



A synthesis of Eurasian Curlew (*Numenius arquata arquata*) demography and population viability to inform its management

DUARTE S. VIANA,*¹  SIMONE SANTORO,²  RAMÓN C. SORIGUER¹  & JORDI FIGUEROLA¹ 

¹Estación Biológica de Doñana, CSIC, C/ Américo Vespucio, 26, 41092, Seville, Spain

²Department of Integrated Sciences, Faculty of Experimental Sciences, University of Huelva, 21007, Huelva, Spain

The European population of Eurasian Curlew *Numenius arquata arquata*, a near-threatened wader subspecies, has undergone pronounced population declines over the past 30 years. To assess the demography and viability of its global population, we surveyed studies quantifying demographic rates (productivity and survival) and complemented this review with new estimates of survival probability at the flyway scale. Then, using a demographic model, we estimated population growth rates while accounting for the range of variation of demographic parameters, and compared these estimates (expected based on demographic rates) with those observed based on population censuses. Both observed and expected average growth rates were negative but the observed rates were higher than estimates from demographic models ($\lambda = 0.98\text{--}0.99$ compared with $0.85\text{--}0.95$). This discrepancy implies that there is geographical variation in the demography of different populations that is not fully covered by current demographic data, namely unstudied regions with higher productivity. According to our calculations, at the flyway scale, productivity is currently *c.* 0.57 fledglings per pair per year, higher than the average reported productivity of 0.29, but lower than the 0.68 needed to achieve a stable global population size ($\lambda = 1$). Adult survival, estimated at 0.90, was the most sensitive parameter determining population growth rates, but the low productivity levels over the last few decades seems to be the most probable cause of population declines. The negative population growth rates require immediate conservation actions to preserve adult survival and increase the extremely low productivity in western and northern European populations to values above 0.68 fledglings per pair per year. We hope our synthesis on the demographic status of Curlew in Europe will encourage the collection of more demographic data and allow concrete management goals at the flyway scale to be established in order to recover the global population of this iconic species.

Keywords: population model, productivity, review, survival, vital rates.

Migratory birds are important biodiversity conservation flags (Caro & O'Doherty 1999, Home *et al.* 2009) and provide important ecosystem services, including dispersal services for many organisms (Viana *et al.* 2016) as well as provisioning, cultural, supporting and regulating services (Whelan *et al.* 2008, Green & Elmberg 2014). However, the populations of many migratory bird species have declined in recent decades (Sanderson

et al. 2006, Gilroy *et al.* 2016) due to several factors such as habitat alterations and climate change (Møller *et al.* 2008, Vickery *et al.* 2014).

Among migratory bird species, the wading birds Numeniini include several species with increasing conservation concerns (Brown *et al.* 2014, Pearce-Higgins *et al.* 2017). The Eurasian Curlew *Numenius arquata* is a widespread species that remains common in many parts of its range (Keller *et al.* 2020) but has a deteriorating conservation status: it is presently classified globally as near threatened (NT) by the International Union for

*Corresponding author.
Email: dviana@ebd.csic.es

Conservation of Nature (Birdlife International 2016). This species is divided into three subspecies distributed across Africa and Europe (*N. a. arquata*), Russia and Kazakhstan (*N. a. suschkini*) and Asia (*N. a. orientalis*). The population trends of these subspecies are partly unknown, although some estimations suggest that the species may have declined by 20–30% in the past 15 years or three generations (Birdlife International 2016). The *arquata* subspecies (Curlew hereafter), the nominate subspecies, is currently classified as vulnerable across its European range (BirdLife International 2015). This negative trend has been mainly attributed to changes in land use, agricultural practices, and nest and chick predation resulting in low productivity rates (Grant *et al.* 1999, Jensen & Lutz 2007, Roodbergen *et al.* 2012, Douglas *et al.* 2014, Franks *et al.* 2017).

The Curlew breeds across northern Europe up to east Siberia, and winters in the coasts of north-west Europe, the Mediterranean and West Africa (Jensen & Lutz 2007, Birdlife International 2016). The breeding populations have shown marked declines in several European countries. In the UK, the situation is particularly worrying, with population estimates showing steep declines in the breeding populations ranging from 42% to 54% in the last 23 years (Woodward *et al.* 2020). Future projections for the breeding population in the UK are also pessimistic, according to different climate change scenarios (Renwick *et al.* 2012). This has placed the Curlew as the bird species of highest conservation priority there (Brown *et al.* 2015). In contrast, the wintering populations in Europe show a stable or even increasing trend in most countries (Birdlife International 2016, Woodward *et al.* 2022). The cause of such discrepancy between breeding and wintering trends is unknown, with possible explanations including shifts in their latitudinal distribution or population estimation biases.

Previous population viability analyses have indicated negative growth in some Curlew populations (Klok *et al.* 2009, Cook *et al.* 2021) but estimated demographic parameters vary greatly among different regions, studies and years (see Table 1). We reviewed literature reporting information on demographic parameters of Curlew populations and performed population viability analyses to assess the conservation status and prospects of the global Curlew population. In particular, we used demographic matrix models to explore the range

of potential population growth rates according to variations in demographic parameters and population size estimates. First, we used the reviewed estimates of demographic parameters (productivity, juvenile survival, sub-adult survival and adult survival) from studies across Europe and our own estimates of survival probabilities at the flyway scale to estimate the range of expected population growth rates. Secondly, we compared these expected growth rates with the observed growth rates calculated according to temporal trends in population size. Thirdly, we evaluated which combinations of demographic parameters would be compatible with the range of observed growth rates and with a stable breeding population, in comparison with the set of reviewed demographic parameters. Finally, because the Eurasian Curlew is a game species, we assessed the impact of mortality caused by hunting activity, using the hunting bag in France as a case study.

