



Long-term decline despite conservation efforts questions Eurasian Stone-curlew population viability in intensive farmlands

ELIE GAGET,^{1,2,3*}  REMI FAY,¹ STEVE AUGIRON,^{1,4} ALEXANDRE VILLERS^{1,5}  & VINCENT BRETAGNOLLE^{1,6}

¹Centre d'Etudes Biologiques de Chizé, UMR 7372, CNRS and Université de La Rochelle, 79360 Beauvoir sur Niort, France

²Tour du Valat, Institut de recherche pour la conservation des zones humides Méditerranéennes, 13200 Le Sambuc Arles, France

³Muséum National d'Histoire Naturelle, Centre d'Ecologie et des Sciences de la Conservation-CESCO - UMR 7204 MNHN-CNRS-UPMC, 43 rue Buffon, 75005 Paris, France

⁴GeolinkX, P-A Côte Rousse, 180 rue du Genevois, 73000 Chambéry, France

⁵INRA, Biostatistics & Spatial Processes (BioSP), Domaine Saint-Paul, Site Agroparc, 84914 Avignon, France

⁶LTSER 'Zone Atelier Plaine & Val de Sèvre', CNRS, 79360 Beauvoir sur Niort, France

Agricultural intensification over the past decades has led to a generalized decline in farmland biodiversity. Farmland birds are particularly exposed to rapid changes in habitat and reduced food resources or availability. Understanding how farmland specialists can be preserved and their populations enhanced are major challenges for this century. Based on a long-term (19-year) study of a Eurasian Stone-curlew *Burhinus oedicnemus* population, we estimated the demographic parameters, including clutch size, egg volume, hatching success, survival rate and apparent population size. Demographic rates found for this French population were, on average, comparable to those found elsewhere in Europe. However, all demographic parameters showed negative trends, including a dramatic decline in the local population (26% decline over 14 years) and a 10% decline in adult survival rate over 11 years. Such a long-term decline, despite on-going conservation efforts, calls into question the overall sustainability of arable Stone-curlew populations. We infer some of the possible causes of this decline, in particular food shortage, and discuss how this pattern could be reversed through conservation measures applicable at very large spatial scales.

Keywords: breeding, *Burhinus oedicnemus*, demographic rate, farmland birds, population dynamics, population monitoring, protection status.

Agricultural expansion over the last 10 000 years has created a complex mosaic of landscapes which replaced primeval forests and steppe habitats (Kaplan *et al.* 2009). Extensive farming allowed the colonization of these new habitats by numerous species of birds, usually of steppe origin (O'Connor & Shrubbs 1986). However, over the past century, intensive agriculture has replaced traditional farming, a trend that has been accelerated

by the Common Agricultural Policy (CAP) in Western Europe since 1962. CAP-induced changes in agricultural practices are a major cause of farmland biodiversity loss, especially birds (Krebs *et al.* 1999, Donald *et al.* 2001). Farmland specialist birds have been extensively studied to understand the multifactorial causes of decline linked to intensive farming practices (Aebischer & Ewald 2012, Kentie *et al.* 2013, Chiron *et al.* 2014, Barré *et al.* 2018). However, the breeding ecology of several farmland birds, including some threatened species, and the detailed mechanisms by which they are

*Corresponding author.
 Email: elie.gaget@gmail.com

affected by intensive farming practices, still remain to be elucidated in many cases (Fuller *et al.* 1995, Chamberlain *et al.* 2000, Heldbjerg *et al.* 2017, Stanton *et al.* 2018).

The Eurasian Stone-curlew *Burhinus oedicnemus* (Charadriiformes, Burhinidae; hereafter Stone-curlew) is a steppic Palaearctic bird occurring in European farmlands and pseudo-steppes (Vaughan & Vaughan-Jennings 2005). The species suffered a rapid and important population decline over the second half of the last century (Cramp & Simmons 1983). However, despite the scarcity and imprecision of national trend data, its European conservation status has remained in the 'least concern' category, with an estimated 53 400–88 200 pairs in the EU (BirdLife International 2017). Indeed, the population trend is unknown for 46% of European countries, shows positive trends for only 14%, is stable or fluctuating for 21% and is negative for 18% (BirdLife International, 2017). Apart from countries where the species is highly localized (e.g. in the UK), trends should probably be best considered tentative. A decrease in geographical range and breeding population was reported in France over the second half of the 20th century (Yeatman-Berthelot & Jarry 1994), with an estimated breeding population of 5000–9000 pairs between 1980 and 1993 (Malvaud 1996), with most recent estimates for the French population size of c. 19 000–28 000 breeding pairs (Issa & Muller 2015). In the UK, the situation in the 1980s was almost desperate, but over the last three decades, owing to a major conservation effort of the RSPB (Evans & Green 2007), the population reached c. 400 breeding pairs (Eaton *et al.* 2011).

Stone-curlew population monitoring data are scarce because there are very few long-term field studies that could provide accurate trends, partly because of the elusive behaviour, shyness and excellent camouflage of the species. In addition, Stone-curlew breeding habitat choice is surprisingly flexible: any kind of habitat with drained soils, low vegetation height and density, and stones on the ground to optimize anti-predation strategies for this cryptic species, seems to fulfil its habitat requirements (Green *et al.* 2000). Breeding habitat includes heathlands, semi-natural grasslands, pseudo-steppes, gravel riverbeds, vineyards, orchards, spring-sown crops and brownfields (Vaughan & Vaughan-Jennings 2005). Conservation success in the UK relied to a large extent on detailed

breeding biology and habitat selection studies (Gibbons *et al.* 1996) which helped shape Agri-Environmental Scheme (AES) implementation (Grice *et al.* 2007). The latter mainly consisted of nesting plots in an uncultivated area within spring-sown crops of 1–2 ha, away from field boundaries and near pastureland (Evans & Green 2007). However, implementing this AES elsewhere in Europe requires extended knowledge of the breeding biology of the species, either in arable crops or in more natural steppic or pseudo-steppe habitats.

France, with 21% of the European population, represents the second largest European breeding population after Spain (BirdLife International 2017). In France, farmland landscapes are the major breeding habitat, with over 60% of breeding pairs being located in arable crops of the central-western region (Malvaud 1996, Issa & Muller 2015). In such habitat, however, the species is threatened by nest destruction through agricultural work (Berg *et al.* 2002, Whittingham & Evans 2004), and chick survival as well as adult fitness are potentially threatened by a decrease in food resources, which is known adversely to affect farmland specialists (Donald *et al.* 2001). The aim of this study was to assess the status and trends (over 19 years) of demographic parameters of a Stone-curlew population breeding in an intensive farmland landscape and benefiting indirectly from agri-environmental conservation measures.

