Survival estimation and population modelling for Swedish Lesser White-fronted Geese

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1. Introduction

1.1. Background

The Lesser White-fronted Goose *Anser erythropus* (hereafter LWfG) is a small, migratory, Arctic-nesting goose that occupies a breeding range from Scandinavia eastward to Chukotka in eastern Siberia. During the 19th and 20th centuries, the species underwent a massive population decline across all parts of its range. In Scandinavia, nowadays essentially just two small subpopulations remain, one in northern Norway and one in Swedish Lapland (county of Norrbotten). Since the early 1980s, the Swedish breeding population has been reinforced by 'Projekt Fjällgås' of the Svenska Jägareförbundet and foundation Nordens Ark, by releasing captive-bred young birds. Until the year 2000 this was carried out with Barnacle Goose foster parents and from 2010 onwards by releasing groups of young birds on the breeding grounds just before they are able to fly (von Essen 1991, Andersson & Holmqvist 2010, Andersson 2016). The foster-parenting approach resulted in the population establishing new migration habits with wintering areas concentrated in The Netherlands.

Both in the 1980s-1990s and after 2010, released birds have been individually marked with colour rings, as were a small number of wild-born birds captured outside the breeding season around 2010. A database containing all ringing data and resightings has been set up to enable analyses of the fates and demography of birds from this project. In 2018, the resightings were analysed in order to obtain estimates of annual (apparent) survival of released birds in this population, in both the 'old' (1984-2003) and the 'new' introduction periods (2012-2018) (Schekkerman & Koffijberg 2019).

In this report, survival estimates for the 'new' period after 2010 are updated using an additional year of resighting data (2018-2019). In addition, these updated estimates are combined in a population model with data on the reproduction of free-living LWfG of this population and on the numbers of young birds released in the breeding area, to explore what population development can be expected given the current demographics, and how important the reinforcement with captive-bred young is to the population.

1.2. Aims of the study

- Extend the analysis of annual survival in the 'new' period by adding one year of data, with consideration of effects of age, sex, time, and age at release of captive-bred individuals;
- Construct a population model incorporating the survival estimates, data on reproduction of the free-living LWfG population, and annual numbers of young birds introduced;
- Explore the population trajectory (growth rate) expected without reinforcement;
- Explore the effect of reinforcement with captive-bred birds on the population growth rate and expected future population trajectory.

2. Survival estimation update

2.1. Data and methods

Data sources and methods employed in the survival update are identical to those used in Schekkerman & Koffijberg (2019) for 'period 2', with minor amendments. Birds marked and released in 2018 (87) and resightings of all birds up to the spring of 2019 (per 1 May 2019, see Schekkerman & Koffijberg 2019 for delineation of annual cycle) were added to the data set. As in the previous analysis, we estimated survival from the year 2012 onwards, as too few marked individuals were available in the first two years of the 'new' period of introductions. However, 15 birds released in 2010-11 that became adults (i.e. ≥2 years old) in 2012 were now included in the dataset, treating them as if they were marked as adults in 2012. (Note that there was insufficient data to distinguish adult survival of wild-borns and birds introduced as young). Hence estimates were obtained for the years 2012 (i.e. survival from 2012 to 2013) to 2018.

Survival analysis was carried out with the Cormack-Jolly-Seber (CJS) model option in program MARK v. 9.0 (White & Burnham 1999). In the initial analyses, effects of sex (male/ female/unknown), age at release (fledgling/yearling), absolute age (1st-year/2nd-year/older), and time (year) were considered, with interactions. An initial model was constructed including all the above factors and their interactions for both apparent survival (φ) and resighting probability (p). This model was then simplified by dropping first interactions and then main effects, and by considering a linear time effect instead of independent estimates for each year. Selection of the most parsimonious models was based on the Quasi Akaike Information Criterium (QAICc, Burnham & Anderson 2002), using an overdispersion parameter estimated by the *median ĉ* method for the fullest model in which most of the parameters were estimable (in this case ĉ=2.3). We first identified the most parsimonious parametrisation for the resighting probability p and then optimised the model structure for survival φ. Finally we checked whether the most parsimonious model thus found could yet be improved by a slightly different parametrisation for p.