METHODS

Literature review

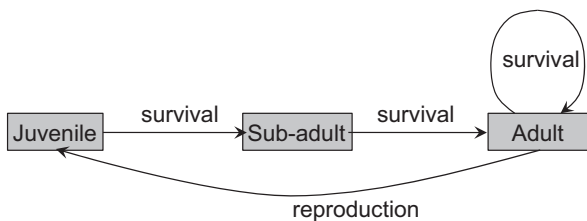
We extensively reviewed available literature reporting estimated demographic parameters, including productivity (number of fledglings per pair per year), juvenile (first-year) survival, sub-adult (second-year) survival and adult survival (see model structure below). Whenever possible, we took the information from original studies, but in a few cases where we could not access the original source, we completed the parameter dataset with cited information, taking special care not to include repeated information in our analysis. The final dataset had information from 23 publications (Table 1). To analyse temporal trends in the demographic parameters, we took the middle year of the period in each study and regressed the parameter values on year.

Demographic analysis

We used a stage-structured population model (hereafter 'demographic model') where only females are explicitly modelled, and the life cycle is based on juvenile (first-year birds), sub-adult (second-year birds) and adult (2+ year birds) stage classes, each showing different demographic rates (Fig. 1). The model assumed that (i) the sex ratio at birth is 1:1, (ii) survival rates are independent

Table 1. Summary results of the reviewed information on demographic parameters.

Region	Study year	Productivity	1st year survival	2nd year survival	Adult survival	Reference
Great Britain	1909–1975	–	0.47	0.63	0.736	Bainbridge and Minton (1978)
–	1950	–	0.38	0.33	0.670–0.748	Boyd (1962)
Netherlands	1972	–	0.34	–	0.72	Speek in von Blotzheim <i>et al.</i> 1984 in Roodbergen <i>et al.</i> (2012)
Germany	1973–1980	0.3	–	–	0.885	Kipp 1982 in Klok <i>et al.</i> (2009)
Germany	1975–1998	0.11	–	–	–	Kipp and Kipp (2009)
England	1977–1981	NA	–	0.70–0.82	0.70–0.82	Evans and Pienkowski (1984)
Germany	1977–1986	0.4	–	–	–	Dornberger and Ranftl (1986)
Germany	1977–1990	0.32	–	–	–	Boschert and Rupp (1993)
Europe	1980 (1985, 2006)	0.34–0.40	–	–	–	Roodbergen <i>et al.</i> (2012)
Wales	1974–2011	–	–	–	0.869–0.905	Taylor and Dodd (2013)
Finland	1982–1986	0.72	–	–	0.88	Ylimaunu <i>et al.</i> (1987)
Sweden	1986–1992	–	–	–	0.588–0.917	Berg (1994)
Sweden	1987–1989	0.25–1.4	–	–	–	Berg <i>et al.</i> (1992)
England	1990	–	–	–	0.832	Evans 1991 in Berg (1994)
Germany	1991–2003	0.05	–	–	–	Boschert 2004 in Jensen and Lutz (2007)
N. Ireland	1993–1995	0.14–0.56	–	–	–	Grant <i>et al.</i> (1999)
Finland	1995–1998	0.32	–	–	0.844	Valkama and Currie (1999)
Great Britain	1970–2018	–	0.326	–	0.898	Cook <i>et al.</i> (2021)
England	2017–2018	0.16	–	–	–	Zielonka <i>et al.</i> (2019)
England	2018–2019	0.1	–	–	–	Colwell <i>et al.</i> (2020)
Ireland	2017–2020	0.38–0.81	–	–	–	O'Donoghue and Carey (2020)
England	2010–2019	–	–	–	0.92	Robinson <i>et al.</i> (2020)
Wales	–	0.31	–	–	–	Taylor <i>et al.</i> (2020)



$$M = \begin{bmatrix} 0 & 0 & a\frac{p}{2} \\ j & 0 & 0 \\ 0 & s & a \end{bmatrix}$$

Figure 1. Schematic life-cycle of the Eurasian Curlew used for the demographic models.

of density, (iii) female and male survival is equal and (iv) breeding occurs over a short period during spring, after which the model is censused. In the Leslie matrix (M) with three age classes underlying the population model, the age for adulthood is 2 years:

where p is the productivity, i.e. the number of fledglings per breeding pair and year, j is the survival rate during the first year (from fledgling until 1 year old), s is the survival rate during the second year (from 1 to 2 years old) and a is the yearly adult survival (from 2 years old). Only adult birds can reproduce in our model (Fig. 1). We also tried adding the 3+ age class, assuming that many Curlew do not commence breeding until 3 years old, but the population projections of this model only differ from the three-stage class model if we assume different survival rates for 2+

and 3+ year-old birds. The only estimate we could find for third year (2+) birds (0.82; van Gils & Wiersma 1996) was in line with adult survival estimates reviewed by us (median = 0.81), and thus we retained the simplest three-stage class model.

