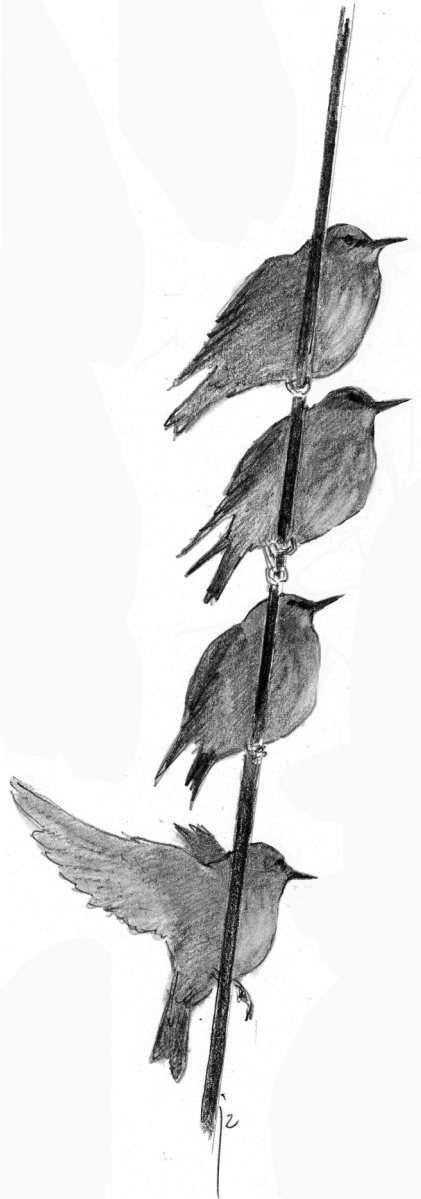


Demographic changes underpinning the population decline of Starlings *Sturnus vulgaris* in The Netherlands

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Declines in farmland bird populations are often linked to changes in agricultural practices, but little is known about the demographic changes underlying these adverse trends. Identifying the demographic drivers of population change is critical for understanding why populations are declining. In this study we assessed the demographic changes in the declining Dutch Starling *Sturnus vulgaris* population. We estimated productivity per breeding attempt and survival rates over a period of 52 years (1960–2012). The results show that juvenile survival decreased significantly over time. Adult survival fluctuated between years, with (non-significant) lower survival rates between 1990 and 2012. No trend in reproductive output was found over the study period. A population model was built for three different phases of population change within the study period: 1960–1978, 1978–1990 and 1990–2012. The contribution of changes in demographic parameters to population growth rate (λ) between the different periods was examined by performing a life table response experiment (LTRE). The LTRE analysis showed that changes in juvenile survival explained most of the differences in population growth rate between periods. Our results therefore suggest that a decline in juvenile survival rather than changes in adult survival or reproductive success is the most important cause of the decline of the Starling population in The Netherlands.

Key words: LTRE, mark-recovery, population matrix model, reproduction, survival

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Large scale declines in farmland bird populations are of major conservation concern in many European countries (Donald *et al.* 2001, Sanderson *et al.* 2013). Studies explaining the causes of these population changes often focus on changes in agricultural practices, such as increased levels of mechanization, changes in sowing and harvesting times and frequencies, pesticide use and drainage (Chamberlain & Fuller

2000, Gregory *et al.* 2004, Newton 2004, Donald *et al.* 2006, Kleijn *et al.* 2010, Hallmann *et al.* 2014). These processes will affect vital rates such as fecundity, survival and emigration/immigration, which in turn determine population size. In order to formulate effective habitat management to enable declining populations to recover, a thorough understanding of the biological processes underlying these declines is

required. Determining demographic changes that are linked to changes in population size is a critical step in identifying the mechanisms underlying population declines.

One species that has strongly declined over much of its Northern and Western European range is the Starling *Sturnus vulgaris* (Solonen *et al.* 1991, Robinson *et al.* 2005, Wahl *et al.* 2011, Boele *et al.* 2014). Starlings are among the most common birds in Europe, yet they are declining at an alarming rate, and it has now become clear that most of the decline in avian abundance and biomass can in fact be attributed to more common species like the Starling (Inger *et al.* 2014). The Starling is a passerine bird species that is strongly associated with agricultural landscapes. High quality foraging habitats, such as extensively managed pastures, tend to be preferred; within this habitat soil-living invertebrates, e.g. larvae of crane flies (Tipulidae), butterflies (Lepidoptera) and beetles (Coleoptera), are the Starlings' main food source (Tinbergen 1981, Olsson *et al.* 2002, Rhymer *et al.* 2012). Starlings frequently forage in association with cattle, and will also forage in crops grown for stock fodder (Feare 1984). Starlings are likely to be negatively affected by agricultural intensification; which results in loss of extensively managed pastures, decrease in soil moisture by drainage of grasslands and a decrease of invertebrate biodiversity because of increased fertilizer use (Smith & Bruun 2002, Devereux *et al.* 2004, Newton 2004, Rhymer 2012). Additionally, an increase in pesticide use negatively affects the availability of soil-living invertebrates (Wilson *et al.* 1999, Geiger *et al.* 2010, Hallmann *et al.* 2014). In Northern Europe, Starlings may also be affected by agricultural abandonment (Svensson 2004).

Little is known about the underlying changes in vital rates and exact mechanisms causing the large scale population declines in Northern and Western Europe. Contradictory results were found in previous studies. Although it was found that in Fennoscandia brood size increased during the time of population decline (Solonen *et al.* 1991), it was shown that reproductive success, measured as the number of fledglings leaving the nest, was negatively affected by regional changes in land use (Smith & Bruun 2002, Rintala & Tiainen 2008, Smith *et al.* 2012). Agricultural intensification and a shift from mixed farming to specialized cultivation were found to be the main drivers affecting optimal foraging habitat within a range of 500 meters from nest sites (Smith & Bruun 2002). In contrast to the Fennoscandian population, reproductive success gradually increased in the declining Starling population

in the United Kingdom (Freeman *et al.* 2007). Here, it was demonstrated that survival rates in the first-year and adult age-class tended to be lower, albeit not significantly, during the period of population decline. Nevertheless, further analysis demonstrated that juvenile survival outside the breeding season was the crucial parameter explaining the national population decline over time (Freeman *et al.* 2007). Changes in adult survival may play a role in driving population changes at a local level; however, at the national population level the changes in adult survival did not explain the declining trend as accurately as changes in juvenile survival did. It is expected that due to a decrease in overall habitat quality or in the area of optimal foraging habitats in winter, competition between juvenile and adult birds may have increased, which could result in higher mortality in this age class (Cresswell 1994).

