i.e. intermediate between the Collared Flycatcher *Ficedula albicollis* or the House Sparrow *Passer domesticus* and the Barn Owl *Tyto alba* or the Mauritius Kestrel *Falco punctatus* (Jones *et al.* 2008). All age-classes contributed nearly equally to the total reproductive value as expected for such a demographic tactic (Sæther *et al.* 2013). Accordingly, the highest elasticities of the population growth rate were for juvenile

survival and fecundity parameters, followed by breeding proportions and by survival of older age-classes. Interestingly, age-specific survival indicated that survival at age 3 was relatively high (0.734), but declined to 0.580 for older age-classes. Confidence intervals on age-specific survival probabilities were large but this result suggests senescence and early age at onset of senescence (3 years), as expected from the relationships between senescence rate, age at onset of senescence and generation time in birds and mammals (Jones *et al.* 2008).

### Relationships between survival and winter climate in Africa

As found in other European trans-Saharan migratory species (Kanyamibwa *et al.* 1989, Barbraud *et al.* 1999, Johnston *et al.* 2016, Millon *et al.* 2019, Boano *et al.* 2020), there was a positive effect of Sahel rainfall on survival. For the Scops Owl, the results suggest that September precipitation conditions in the Sahel are important. Over the course of the study (1981–2019), the amount of September rainfall increased slightly (slope  $\pm$  se =  $8.298 \pm 3.073$ , Student's *t*-test = 2.701,  $P = 0.01$ ; Supporting Information Fig. S7; Panthou *et al.* 2018), indicating favourable overwintering conditions for Scops Owls and other trans-Saharan migrants. Interestingly, there was also a negative relationship between winter NAO and survival. The effects of NAO have recently been documented on survival of Palaearctic trans-Saharan migrants (Johnston *et al.* 2016) but not in others (Boano *et al.* 2020). We suspect that the negative association between winter NAO and the amount of precipitation and vegetation productivity in the Mediterranean and northwestern African regions (Stige *et al.* 2006, Vicente-Serrano & Trigo 2011) partly explains this relationship. As most Scops Owl populations, including our study population, appear to winter further south in the sub-Saharan zone, this would suggest an effect of climate conditions on stopover sites. No temporal trend was detected for the winter NAO during the study period (slope  $\pm$  se =  $-0.305 \pm 0.305$ , Student's *t*-test =  $-1.002$ ,  $P = 0.323$ ; Supporting Information Fig. S7). The effect sizes (standardized slopes) of Sahel rainfall and winter NAO on survival were similar (*z*-test = 0.431,  $P = 0.667$ ) and explained 57% of the deviance in survival,

revealing a similar importance of climate conditions on both overwintering grounds and stopover sites and migration routes. Further knowledge of the wintering areas and migration routes of different populations is therefore required fully to understand how climate processes affect survival of Scops Owls along their migratory flyway and within their overwintering distribution. This could be achieved in the near future thanks to the miniaturization of electronic tracking devices.

### Demography and population dynamics of Scops Owls in a landscape with agricultural abandonment

Our results indicate that between 1981 and 2019, the population of Scops Owls at Oléron Island increased. The retrospective analysis suggests that this increase was mainly due to high survival of juveniles and first-year birds and high fecundity parameters (particularly clutch size and fledging success), and to a lower extent due to high adult survival. Our mean apparent survival estimate (excluding juveniles) was  $0.611 \pm 0.083$ , very similar to the apparent survival of adult Scops Owls in northwest Italy ( $0.58 \pm 0.07$ , Boano & Silvano 2015) and to other small owl species (Newton *et al.* 2016) but higher than the one reported for Scops Owls in southeast Spain ( $0.40 \pm 0.04$ , Parajo *et al.* 2018) and lower than adult survival estimated for larger owl species (Newton *et al.* 2016). The results indicate that overwintering conditions in sub-Saharan Africa were favourable for Scops Owls given the positive trend in Sahel rainfall.