The demographic analysis was performed by estimating deterministic and stochastic population growth rates (λ) and extinction probabilities, as well as parameter sensitivity and elasticity using the R package *popbio* (Stubben & Milligan 2007, R Development Core Team 2020). Initial population sizes for each stage in the stochastic analysis were determined as the proportions of the current population size (640 000–920 000 individuals according to Wetlands International; Nagy *et al.* 2015) corresponding to the stable stage distribution inferred from the deterministic matrix model. We estimated population growth rates according to (*Model 1*) the set of demographic parameters taken from the literature (Table 1), (*Model 2*) our own estimates of flyway-scale survival of birds ringed when chicks in the UK, Ireland, the Netherlands, Germany, Finland and Sweden (see below), while taking the remaining parameters (i.e. productivity) from the literature review, and (*Model 3*) our estimates of survival and the range of productivity values that resulted in growth rates within the range of observed growth rates (λ_{obs} ; i.e. estimated according to population censuses). Our estimates of survival agree with the few post-2000 estimates in other studies, and thus we used *Model 3* as our reference model at the flyway scale for posterior viability analysis and discussion. For each model, we estimated the deterministic and stochastic growth rates, extinction probabilities and extinction year (probability of extinction > 0.95), assuming an extinction threshold of 10 individuals, as well as parameter sensitivity (additive effect of an absolute change in the parameter value on the population growth rate) and elasticity (proportional effect of a proportional change in the parameter value).

Model 1

To account explicitly for all the uncertainty associated with demographic parameters taken from the literature, we first modelled the frequency distributions of each parameter by fitting a parametric probability distribution using maximum likelihood estimation with the R package *fitdistrplus* (Delignette-Muller & Dutang 2015) and truncating

the fitted distributions to range between the minimum and maximum observed values using the R package *distr* (Ruckdeschel *et al.* 2006). Based on visual inspection of the empirical frequency distributions and the type of variables, we fitted a log-normal distribution to productivity values, a uniform distribution to juvenile survival, as we had only three data points, and a beta distribution to sub-adult and adult survival (see Supporting Information Appendix S1). To cover the whole spectrum of possible parameter combinations (conforming to different Leslie matrices), we sampled the parameter probability distributions according to a Latin Hypercube using the R package *lhs* (Carnell 2022), which allowed us to use different probability distributions for each parameter (see Supporting Information Figs S1 and S2). We then built the respective Leslie matrix for each parameter combination and performed the demographic model.

Model 2

This demographic model was performed by using survival rates estimated according to a capture-recapture model (productivity values were taken from the literature, as in *Model 1*). Capture-recapture models provide more robust survival estimates than the mere observation of the proportion of marked birds returning to the breeding grounds, as reported in most surveyed studies in our review. Based on EURING ring-recovery data, we used E-SURGE (Choquet *et al.* 2009) to model the recovery and survival probabilities of 1047 Curlews ringed as chicks between 1968 and 2016 in three regions: Fennoscandia ($n = 582$), Germany/Holland ($n = 367$) and the British Isles ($n = 241$); and recovered in four areas: France ($n = 318$), the British Isles ($n = 267$), Fennoscandia ($n = 264$) and other countries ($n = 194$). Our modelling approach mimicked that used by Souchay and Schaub (2016) for Northern Lapwing *Vanellus vanellus* but, in this case, we did not model the cause of mortality. The estimates of survival were extrapolated from a model in which the survival probability depended on age (1 year old, 2 years old, >2 years old), and the recovery probability depended on the recovery location and temporal variation between blocks of four consecutive years. Specifying temporal variation in survival probability did not improve model fitting. A detailed explanation of the modelling framework and model selection is given in Appendix S1.

According to our estimates, juvenile survival was 0.43 (95% confidence interval (CI) 0.39–0.46), sub-adult survival was 0.75 (95% CI 0.70–0.79) and adult survival was 0.90 (95% CI 0.88–0.92). These estimated survival rates together with the productivity values taken from the reviewed studies were used for performing the demographic model. To account for the uncertainty in survival estimates, we took the Gaussian distribution of survival estimates defined by the mean model estimate and its standard deviation (equivalent to the standard error of the model estimate). Then, similarly to *Model 1*, we sampled the parameter probability distributions according to a Latin Hypercube and built the respective Leslie matrix for each parameter combination.

Model 3

We calculated the observed growth rate (λ_{obs}) according to a geometrical growth rate model in which the population size after t years (N_t) was given by

$$N_t = N_0 * \lambda_{\text{obs}}^t$$

and where N_0 was the initial population size. The minimum and maximum rates of population decline (0.30 and 0.49, respectively; BirdLife International 2016) were used to calculate the range of possible initial population sizes 31 years ago and, in turn, the range of possible growth rates. To infer possible parameter combinations resulting in observed growth rates, we simulated parameter combinations across the whole possible range of each parameter (0–4 for productivity according to the average biological potential reported by Mulder & Swaan 1992; 0–1 for juvenile, sub-adult and adult survival) and extracted the combinations yielding growth rates lying within the observed range. In addition, because productivity is highly variable across space (due to local factors related to habitat alterations, predation and human disturbance) and is usually measured in managed rather than natural habitats, we decided to infer productivity according to our estimates of survival that yielded the observed (negative) growth rates. This allowed us to obtain more realistic productivity values (congruent with observed growth rates) and thus more realistic stochastic growth rates and extinction year.