METHODS

Study area and conservation measures

The Long Term Social-Ecological Research site (LTSER) 'Zone Atelier Plaine & Val de Sèvre' (<http://www.za.plainevalsevre.cnrs.fr/>, Bretagnolle *et al.* 2018) is located within an intensively managed farmland area in the Poitou-Charentes Region, Deux-Sèvres district, central-western France (Fig. 1). The site covers 450 km² of farmland, where crops are dominated by winter annuals (cereals c. 40% and rapeseed c. 15% of the arable surface), followed by spring crops (sunflower 15% and maize 10%) and perennial covers (10%; Bretagnolle *et al.* 2018). The plain lies upon a Jurassic sedimentary basin, with well-drained and poor soil, typical of a rendzina (INRA 1998).

Half of the LTSER was designated as a Special Protected Area (SPA Natura2000, FR5412007, 207.6 km²) in 2004 due to the presence of 17

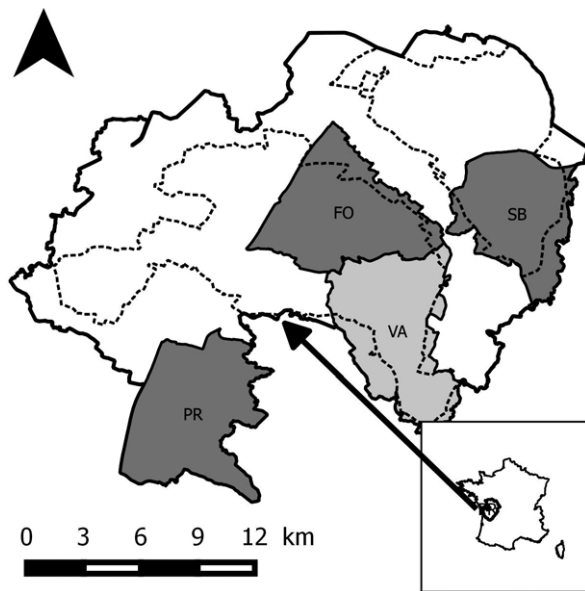


Figure 1. Map of the study area, the Long-term Social-Ecological Research Site (LTSER) 'Zone Atelier Plaine & Val de Sèvre'. The grey polygons correspond to the four sub-sites used for the survey of the Stone-curlew population, of which 'VA' in light grey corresponds to the monitoring sub-site. The dotted lines delimit the Special Protected Area (SPA Natura2000, FR5412007).

species listed in Annex I of the Birds Directive. Some AES have been implemented on the LTSER since 1999, but since 2004, AES have been implemented more strongly within the framework of the CAP (Bretagnolle *et al.* 2011, Berthet *et al.* 2012). AES have been mainly targeted toward the conservation of Little Bustards *Tetrax tetrax* and consist of increasing grassland cover and fodder crops, decreasing mowing frequency in alfalfa and permanent grasslands from May to August in order to limit nest destruction and the killing of incubating females, and banning pesticides to increase food resources for the chicks (Bretagnolle *et al.* 2011). Up to 10 000 ha of contracts have been established (Bretagnolle *et al.* 2011, Caro *et al.* 2016). These measures have increased the overall amount of preserved nesting habitat as well as food resources for many farmlands birds (Bretagnolle *et al.* 2011, Brodier *et al.* 2014). Stone-curlews breeding on the LTSER have thus probably benefited from habitats that were on average of higher quality regarding food resources. In addition, since the beginning of monitoring in 1998, the species has benefited from an awareness programme aimed at farmers on a sub-site of 4300 ha

(the one where all breeding parameters were collected for this study, see VA sub-site below): nests found following intensive searches were reported to farmers, and nest locations were marked in the field, to avoid destruction during agricultural work. Overall, measures to improve food availability as well as nest protection were expected to maintain, if not increase, reproductive investment (clutch size, egg volume and hatching rate) and hence population size on the VA sub-site.

Stone-curlew breeding biology

Breeders were monitored in a delimited sub-site of the LTSER of c. 4300 ha (hereafter, VA), over 19 consecutive years (1998–2016). Each year, from March to June, all fields with favourable vegetation height (< 15 cm) were monitored on a weekly basis (approximately 200–400 fields covering 500–1200 ha). Nests were located from distant vantage points by using a telescope (20 × 60 mm) and subsequently visited to determine breeding stage precisely. The first visit usually occurred before hatching, when egg biometric measurements allowed the determination of laying and hatching dates with the use of a calibration density curve (Hoyt 1979, V. Bretagnolle unpubl. data, Fig. S1). Egg weight, length and width were recorded (precision of 0.1 g and 0.1 mm, respectively; Table S1). Egg density (mass/volume), which decreases during incubation (Green & Griffiths 1994), was used to estimate egg laying date at a precision of 1.52 days (V. Bretagnolle unpubl. data, Fig. S1). Pairs were then re-checked at least once a week to ensure they were still present and incubating. The nests were re-visited if pairs were not observed for two consecutive days, or around the hatching date, to determine the fate of the clutch (hatching, destruction by agricultural work, desertion/predation). Because it was not possible to determine with certainty whether an empty nest had been deserted before eggs were removed by a predator, we used a single category 'desertion/predation'. If at the first nest visit, eggs had already hatched and chicks were still close to the nest, the laying date was retrospectively calculated with reference to the incubation period of 26 days (Vaughan & Vaughan-Jennings 2005) and the chicks' age (estimated with a precision of 2.6 days with the use of a wing measure calibration curve, V. Bretagnolle unpubl. data; Fig. S2).

For each nest, laying date was thus obtained (for two-egg clutches, the mean laying date) and expressed in Julian calendar days, starting from 1 March. Clutches from July to early September (< 3% of recorded breeding events) were discarded from the analyses because observation pressure during those months varied over time. Stone-curlews are able to lay replacement clutches after nest failure, as well as true second clutches (Vaughan & Vaughan-Jennings 2005). To estimate the number of breeding attempts per pair, we used a mixture distribution method (log-normal, Bealey *et al.* 1999) using the observed distribution of the laying dates (R package 'mixdist', Macdonald & Du 2012). We parameterized the model with the laying date of nests with ringed breeding birds ($n = 130$) and then fitted it on the complete dataset ($n = 513$). This analysis is a combination of the Newton-type method and the estimate mean algorithm (O'Neil 1971). The unconstrained model finds a set of overlapping distributions of laying dates (we used three log-normal distributions, accounting for the possibility of three successive clutches for a given pair) that provides the best fit to grouped data. The quality of the model (comparison between observed data and estimated distributions) was tested with a Chi-square goodness-of-fit test (Macdonald & Du 2012).