The aim of this study was to investigate demographic changes underpinning the population decline of Starlings in The Netherlands. The Dutch Starling population has decreased by 50% since 1990 (Boele *et al.* 2014) and therefore interest in this species is increasing. In this study we estimated productivity per breeding attempt from nest records, and estimated survival rates by using a large dataset of ringed Dutch Starlings, spanning a period of 52 years. We then integrated these demographic parameters into a population model and compared the model outcome with the realised population growth based on population trends for three distinct periods. Finally, we quantified the contribution of all demographic parameters to the observed differences in population growth between the different periods by performing a life table response experiment (LTRE; Caswell 1989, Cooch *et al.* 2001).

METHODS

Reproduction

Estimates of productivity per breeding attempt are based on the Dutch Nest Record Scheme, a citizen science program for monitoring reproductive parameters of breeding birds, including nest success. It is coordinated by Sovon Dutch Centre for Field Ornithology, in collaboration with Statistics Netherlands, and has a set-up comparable to its British equivalent (Crick *et al.* 2003). Data are collected by volunteer birdwatchers throughout The Netherlands who search for nests and revisit these several times to collect information on laying date, clutch size, hatching and fledging success (successful, failed or ultimate fate unknown) and



Colour-ringed male Starling with ring combination 'green ZE', ringed in 2015 in Alpen aan den Rijn, The Netherlands (photo Arie Kwakernaak, 25 mei 2015).

number of fledged young. Since 1960, data from around 3000 Starling nests have been recorded. However, annual sample sizes are small and vary greatly between years: mean of 57 in the period 1984–2012 ($SD = 21.8$, range: 20–95). Moreover, there was not sufficient data from the years prior to 1984 to calculate reproductive success on an annual basis. Therefore, we calculated average reproductive success for three distinct periods of population growth: 1960–1978, 1978–1990 and 1990–2012 (Figure 1). Nest success and number of fledglings leaving the nest were analysed with the Mayfield method (Mayfield 1961). Changes over time were tested using a Spearman rank correlation as the data were not normally distributed.

We estimated the frequency of second broods using an independent dataset gathered between 2010 and 2012 by working group NESTKAST. This dataset is based on registrations of occupancy of 237 nest boxes in several study areas which included the frequency of presumed second or replacement clutches. This refers to a second breeding attempt in the same nest box, after the first attempt either succeeded (second) or failed (replacement). Since breeding parents were not

colour-ringed we could not rule out the possibility that nest boxes were occupied by new birds. These data therefore provide only a rough estimate of second breeding attempts, but we preferred to use these estimates rather than disregard second breeding attempts entirely. In 2010, 2011 and 2012 the frequency of second clutches was 9% ($n = 143$ nests), 5% ($n = 237$ nests) and 4% ($n = 237$ nests), respectively. The average frequency of second clutches in 2010–2012 was used to inflate the fledging success, assuming that the frequency of second broods did not change during the study period.

Ring recoveries and survival analysis

For the survival analysis, ringing data were derived from the database of the Dutch Centre for Avian Migration and Demography (Vogeltrekstation), which collects all the ringing and recovery data of birds in The Netherlands. The study period was defined from 1960 until 2012, and we included all dead recoveries until 31 March 2013. In order to restrict this analysis to the Dutch breeding population, we only used data from birds caught and ringed in the period from 1 April to 31

June. By using this short period we reduced the chance that our dataset included birds ringed during migration, and originating from Northern and Eastern breeding populations (Fliege 1984). The Starling is the most frequently ringed bird species in The Netherlands, with high numbers of birds ringed in all years.

To perform the survival analyses the number of Starlings ringed annually per age-class has to be known. From 1990 onwards, all ringing data were digitally available. Prior to 1990, however, only ringing data of birds that were subsequently recovered were digitally available. Ringing data of birds that were not recovered afterwards are available on paper but have not yet been digitized. However, the total numbers of birds ringed as nestlings (EURING age code 1), and of birds ringed as full-grown individuals (i.e. both adults, EURING code 4, and birds ringed as free-flying juveniles after fledging, EURING code 3) is known for each calendar year. We used these data to estimate the annual numbers of Starlings ringed during the Dutch breeding period as first-year birds and adults in the period prior to 1990. First, we estimated the numbers of full-grown Starlings ringed annually during the breeding season. This was done by calculating the average proportion of full-grown Starlings ringed during the breeding season in the period 1990–2012. This proportion was then multiplied with the number of full-grown Starlings per calendar year to obtain the estimated numbers of full-grown birds ringed during the breeding season each year in the period prior to 1990. Secondly, we calculated the average proportion of full-grown birds ringed as juveniles (EURING age code 3) and adults (EURING age code 4) during the breeding season for the period 1990–2012. We then multiplied these average proportions by the estimated number of full-grown birds ringed during the breeding season to obtain estimates of the annual numbers of birds ringed within both age-classes for the period prior to 1990. These calculations assume that the proportion of Starlings ringed during the breeding season has remained constant throughout the study period. To test this assumption we calculated the proportion of birds annually ringed as nestling, first-year bird and adult. We compared the proportional distribution in ringing ages between the period before 1990 and in the period after 1990. We found only small differences between 1 and 5%. We therefore assume that our estimates are acceptable, taking into account that small differences in the numbers of birds ringed in each cohort result in rather similar estimates of survival (Robinson 2010). Our final dataset contains in total 75,218 individual ringed birds, of which 54,779 birds were ringed as