Mortality scenarios

Hunting of Curlew is a regulated activity, and although it can be currently considered a minor pressure on the Curlew population in Europe compared with threats to breeding success such as intensive agriculture or nest predation (Brown 2015), the impact is unknown. For example, a mortality rate of 0.019 due to illegal killing and taking (as reported in Brochet *et al.* 2016 for the *orientalis* population) can cause significant impacts. In Europe, hunting is only possible in France, though it is annually revised; e.g. the French government fixed the quota for the 2020–2021 hunting season to zero (<https://www.legifrance.gouv.fr/jorf/id/JORFTEXT000042176842>). Curlew was hunted in the past in several European countries, including Denmark, Ireland and UK, according to the Annex II/2 of the EU Birds Directive. In practice, Curlews have not been hunted in most of the UK since 1982 (except N. Ireland and only in 2011), 1994 in Denmark and 2012 in Ireland. To investigate the relative demographic effects of different mortality scenarios associated with varying hunting pressures or other causes, we simulated increased mortality rates translated into reduced survival rates. As an example, we analysed the relative importance of the French hunting bag on Curlew population dynamics using the recent estimate of 6961 Curlews (95% CI 4394–9529) reported in Aubry *et al.* (2016) for the hunting season of 2013–2014. Starting with our estimates for current survival, we progressively increased the mortality rate (by 0.001 each time) to assess its impact on the population growth rate. We then estimated the relative importance of such annual hunting bag compared with the overall annual mortality of Curlew.

RESULTS

Demographic parameters

Demographic information of Curlew populations was highly heterogeneous across its European distribution range (Table 1). The majority of studies were carried out in Great Britain ($n = 11$) and Germany ($n = 5$), with a few in Sweden ($n = 2$), Finland ($n = 2$) and the Netherlands ($n = 1$). One study reported aggregated values from multiple European regions. Adult survival ranged from 0.59

to 0.92 and showed a positive temporal trend (Fig. 2; $F_{1,22} = 8.395$, $P = 0.008$), though the latter trend might be the result of more sophisticated estimations of survival towards recent years (see Discussion). Juvenile (first year) survival ranged from 0.33 to 0.47 and sub-adult (second year) survival from 0.33 to 0.82, but it was not possible to estimate temporal trends due to the low number of studies reporting such data. Productivity ranged from 0.05 to 1.4, and although we expected a negative temporal trend, the data were too idiosyncratic and noisy to detect any significant trends. Still, the reviewed values of productivity were in general lower than those inferred from observed population growth rates (obtained according to *Model 3*; Fig. 3).

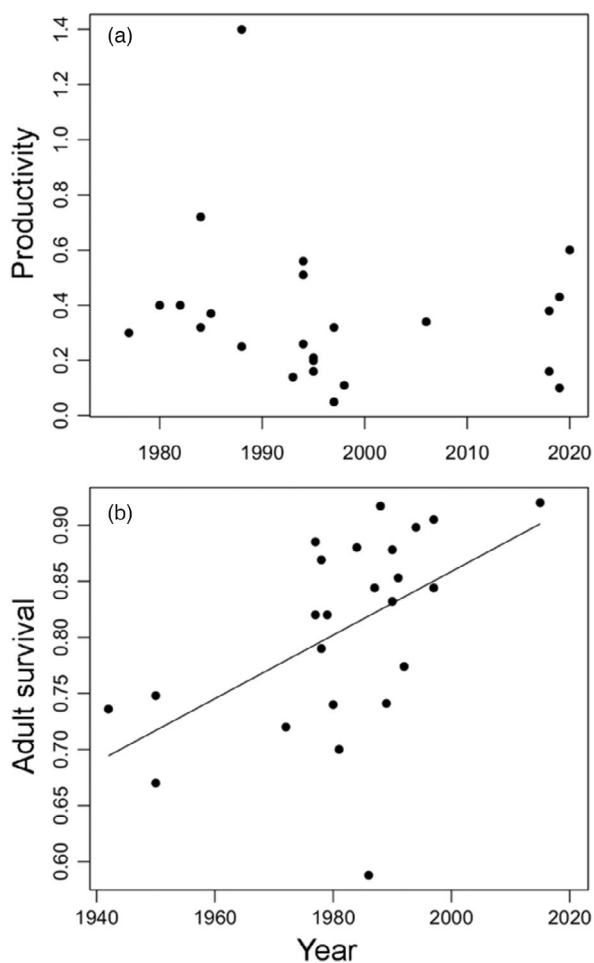


Figure 2. Temporal trend in demographic parameters obtained from the reviewed studies: (a) productivity and (b) adult survival. Data for juvenile and sub-adult survival were not sufficient for analysis ($n < 5$).