Temporal trends in breeding parameters were then evaluated successively in different models. Trends in laying date, clutch size and egg volume were investigated using a generalized linear model (GLM) with either a Gaussian error distribution (laying date and egg volume) or a binomial error distribution (clutch size, modelling the probability of a one- or two-egg clutch). For the laying date, we tested the temporal trend over years on two subsets: over the breeding season (from March to June) and over the first half of the first breeding attempts, which does not include replacement clutches (from March to 27 April). For egg volume and clutch size, we considered the effect of laying date and its interaction with year (Christians 2002). Nest fate was investigated using the Mayfield model based on a maximum likelihood approach. Compared with the initial Mayfield model (Mayfield 1975), no assumption about when the failure occurs is required, and covariates can be easily incorporated (Rotella 2014). We used a multi-state model to include directly the two identified causes of failure, i.e. 'destroyed by agricultural work' or 'deserted/predated' (Darrah

et al. 2018). We tested whether nest survival and causes of failure changed according to year, laying date and clutch size considering linear relationships. Additionally, we tested the effect of the interaction between laying date and year. Nest survival from laying until hatching was calculated by raising the daily survival rate to the power of 26 (i.e. the incubation period) and the corresponding variance was estimated by the delta method (Powell 2007). Nest fate model building and parameter estimates were obtained using E-SURGE v.1.8.5 (Choquet *et al.* 2009a). For all these models investigating the breeding parameters and their temporal trend, we used a model selection inference with corrected Akaike information criterion (AICc). The ability of two models to describe the data was assumed to be identical if the difference in their AICc was < 2. However, in particular cases where models within the two units of the best model have only one more parameter, the larger model is not necessarily supported or competitive. A closer examination considering the deviance is required to see whether the fit is really improved, or whether the model is 'close' in terms of AICc because it adds only one parameter (Burnham & Anderson 2002). In the latter case, we selected the most parsimonious model (i.e. that with the lowest number of parameters).

Trend in apparent population size

To evaluate the trend in population size, two different methods were used. First, counts were performed every year on four different sub-sites from 2003 to 2016, totalling 16 000 ha including the monitoring VA sub-site (Fig. 1). All ploughed fields (an area of *c.* 3000 ha), i.e. those sown with sunflower or maize (vegetation height under 15 cm), were systematically inspected for 1–5 min according to field size and topography. Observations were carried out at the beginning of May over 8–15 days (the precise dates varied from year to year according to spring crop growth). As the LTSER is very varied in topography and cropping systems, there were substantial differences between the four sub-sites. Observations were always performed in good sighting conditions (no heavy rainfall or heat haze), usually at 07:00–11:00 h and 16:00–20:00 h. As detection probability was not accounted for, we measured apparent population size rather than true population size. We used a GLM with a Poisson error-

distribution (and log link) with a hypothesis testing approach (i.e. based on P -value with $\alpha = 0.05$) to test for the temporal trend in abundance, number of pairs detected (simply defined as two birds seen together in the same field) and number of fields occupied by one or more birds. Explanatory variables included: sub-site identity (a factor with four levels), year (as a continuous variable) as well as their interaction. In addition, the surface of the surveyed area and the number of fields surveyed, which varied between years and sub-sites, were entered as offsets after log-transformation. Because 75% of the observers were involved for only 1 year, and only 5% for more than 3 years, we did not include observer identity in a mixed effect modelling framework. We investigated whether residuals displayed spatial autocorrelation thanks to a spatial variogram (R package 'spatial', Venables & Ripley 2002). The exponential growth rate of the abundance was extracted from the year term.

The second monitoring survey relied on the breeding biology monitoring scheme (see above) and concerned only the VA sub-site, where a thorough nest search was carried out every year from March to June. The long-term trend in number of nests was tested using a generalized additive model with a smoothed term on the year (GAM, Gaussian error distribution) and a hypothesis testing approach (based on P -value with $\alpha = 0.05$). However, as the monitored period differed slightly between years, we tabulated the number of pairs for the extended period (15 March–30 June) and for reduced, better standardized periods: 15 March–30 May and 1 April–10 May.

Survival rates

Stone-curlews were captured in the monitored breeding sub-site VA from 2005 between March and September. Birds were ringed with a metal ring (National Museum of Natural History, MNHN, Paris, France) and a combination of two or four colour rings (<http://cr-birding.org/node/89>). Chicks were ringed only if older than 10 days. Between 2005 and 2015, 93 adults and 68 chicks/fledglings were ringed, resulting in a total of 254 re-sightings. Adult bodyweight (g) and wing length (mm) were measured for captures ($n = 57$) and recaptures ($n = 6$). Body condition was estimated using the scale mass index (SMI) that explicitly accounts for the allometrical relations (Peig &

Green 2009). Body mass was standardized for a given size using the following equation:

$$\widehat{M}_i = M_i * \left[\frac{L_0}{L_i} \right]^{b_{sma}}$$

Where \widehat{M}_i is the predicted body mass for individual i when the body measure is standardized to L_0 , an arbitrary value of L . M_i and L_i are the body mass and the body measurement of individual i , respectively; b_{sma} is the scaling exponent estimated.

Survival estimates were obtained by capture–recapture analysis using a Cormack–Jolly–Seber model. Parameters directly estimated by the model were ϕ , the apparent survival probability, and p , the re-sighting probability. To avoid over-parameterization, we used a two-step model selection procedure. First, we selected the best model structure based on a full general model with an AICc-based model selection. Secondly, we assessed the presence of a trend over the study period on juvenile and adult survival, and tested the possible effect of body condition at capture year t on adult survival in year $t + 1$. In our general model, survival probability was age- and sex-dependent. For the effect of age, we distinguished two classes, juvenile (first year) and adult (> 1 year; Green *et al.* 1997). Re-sighting probability was time- and sex-specific because brooding is mainly performed during the day by the female (preventing rings from being read), and the male is predominantly in the 'spotter' position (V. Bretagnolle pers. obs.). We considered only an additive effect of time for re-sighting probability because an interactive effect with sex leads to an over-parameterized model. Thus our general model was $\phi_{juv.sex\ ad.sex} p_{t+sex}$ where juvenile is denoted by 'juv', adult by 'ad', additive effect by '+' and interactive effect by '.'. To assess the effect of body condition on survival, we included in the best model the logistic regression: $\text{logit}(\phi) = \beta_0 + \beta_1 \times x_i$, where ϕ is the survival probability the year following the first capture, β_0 is an intercept parameter, β_1 is a slope parameter, and x_i is the body condition of individual i at first capture time. Model building, model selection (AICc, Burnham & Anderson 2002) and parameter estimates were obtained using E-SURGE (v.1.8.5, Choquet *et al.* 2009a). The model selection method was identical to that presented above (see section on breeding biology). Following Grosbois *et al.* (2008), we used a likelihood ratio test (LRT, hypothesis testing approach,

$\alpha = 0.05$) to estimate the significance of a trend in survival, because residual survival variation is null after integrating. We performed goodness-of-fit (GOF) tests using the program U-CARE (v.2.3.2, Choquet *et al.* 2009b). Finally, the temporal trend in body condition index was tested under a hypothesis testing approach ($\alpha = 0.05$) with a linear mixed effect model (LMM), with year and date of capture as fixed effects and individual as a random effect.

All statistical analyses were run in R 3.2.0 (R Development Core Team 2015). For GLM and LMM, residuals of the models were checked using graphic methods to verify the assumptions of normality, non-overdispersion and homoscedasticity. Means are presented \pm sd unless stated otherwise.