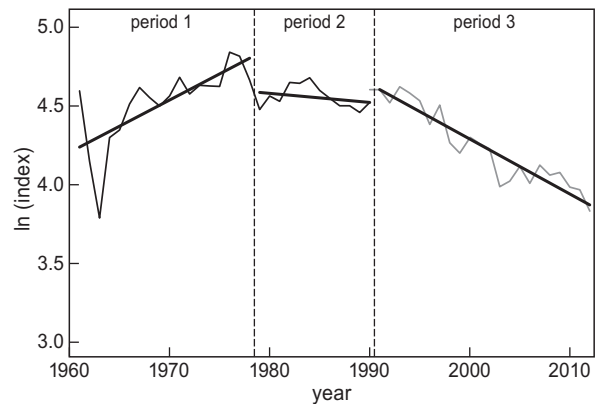


Figure 1. Year indices (relative population size) and trends of the Starling *Sturnus vulgaris* population in The Netherlands (updated from Sovon 2002). The black line represents the trend derived from the 'Old time series database' (see Methods), the grey line is the trend based on data from the Common Breeding Bird Monitoring Scheme (BMP). Three distinct trend periods have been defined for further analyses. Thick black lines represent the linear trend in each of the time periods.

nestlings, 14,732 as first-year birds, and 5707 as adult birds. In total, 885 dead recoveries of these birds were available. Hence, the overall reporting rate was 1.6%.

Exploratory analyses showed that the numbers of recoveries of birds from each age-class were too small to allow separate treatment in the survival analyses, with many estimates arriving at, or close to, the boundary of their parameter space (i.e. 0 or 1). Therefore birds ringed as nestlings (EURING age code 1) and first-year birds (EURING age code 3) were merged into a juvenile class. Nestlings are ringed on average 10 days before they fledge and therefore the juvenile age-class includes a small component of the nestling mortality. Juvenile recoveries were taken to be those occurring before April the year after ringing. Recoveries after April were classed as adult. Birds ringed as adults and recovered before 31 March the following year were classified as having been recovered in the year of ringing. Thereafter the reporting period lasts from 1 April to the following 31 March.

Survival rates over the two age-classes (juvenile (j), adult (a)) were estimated using a dead encounters model (Seber-model). We used R v. 3.2.3 (R Core Development Team 2015) with the statistical package RMark (Laake 2012) to build survival models. This package fits models in the program MARK (White & Burnham 1999), but has the advantage that model definition is straightforward and does not require specifying the design matrix. The parameters that are used in this model are true survival (S) and the probability

of being found dead and reported (r). Both parameters are estimated as being constant over time (\cdot), time dependent (t) and linear over time (T). Models fitted to estimate annual survival rates performed poorly because of the sparse data set. Many model parameters estimated the maximum likelihood estimations at the boundary of their parameter space (i.e. 0 or 1). Consequently, to obtain a trend over time we decided to estimate survival for 13 consecutive time periods of four years. We choose time periods of four years because this increased sample size in such a way that estimates became more accurate without losing the trend over time. We also tested whether survival differed during different trend periods (Figure 1) therefore we modelled survival and reporting parameters as being constant over periods (\cdot) and different between periods (p).

A bootstrap goodness-of-fit test was applied to evaluate to what extent the general model ($S(j,t)$, $S(a,t)$, $r(j,t)$, $r(a,t)$) fitted the data. We checked for overdispersion by calculating the \hat{c} as the observed deviance divided by the mean deviance of the simulated data that we derived from the bootstrap simulation (Cooch & White 2005). A value of $\hat{c} > 1$ indicates a certain degree of overdispersion in the data. For the selection of the best fitting model we used the modified Akaike's Information Criterion adjusted for overdispersion (QAIC_c; Anderson *et al.* 1994, Burnham & Anderson 2002, Cooch & White 2005). Models differing less than $2 \times \Delta\text{QAIC}_c$ were not considered different (Cooch & White 2005).

Population modelling

The trend in population size of Starling in The Netherlands is derived from Sovon (2002), and was updated for later years. It is based on the Dutch Common Breeding Bird Monitoring Scheme (BMP), a standardized

monitoring scheme coordinated by Sovon in collaboration with Statistics Netherlands. The scheme has been running since 1984. Data originating from this scheme are considered to be adequately representative and reliable for population trend estimation (van Turnhout *et al.* 2010a, Kampichler *et al.* 2012). The monitoring plots are well scattered throughout The Netherlands and range in size between 10 ha and 1000 ha. Before the start of BMP, annually repeated breeding bird surveys were already carried out in The Netherlands, be it on a smaller scale and using less standardized methods than nowadays. In the past decades Sovon has collected such data in order to reconstruct long-term population trends of as many bird species as possible. Time series of individual study plots were considered useful if fieldwork and interpretation methods were more or less constant between years. The resulting 'Old Timeseries' database contains census data for some 2000 study sites (Sovon 2002, van Turnhout *et al.* 2010b).