2.2. Results and discussion

Resighting probability
In total 51 different models were explored; table 1 summarises the performance of a subset of these. The best model structure for p was p(T), with resighting probability increasing linearly over time,

from 0.41 in 2013 to 0.92 in 2019. Compared to the previous analysis an age effect was no longer apparent; Schekkerman & Koffijberg (2019) already noted that this effect was not very clear. In this update the evidence for a time effect on p became stronger. Out of the four best-fitting models for φ, the corresponding model with constant p(.) scored c. 6 AIC units lower in three. The remaining one however (model 4 with survival differing between years as well), differed by only 1 unit (table 1).

Survival
Top-ranking model for survival was φ(Ag+Sx+R. Ag), with an effect of true age interacting with that of age at release (fledgling/yearling), plus an independent effect of sex, but no time effect. The parameter estimates from this model (and other high-ranking models) show the same general age pattern as found in the previous analysis up to 2018: low survival (~0.4) in the first year of birds released as fledglings, followed by a much higher value close to that of adults (~0.7) in their second year, but a very low survival (~0.2) in the second (i.e. release) year of birds released as yearlings (figure 1). According to this model females survive slightly better than males. Potential explanations for this could be that most losses of adult birds seem to take place during the breeding season during which predation by White-tailed Eagles and possibly foxes plays a role (N. Liljebäck *unpubl. data.*) and that males could be more vulnerable to such predation due to their greater share in nest and brood defence, or that the difference reflects a slightly greater tendency of males to permanently emigrate from the population. However, the corresponding model without a sex effect is not much less supported by the data (ΔQAICc =0.85; table 1) so the evidence for it is weak. Moreover, it is unexpected that birds of unknown sex seem to survive less well than both known males and females, instead of intermediate between these (figure 1). This might be a 'hidden time effect'; relatively more birds of unknown sex were released in the early years of this period, when survival was lower according to several of the models (although models with a sex.time interaction were not among the top-ranking ones). A second potential explanation is that the younger or slowest-growing goslings which were found most difficult to sex (by cloacal inspection) are also of a lower 'quality' with respect to survival. Females are likely to be overrepresented among unsexed birds since it is more difficult to be 100% sure of females.

The third and fourth-best ranking models have

Table 1. Summary of MARK results showing the 15 top ranking models, the four best models with a 'full' structure ('MAX') for φ used to find the best structure for p, and the 'full' model with complete time and group effects for both φ and p. Models are ranked by decreasing QAICc value. QAIC weights represent the relative support within the total set of 51 models. Ag= age, Sx= sex, R= age at release, t/T= time (categorical/linear effect), '.'= constant.

nr	Model	QAICc	Δ QAICc	Weight	Model Likelihood	N par.	QDeviance
1	φ(Ag+Sx+R.Ag) p(T)	336.31	0.00	0.249	1.000	8	84.06
2	φ(Ag+R.Ag) p(T)	337.16	0.85	0.163	0.653	6	89.04
3	φ(Ag+T+R.Ag) p(T)	337.58	1.27	0.132	0.530	7	87.40
4	φ(Ag+t+R.Ag) p(T)	338.67	2.37	0.076	0.306	11	80.17
5	φ(R+Ag+T+R.Ag) p(T)	339.54	3.23	0.050	0.199	9	85.21
6	φ(Ag+T+R.Ag+Ag.T) p(T)	339.63	3.32	0.047	0.190	9	85.31
7	φ(Ag+t+R.Ag) p(.)	339.67	3.36	0.046	0.187	10	83.25
8	φ(R+Ag+R.Ag) p(T)	339.95	3.64	0.040	0.162	8	87.70
9	φ(R+Ag+Sx+R.Ag) p(T)	340.15	3.84	0.037	0.147	10	83.74
10	φ(Ag+T+R.Ag) p(.)	340.64	4.33	0.029	0.115	6	92.52
11	φ(R+Ag+t+R.Ag) p(T)	340.91	4.60	0.025	0.100	13	78.19
12	φ(Ag+Sx+T+R.Ag+Ag.T) p(T)	341.01	4.70	0.024	0.095	11	82.51
13	φ(R+Ag+Sx+T+R.Ag) p(T)	341.32	5.01	0.020	0.082	11	82.81
14	φ(Ag+Sx+R.Ag) p(.) 7}	341.69	5.38	0.017	0.068	7	91.51
15	φ(R+Ag+T+R.Ag) p(.)	342.59	6.28	0.011	0.043	8	90.34
28	φ(MAXT) p(T)	369.57	33.26	0.000	0.000	27	76.31
29	φ(MAXT) p(.)	370.79	34.48	0.000	0.000	26	79.77
30	φ(MAXT) p(Ag+T)	371.41	35.11	0.000	0.000	28	75.90
31	φ(MAXT) p(R+T)	371.50	35.19	0.000	0.000	29	73.72
51	φ(MAX) p(MAX)	522.40	186.09	0.000	0.000	102	27.31