RESULTS

Breeding biology

Over the 19 survey years, 566 nests were found, of which 513 provided an estimated laying date. Nests with at least one ringed bird ($n = 130$) allowed us to confirm the existence of true second clutches after a successful attempt (i.e. double brooding, $n = 5$) and even that of pairs having three successive breeding attempts ($n = 2$). After successful fledging (at the age of 50 days, Green *et al.* 1997) or a breeding failure, a new reproductive attempt was started on average 13.5 ± 4.2 days later (range 10–20 days, $n = 5$). The first peak of laying dates was around 18 April (Fig. 2, median of the log-normal distribution around 27 April \pm 17 days), with the earliest clutch being laid on 15 March. The second peak of laying dates was around 22 May (Fig. 2, median of the log-normal distribution around 25 May \pm 11 days). A few late clutches were laid by the end of June (Fig. 2). Some laying occurred up to mid-September, although these were not included in the analysis for protocol consistency (< 3% of nests). The mixture distribution model provided an estimate of 1.17 ± 0.11 breeding attempts per pair ($\chi^2_5 = 5.66$, $P = 0.34$). Most clutches (85.0%, $n = 533$) were two-egg clutches (mean 1.85 ± 0.36 eggs), although some one-egg clutches may have been two-egg clutches subject to accidental loss or partial predation. On average, two- and one-egg clutches were visited respectively 9.9 ± 6.9 and 13.0 ± 7.7 days after the laying date. In addition, the first visit occurred in the

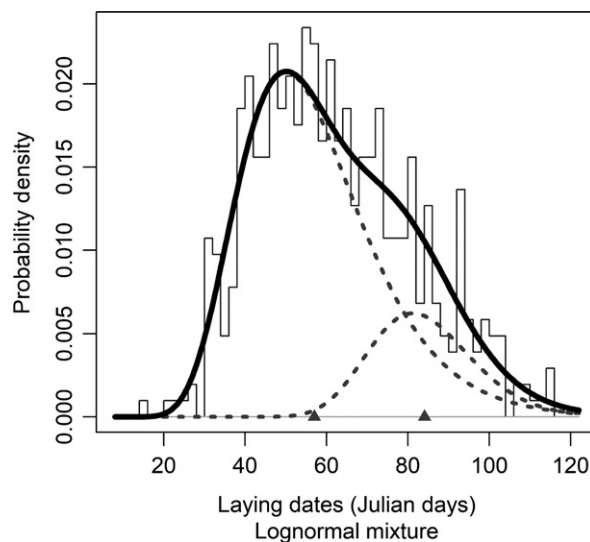


Figure 2. Distribution of laying dates (histogram, $n = 513$, 1998–2016), of the fitted log-normal distributions (dotted lines, see Methods) and of the total fitted laying date (thick line). The x-axis represents the laying date in Julian days since 1 March (31 = 1 April, 61 = 1 May, 92 = 1 June). The laying peaks are around 18 April and 22 May, and the medians (triangles on the x-axis) are around 27 April and 25 May.

first 3 days after laying for 24% and 14% of the two- and one-egg clutches, respectively.

On average, raw hatching success was $53 \pm 15\%$, which was reduced to $32 \pm 3\%$ after correction using the Mayfield method ($n = 441$). Desertion/predation accounted for $85 \pm 3\%$ of clutch failures, and direct destruction caused by mechanical agricultural work caused $15 \pm 3\%$ of failures. Once nests were discovered, however, they were marked and farmers were immediately informed and asked to avoid them during farm work. The proportion of nests lost due to agricultural activity is expected to be higher during the period between egg-laying and nest detection, and therefore nest destruction from sowing or hoeing was probably underestimated. There was no strong evidence that clutch size had an effect on nest survival or on the cause of failure (i.e. each Akaike information criterion size had $\Delta\text{AICc} > 2$, Tables 1 and S2).

Long-term and seasonal trends in breeding parameters

Model selections provided support for a temporal trend for all breeding parameters, except laying date (Table 1). We found that nest survival and

Table 1. Results from model selection testing for a linear effect of time (period 1998–2016) on laying date (LD), nest survival, nest desertion/predation probability given failure, clutch size and egg volume.

Model	k	DEV	AICc	Δ AICc	Slope 1	Slope 2	Interaction
Laying date (March–June)							
Constant model	1	4492.6	4496.7	0.0			
Year	2	4491.8	4497.8	1.1	-0.21 ± 0.14		
Laying date (March–27 April)							
Constant model	1	1702.2	1706.2	0.0			
Year	2	1701.2	1707.2	1.0	0.10 ± 0.10		
Nest survival							
Year + LD + Year:LD	10	1245.0	1265.0	0.0	-0.95 ± 0.27	-0.42 ± 0.16	0.53 ± 0.27
Year + LD	9	1249.0	1267.0	2.0	-0.44 ± 0.08	-0.15 ± 0.08	
Nest desertion/predation probability given failure							
Year + LD	10	1245.0	1265.0	0.0	0.79 ± 0.25	0.85 ± 0.25	
Year + LD + Year:LD	11	1244.7	1266.8	1.8	0.39 ± 0.79	0.63 ± 0.47	0.49 ± 0.92
Clutch size							
Year	2	399.3	403.4	0.0	0.22 ± 0.13		
Constant model	1	402.2	404.2	0.8			
Year + LD	3	398.9	404.9	1.5	0.22 ± 0.13	-0.09 ± 0.13	
Egg volume							
Year + LD + Year:LD	4	4052.2	4062.3	0.0	-0.23 ± 0.10	-0.57 ± 0.10	0.19 ± 0.09
Year + LD	3	4055.2	4063.2	1.0	-0.22 ± 0.10	-0.57 ± 0.10	

Tested variables include the laying date (LD) for all breeding parameters, excluding the laying date, and clutch size for nest survival and nest desertion/predation probability given failure. For each model, results include the number of parameters (k), deviance (DEV), AIC value corrected for small sample size (AICc), difference between current model and the best model within each sub-set of model (Δ AICc) and the estimated slope and intercept \pm se of the highest ranked model. '+' indicates an additive effect and ':' an interaction. All covariates were standardized. Only the highest ranked models (Δ AICc \leq 2) are shown. Details of other models are given in Table S2.

egg volume had declined over the study duration by 80% and 2%, respectively (Fig. 3). Decrease in nest survival over the years was the consequence of increasing desertion/predation rate, which varied from $30 \pm 9\%$ at the beginning of the study period (1998) to $80 \pm 4\%$ during the last years (2014–2016, Fig. S3). Over the same period, destruction rate was relatively stable at around $11 \pm 4\%$ (Fig. S3). Results suggested an increase in clutch size over time, but evidence for this trend was weak, as the constant model was also in the best model set (Δ AICc = 0.8). Within years, we found clear support for a seasonal trend in all breeding parameters, except clutch size (Tables 1 and S2). Nest survival and egg volume decreased over the breeding season (Table 1). The cause of failure also changed, with the highest proportion of nests lost due to desertion/predation for late clutches (Table 1, Fig. S4). Finally, the results provided moderate support for a positive interaction between laying date and year on nest survival and egg volume (Δ AICc = 2 and 1, respectively), suggesting that the negative seasonal trend previously described has been attenuated over the study duration (Table 1). An interaction

between laying date and year was not supported as the cause of failure and clutch size (Tables 1 and S2).