The long-term trend of the Dutch Starling population (Figure 1) demonstrates three different phases of population growth within the study period (a regression analysis was used to determine a significant trend per period; Table 1): (1) the period 1960–1978, with a significantly increasing population ($\lambda = 1.034$, C.I. 0.921–1.161), (2) 1978–1990 when the population was fairly stable ($\lambda = 0.994$, C.I. 0.953–1.035) and (3) 1990–2012, with a significantly decreasing trend ($\lambda = 0.966$, C.I. 0.873–1.068; Table 1). For each of these periods we calculated the finite rates of population change (the dominant eigenvalue λ) by modelling population changes with the obtained demographic parameters. We used a stage-structured matrix population model with two age classes. This matrix model assumed that the population grows in a density-independent manner, survival between sexes is identical

Table 1. Results of population models for three distinct time periods. Trend shows the observed population growth rates based on regression analysis. Model parameter estimates are split into fecundity, juvenile and adult survival. Estimates are used in a matrix population model and LTRE analysis. Model results show estimated trends of the matrix population model and regression analysis, displayed by the λ with 95% bootstrap confidence intervals.

| Period | Regression trend | | | Model parameters | | | Model results | |
|-----------|------------------|---------|--------|--------------------------|-------------------------------------|----------------------------------|-------------------------------|---------------------|
| | df | t | P | Fecundity (\pm SE) | Juvenile survival (\pm SE) | Adult survival (\pm SE) | Population λ model | λ Trend |
| 1960–1978 | 16 | 3.991 | 0.001 | 2.56 \pm 0.35 | 0.33 \pm 0.02 | 0.67 \pm 0.02 | 1.080 (1.017–1.141) | 1.034 (0.921–1.161) |
| 1978–1990 | 10 | –1.011 | 0.336 | 4.20 \pm 0.44 | 0.17 \pm 0.03 | 0.62 \pm 0.02 | 0.988 (0.881–1.096) | 0.994 (0.953–1.035) |
| 1990–2012 | 20 | –11.970 | <0.001 | 3.70 \pm 0.50 | 0.12 \pm 0.02 | 0.58 \pm 0.03 | 0.821 (0.751–0.891) | 0.966 (0.903–1.038) |

and the sex ratio is 1:1. The general matrix model formulation (Caswell 2001) that matches the population structure of Starlings is given in Equation 1.

$$\begin{pmatrix} N_j \\ N_a \end{pmatrix} = \begin{pmatrix} j \times \frac{f}{2} & a \times \frac{f}{2} \\ a & a \end{pmatrix} \begin{pmatrix} N_{j-1} \\ N_{a-1} \end{pmatrix} = c \begin{pmatrix} N_{j-1} \\ N_{a-1} \end{pmatrix} \quad \text{Eqn. 1}$$

where f is the fecundity value of the female Starling, j the probability that juveniles will survive until the next breeding season, and a the survival probability from their first year onwards. In the model only female birds are considered, hence the division by 2 in the upper row of the matrix that refers to the fecundity. Values for annual survival for the two age classes are derived from the MARK analysis of dead recoveries. A Monte Carlo simulation (10,000 replicates) of the population model was performed to calculate the 95% confidence intervals for the dominant eigenvalue. Analyses were performed with the Poptools add-in (Hood 2010) for Microsoft Excel.

Finally, we explored which demographic parameters drive differences in population growth rate between the three periods, by decomposing these into the contributions of each vital rate in a Life Table Response Experiment (LTRE; Caswell 1989, Cooch *et al.* 2001). By doing this, we answer the question how much each of the parameter differences contributes to the difference in population growth rates between the three periods. We used a one-way design where the difference between the control and treatment matrix in a given period, $\Delta\lambda$, is given in Equation 2.

$$\Delta\lambda = \lambda^a - \lambda^b \approx \sum_{ij} (a_{ij}^a - a_{ij}^b) \times \left(\frac{\partial\lambda}{\partial a_{ij}} \right) \Big|_{(a^a + a^b)/2} \quad \text{Eqn. 2}$$

where $(a_{ij}^a - a_{ij}^b)$ represents the difference in parameter a_{ij} between the treatment matrix and the control matrix. $\partial\lambda/\partial a_{ij}$ is the sensitivity of λ to changes in a_{ij} . Sensitivity is evaluated based on the treatment matrix a^a and the control matrix a^b (Caswell 2001). Some of the matrix entries are expressed as a combination of two underlying vital rates. Because the contribution of a_{ij} to changes in λ could reflect the effects of the different subcomponents of a_{ij} , we analysed the contribution of the different subcomponents rather than the matrix entries themselves (Caswell 1996). If a matrix entry is defined by the contribution of subcomponents (i.e., $a_{ij} = f\{\theta_1, \theta_2, \dots, \theta_n\}$) then Equation 2 can be rewritten in terms of the contributions of the subcomponents, as given in Equation 3.

$$\Delta\lambda = \lambda^a - \lambda^b \approx \left(\begin{array}{l} \sum_{ij} (\theta_{1ij}^a - \theta_{1ij}^b) \times \left(\frac{\partial\lambda}{\partial \theta_{1ij}} \right) \\ + \sum_{ij} (\theta_{2ij}^a - \theta_{2ij}^b) \times \left(\frac{\partial\lambda}{\partial \theta_{2ij}} \right) \\ + \sum_{ij} (\theta_{nij}^a - \theta_{nij}^b) \times \left(\frac{\partial\lambda}{\partial \theta_{nij}} \right) \end{array} \right) \Big|_{(a^a + a^b)/2}$$

Eqn. 3

Every summation term is the contribution of a treatment effect to the overall effect on λ , expressed by the underlying vital rates, rather than the matrix entries themselves (Caswell 2001, Cooch *et al.* 2001). The contribution of a different subcomponent on $\Delta\lambda$ could have a negative or positive effect. With a positive LTRE output, the subcomponent should have a positive influence on λ and thus λ^b should be higher than λ^a . A negative output has the opposite effect; however, the sum of all subcomponent represents $\Delta\lambda$. In total, we conducted two LTRE comparisons; period 1 (1960–1978) vs. period 2 (1978–1990) and period 2 (1978–1990) vs. period 3 (1990–2012).