MAX= Sx+R+Ag+t+R.Ag+Ag.t+Sx.R+Sx.Ag+Sx.t+Sx.R.Ag+R.Ag.t+Sx.Ag.t+Sx.R.Ag.t; MAXT= T instead of t.

the same age/release structure as described above, and no sex difference, but do include a time effect on φ, either a linear increase (model 3) or separate values for each year which also tend to be higher in the later years (model 4). Model 3 differs less than 1.27 QAICc-units from the top model, while model 4 just exceeds the value of 2 units generally used as a threshold to consider models 'significantly less well supported'.
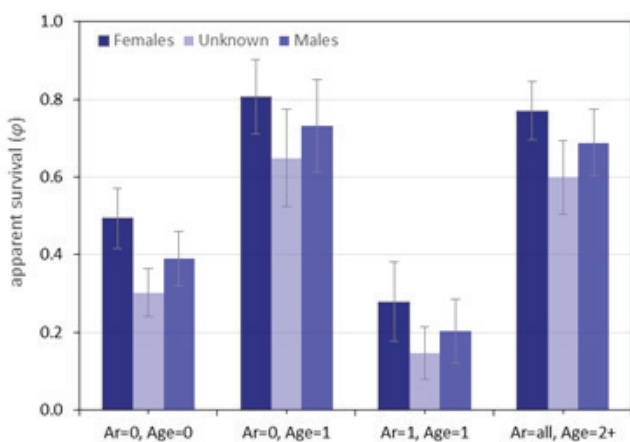

Figure 1. Estimates of mean survival probabilities (φ) in 2012-2019 according to the top-ranking model φAg+Sx+R.Ag p(T). Bars denote standard errors. Ar = age at release, Age=true age, in years. Thus Ar=0 represents birds released as fledglings, Ar=1 released yearlings.

Given that differences in support (QAICc weights) were generally slight among top-ranking models, model averaging was used to obtain parameter estimates for use in population modelling. In doing so we excluded models with a sex difference. As we essentially model the female half of the population, it would seem preferable to use an explicit estimate of female survival (e.g. from model 1), but given that the estimates for unsexed birds are systematically lower, this is likely to result in a high-biased value. The model-averaged estimates were calculated over the nine top-ranking models without sex, weighted according to their relative support (QAICc-weight) within this set. The accumulated weight of these nine models, which include two assuming a time-constant p(.), amounted to 61% in the original set of 51 models.

The model-averaged estimates are presented in figure 2. Changes from year to year run virtually parallel among age groups, as only one model in the set included an age.time interaction. They show a generally upward trend with some irregularity between years. The mean value of adult survival calculated over this new period is 0.71, slightly lower than the value found in the 'old' release period up to 2003 (0.70-0.82 with increasing trend; Schekkerman & Koffijberg 2019). The mean survival in their first (release) year of birds released as fledglings (0.37)

is markedly lower than that of fledglings released with Barnacle Goose foster parents in the 'old' period (0.60-0.76), but this difference becomes much smaller in their second year of life (0.71 vs. 0.80-0.90). The very low survival in the release year of birds introduced as yearlings in the new period (mean 0.21) is also similar to that in the old period (0.21-0.33). Release conditions for these birds were also similar in both periods.