Trends in apparent population size

Using data from the four sub-sites, we found that abundance decreased significantly over the 14 years (Fig. 3, GLM, $\beta = -0.03$, $z = -3.1$, $P = 0.002$) with an exponential growth rate of $r = 0.979$, 95% CI: 0.958–0.989. The same results were verified for the number of pairs detected (GLM, $\beta = -0.03$, $z = -2.0$, $P = 0.05$) and for the number of occupied fields (GLM, $\beta = -0.03$, $z = -2.9$, $P = 0.004$). The sub-site effect was significant as well as its interaction with year for the three investigated variables (total abundance, number of pairs and number of occupied fields, $P < 0.0001$). In the VA sub-site, the values were significantly higher and trends were more negative ($P < 0.0001$). The PR sub-site, outside of the SPA, was not significantly different from the FO and SB sub-sites in mean or interaction effects ($P > 0.4$). No significant linear or polynomial trends were detected for the number of nests

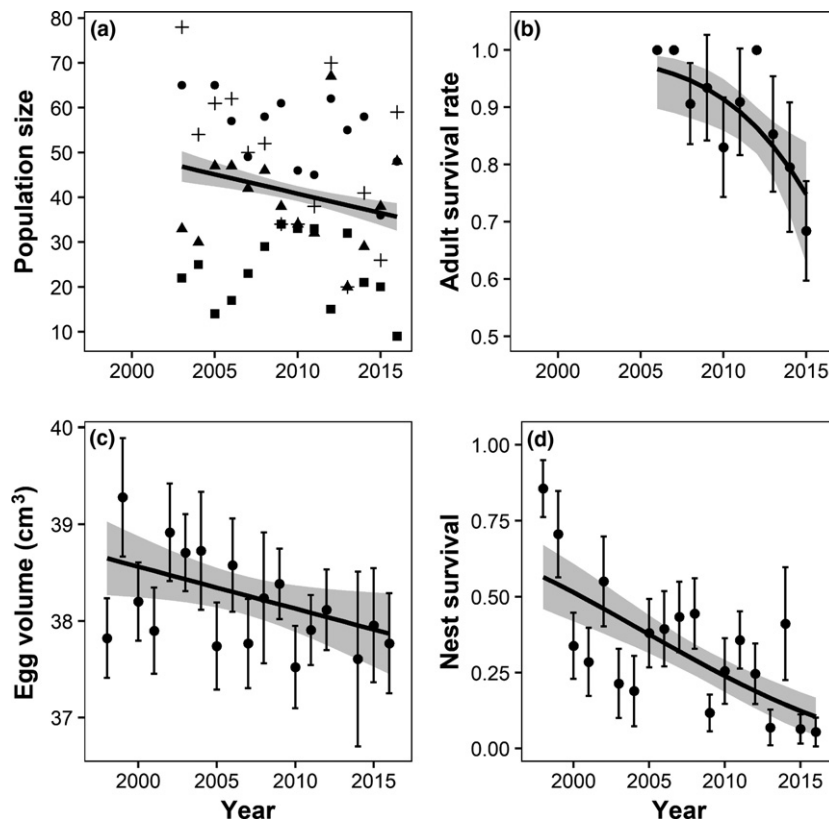


Figure 3. Trends in (a) population size (four sub-sites: cross for VA, triangle for PR, circle for FO and square for SB), (b) adult apparent survival rate \pm se, (c) egg volume \pm se and (d) nest survival \pm se. The predicted values were extracted from the corresponding GLMs (see Methods) and shown with their 95% CI. All trends are significant.

found at the VA sub-site, irrespective of the survey period retained (GAM, $P > 0.05$; Fig. S5).

Survival rates

Goodness of fit tests ($\chi^2 = 52.7$, $P = 0.60$) provided no indication of lack of fit. The first step of model selection suggested that resighting probability was time- and sex-specific (Table 2). As expected, males had an average resighting probability higher than that for females (males 0.76, 95% CI: 0.62–0.86; females 0.53, 95% CI: 0.38–0.67). We did not find any evidence for sex-specific survival rates, but there was strong support for different apparent survival rates between juveniles and adults (Table 2, M5 vs. M8 Δ AICc = 14.92). Juvenile survival was 0.55 (95% CI: 0.41–0.69) and adult survival was 0.88 (95% CI: 0.83–0.91). For the second step of the model selection, LRT supported a linear trend in adult survival over the study period ($F_{\text{cst}/\text{trend}/t} = 8.11$, $P = 0.004$;

Table S3), with an average decrease in apparent survival of 2.3% per year (Fig. 3). Finally, adult body condition index (average mass = 490.0 ± 38.6 g) decreased, but not significantly, over the study period (LMM, $\beta = -2.00$, $t_{1,89} = -1.67$, $P = 0.23$). We found a positive relationship between body condition and female adult survival (Table S3).

DISCUSSION

Our study provides detailed information on the breeding biology and population trends of the Stone-curlew using one of the longest time-series available, and the only available one for France. In addition, the study was located in one of the strongholds of the species, the Poitou-Charentes region, which harbours *c.* 13–21% of the French population (Issa & Muller 2015). Our results indicate a long-term decline in this population. Such a decline, despite on-going conservation efforts, calls

Table 2. Survival (ϕ) and resighting (p) modelling as a function of age and sex between 2005 and 2015.

No.	Model	k	DEV	AICc	Δ AICc
Resighting					
1	$p_{\text{sex}+t}$	22	797.43	844.02	0
2	p_{sex}	10	826.31	846.85	2.84
3	p_t	21	802.57	846.93	2.91
4	p_{cst}	9	831.31	849.76	5.74
Survival: sex effect					
5	$\phi_{\text{juv_ad}}$	20	798.07	840.21	0
6	$\phi_{\text{juv.sex_ad}}$	21	797.76	842.11	1.90
7	$\phi_{\text{juv_ad.sex}}$	21	797.80	842.16	1.95
1	$\phi_{\text{juv.sex_ad.sex}}$	22	797.43	844.02	4.78
Survival: age effect					
5	$\phi_{\text{juv_ad}}$	20	798.07	840.21	0
8	ϕ_{cst}	19	815.20	855.13	14.92

Results of model selection include: number of mathematical parameters (k), the deviance (DEV), AIC value corrected for small sample size (AICc) and difference between the current model and the best model within each sub-set of models (Δ AICc). The final selected model is in bold type. For model notation, 'juv' indicates juvenile, 'ad' indicates adult, 'cst' indicates a constant parameter, '+' indicates an additive effect and '.' indicates an interactive effect.

into question the overall sustainability of arable Stone-curlew populations.