RESULTS

Reproduction

Over the period 1984–2012, for which reproductive success could be estimated on an annual basis, Starling nest success did not change significantly ($r_s = -0.088$, $P = 0.673$; Figure 2). For the three different periods we found an average nest success (at least one fledged young) of 68% (C.I. = 61.4–75.3, $n = 236$) for 1960–1978, 90.7% (C.I. = 87.8–93.7, $n = 527$) for 1978–1990 and 77.8% (C.I. = 74.3–81.5, $n = 764$) for 1990–2012. The average number of fledglings per successful nest was 3.55 (C.I. = 3.14–3.97, $n = 47$) for 1960–1978, 4.37 (C.I. = 4.1–4.64, $n = 81$) for 1978–1999 and 4.43 (C.I. = 4.28–4.58, $n = 269$) for 1990–2012. Sufficient data for calculating the number of fledglings per successful nest per year were available for 1989, and for most years between 1995 and 2012 (Figure 3). The mean number of fledglings per successful nest did not change significantly during this period ($r_s = 0.253$, $P = 0.380$; Figure 3), in which the population decline was strongest. The overall breeding success in 1960–1978, 1978–1990 and 1990–2012 is 2.42, 3.96 and 3.45 fledglings per nesting attempt respectively. Starlings may have either one or two clutches within the breeding season, however, the exact annual proportion of second clutches is unknown. For further analyses we inflated reproductive success within the

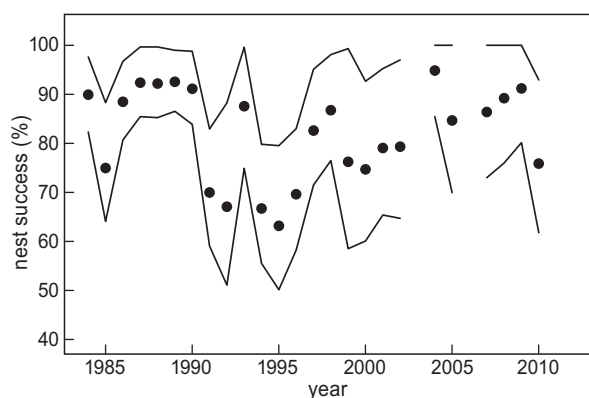


Figure 2. Trend in annual nest success (% of nests with at least one fledged young) of Starling, with 95% confidence interval (solid line), for the period 1984–2010. Only years with at least 25 nests are included.

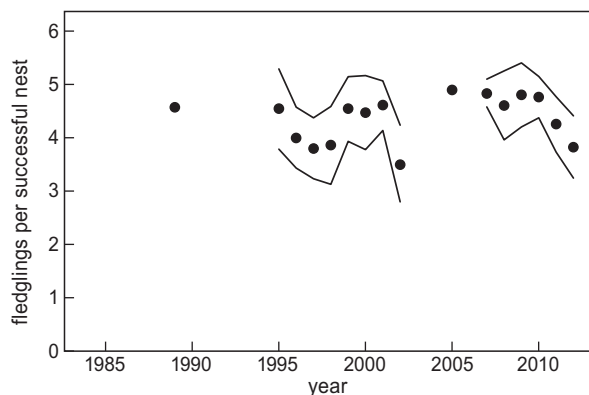


Figure 3. Trend in the mean number of fledglings per successful nest, with 95% confidence interval (solid line), for the period 1984–2012. Only years with at least 10 nests are included.

different periods using the average frequency of second clutches in the period 2010–2012, by 6% to 2.56 for 1960–1978, 4.20 for 1978–1990 and 3.70 for 1990–2012 (see Methods).

Estimates of survival

The bootstrap goodness-of-fit test of the general model indicated some overdispersion ($\hat{c} = 1.6$). Therefore, we used the adjusted \hat{c} and the $QAIC_c$ for further model selection. The five best fitting models are shown in Table 2. The two best models did not differ ($\Delta QAIC_c < 2$); therefore, we used model averaging to compute the average of the parameters from the models.

The average survival rate for adults was 0.63; the best fitting model included a significant effect of time period on survival. Adult survival rates varied between the different time periods (Figure 4), with lower survival during the last 15 years. However, a linear trend in survival over time was not significant. For the juvenile period we found an average survival rate of 0.20. The best model for juveniles included a linear trend in survival: juvenile survival decreased significantly during the study period, with a long-term decline starting in the late 1970s (Figure 4). Reporting rates over the 13 consecutive time periods were not correlated with the estimated survival rates in both age-classes: juvenile ($r = -0.095$, $P = 0.757$) and adult ($r = 0.068$, $P = 0.826$). However, reporting rates in the adult age-class were lower in the last 20 years (Figure 5).

Population modelling

Within the long-term trend (1960–2012) of the Dutch Starling population we distinguish three different periods with contrasting population trends (Figure 1). For each period the population growth rate was modelled by using the modelled survival rates per period (Table 3) and reproductive success per period (Table 1). Projected population growth rate for the period 1960–1978 showed an annual increase in numbers of 8% ($\lambda = 1.080$ C.I. = 1.017–1.141). For the period 1978–1990 the population was projected to be rather stable -1.2% ($\lambda = 0.988$, C.I. = 0.988–1.096), and for the period 1990–2012 an annual

Table 2. The five best-fitting models for survival of juvenile (*j*) and adult (*a*) Starlings, in The Netherlands. Models consider survival (*S*) and the probability of being found dead and reported (*r*). Parameters are modelled as being constant over time (\cdot), time dependent (*t*), and linear over time (*T*). The models used to estimate survival probabilities are given in bold.

| Model | $QAIC_c$ | $\Delta QAIC_c$ | $QAIC_c$ weight | Number of parameters | QDeviance |
|---|-----------|-----------------|-----------------|----------------------|-----------|
| <i>S(j T)</i>, <i>S(a t)</i>, <i>r(j t)</i>, <i>r(a t)</i> | 14070.389 | 0.000 | 0.576 | 20 | 1131.337 |
| <i>S(j T)</i>, <i>S(a t)</i>, <i>r(j t)</i>, <i>r(a \cdot)</i> | 14072.243 | 1.854 | 0.228 | 19 | 1135.192 |
| <i>S(j t)</i> , <i>S(a T)</i> , <i>r(j t)</i> , <i>r(a \cdot)</i> | 14072.716 | 2.327 | 0.180 | 18 | 1137.666 |
| <i>S(j t)</i> , <i>S(a T)</i> , <i>r(j \cdot)</i> , <i>r(a t)</i> | 14079.154 | 8.765 | 0.007 | 18 | 1144.104 |
| <i>S(j T)</i> , <i>S(a \cdot)</i> , <i>r(j t)</i> , <i>r(a t)</i> | 14080.044 | 9.655 | 0.005 | 7 | 1167.001 |