Figure 2. Model-averaged annual estimates of survival probability (φ) in 2012-2019. Bars denote standard errors. Ar = age at release, Age=true age, in years.
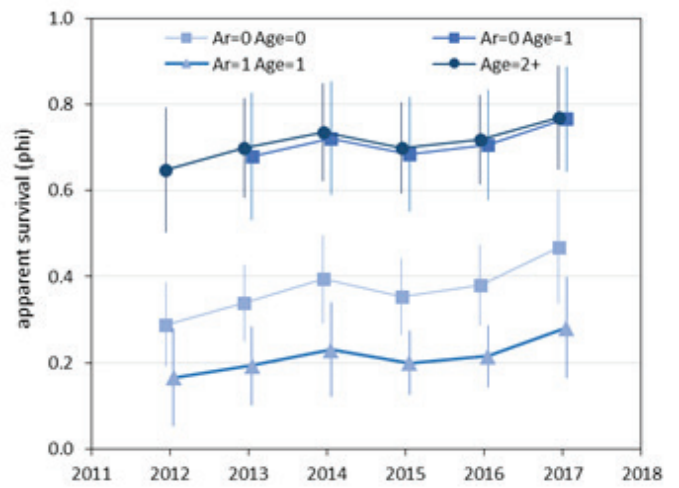
3. Population modelling

3.1. Model structure

In order to explore the expected population development given the above survival rates and existing data on reproduction of the wild LWfG, we applied a matrix population model (Caswell 2001). We implemented the model and performed calculations in Excel by using the add-in toolpack Poptools (Hood 2010). We modelled the female half of the population, assuming an equal sex ratio throughout, and formulated models for both post- and pre-breeding censuses. Here, we present (results for) the post-breeding model, which describes the population present at the end of the breeding season. It contains four age classes (figure 3):

(1) juveniles just fledged in the current breeding season,
(2) one-year old birds (yearlings) which are assumed not to have reproduced yet,
(3) two-year olds which might or might not have bred already, and
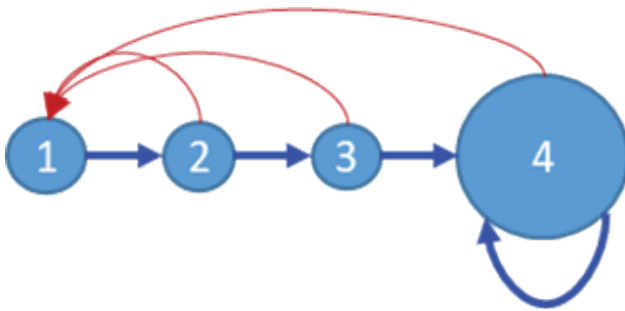(4) all older birds.

Figure 3. General structure of the population model (post-breeding census). Blue circles denote age classes: 1 juveniles, 2 yearlings, 3 two-year olds, and 4 older birds; circle sizes mirror proportions in the total population once a steady age composition has been reached. Blue arrows denote survival, red arrows reproduction.

The core of the population model is the projection matrix (figure 4), by which numbers of individuals in each age class (represented by the column headings) in one year can be projected (by multiplication with the corresponding matrix elements) into appropriate age classes in the next year (represented by the row headings). For the post-breeding model, this matrix is shown in figure 4.

The matrix is defined by the following demographic parameters:

S_j, S_1, S_a are the mean annual survival probabilities in, respectively, the first (fledging), second, and later years of life (adult). Note that here we assume the survival of two-year olds to equal that of older birds.

B_1, B_2, B_a are the probabilities that a bird of 1, 2 or >2 years old, respectively, starts a breeding attempt.

R is the mean reproductive output in fledglings per breeding pair, which is multiplied by 0.5 as only female offspring 'count'. Note that we assume that breeding success does not depend on age once recruited.

For instance, the left-most column describes the contribution of a (female) juvenile fledged in year t to the population in year t+1. In order to add another juvenile at t+1 it must first survive the year (S_j), then attempt to breed (B_1) and produce female young ($R*0.5$). In this case, we assume that yearlings do not yet breed, so B_1=0 and the outcome in this matrix cell is 0. However, a juvenile does contribute to the next-year class of yearlings, through S_j.

If this matrix projection is repeated year after year with constant values of the demographic parameters, after several iterations the population reaches a steady state with respect to age composition (proportions of individuals in each age class) and relative (*per capita*) growth rate. This 'asymptotic growth rate' is denoted by λ (lambda): λ = N_{t+1}/N_t, where N is number of individuals in the population and t is time. If λ=1, the population size is stable, if λ>1 it grows, otherwise it shrinks. For instance, λ=0.96 denotes a decline of about 4% per year.