Breeding success and survival rate in an intensive farmland landscape

Within a European context, the observed nest survival rate and survival of individuals in this study are comparable to those obtained for the UK, Spain and Italy (Table S4). Nest destruction due to agricultural work was responsible for 11% of nest failures in our study, mainly occurring at a very early stage of incubation, i.e. before signalling the presence of the nest to the farmers, and which is underestimated. The rate of nest destruction without protection was estimated at 33% in 2001 and nearly 50% in 2012 (V. Bretagnolle unpubl. data), thus constituting the major threat encountered by the species in such farmland habitat. Additionally, predation has been reported as the main cause of nest failure (Solis & Lope 1995, Bealey *et al.* 1999) and probably accounts for most of the desertion/predation events reported in this study, even if the effect of crop growth was not estimated. Some one-egg clutches could also have resulted from partial egg predation before the first nest visit. The increase in desertion/predation over time could result either from a reduction in nest

protection, given that parents in weak body condition cannot ensure proper parental care such as nest defence or nest attendance after predator encounters (Winkler 1992), or by an increase in the predator populations.

The long-term decline of the Stone-curlew in intensive farmlands

All investigated demographic parameters displayed negative trends over time. Although apparent rather than true survival rate was estimated, which may not exclude permanent emigration from the study area (an unlikely scenario given the species is known to be highly philopatric; Green 1990), a decrease in adult survival is of concern for population stability, as population growth rate is highly sensitive to adult mortality in long-lived species (Sæther & Bakke 2000). Although this study took place at a relatively small spatial scale (c. 4300 ha), which may limit the generality of the conclusions, this population benefitted from AES dedicated to the preservation of trophic resources for farmland birds (Bretagnolle *et al.* 2011) and from active nest protection from agricultural work. Consequently, the decrease in breeding success and survival which resulted in a rapid population decline (26% in 14 years) occurred in what could be described as the best current possible conditions for the species in intensive French agricultural landscapes.

Which factors, affecting both survival and breeding process, may have caused the population decline? As suggested, nest destruction during sowing or mechanical weeding is a well-known major factor, but with limited impact in our case thanks to the nest awareness programme. In addition, we suggest that food limitation may play an important but often overlooked role. Of particular interest in this respect is the decrease in egg volume (2% in 19 years), despite AES implementation since the first years of monitoring, enhancing overall habitat quality (Bretagnolle *et al.* 2011). Within a given season, a decrease in egg volume is found in many bird species, as in our population, due to early breeders being of higher quality than late breeders (Christians 2002, Verhulst & Nilsson 2008). However, food availability can also affect egg volume (Robb *et al.* 2008). Agricultural intensification is considered a key factor which adversely impacts the diversity and abundance of insects (Donald *et al.* 2001, Johnson 2007, Geiger *et al.* 2010).

Recent studies have demonstrated a relationship between widespread application of pesticides, neonicotinoids in particular, with concomitant declines in insect and plant communities, and decreases in insectivorous or granivorous birds (Mineau & Whiteside 2013, Hallmann *et al.* 2014, Gilburn *et al.* 2015). The diet of the Stone-curlew is based on earthworms and beetles (Amat 1986, Green *et al.* 2000). Even though a detailed analysis of food availability and diet may be lacking in our study, it is perhaps relevant to note that *Poecilus cupreus*, the most abundant carabid species in our study site (Marrec *et al.* 2015), has shown an average 80% decline in 20 years (V. Bretagnolle unpubl. data). A further mechanism which may be involved in the decrease in adult survival is that of carry-over effects in wintering areas (Harrison *et al.* 2011). Preliminary data from GPS tracking of our breeding population has indicated a fairly high diversity of wintering sites (France, Portugal and Morocco, V. Bretagnolle & Groupe Ornithologique des Deux-Sèvres unpubl. data).

Implications for conservation

The French Stone-curlew population has been claimed to have increased in the period 2001–2011 (BirdLife 2017). We question this conclusion, especially given the absence of standardized and dedicated protocols to monitor Stone-curlews in France, and the cryptic nature of the species. We suggest these positive trends actually result from an increase in survey quality, i.e. a better knowledge of the species habitat, and better data transfer from observers (Issa & Muller 2015). Based on our results, we suggest that Stone-curlews breeding in farmland habitats may be currently in decline. Indeed, many farmland birds, especially the largest species, are currently highly threatened. For some, a dedicated AES framework has proved useful (e.g. Verhulst *et al.* 2007, Bretagnolle *et al.* 2011), despite AES having been much criticized in the early years of its implementation (Kleijn & Sutherland 2003). AES schemes dedicated to Stone-curlews are non-existent in France, whereas in the UK, such AES schemes consist of fallow plots providing suitable breeding and foraging areas (Natural England 2010). In our study area, however, we expected the species to have potentially benefited from AES dedicated to the Little Bustard. Such practices may provide suitable habitat for the Stone-curlew and improve

food availability (Bretagnolle *et al.* 2011, Caro *et al.* 2016). However, despite the fact that up to 10 000 ha of AES were established within the LTSER (43 000 ha), Stone-curlew demographic parameters have been declining. AES at a field scale may not be appropriate because this species forages over large areas (Green *et al.* 2000). Nevertheless, AES for Stone-curlews can work, as the RSPB Stone-curlew programme has successfully demonstrated (Evans & Green 2007). However, the success of this latter programme required a strong investment in fieldworkers, applied research, networking and funds for some hundreds of breeding pairs.

In our case, there are possible efficient conservation measures that could be implemented at a far larger spatial scale. Given the current restricted knowledge of this species, there is a clear and urgent need to evaluate accurately whether this decline is general (at the nationwide scale) or restricted to some specific agricultural areas. Implementing long-term monitoring of demography and breeding parameters in this and other French populations is therefore needed to assess the potentially widespread and generic decline of the species, not only in arable farmland landscapes, but also in all semi-natural or artificial habitats. This would require an assessment of: (1) the spatial distribution and population size at the country scale; (2) local/regional population trends in several habitats; (3) diet in and outside the breeding season; (4) the effects of predation and human disturbance; (5) exposure to pesticides; and (6) migratory strategies.

The creation of safe habitats to reduce brood destruction and promote food availability, based on the UK experience (Thompson *et al.* 2004), should be explored. If similar patterns of population decline were to be confirmed in other parts of France, such conservation plots should be established over hundreds of thousands of hectares to be efficient, given the very large breeding distribution of Stone-curlew. It should be also adapted to a range crops (e.g. maize, sunflower, grasslands, vineyard). This would be challenging, as it would require either pro-active campaigns targeting farmers to adopt voluntary practices, or a consistent funding scheme to compensate for the potential yield loss to farmers at very large scales (Evans & Green 2007), in a context of budgetary restriction in agricultural subsidies. Alternatively, we may target the species environment and habitat rather than

the species itself. For instance, to improve food availability, a reduction or ban of inputs may be targeted. Some AES, organic farming or the recent complete ban of neonicotinoids in France may help. An increase of perennial crops, such as grasslands, and the enhancement of more extensive practices should be strongly promoted as they support higher prey resources (Bretagnolle *et al.* 2011, Badenhauer & Cordeau 2012, Caro *et al.* 2016).