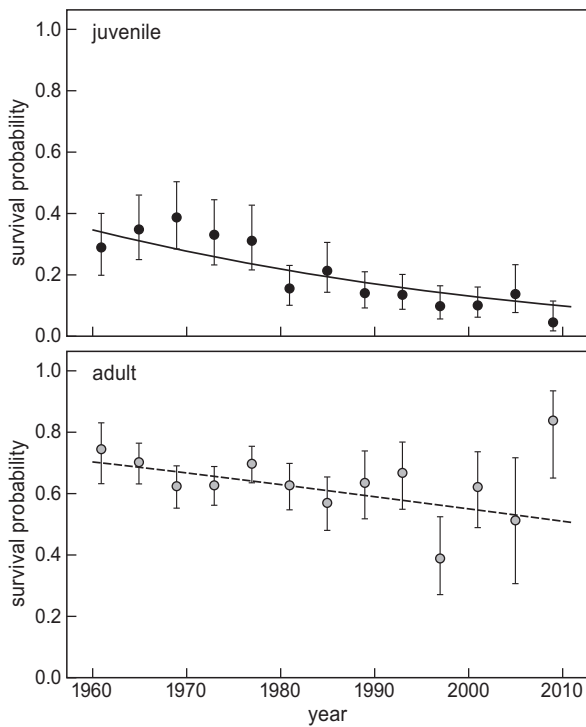


Figure 4. Trend in estimated survival for juvenile and adult Starlings, based on time periods of four years, for the period 1960–2012. Bars represent the 95% confidence intervals. The solid line in the upper panel represents a significant (log)linear trend and the dashed line in the lower panel a non-significant linear trend.

decrease in numbers with 17.9% ($\lambda = 0.821$, C.I. = 0.751–0.891) was projected (Table 1). The observed population trends in the periods 1960–1978 and 1978–1990 lie well within the 95% confidence intervals of the model predictions. For the period 1990–2012, however, the 95% confidence interval of the model prediction does not include the observed λ . The model prediction is considerably lower than the value calculated from the observed population trend (0.966).

Table 3. The five best-fitting models for survival of juvenile (*j*) and adult (*a*) Starlings for three different phases of population change. Models consider survival (*S*) and the probability of being found dead and reported (*r*). Parameters were modelled as being constant between periods (.) or different between periods (*p*). The models used to estimate survival probabilities are given in bold.

| Model | QAIC _c | ΔQAIC _c | QAIC _c weight | Number of parameters | QDeviance |
|--|-------------------|--------------------|--------------------------|----------------------|----------------|
| <i>S(j p), S(a p), r(j p), r(a p)</i> | 9742.418 | 0.000 | 0.754 | 10 | 792.310 |
| <i>S(j p), S(a .), r(j p), r(a p)</i> | 9746.217 | 3.799 | 0.113 | 9 | 798.110 |
| <i>S(j p), S(a p), r(j .), r(a p)</i> | 9747.723 | 5.306 | 0.053 | 9 | 799.616 |
| <i>S(j p), S(a p), r(j .), r(a .)</i> | 9748.260 | 5.842 | 0.041 | 8 | 802.152 |
| <i>S(j p), S(a .), r(j .), r(a .)</i> | 9749.362 | 6.944 | 0.023 | 6 | 807.256 |

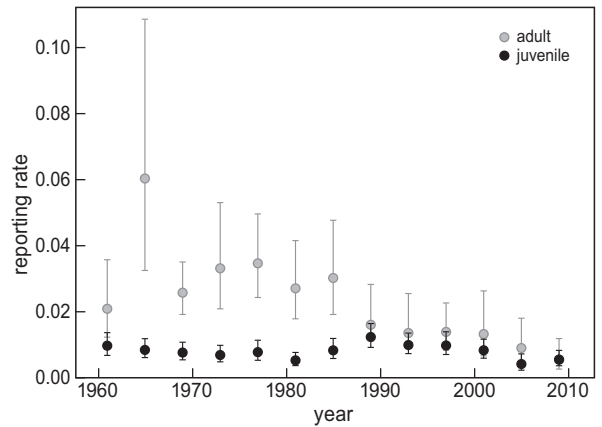


Figure 5. Reporting rates estimated for juvenile and adult Starlings. Estimates are based on time period of four years, for the period 1960–2012. Bars represent the 95% confidence interval. Estimates based on the first model in Table 2.

Table 4. Results of the life table response experiment (LTRE), the contributions of differences in vital rates to changes in population growth rates. LTRE analyses were conducted between different periods as defined in Figure 1 (see Methods).

| Individual vital rates | Contribution to differences in λ | |
|-----------------------------|--|----------------|
| | Period 1 vs. 2 | Period 2 vs. 3 |
| Juvenile fecundity | 0.053 | -0.005 |
| Adult fecundity | 0.118 | -0.014 |
| Juvenile survival (f^1) | -0.127 | -0.046 |
| Adult survival (a^1) | -0.024 | -0.013 |
| Juvenile survival (f^2) | -0.161 | -0.068 |
| Adult survival (a^2) | -0.030 | -0.027 |

We decomposed differences in population growth rates into contributions from differences in the vital rates between the three periods (Table 4). The difference in λ between period 1 and 2 was -0.11. Changes

in juvenile (f^1+f^2) survival had the largest negative contribution to this change in λ . The increase in fecundity had a positive effect on λ . However, the smaller positive contribution of fecundity to the change in λ does not outweigh the larger negative effect of the change in juvenile survival. The second comparison was made between period 2 and 3: the difference in λ was -0.16 . Changes in juvenile survival had the largest contribution to the change in the modelled λ , with -0.10 while changes in adult survival had only a contribution of -0.04 to the differences.