The values of the demographic variables input into the basic model are estimates, subject to some

Figure 4. Projection matrix for the post-breeding model.

	juvenile	1yr old	2yr old	≥3yr old
juvenile	Sj*B1*R*0.5	S1*B2*R*0.5	Sa*Ba*R*0.5	Sa*Ba*R*0.5
1yr old	Sj	0	0	0
2yr old	0	S1	0	0
≥3yr old	0	0	Sa	Sa

amount of uncertainty. In addition they are multi-year means, whereas in practice these values will vary between years. We explored how this translates to uncertainty around the prediction of λ by resampling the probability distributions of the parameters. For uncertainty surrounding the mean parameter values, we took 5000 draws from normal distributions defined by the mean and associated standard *error* (SE) of each parameter, and calculated the mean and 2.5% and 97.5% percentiles of the resulting λs to obtain a confidence interval. For the effect of annual stochasticity in the demographic parameters, we sampled normal distributions defined by the mean and standard *deviation* (SD) of yearly values of the parameters at each of 30 yearly iterations of the model, calculated λ and repeated this 5000 times to obtain the mean and confidence interval.

In addition to asymptotic growth rate λ and stable age composition, a number of other useful metrics are obtained from the population model. One is measures of how much the growth rate changes when the values of different demographic parameters change (sensitivity and elasticity; see §3.4). This informs on how much greater (or smaller) the potential effect on population growth of one parameter is than that of others. Related to this is the option to explore different (conservation or management) scenarios by changing the values of demographic parameters.

3.2. Parametrisation

Survival
Values for survival were derived from the analysis of colour-mark resightings presented in chapter 2 and in Schekkerman & Koffijberg (2019). These estimates however essentially pertain to introduced captive-bred birds, as these make up the vast majority of the marked individuals. So if we are to model the entire free-living population, several assumptions have to be made. First, we assumed that survival of adults (≥2 years old) does not depend on whether they are captive-raised or wild-born. The observation that the survival of young birds introduced as either fledglings or yearlings was low in their release year, but increased to adult levels in the following year, may

indicate that the negative effect of introduction on survival has largely 'worn off' at this time. Therefore, the estimate of second-year survival of birds released as fledglings was used for S1 of both introduced and wild-born birds and that of all adult birds for Sa. Second, since we have no direct information on the first-year survival (Sj) of wild birds, we have taken this estimate from the first-year survival of fledglings released in the companion of Barnacle Goose foster parents in the 'old' period of releases in the 1990s. The presence of foster parents creates a social environment not too dissimilar from that of wild-born young and their survival (mean 0.68) was markedly higher than that of fledglings released without foster parents in the 'new' period, and not unlike what could be expected for young wild geese (e.g. ~0.68 in first-year Greenland White-fronted Geese, Fox 1999; ~0.67 in Barnacle Geese, Layton Matthews *et al.* 2019). This leads to the parameter values summarised in table 2.

Reproduction
In the model structure used, reproductive output is represented by two (groups of) parameters: the probability that a bird of a given age starts a breeding attempt (B1, B2, Ba) and the average number of fledglings produced by pairs that do (R). This formulation allows implementing variation in age at first breeding, and is suited to the common case where reproduction in a population is quantified by measuring the number of young raised by a sample of breeding pairs. For the LWfG however, which breeds well-hidden and in low density in remote and poorly accessible terrain, such data hardly exist. Information on the reproductive output of this LWfG population is available however in the form of numbers of (wild-born) juvenile and older birds counted in autumn flocks (table 3). From these and the numbers of released birds, the average number of young produced per pair can be estimated for each year, by dividing the observed number of wild-born juveniles by half the number of at least two-year old birds, i.e. the total count minus the numbers of juveniles and yearlings. LWfG generally do not yet breed as yearlings; during the entire project this has only been observed once in females and never in males (Andersson 2016). The number of yearlings is not established directly during the counts but can be

Table 2. Mean survival values used in the population model, with standard error and standard deviation of variation between years.

parameter	age	wild-born	released fledgling	released yearling
Sj	1st-year	0.68 ± 0.04 (0.06)	0.37 ± 0.10 (0.06)	
S1	2nd-year	0.71 ± 0.13 (0.04)	0.71 ± 0.13 (0.04)	0.21 ± 0.10 (0.04)
Sa	older	0.71 ± 0.12 (0.04)	0.71 ± 0.12 (0.04)	0.71 ± 0.12 (0.04)

