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DR. ELIE GAGET (Orcid ID : 0000-0003-3462-9686)

DR. ALEXANDRE VILLERS (Orcid ID : 0000-0003-3050-4106)

**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}

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

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

³ *CESCO, UMR 7204 UPMC-CNRS-MNHN, 55 rue Buffon, 75005 Paris, France*

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

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

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

elie.gaget@gmail.com; steve.augiron@geolinkx.com; fay.remi@gmail.com;

villers.alexandre@gmail.com; breta@cebc.cnrs.fr

Corresponding author.

Email: elie.gaget@gmail.com

Agricultural intensification over the past decades has led to a generalised 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 oedicanus* 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, questions 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: *Burhinus oedicanus*, breeding, demographic rate, farmland birds, population dynamics, population monitoring, protection status.

Agricultural expansion over the last 10000 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 in order 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 affected by intensive farming practices, still have 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; henceforth Stone-curlew) is a steppic Palearctic 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 under the 'least concern' category, with an estimated 53400 - 88200 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 as 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. 19000-28000 breeding pairs (Issa & Muller 2015). In the UK, the situation in the eighties 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 may 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 to negatively 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%, 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 species listed in Annex I of the Birds Directive. Some Agri-Environmental Schemes have been implemented on the LTSER since 1999, but since 2004, AES have been implemented more strongly within the framework of 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 program toward 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 those toward 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. 4 300 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 (20x60) 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 and V. Bretagnolle, unpubl. data, SOM1,). Egg weight, length and width were recorded (precision of 0.1 g and 0.1 mm, Table SOM1). Egg density (mass/volume), which decreases during incubation (Green 1994), was used to estimate egg laying date at a precision of 1.52 days (V. Bretagnolle, unpubl. data, SOM2). 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, or desertion/predation). Because it was not possible to determine with certainty if 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; SOM3).

For each nest, laying date was thus obtained (for 2-egg clutches, the mean laying date) and expressed in Julian days, starting from the 1st 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 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 χ^2 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) either with a Gaussian error distribution (laying date and egg volume) or with a binomial error distribution (clutch size, modelling the probability of a 1-egg clutch or a 2-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 the 27th of 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 to 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 if 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 AICc criteria. 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 if the fit is really improved, or rather if the model is 'close' in term of AICc because it adds only one parameter (Burnham and 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 minutes 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). Since 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 7-11 a.m. and 4-8 p.m. Since 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 in just one year, and only 5% more than three 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, since the monitored period differed slightly between years, we tabulated the number of pairs for the extended period (15th March - 30th June) and for reduced, better standardised periods: 15th March - 30th May, and 1st April - 10th 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 2 or 4 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, yielding to a total of 254 re-sightings. Adult body weight (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 allometric relationships (Peig & Green 2009). Body mass was standardized for a given size using the following equation:

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

where \hat{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. Second, 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 2 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 to be read), and the male is predominantly in the 'spotter' position (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: $\text{logit}(\Phi) = \beta_0 + \beta_1 * x_i$, 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 since residual survival variation is null after integrating. We performed goodness-of-fit (GOF) tests using 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 on R 3.2.0 (R Development Core Team 2015). For LM, GLM and LMM, residuals of the models were checked using graphical methods in order to verify the assumptions of normality, non-overdispersion and homoscedasticity. Means are presented \pm sd unless stated.

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 the 18th of April (Fig. 2, median of the log-normal distribution around the 27th of April \pm 17 days), with the earliest clutch being laid on the 15th of March. The second peak of laying dates was around the 22th of May (Fig. 2, median of the log-normal distribution around the 25th of 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 2-egg clutches (mean 1.85 ± 0.36 eggs), although some 1-egg clutches may have been 2-egg clutches subject to accidental loss or partial predation. On average, 2-egg and 1-egg clutches were visited respectively 9.9 ± 6.9 days and 13.0 ± 7.7 days after the laying date. In addition, the first visit occurred in the first three days after laying for 24% and 14% of the 2-egg and 1-egg clutches, respectively.

On average, raw hatching success was $53 \pm 15\%$, reduced to $32 \pm 3\%$ after correction using the Mayfield method ($n = 441$). Desertion/predation accounted for $85 \pm 3\%$ of clutch failures, while 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, nor on the cause of failure (i.e. each model including clutch size had $\Delta\text{AICc} > 2$, Table 1, SOM4).