DISCUSSION

The Starling is one of the most widespread and abundant bird species in the world (Feare 1984). Nevertheless, in recent decades, it has experienced a significant decline in large parts of Europe. Large declines of relatively few very common birds in fact contribute more to the overall loss in avian abundance and biomass in Europe than declines in already rare species, but have received relatively little attention so far (Inger *et al.* 2014). In The Netherlands, the Starling showed an increase in numbers in the 1960s and the early 1970s. The population stabilized in the late 1970s, and around 1990 the numbers started to decline rapidly. The results from our population modelling suggest that the stabilization of the Starling population in the late 1970s, and the subsequent decline after 1990, was mainly caused by a significant decline in survival of juvenile birds. This is supported by the LTRE analyses which suggest that juvenile survival is the vital rate that best explains differences in population growth rate between periods. Furthermore, adult survival tended to be lower as well in the period 1990–2012, albeit not significantly. These results are comparable with the British population, however, we estimated on average lower adult survival rates: 0.63 compared to 0.69, respectively (Freeman *et al.* 2007). Most likely changes in adult survival also contributed to the negative population trend of the Starling in the last two decades of our study period.

We tested the robustness of the S -parameter by rerunning the survival models where we fixed the S -parameter while the r -parameter differed between models. The results showed that juvenile survival rates differ between 1 and 6% when using different r -parameters and adult survival rates between 0.5 and 2%. This indicates that the survival rates are quite robust. However, the numbers of ringed birds found dead and reported declined from 2–9% in 1960–1990 to only

0.5–1.5% in 1990–2012. This may have caused larger variation and possible bias in survival rates in the last period. There is a general tendency for ring recoveries of bird species to decline over time (Dunn 2001, Besbeas *et al.* 2002), which according to Robinson *et al.* (2009) is due to changes in reporting behaviour, rather than factors associated with the ecology of species.

In Fennoscandia and in urban areas in France, Starling population declines have been linked to changes in reproductive output of populations (Tiainen *et al.* 1989, Mennechez & Clergeau 2006, Wretenberg *et al.* 2006, Smith *et al.* 2012). In this study, the long-term trend does not suggest that reproductive success has changed during 1984–2012, the period of population decline. However, our estimates are based on relatively small annual sample sizes. Therefore, additional effort is required to acquire more reliable reproductive data in the future. In 2014, Sovon made a huge effort in gathering a large sample of nest record data, as part of the ‘Year of the Starling’. The number of fledglings per successful nest and the number of fledglings per breeding attempt in this much larger sample appeared similar to the long-term averages: 4.37 ± 1.29 (SD; $n = 262$) and 3.80 ± 1.13 ($n = 262$), respectively. Hence, small annual sample sizes may be sufficient to calculate average reproductive success. For modelling population changes we used reproductive success calculated over the three distinct periods. Reproductive success tends to be lower in the first period (1960–1978) compared with the two latter periods. Due to low sample size in this period we are not very confident that a true positive trend exists. Nevertheless, the modelled population growth rate for period 1960–1978 is comparable to the observed trend, 8% ($\lambda = 1.080$, C.I. = 1.017–1.141) and 3.4% ($\lambda = 1.034$, C.I. = 0.921–1.161) respectively. A positive trend in reproductive success was also observed in the United Kingdom, where the number of fledglings per breeding attempt increased over 1965–2000 (Siriwardena & Crick 2002, Freeman *et al.* 2007). Comparing both studies shows that the average reproductive success in the Dutch population was higher over the latter part of the study period (1978–2000), 3.5 compared to 3.7, respectively. Over the first period (1960–1978) reproductive success in the British population was higher, 3 compared to 2.56 in the Dutch population. However, the estimates from the Dutch population are not accurate due to very low sample sizes. In other parts of Europe it has been found that reproductive success was considerable higher than in both the Dutch and British population. In the Finnish population, the average number of fledglings per breeding attempt over the period 1951–2005 was 4.1

(Rintala & Tiainen 2008). However, in the 1970s and 1980s when the Finnish population declined by 80%, reproductive success was lower, between 3.5 and 4 fledglings per breeding attempt. This is still higher than in the British population but similar to the Dutch population. In France, reproductive success was estimated to be higher than the Dutch and Finnish population: over a period of three years (1995–1997) they found reproductive success to be between 4.6 and 5.3 (Mennechez & Clergeau 2006).

We assumed that the proportion of second or replacement clutches did not change over time. Since second clutches are rare, they have a very low impact on the total reproductive output and thus on the modelled population growth rates. The proportion of Starlings laying second clutches varies annually (Siriwardena & Crick 2002) and is largely dependent on the date of laying of the first clutch. In years with high April temperatures, first clutches are laid earlier in the season (Meijer *et al.* 1999), and more pairs can produce a second clutch. According to Bijlsma (2013) and Tinbergen (1981), the proportion of second clutches within the Dutch breeding population is low, between 1 and 3%. It is expected that the proportion of second clutches might increase in the future due to an increasing trend in April temperatures (KNMI 2014) which suggests that this parameter requires more reliable estimation in the future, preferably using colour ringed parents.

Our findings that lower survival rates in juveniles drive the current population decline of the Dutch Starling population is in line with the findings of Freeman *et al.* (2007), who found that changes in juvenile survival play an important role in determining the population trend of Starlings in the United Kingdom. In contrast to the British population where juvenile survival did not significantly change over time but varied greatly annually, juvenile survival in the Dutch population decreased significantly between 1960 and 2012 from 0.33 to 0.12. When comparing these results we should take into account that in this study the post-fledging period is included in the juvenile age-class, while in Freeman *et al.* (2007) the post-fledging period was excluded. The post-fledging survival in Freeman *et al.* (2007) was kept constant in the population model and thus did not contribute to the decline. However, Freeman *et al.* (2002) give more detailed insight into juvenile survival (post-fledgling and first-year) within the British population. They found an overall survival rate during the first twelve months of life of 0.15 over the period 1966–2000. Although we found for the period 1990–2012 a juvenile survival rate of 0.12, the

average survival rate over the whole study period was 0.20. This is considerably higher than that found in the United Kingdom.