Juvenile survival appeared as a key demographic parameter regarding its contribution to the variance in population growth rate and the high sensitivity and elasticity of population growth rate to this parameter. However, our initial estimate of juvenile apparent survival was clearly biased downwards (0.052). We suspect this could be explained by two non-mutually exclusive hypotheses: natal dispersal of juveniles outside the study area and natal dispersal of juveniles outside our network of nestboxes. Natal dispersal of juvenile Scops Owls is unknown and, despite evidence for natal philopatry, distance of natal dispersal is highly variable in owls (Korpimäki & Lagerstrom 1988, Luna *et al.* 2020). In addition, Scops Owls are known to use different types of cavities for breeding as well as abandoned nests of Eurasian Magpie, Common Crow and Woodpigeon

(Bavoux *et al.* 2011, Grieco 2018). Therefore, we strongly suspect that a significant proportion of philopatric juvenile Scops Owls bred in tree cavities and in nests of other species, where they could not be monitored. This could also explain the relatively low proportion of occupied nestboxes. Nevertheless, juvenile survival was deduced from the inconsistency between the observed and predicted population trajectory, and we cannot exclude other explanations to explain this discrepancy. Although we lacked data on immigration, we speculate that it was probably extremely low, as the overall population abundance of Scops Owls in France has been declining since the 1980s (Barnagaud & Caupenne 2015, Herrando *et al.* 2020) and continental areas nearby Oléron Island host very small breeding densities (our pers. obs.). Fecundity parameters recorded in our study were very similar to those reported elsewhere in the literature (del Hoyo *et al.* 1999). Our apparent adult survival estimate was similar (albeit slightly higher) than the one reported by Boano and Silvano (2015) using mist-nets and capture–recapture models. We cannot exclude that our population size estimation was biased, but it is extremely unlikely that such a bias would explain the entire discrepancy. Therefore, it is likely that most of the discrepancy was due to low apparent juvenile survival.

The Scops Owl population trend is uncertain in Europe due to a lack of large-scale monitoring data (Herrando *et al.* 2020). Between the early 1990s and the 2010s, the species seems to have expanded its range northward in eastern Europe, but range retractions were observed in northwest France and west of the Iberian Peninsula (Herrando *et al.* 2020). Contrary to the negative population trend in France during 1980–2012 (Barnagaud & Caupenne 2015), our results indicate that the Oléron Island population has increased over the past 39 years. This suggests that this increase was partly driven by local factors. Indeed, the increase coincided with a major ( $\approx 65\%$ ) decrease of intensive farming areas. This is consistent with the hypothesis that Scops Owls declines have been driven by changes in land use, namely agricultural changes that occurred in Europe, accelerated by the Common Agricultural Policy, leading to an intensification of agricultural practices and losses of some habitats, resulting in changes in resource availability (Bavoux *et al.* 1997). Indeed, fecundity parameters (clutch size and breeding success) of Scops Owls at Oléron Island were relatively high (Cramp 1985, del Hoyo

*et al.* 1999, Marchesi & Sergio 2005), suggesting high prey availability, which contributed heavily to the variation in population growth rate. The main prey of Scops Owls are large insects such as Great Green Bush-crickets, Lepidoptera and stick insects (Bavoux *et al.* 1993), which are particularly vulnerable to intensive agricultural practices relying on pesticide use and frequent ploughing. Thus, on Oléron Island the replacement of areas of intensive agriculture with areas of woodland, wooded areas, shrubs and wasteland due to abandonment of farming practices (Bavoux *et al.* 2012) has probably favoured large insect populations (Hallmann *et al.* 2017, Pilotto *et al.* 2020). This is also in line with results from habitat selection studies on Scops Owls on Oléron Island, suggesting that the density of singing males was positively influenced by the importance of wooded areas resulting from abandonment of farming practices, and negatively influenced by urbanized areas (Bavoux *et al.* 2012). This is consistent with conclusions from studies on habitat use at other localities (Treggiari *et al.* 2013, Denac *et al.* 2019) but not entirely with others. For example, Denac (2009) found a negative effect of settlements but also of the surface area of woodland on Scops Owl occupation in Slovenia. These differences may reflect differences in the types of woodland habitats between Oléron Island and Slovenia. In addition, in December 1999, forests on Oléron Island were affected by one of the strongest hurricanes (Martin) that France has suffered in centuries (Ulbrich *et al.* 2001). This resulted in openings in the forests, which were occupied by male Scops Owls during the following breeding seasons (C. Bavoux unpubl. data). Therefore, we cannot exclude that hurricane Martin created good habitats for Scops Owl and contributed to the population increase during the 2000s.