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 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 that varied from $30 \pm 9\%$ at the beginning of the study period to $80 \pm 4\%$ during the last years. Over the same period, destruction rate was relatively stable at around $11 \pm 4\%$ (SOM5). Results suggested an increase in clutch size through time, but evidence for this trend was weak since the constant model was also in the best model set ($\Delta\text{AICc} = 0.8$). Within years, we found a clear support for a seasonal trend in all breeding parameters, except clutch size (Table 1, SOM4). 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, SOM6). Finally, the results provided moderate support for a positive interaction between laying date and year on nest survival and egg volume ($\Delta\text{AICc} = 2$ 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 (Table 1, SOM4).

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 to 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 found at the VA sub-site, irrespective of the survey period retained (GAM, $P > 0.05$; SOM7).

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 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 $\Delta AICc = 14.92$). 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 ($F_{cst/trend/t} = 8.11$, $P = 0.004$; SOM8), 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 (SOM8).

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 that 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 ongoing conservation efforts, questions 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 (SOM9). Nest destruction through agricultural work was responsible for 11% of nest failures in our study, which mainly occurred at a very early stage of incubation, i.e. before signalling the nest's presence 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 (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 1-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 populations of predators.

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 since population growth rate is highly sensitive to adult mortality in long-lived species (Sæther & Bakke 2000). While this study took place at a relatively small spatial scale (c. 4 300 ha), which may limit the generality of the conclusions, this population benefited 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) that 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 program. In addition, we suggest that food limitation may play an important, 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 ones (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 negatively impacts the diversity and abundance of insects (Donald *et al.* 2001, Johnson 2007, Geiger *et al.* 2010). Recent studies have demonstrated relationships 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.* 2016) has shown an average 80% decline in 20 years (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, 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 standardised and dedicated protocols to monitor Stone-curlew 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 declining. 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 criticised in the early years of implementation (Kleijn & Sutherland 2003). AES dedicated to Stone-curlews are non-existent in France, while in the UK, such AES 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 program has successfully demonstrated (Evans & Green 2007). However, the success of this latter program 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 accurately evaluate whether this decline is general (at the nation-wide 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, since 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 of farmers at very large scale (Evan & 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, in order 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, Badenhausser *et al.* 2012, Caro *et al.* 2016).

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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. Tested variables include the laying date ('LD') for all breeding parameters, excluding the laying date, and clutch size ('CS') 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 ($\Delta AICc$) and the estimated slope and intercept \pm se of the highest ranked model. '+' indicates additive effect and ':' an interaction. All covariates were standardized. Only the highest ranked models ($\Delta AICc \leq 2$) are shown. Details of other models are given in SOM4.

| Model | k | DEV | AICc | $\Delta AICc$ | 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 \pm 0.14 | | |
| Laying date (March-27thApril) | | | | | | | |
| constant model | 1 | 1702.2 | 1706.2 | 0.0 | | | |
| year | 2 | 1701.2 | 1707.2 | 1.0 | 0.10 \pm 0.10 | | |
| Nest survival | | | | | | | |
| year + LD + year:LD | 10 | 1245.0 | 1265.0 | 0.0 | -0.95 \pm 0.27 | -0.42 \pm 0.16 | 0.53 \pm 0.27 |
| year + LD | 9 | 1249.0 | 1267.0 | 2.0 | -0.44 \pm 0.08 | -0.15 \pm 0.08 | |
| Nest desertion/predation probability given failure | | | | | | | |
| year + LD | 10 | 1245.0 | 1265.0 | 0.0 | 0.79 \pm 0.25 | 0.85 \pm 0.25 | |
| year + LD + year:LD | 11 | 1244.7 | 1266.8 | 1.8 | 0.39 \pm 0.79 | 0.63 \pm 0.47 | 0.49 \pm 0.92 |
| Clutch size | | | | | | | |
| year | 2 | 399.3 | 403.4 | 0.0 | 0.22 \pm 0.13 | | |
| constant model | 1 | 402.2 | 404.2 | 0.8 | | | |
| year + LD | 3 | 398.9 | 404.9 | 1.5 | 0.22 \pm 0.13 | -0.09 \pm 0.13 | |
| Egg volume | | | | | | | |
| year + LD + year:LD | 4 | 4052.2 | 4062.3 | 0.0 | -0.23 \pm 0.10 | -0.57 \pm 0.10 | 0.19 \pm 0.09 |
| year + LD | 3 | 4055.2 | 4063.2 | 1.0 | -0.22 \pm 0.10 | -0.57 \pm 0.10 | |