Survival of juvenile birds is thought to be affected by a decrease in good foraging habitat and food availability. Large-scale changes in agricultural land use affect vegetation structure and food resources, as drainage, increased harvesting frequencies and more efficient techniques and use of fertilizers and pesticides, create improved conditions for competitive grass species, resulting in homogeneous and species poor swards and impenetrable soils (McCracken & Tallwin 2004). Productive grass monocultures have reduced arthropod abundance and diversity (Morris 2000, Schekkerman & Beintema 2007). Starlings prefer to forage on permanent, extensively used pastures where densities of soil living invertebrates are highest (Bruun 2002). In The Netherlands, the area of these permanent pastures has declined by 35% since 1980 (CBS 2013). Food availability and accessibility within the remaining grasslands are affected by increased insecticide use (Geiger *et al.* 2010), increased fertilizer use and lower moisture content of the soil top layer (Rhymer *et al.* 2012). The percentage of dairy cows kept permanently inside stables increased from 8 to 30% in The Netherlands between 1997 and 2012 (CBS 2014), which also has a potential impact on the availability and accessibility of food. Starlings are frequently associated with livestock (Tinbergen 1981, Perkins *et al.* 2000), as livestock generally increase the availability of soil-living invertebrates. Ungrazed parcels with dense grass swards are unattractive for Starlings, as livestock disturbs the soil substrate through trampling, which leads to an increase of invertebrate activity in the top layer of the soil. This has a positive effect on the foraging efficiency of Starlings (Devereux *et al.* 2004, McCracken & Tallwin 2004).

Predation risk for Starlings may have increased as well. The main period of the decline in juvenile survival coincides with an increase in numbers of potential predators. For example, the Dutch Northern Goshawk *Accipiter gentilis* population has increased from an estimated 50 breeding pairs in 1960–1970 to 1800–2000 pairs in 2000 (Sovon 2002, Rutz *et al.* 2006). Between 4–20% of the Northern Goshawk diet consists of Starlings (Opdam *et al.* 1977, Rutz *et al.* 2006). Different studies have shown that predator removal can produce significant increases in breeding population numbers and increase hatching and fledging success (Côté & Sutherland 2006, Smith *et al.* 2010), suggesting that higher densities of potential predators (i.e. Northern Goshawk, Eurasian Sparrowhawk *Accipiter nisus* and

Pine Marten *Martes martes*) can have a negative effect on the population growth rate (Bell *et al.* 2010).

It is perhaps not surprising that juvenile Starlings show more pronounced changes in survival rates than adults. It is widely acknowledged that the post-fledging period is the critical phase in the avian life-cycle; unexperienced naïve birds in an unfamiliar environment often suffer severe mortality while learning to forage independently and avoid predation (Krementz *et al.* 1989, Anders *et al.* 1997). Juveniles may be more vulnerable to environmental stress, such as food shortage during the winter period, because in times of food shortages subordinate juveniles are the first to be competitively excluded from rich feeding patches (Ekman & Askenmo 1984, van den Hout *et al.* 2014). Furthermore, juveniles are less efficient foragers due to poorer knowledge of their winter environments (Marchetti & Price 1989, Heise & Moore 2003). Lower energy intake rates and associated reduced body condition may subsequently lead to higher (predation related) mortality rates in juveniles (Cresswell 1994, Adams *et al.* 2006).

In conclusion, our results suggest that a change in juvenile survival rather than changes in adult survival or reproductive success is the underpinning demographic cause of the decline of the Dutch Starling population. The most likely factors contributing to declining juvenile survival include a decrease in the quality of potential foraging habitat and a higher predation risk caused by increasing predator populations. Further studies are necessary to elucidate the causal factors, in order to formulate effective conservation management strategies.

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SAMENVATTING

De recente populatieafname van veel boerenlandvogels wordt vaak in verband gebracht met de intensivering van het agrarisch landgebruik gedurende de afgelopen decennia. Er is echter maar weinig bekend over de demografische veranderingen die aan deze negatieve trends ten grondslag liggen. In deze studie hebben wij over een tijdsperiode van 52 jaar (1960–2012) de veranderingen in het broedsucces en de overleving van de afnemende populatie Spreeuwen *Sturnus vulgaris* in Nederland onderzocht. De resultaten laten zien dat de overleving van juveniele Spreeuwen significant is afgenomen gedurende de onderzoeksperiode. De overleving van adulte Spreeuwen fluctueerde sterk tussen jaren, maar lijkt in 1990–2012 ook wat lager te zijn geweest dan daarvoor, al was het verschil niet significant. Wij hebben geen aanwijzingen gevonden dat het broedsucces gedurende de onderzoeksperiode is afgenomen. Op basis van de demografische cijfers hebben we met behulp van een populatiemodel de populatieverandering in drie perioden (1960–1978, 1978–1990 en 1990–2012) berekend en die vergeleken met de waargenomen populatieverandering op basis van monitoringgegevens. Voor de eerste twee perioden komt de uitkomst van het populatiemodel overeen met de waargenomen populatieverandering; de laatste periode wijkt echter erg af van de waargenomen trend. Dit verschil is waarschijnlijk het gevolg van een onnauwkeurige schatting van de overleving van de adulte vogels veroorzaakt door een afname van het aantal terugmeldingen in die periode. De bijdrage van de veranderingen in demografische parameters op de populatieontwikkeling is daarnaast geanalyseerd met behulp van een Life Table Response Experiment (LTRE). Deze analyse laat zien dat de veranderingen in juveniele overleving het meeste hebben bijgedragen aan de populatieontwikkeling. Onze resultaten suggereren daarom dat de afname in juveniele overleving de belangrijkste oorzaak is van de populatieafname van de Nederlandse Spreeuwenpopulatie.

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