Demographic analysis

Model 1

Based on reviewed demographic parameters, the estimated deterministic rate of population growth (λ) for the most probable parameter combination (median $P = 0.29$, $j = 0.40$, $s = 0.67$, $a = 0.81$) was 0.85, which indicates a steep negative growth yielding population declines of 15%. The population growth rates resulting from all the sampled parameter combinations ranged from 0.616 to 1.032 (mean 0.850, 95% CI 0.845–0.855). Considering this variation in demographic parameters, the estimated stochastic growth rate was 0.848 when the probability of each parameter combination was equal and 0.791 when the probability of the different parameter combinations differed according to their frequency of occurrence. The estimated extinction time for the global population ranged from 49 to 50 years (probability > 95%), assuming either minimum (640 000) or maximum (920 000) population estimates, respectively (Fig. 4). Both sensitivity and elasticity were higher for adult survival and lower for productivity and juvenile and sub-adult survival (Table 2), meaning that adult survival is the most influential factor affecting population growth rate.

Model 2

When the growth rates were calculated according to the survival estimates obtained from our capture–recapture model, the estimated deterministic rate of population growth (λ) for the most probable parameter combination (median $P = 0.29$, $j = 0.43$, $s = 0.75$, $a = 0.90$) was 0.95, which indicates a negative growth rate of 5%. The population growth rates resulting from all the sampled parameter combinations ranged from 0.896 to 1.089 (mean 0.953, 95% CI 0.951–0.955). Considering this variation in demographic parameters, the estimated stochastic growth rate was 0.954 when the probability of each parameter combination was equal, and 0.932 when the probability of the different parameter combinations differed according to their frequency of occurrence. The estimated extinction time ranged from 155 to 159 years (probability > 95%), assuming either minimum (640 000) or maximum (920 000) population estimates, respectively (Fig. 4). Both sensitivity and elasticity were higher for adult survival, and lower for productivity and juvenile and sub-adult survival (Table 2).

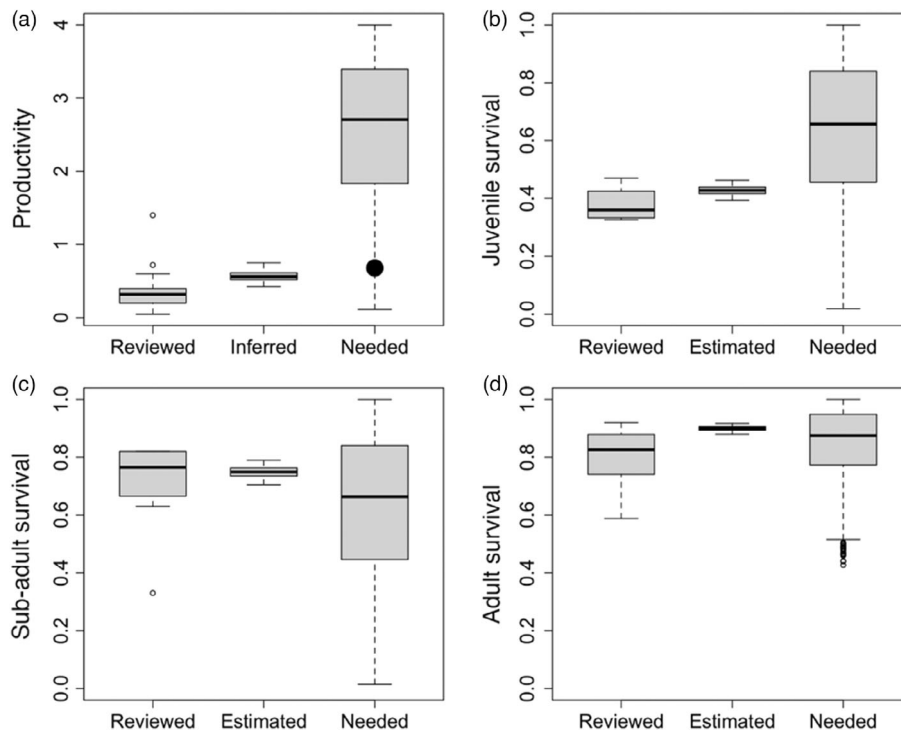


Figure 3. Comparison of demographic parameter values (a, productivity; b, juvenile survival; c, sub-adult survival; d, adult survival) between reviewed information, our own estimations (or inference in the case of productivity), and the range of values needed for positive rates of population growth ($\lambda > 1$). Note that the latter are the result of all possible parameter combinations leading to positive population growth. The black dot in panel (a) indicates the productivity value needed for achieving a stable population size ($\lambda = 1$).