We would like to thank C. Attié, V. Rocheteau, M. Liaigre, R. Bonnet, A. Millon, A. Desternes as well as all fieldworkers who have helped to collect these data over the years and spent much time in the field, and L. Inchboard for improving the English text. Partial funding was allocated by DREAL Poitou-Charentes and Fondation LISEA to V.B. We also thank the reviewers for their very helpful comments and suggestions.

REFERENCES

- Aebischer, N.J. & Ewald, J.A.** 2012. The grey partridge in the UK: population status, research, policy and prospects. *Anim. Biodivers. Conserv.* **35**: 353–362.
- Amat, J.A.** 1986. Information on the diet of the Stone Curlew *Burhinus oedicephalus* in Doñana, southern Spain. *Bird Study* **33**: 71–73.
- Badenhauer, I. & Cordeau, S.** 2012. Sown grass strip – A stable habitat for grasshoppers (Orthoptera: Acrididae) in dynamic agricultural landscapes. *Agric. Ecosyst. Environ.* **159**: 105–111.
- Barré, K., Le Viol, I., Julliard, R. & Kerbiriou, C.** 2018. Weed control method drives conservation tillage efficiency on farmland breeding birds. *Agric. Ecosyst. Environ.* **256**: 74–81.
- Bealey, C.E., Green, R.E., Robson, R., Taylor, C.R. & Winspear, R.** 1999. Factors affecting the numbers and breeding success of Stone Curlews *Burhinus oedicephalus* at Porton Down, Wiltshire. *Bird Study* **46**: 145–156.
- Berg, Å., Jonsson, M., Lindberg, T. & Källebrink, K.G.** 2002. Population dynamics and reproduction of Northern Lapwings *Vanellus vanellus* in a meadow restoration area in central Sweden. *Ibis* **144**: 131–140.
- Berthet, E.T., Bretagnolle, V. & Segrestin, B.** 2012. Analyzing the design process of farming practices ensuring Little Bustard conservation: lessons for collective landscape management. *J. Sustain. Agric.* **36**: 319–336.
- BirdLife International** 2017. *European Birds of Conservation Concern: Populations, Trends and National Responsibilities*. Cambridge: BirdLife International.
- Bretagnolle, V., Villers, A., Denonfoux, L., Cornulier, T., Inchausti, P. & Badenhauer, I.** 2011. Rapid recovery of a depleted population of Little Bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme. *Ibis* **153**: 4–13.
- Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., Badenhauer, I., Monceau, K., Allier, F., Monestiez, P. & Gaba, S.** 2018. Towards sustainable and multifunctional agriculture in farmland landscapes: lessons from the integrative approach of a French LTSE platform. *Sci. Total Environ.* **627**: 822–834.
- Brodier, S., Augiron, S., Cornulier, T. & Bretagnolle, V.** 2014. Local improvement of Skylark and Corn Bunting population trends on intensive arable landscape: a case study of the conservation tool Natura 2000. *Anim. Conserv.* **17**: 204–216.
- Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*, 2nd edn. New York: Springer.
- Caro, G., Marrec, R., Gauffre, B., Roncoroni, M., Augiron, S. & Bretagnolle, V.** 2016. Multi-scale effects of agri-environment schemes on carabid beetles in intensive farmland. *Agric. Ecosyst. Environ.* **229**: 48–56.
- Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubbs, M.** 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J. Appl. Ecol.* **37**: 771–788.
- Chiron, F., Chargé, R., Julliard, R., Jiguet, F. & Muratet, A.** 2014. Pesticide doses, landscape structure and their relative effects on farmland birds. *Agric. Ecosyst. Environ.* **185**: 153–160.
- Choquet, R., Rouan, L. & Pradel, R.** 2009a. Program E-SURGE: a software application for fitting multievent models series. *Environ. Ecol. Stat.* **3**: 845–865.
- Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.-M. & Pradel, R.** 2009b. U-CARE: utilities for performing goodness of fit tests and manipulating CAPTURE-RECAPTURE data. *Ecography* **32**: 1071–1074.
- Christians, J.K.** 2002. Avian egg size: variation within species and inflexibility within individuals. *Biol. Rev.* **77**: 1–26.
- Cramp, S. & Simmons, K.E.L.** 1983. *The Birds of the Western Palearctic Volume III*. New York, NY: Oxford University Press.
- Darrah, A.J., Cohen, J.B. & Castelli, P.M.** 2018. A Bayesian multinomial logistic exposure model for estimating probabilities of competing sources of nest failure. *Ibis* **160**: 23–35.
- Development Core Team, R.** 2015. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Donald, P.F., Green, R.E. & Heath, M.F.** 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B* **268**: 25–29.
- Eaton, M.A., Balmer, D.E., Cuthbert, R., Grice, P.V., Hall, J., Hearn, R.D., Holt, C.A., Musgrove, A.J., Noble, D.G., Parsons, M., Risely, K., Stroud, D.A. & Wotton, S.** 2011. *The State of the UK's birds 2011*. Sandy: RSPB, BTO, WWT, CCW, JNCC, NE, NIEA & SNH.
- Evans, A.D. & Green, R.E.** 2007. An example of a two-tiered agri-environment scheme designed to deliver effectively the ecological requirements of both localized and widespread bird species in England. *J. Ornithol.* **148**: 279–286.
- Fuller, J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, I.D., Baillie, S.R. & Carter, N.** 1995. Population declines and range contractions among lowland farmland birds in Britain. *Cons. Biol.* **9**: 1425–1441.
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharrntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantagenest, M., Clement, L.W.,**

- Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W. & Inchausti, P. 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic App. Ecol.* **11**: 97–105.
- Gibbons, D.W., Avery, M., Baillie, S., Gregory, R., Kirby, J., Porter, R., Tucker, G. & Williams, G. 1996. *Bird Species of Conservation Concern in the United Kingdom, Channel Isles and Isle of Man: Revising the Red Data List*. Sandy: RSPB Conservation Review No. 10.
- Gilburn, A.S., Bunnefeld, N., Wilson, J.M., Botham, M.S., Breton, T.M., Fox, R. & Goulson, D. 2015. Are neocotinoid insecticides driving declines of widespread butterflies? *PeerJ* **3**: e1402.
- Green, R.E. 1990. Saving the stone curlew. *Sanctuary Bull.* **19**: 37–39.
- Green, R.E. & Griffiths, G.H. 1994. Use of preferred nesting habitat by Stone Curlews *Burhinus oedicanus* in relation to vegetation structure. *J. Zool.* **233**: 457–471.
- Green, R.E., Hodson, D.P. & Holness, P.R. 1997. Survival and movements of Stone Curlews *Burhinus oedicanus* ringed in England. *Ring. Migr.* **18**: 24–34.
- Green, R.E., Tyler, G.A. & Bowden, C.G.R. 2000. Habitat selection, ranging behavior and diet of the stone curlew (*Burhinus oedicanus*) in southern England. *J. Zool.* **250**: 161–183.
- Grice, P., Radley, G., Smallshire, D. & Green, M. 2007. Conserving England's arable biodiversity through agri-environment schemes and other environmental policies: a brief history. *Aspects Appl. Biol.* **81**: 7–22.
- Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P. & Weimerskirch, H. 2008. Assessing the impact of climate variation on survival in vertebrate populations. *Biol. Rev.* **83**: 357–399.
- Hallmann, C.A., Foppen, R.P.B., van Turnhout, C.A.M., de Kroon, H. & Jongejans, E. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* **511**: 341–343.
- Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. 2011. Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.* **80**: 4–18.
- Heldbjerg, H., Sunde, P. & Fox, A.D. 2017. Continuous population declines for specialist farmland birds 1987–2014 in Denmark indicates no halt in biodiversity loss in agricultural habitats. *Bird Conserv. Int.* **28**: 278–292.
- Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* **96**: 73–77.
- INRA 1998. *La base de données géographique des sols de France au 1/1 000 000*. Paris: INRA, Service d'étude des sols et de la carte pédologique de France.
- Issa, N. & Muller, Y. 2015. *Atlas des oiseaux de France métropolitaine; nidification et présence hivernale*. Paris: Delachaux & Niestlé.
- Johnson, M.D. 2007. Measuring habitat quality: a review. *Condo* **109**: 489–504.
- Kaplan, O.J., Krumhardt, K.M. & Zimmermann, N. 2009. The prehistoric and preindustrial deforestation of Europe. *Quat. Sci. Rev.* **28**: 3016–3034.
- Kentie, R., Hooijmeijer, J.C., Trimbos, K.B., Groen, N.M. & Piersma, T. 2013. Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. *J. Appl. Ecol.* **50**: 243–251.
- Kleijn, D. & Sutherland, W. 2003. How effective are European agri-environmental schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* **40**: 947–963.
- Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. 1999. The second silent spring? *Nature* **400**: 611–612.
- Macdonald, P. & Du, J. 2012. *mixdist: finite mixture distribution models. R package version 0.5-4*. Available at: <http://cran.r-project.org/web/packages/mixdist/index.html>. (accessed 16 May 2011) (08 February 2013)
- Malvaud, F. 1996. *L'Oedicnème criard en France, (Burhinus oedicanus)*. Caen: Groupe Ornithologique Normand.
- Marrec, R., Badenhausser, I., Bretagnolle, V., Börger, L., Roncoroni, M., Guillon, N. & Gauffre, B. 2015. Crop succession and habitat preferences drive the distribution and abundance of carabid beetles in an agricultural landscape. *Agric. Ecosyst. Environ.* **199**: 282–289.
- Mayfield, J. 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**: 456–466.
- Mineau, P. & Whiteside, M. 2013. Pesticide acute toxicity is a better correlate of U.S. grassland bird declines than agricultural intensification. *PLoS ONE* **8**: e57457.
- Natural England 2010. *Entry Level Stewardship: Environmental Stewardship Handbook*, 3rd edn. Sheffield: Natural England. February 2010.
- O'Connor, R.J. & Shrubbs, M. 1986. *Farming and Birds*. Cambridge: Cambridge University Press.
- O'Neill, R. 1971. Algorithm AS 47. Function minimization using a simplex procedure. *Appl. Stat.* **20**: 338–345.
- Peig, J. & Green, A.J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* **118**: 1883–1891.
- Powell, L.A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *Condor* **109**: 949–954.
- Robb, G.N., McDonald, R.A., Chamberlain, D.E. & Bearhop, S. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* **6**: 476–484.
- Rotella, J.J. 2014. Nest survival models. In Cooch, E. & White, G., eds. *Program MARK: A gentle introduction. Chapter 17*: 20 p. Available at: <http://www.phidot.org/software/mark/docs/book/> (accessed 5 May 2018).
- Sæther, B.E. & Bakke, Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**: 642–653.
- Solís, J.C. & Lope, F. 1995. Nest and egg crypsis in the ground-nesting Stone Curlew *Burhinus oedicanus*. *J. Avian Biol.* **26**: 135–138.
- Stanton, R.L., Morrissey, C.A. & Clark, R.G. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. *Agric. Ecosyst. Environ.* **254**: 244–254.
- Thompson, S., Hazel, A., Bailey, N., Bayliss, J. & Lee, J.T. 2004. Identifying potential breeding sites for the Stone Curlew (*Burhinus oedicanus*) in the UK. *Agric. Ecosyst. Environ.* **12**: 229–235.
- Vaughan, R. & Vaughan-Jennings, N. 2005. *The Stone Curlew Burhinus oedicanus*. Falmouth: Isabelline Books.
- Venables, W.N. & Ripley, B.D. 2002. *Modern Applied Statistics with S*, 4th edn. New York, NY: Springer.
- Verhulst, S. & Nilsson, J.-Å. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated

timing of breeding. *Philos. Transact. R. Soc. Lond.* **363**: 399–410.

- Verhulst, J., Kleijn, D. & Berendse, F.** 2007. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. *J. Appl. Ecol.* **44**: 70–80.
- Whittingham, M.J. & Evans, K.L.** 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* **146**: 210–220.
- Winkler, D.W.** 1992. Causes and consequences of variation in parental defence behaviour by tree swallows. *Condor* **94**: 502–520.
- Yeatman-Berthelot, D. & Jarry, G.** 1994. *Nouvel Atlas des Oiseaux nicheurs de France. 1985-1989*. Paris: Société Ornithologique de France.

Received 29 May 2017;
revision accepted 24 June 2018.
Associate Editor: Niall Burton.

SUPPORTING INFORMATION

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

Table S1. Egg biometrics of the two-egg (smallest and largest egg) and one-egg clutches (single egg).

Table S2. Details of the model selection on laying date (LD), nest survival, nest desertion/predation probability given failure, clutch size and egg volume.

Table S3. Testing for decreasing juvenile and adult survival from 2005 to 2015 and body condition effect on adult survival.

Table S4. Demographic parameters of Stone-curlew populations in the European context.

Figure S1. Calibration density curve for eggs, to determine the laying date with the egg biometric measurements (data collected in captivity or directly in the field, V. Bretagnolle, unpubl. data; Augiron 2007).

Figure S2. Calibration wing length curve for chicks, to determine the hatching date (data collected in captivity or directly in the field, V. Bretagnolle, unpubl. data; Augiron 2007).

Figure S3. Desertion/predation and destruction rate over the study duration.

Figure S4. Proportion of nest failure due to desertion or predation as a function of laying date (in comparison to the nest failure due to destruction by agricultural work).

Figure S5. Trend in number of nests during the three breeding period subsets in VA.