Table 2. Survival (ϕ) and resighting (p) modelling as a function of age and sex between 2005 and 2015. Results of model selection include: number of mathematical parameters (k), the deviance (Dev), AIC value corrected for small-sample-size (AICc) and difference between current model and the best model within each sub-set of model (Δ AICc). The final selected model is in bold characters. For model notation, ‘juv’ indicates juvenile, ‘ad’ indicates adult, ‘cst’ indicates a constant parameter, ‘+’ indicates an additive effect and ‘.’ indicates interactive effect.

| No. | Model | k | DEV | AICc | Δ AICc |
|----------------------|------------------------------------|-----------|---------------|---------------|---------------|
| Resighting | | | | | |
| 1 | p_{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 | ϕ_{juv_ad} | 20 | 798.07 | 840.21 | 0 |
| 6 | $\phi_{juv.sex_ad}$ | 21 | 797.76 | 842.11 | 1.90 |
| 7 | $\phi_{juv_ad.sex}$ | 21 | 797.80 | 842.16 | 1.95 |
| 1 | $\phi_{juv.sex_ad.sex}$ | 22 | 797.43 | 844.02 | 4.78 |
| Survival: age effect | | | | | |
| 5 | ϕ_{juv_ad} | 20 | 798.07 | 840.21 | 0 |
| 8 | ϕ_{cst} | 19 | 815.20 | 855.13 | 14.92 |

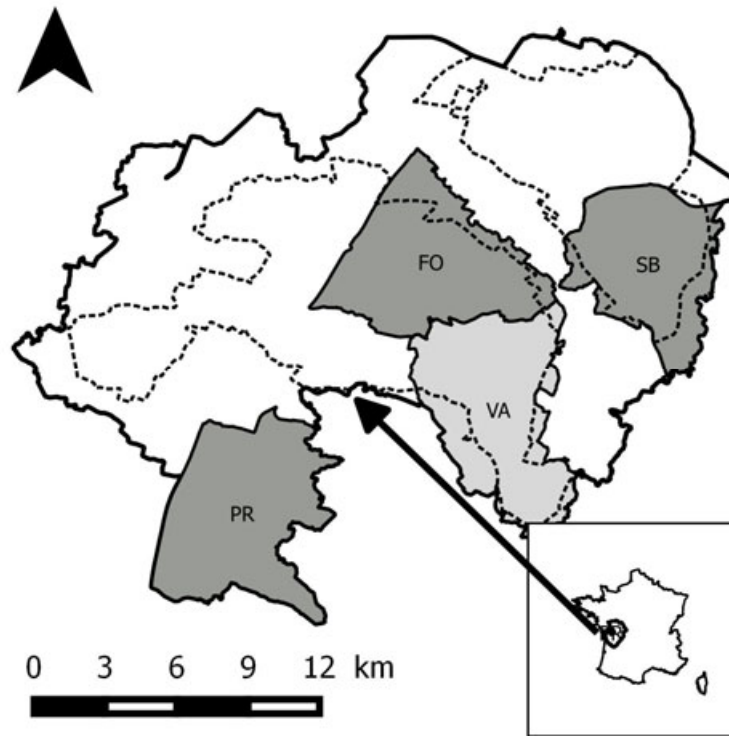


Figure 1. Map of the study area, the Long Term Social-Ecological Research site (LTSER) 'Zone Atelier Plaine & Val de Sèvre'. The grey polygons correspond to the four sub-sites used for the survey of the Stone-curlew population, of which 'VA' in light grey corresponds to the monitoring sub-site. The dotted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