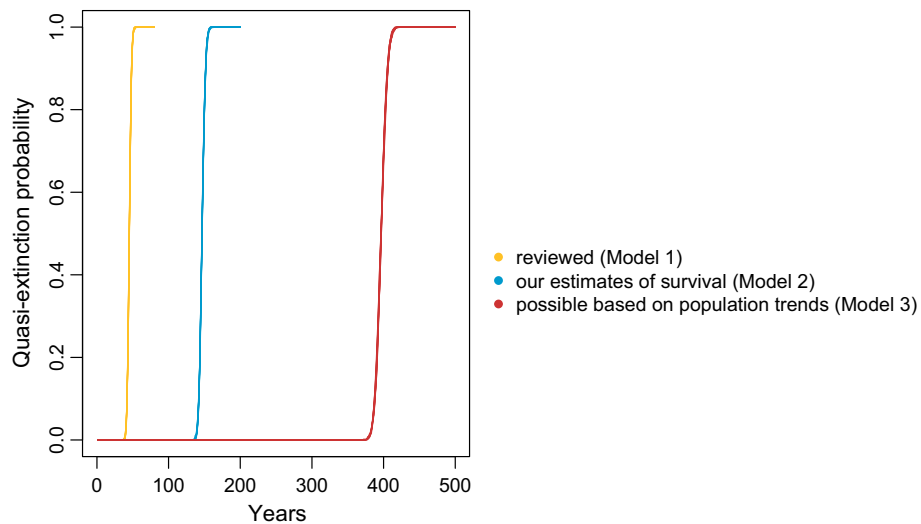


Figure 4. Extinction probability curves for *Model 1* (i.e. viability resulting from reviewed demographic parameters), *Model 2* (i.e. viability resulting from estimated survival; productivity taken from reviewed studies) and *Model 3* (i.e. viability resulting from expected parameter values based on actual population trends), all departing from mean population size estimates (850 000 individuals).

Table 2. Ranges of parameter sensitivity and elasticity for Models 1, 2 and 3.

Parameter	Model	Estimate	Sensitivity	Elasticity
Productivity	Model 1	0.05–1.39	0.06–0.25	0.01–0.15
	Model 2	0.05–1.38	0.09–0.18	0.01–0.12
	Model 3	0.42–0.75	0.11–0.14	0.06–0.09
Juvenile survival	Model 1	0.33–0.47	0.02–0.32	0.01–0.15
	Model 2	0.39–0.46	0.02–0.32	0.01–0.12
	Model 3	0.39–0.46	0.13–0.21	0.06–0.09
Sub-adult survival	Model 1	0.33–0.82	0.01–0.20	0.01–0.15
	Model 2	0.70–0.79	0.01–0.17	0.01–0.12
	Model 3	0.70–0.79	0.08–0.12	0.06–0.09
Adult survival	Model 1	0.59–0.92	0.89–0.99	0.70–0.99
	Model 2	0.88–0.92	0.90–0.99	0.75–0.98
	Model 3	0.88–0.92	0.92–0.95	0.82–0.88

Model 3

The observed population growth rate (λ_{obs}) resulting from a population decline of 20–49% in 31 years was 0.978–0.988. According to the observed population growth rates, and using our estimates of survival, the productivity was estimated to range from 0.42 to 0.75 (adjusted normal distribution: mean 0.57, sd 0.07), which is on average 16% lower than that required to achieve a stable population size (0.68; Fig. 5). In this scenario, and based on the parameter combinations yielding growth rates within the observed range, the stochastic population growth rate was 0.984 or 0.973 for equal or different probabilities of parameter combinations, respectively. The corresponding extinction time for a probability of > 95% extinction was 403–414 years according to the range of population size estimates (Fig. 4).

Mortality scenarios

In a scenario of increased mortality, the population growth rate decreases linearly at a rate of 1.20 ($\lambda = 1.10\text{--}1.20 \times \text{mortality}$). If we take the hunting bag reported in Aubry *et al.* (2016) as an example, considering the hunting mortality as fully additive, the population growth rate increases by 0.007–0.015 after removing the respective mortality (0.005–0.011). If mortality due to illegal killing and taking (0.019 as reported in Brochet *et al.* 2016) could be avoided, a stable population size could be achieved with a productivity 24% lower, from 0.68 to 0.52 fledglings per pair per year.

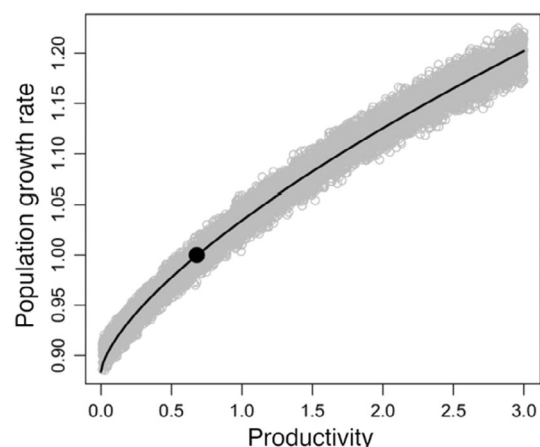


Figure 5. Relationship between simulated population growth rates (λ) and productivity (p ; number of fledglings per pair per year), when survival rates were allowed to vary within the range of our estimates. The large black dot indicates the needed productivity value to achieve a stable population size ($\lambda = 1$) and the line is the fitted exponential model ($\lambda = 0.88 + 0.15 p^{0.68}$).