Our results suggest that the population increase induced a density-dependent response, probably through an increased mortality of chicks between hatching and fledging. Several mechanisms may explain the negative effect of density-dependence on fledging success. First, as the population increased, nest-sites may have become limited and some individuals may have been forced to breed in poor quality nest-sites, thereby increasing chick mortality in the nest. However, we think this is unlikely, as the occupancy rate in nestboxes remained stable and relatively low during the study period. Secondly, direct competition for

food resources may have played a role. Scops Owls are single-prey loaders and feed their chicks 35.4 times per night on average (min = 19, max = 69, Bavoux *et al.* 1993). Assuming that chicks are cared for over 35 days, the population increase from  $\approx 80$  pairs in the early 1980s to  $\approx 450$  pairs in the late 2000s would correspond to an increase from  $\approx 107\,400$  to  $\approx 604\,200$  captured prey items during the chick-rearing period. However, the densities of prey populations are unknown on Oléron Island and would require further studies and monitoring (Jeliazkov *et al.* 2016).

Although density-dependence affected fledging success, breeding success and population abundance, this does not necessarily mean that the species was not limited by resources during the first years of the study period. Indeed, more intensive agricultural practices occurred during this period, with potentially less prey available for Scops Owls, potentially generating density-dependence. During the latter part of the study, although agricultural abandonment was probably an important driver of the increase in population size, prey abundance may have also been limiting (Fig. 5 suggests that the rate of population increase was lower during the latter part of the study).

A potential limitation of our study is that the demographic parameters were all estimated using nestbox monitoring. Therefore, we cannot exclude that some parameters were biased. For example, juvenile and adult survival estimates might have been biased downwards if some individuals had abandoned nestboxes for natural sites, where they remained undetected and considered dead in the context of the capture–recapture analysis. Demographic parameters may also have been biased by the location of the nestboxes depending on nearby prey abundance and habitat quality, as nestboxes were not set up entirely randomly for logistical reasons (Fig. S2). However, to our knowledge this is currently the only way to study fecundity parameters and age-related survival rates for this species, as natural nests are extremely difficult to detect and to access in order to mark birds and measure fecundity parameters. Boano and Silvano (2015) and Parejo *et al.* (2018) used mist-netting to study Scops Owls but could only estimate adult survival. Reassuringly, Vidal *et al.* (1984) found similar clutch sizes and numbers of fledged chicks for Scops Owls breeding in natural cavities or in nestboxes in southern France, suggesting little bias caused by fecundity parameters due to nestboxes.

## Implications for conservation

Several efficient conservation measures could be implemented. First, given the current restricted knowledge of the population trends of the species, there is a clear and urgent need to evaluate accurately trends of Scops Owl populations in different habitats and geographical regions of its breeding distribution range. Long-term monitoring of population abundance and demographic parameters is therefore needed to assess population dynamics in arable farmland landscapes and in landscapes with less intensive agricultural practices.

Secondly, further studies are required to assess diet outside the breeding season in wintering areas, to estimate the effects of exposure to pesticides and to understand the migratory tactics of different populations of Scops Owls.

Thirdly, changes in agricultural practices on breeding and non-breeding grounds should be favoured to enhance the species' environment, habitat quality and food availability. Organic farming and ban of pesticides may help, as well as enhancement of more extensive agricultural practices allowing the maintenance of hedges, grasslands, shrubs and orchards favoured by Scops Owls. Therefore, incentives are urgently needed to sustain traditional farming practices.