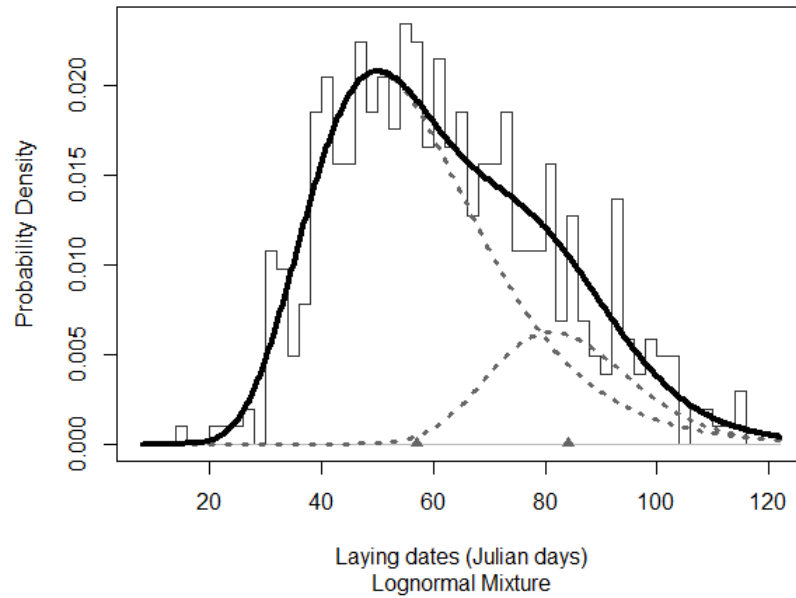


Figure 2. Distribution of laying dates (histogram, $n = 513$, 1998-2016), of the fitted log-normal distributions (dotted lines, see Methods) and of the total fitted laying date (thick line). The x-axis represent the laying date in Julian days since 1st March (31 = 1st April, 61 = 1st May, 92 = 1st June).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

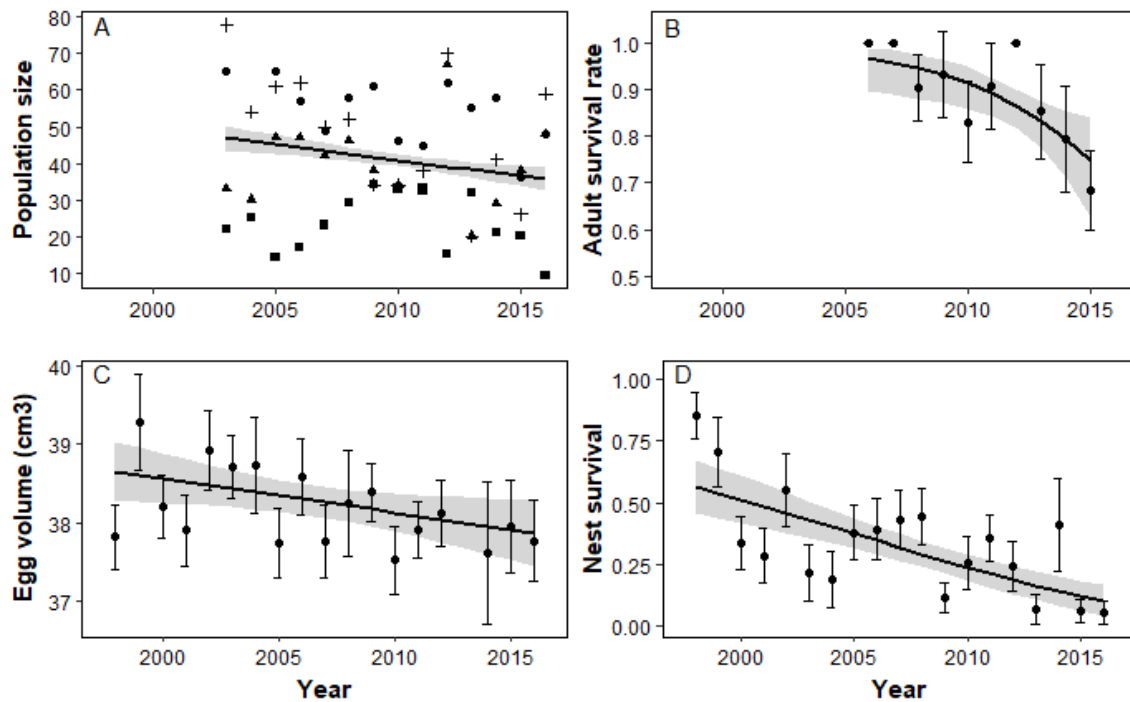


Figure 3. Trends in (A) population size (four sub-sites: cross for VA, triangle for PR, circle for FO and square for SB), (B) adult apparent survival rate \pm se, (C) egg volume \pm se and (D) nest survival \pm se. The predicted values were extracted from the corresponding LM and GLM models (see Methods)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

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