DISCUSSION

The estimated population growth rates calculated according to demographic parameters obtained either from other studies ($\lambda = 0.85$) or from our survival estimates ($\lambda = 0.95$) were lower than the observed growth rates based on population size trends ($\lambda \approx 0.98$). This difference between estimated and observed population growth estimates indicate that the availability of information on demographic parameters may be biased towards regions showing the highest Curlew population declines, or that population declines are more severe than observed according to population censuses. A large proportion of the information on demographic parameters comes from studies carried out in Great Britain, where 19–27% of the global Eurasian *Numenius arquata* population breed (or used to breed; Brown *et al.* 2015) and where population declines are the highest recorded (60%, Eaton *et al.* 2015). Breeding populations in more northern areas are also declining, but allegedly at lower rates. Long-term breeding population counts in both Finland and Russia, where most of the Curlew population breeds (33% and 27%, respectively), show population decreases of up to 30%, although populations have stabilized in Finland over the last two decades (BirdLife International 2015). To make more accurate population

projections, we need to obtain updated estimates of demographic rates in Finland and Russia, where Curlew is more abundant. Higher breeding productivity in these two regions might explain the discrepancies between observed and estimated population growth rates, considering that most productivity values might come from breeding populations experiencing steeper declines. For example, Samigullin (1998) reported much higher productivities of 2.4 fledglings per pair per year in the Russian regions of Orenburg (although that estimate probably refers to the subspecies *N. arquata suschkini* or *N. a. orientalis*). Still, it is relevant to note that the reviewed demographic parameters are within the range of values estimated for other large-bodied wader species with declining populations, including Bristle-thighed Curlew *Numenius tahitiensis*, Eurasian Oystercatcher *Haematopus ostralegus*, Northern Lapwing, Black-tailed Godwit *Limosa limosa* and Common Redshank *Tringa totanus* (Sandercock 2003, Roodbergen *et al.* 2012; see Fig. S2).

The lack of updated demographic data and population size estimates may also hamper our ability to model population status and trends. To partially address such lack of demographic data at the flyway scale, we obtained estimates of Curlew survival using ring-recovery data from different European regions, obtaining higher estimates of survival and thus higher estimates of population growth than with reviewed demographic estimates. In fact, and in line with other studies (e.g. Taylor & Dodd 2013, Cook *et al.* 2021, Woodward *et al.* 2022), adult survival seemed to increase over the years. Increasing survival in declining populations may be the result of density dependence (e.g. Cook *et al.* 2021) but we cannot rule out that such a positive trend may result from methodological differences in the estimation of survival. Many survival estimates were made before 2000, and until the 1990s, survival estimation was mainly based on return rates assuming closed populations and recapture probability equal across years and among age classes. With the advent of maximum likelihood estimation, more restricted models, such as the Cormack–Jolly–Seber (CJS) model, made it possible to calculate more realistic survival rates. Indeed, the most recent adult survival estimates, including ours (0.89–0.92; Taylor & Dodd 2013, Robinson *et al.* 2020, Cook *et al.* 2021), are the highest recorded, which may be partly explained by the

more rigorous estimation method (CJS models). Still, Cook *et al.* (2021) found that the survival rate based on CJS models has increased since 1996 in Great Britain, which can probably be explained by the restrictions on hunting activity in Europe. For example, survival increased in Wales (from 86.9% to 90.5%) after the hunting ban in 1982 (Taylor & Dodd 2013).

Because adult survival is the most sensitive demographic parameter, projected scenarios affecting mortality, such as changes in hunting pressure, significantly impact population growth rate and expected extinction year. If mortality increases, the population growth rate will be reduced, causing an acceleration of the probability of earlier extinction. Although the historical impact of harvesting was not the primary cause of population decreases in other declining wader species (e.g. the Northern Lapwing; Souchay & Schaub 2016), harvesting can hamper the recovery of population growth rates unless productivity rises considerably. Moreover, illegal killing and taking is still a major concern in other Curlew populations (*N. a. orientalis*; Brochet *et al.* 2016). On the other hand, increases in survival rates might lead to density dependence effects and decrease population growth (Cook *et al.* 2021). Such effects should be measured and accounted for in future demographic models.

In contrast to the increasing trend in survival, productivity has remained low over the last 40 years, which explains the negative population growth rates (as also concluded in other studies; e.g. Grant *et al.* 1999, Cook *et al.* 2021). Both reviewed (median 0.29) and inferred (0.57; needed to explain observed population trends) productivity values are largely below the biological potential of this species, which typically lays four eggs (Mulder & Swaan 1992), and is also much lower than the productivity needed to achieve stable population sizes (0.68 fledglings per pair per year). Although many causes for productivity declines have been pointed out, these are most probably related to breeding habitat alterations and increased predation. The Curlew breeds in coastal, lowland and upland habitats of boreal, temperate and steppe regions (Cramp & Simmons 1983, Delany *et al.* 2009), preferably in open areas such as grassland and meadows frequently associated with wetland habitats. However, this type of landscape has been increasingly reclaimed for agriculture, generating habitat

fragmentation and changing natural habitat features. Curlews have been observed breeding in farmland habitats, but with associated nest losses due to farming operations. The disproportionately highest productivity value (1.4 fledglings per pair per year) was observed in Sweden in natural habitats, a much higher reproductive success than that in farmlands observed in that same study (Berg *et al.* 1992). Habitat alterations are often associated with an increase in egg and chick predation by mesopredators, which has been shown to be a major cause of breeding failure. Predation on wader nests has increased in Western Europe over the past four decades (Roodbergen *et al.* 2012), and in some regions of countries such as UK, Germany, Sweden and Finland, high predation levels have been observed (Berg *et al.* 1992, Grant *et al.* 1999, Valkama & Currie 1999, Boschert 2005, Douglas *et al.* 2014, Zielonka *et al.* 2019), reaching extreme values of > 80% (Valkama & Currie 1999). Habitat fragmentation (Douglas *et al.* 2014) and super-abundant prey (e.g. resulting from released gamebirds; Pringle *et al.* 2019) may increase avian predator densities and, therefore, nest predation rates, especially in habitat patches surrounded by woodland. All these threats to breeding may lead to insufficient recruitment every year. According to the reviewed demographic parameters and our model calculations, on average, only 8.2% of the descendants per adult per year recruit in the breeding population (according to *Model 3*), a proportion that is lower than the median adult mortality rate of 10%. Predator control experiments in northern England resulted in a threefold increase in the breeding success of waders (Fletcher *et al.* 2010), suggesting it could be a useful additional measure together with attempts to reduce nest destruction by human activities. Unfortunately, predator control is not always effective (Franks *et al.* 2018) and we still lack studies outside the UK to assess the general effectiveness of these actions.