Finally, the effects of climate change on Scops Owls remain unclear. On breeding grounds, although hurricane Martin had possible positive effects on the reproductive habitat of Scops Owls on Oléron Island, whether it occurred as a result of climate change and enhanced greenhouse gas effects remains highly uncertain (Ulbrich *et al.* 2001). Current climate model projections suggest increases in rainfall in the central and eastern Sahel, and thus favourable climatic conditions for Scops Owls as indicated by our results, but they also suggest decreases in the westernmost regions characterized by more intense and intermittent rainfall (Kirtman *et al.* 2013, Biasutti 2019), although there is uncertainty in future climate projections.

Particular thanks are due to C. Lemarchand, L. Macouillard, L. Mimaud, M. Picard and several trainees of 'Le Marais aux Oiseaux' (Wildlife Rescue Centre in Oléron Island) for help during fieldwork. We thank K. Delord for useful discussions and comments on a previous version of the manuscript. All ringing data used in this

study were collected by qualified, licensed volunteer bird ringers under the coordination of Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Muséum National d'Histoire Naturelle. We thank two anonymous reviewers for their useful comments on an earlier version of the manuscript.

## AUTHOR CONTRIBUTIONS

**Christophe Barbraud:** Conceptualization (lead); Formal analysis (lead); Methodology (lead); Validation (equal); Visualization (equal); Writing-original draft (lead); Writing-review & editing (equal). **Christian Bavoux:** Data curation (lead); Investigation (equal); Validation (equal); Writing-original draft (supporting); Writing-review & editing (equal). **Guy Burneleau:** Data curation (lead); Investigation (equal); Validation (equal); Visualization (equal); Writing-original draft (supporting); Writing-review & editing (equal).

## Data Availability Statement

Data and R code for the analyses in this study are available upon request from the corresponding author.

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Received 7 December 2020;  
revision accepted 21 June 2021.  
Associate Editor: Alexandre Millon

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Fig. S1.** Location of point counts used to monitor the abundance of hooting male Scops Owls on Oléron Island between 1981 and 2019.

**Fig. S2.** Location of next boxes for Scops Owls on Oléron Island during the period 1984–1990 (left) and 2000–2008 (right).

**Fig. S3.** Number of times (years) each nest box was sampled during the periods 1984–1999 and 2000–2008. Numbers indicate proportions of nest boxes sampled during one or multiple years.

**Fig. S4.** Aerial photographs illustrating habitat changes around Saint-Pierre-d'Oléron, France between 1957 (right) and 2018 (left). Maps were downloaded from <https://remonterletemps.ign.fr/comparer>.

**Fig. S5.** Number of installed nest boxes at Oléron Island during the periods 1984–1999 and 2000–2008, number of nest boxes occupied by Scops Owls and proportion occupied.

**Fig. S6.** Relationships between breeding success, fledging success and the estimated number of territorial male Scops Owls on Oléron Island for the periods 1984–1990 and 2000–2008. Dots represent mean annual values ( $\pm$  SE), plain line is the predicted relationship from the individual nest data with 95% confidence intervals (dotted line).

**Fig. S7.** Time series of winter NAO (December, January, February, March) a, Sahel rainfall index in September between 1981 and 2019.

**S1.** Estimating climate effects on adult survival

**S2.** Density-dependence using the Gompertz model

**S3.** Estimating accession to reproduction

**Table S1.** Modelling age-specific probabilities of accession to reproduction of Scops Owls ringed as chicks on Oléron Island, France (1984–2008).

**Table S2.** Modelling age-specific survival probabilities of Scops Owls ringed as chicks on Oléron Island, France (1984–2008).

**Table S3.** Modelling climate effects on adult survival probabilities of Scops Owls on Oléron Island, France (1984–2008).

**Table S4.** Estimates and 95% highest posterior density (HPD) of the parameters of the stochastic Gompertz model testing for density dependence of the number of territorial males of Scops Owls on Oléron Island, 1981–2019.