The observed global Curlew population decline calls for immediate conservation measures. Adult mortality/survival is the most sensitive parameter but it is also the hardest to manipulate upwards. Productivity, on the other hand, has increased following effective and integrated conservation measures. Agri-Environment Schemes (AES) have been implemented in several EU countries and have been shown to be successful management practices for some bird species in the UK and

France (Broyer *et al.* 2014, Smart *et al.* 2014), although other studies have shown that these schemes can be largely ineffective for Curlew (Franks *et al.* 2018). Because agricultural habitats are being increasingly used for breeding, promoting compatible agricultural practices is a priority, but both AES and other management interventions such as site protection and predator control have yielded uncertain success rates in Curlew populations (Franks *et al.* 2018). More studies targeting Curlew in particular are needed to assess the success of potential management measures. A detailed review of the threats and potential conservation actions is provided in the 2015 report of the 'International single species plan for the conservation of the Eurasian Curlew' (Agreement on the Conservation of African-Eurasian Migratory Waterbirds; Brown 2015).

Despite the overall declining population trend, Curlew wintering populations have been increasing in many European countries, especially in southern Europe (according to BirdLife International 2022). Although this might seem paradoxical at first glance, rising winter temperatures under current climate change may lead to extended winter ranges (Nagy *et al.* 2022, Woodward *et al.* 2022), including population shifts towards more northern latitudes, which can increase the importance of Europe, relative to Africa, as a winter quarter for the species. Hence, the Curlew migratory capacity and consequent ability to adjust their wintering distribution to more favourable areas might contribute to explaining the positive or stable population trend during the wintering season. A similar process has been reported for the continental population of Black-tailed Godwit, whose wintering numbers in southern Spain have increased (Márquez-Ferrando *et al.* 2014) despite the significant declines in their breeding population.

The contrasting demographic scenarios of Curlew populations explored in our study, where populations in Western Europe show lower productivity and thus lower population growth rates (as indicated by *Model 2*) compared with the global population, which shows a higher growth rate probably driven by higher productivities in more north-eastern populations (as indicated by *Model 3*), highlight the importance of setting up a flyway-scale programme to estimate productivity and survival accurately across important breeding areas. Although our analysis accounted, to the extent of the reviewed studies, for geographical

variation in the demographic parameters, our mean population growth estimates at the European level may not be indicative of local or regional populations. To obtain regional estimates, this model can be parameterized with the specific demographic parameters of the local populations. Regional estimates are especially urgent in the Russian breeding areas. Together with flyway-scale demographic parameters, real-time tracking of Curlews to study migratory behaviour, for example with GPS devices (e.g. Schwemmer *et al.* 2016), will allow the establishment of a more precise distribution and connectivity map. These data can be then used to build more complex and realistic demographic models such as full annual-cycle population models (Hostetler *et al.* 2015). All these proposed conservation actions fit the short-term objectives outlined in the EU Management Plan for Curlew (Jensen & Lutz 2007), which are (*sensu*): (1) improve management and protection of breeding and wintering sites, (2) improve the protection from disturbance and (3) collect more robust data to better understand the potential importance of hunting and other types of population regulations. Therefore, research, conservation and political efforts are aligned with an effective conservation plan to recover Curlew vital rates and populations. Action is now needed to reverse the negative population growth rates.

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AUTHOR CONTRIBUTIONS

Duarte S. Viana: Formal analysis (lead); methodology (lead); software (lead); writing – original draft (lead); Conceptualization (equal); writing – review and editing (equal). **Simone Santoro:** Formal analysis (equal); methodology (equal); software (equal); writing – review and editing (equal). **Ramón C. Soriguer:** Conceptualization (equal); funding acquisition (equal); project administration (equal); writing – review and editing (equal). **Jordi Figuerola:** Conceptualization (equal); Formal analysis (supporting);

funding acquisition (equal); project administration (lead); writing – review and editing (equal).

CONFLICT OF INTEREST STATEMENT

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ETHICAL NOTE

None.

Data Availability Statement

The data that support the findings of this study (specifically, the ring-recovery data) are available from EURING (<https://euring.org/data-and-codes/obtaining-data>) upon request.

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SUPPORTING INFORMATION

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

Appendix S1. Details of the capture–recovery modelling.

Figure S1. Goodness-of-fit of the fitted probability distributions of the different demographic rates.

Figure S2. Comparison of demographic parameter values between the Eurasian Curlew and other large-bodied wader species with declining populations.