Table 3. Reproduction data for 2010-2019. Results of autumn counts of wild-born juveniles and all older birds, numbers of released fledglings and yearlings, and number of wild-born juveniles per potential breeding pair (2 years old or older).

year	autumn counts			releases		reproduction in the wild	
	total	adults	wild-born juveniles	juveniles	yearlings	Njuv/Ntot	Njuv/(N2$^+$/2)
2010	110	101	9	2	7	0.08	0.24
2011	104	69	35	7	3	0.34	1.13
2012	60	57	3	24	4	0.05	0.20
2013	40	39	1	35	14	0.03	0.07
2014	54	43	11	37	17	0.20	0.76
2015	45	42	3	55	10	0.07	0.29
2016	66	55	11	75	12	0.17	0.69
2017	71	61	10	66	16	0.14	0.80
2018	75	67	8	71	16	0.11	0.46
2019	110	101	9	38	9	0.08	0.26

estimated from the number of juveniles wild-born or released in the previous year, by multiplying by their respective first-year survival (Sj, 0.68 and 0.37 respectively; table 1). The at least two-year olds represent all birds in the population that potentially *could* breed, whether or not they actually did. Hence, when this estimate of R is used in the model, values for B2 and Ba are set to 1. This leads to the parameter settings given in table 4.

Table 4. Mean values of reproduction parameters used in the population model, with standard error and standard deviation of variation between years.

parameter	age	mean ± se (sd)
B1	1 year	0.0 ± 0.0 (0.0)
B2	2 years	1.0 ± 0.0 (0.0)
Ba	older	1.0 ± 0.0 (0.0)
R	all	0.49 ± 0.11 (0.34)

3.3. Basic model results and validation

Population trajectory without releases
The basic model parametrised as described above predicts a growth rate of λ=0.85, i.e. a decline of about 15% per year of the total population size (figure 5). There is considerable uncertainty around this value; the 95% confidence interval for λ obtained by resampling spans 0.63 to 1.06. Note that predictions made by annual resampling from the parameter distributions yield a much narrower interval (but the same mean λ). This is to be expected: by resampling annually instead of only once at the start of each model run, random variation is cancelled out to a large extent. Although the upper confidence limit of λ based on the parameter uncertainty resampling exceeds 1, these results strongly suggest that cur-

rently reproduction does not balance mortality in the Swedish LWfG population. In figure 5 the predicted decline is superimposed on the actual development of the population as documented by the autumn counts. From 2010 onwards, λ based on these counts is 1.00, i.e. a stable population size, but this figure hides a strong decline in 2011-2013 followed by a recovery. The population trajectory predicted by the model follows the decline fairly well, but not the following increase. This can only be explained by a strong upward change in the demographic parameters over this time period (for which there is no clear evidence in the mark-resight and reproduction data) or by the augmentation of the population with captive-reared birds that took place.
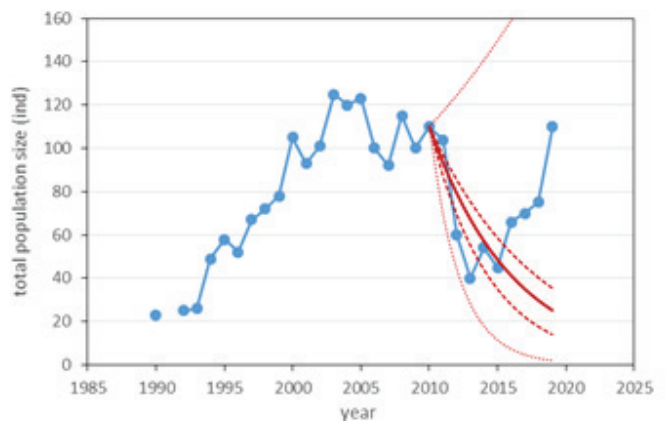

Figure 5. Development of the Swedish LWfG population based on autumn counts (blue), and population trajectory predicted by the basic model from 2010 onwards (red continuous line). Red broken lines denote the confidence intervals resulting from annual stochasticity (broken) and parameter uncertainty (dotted).
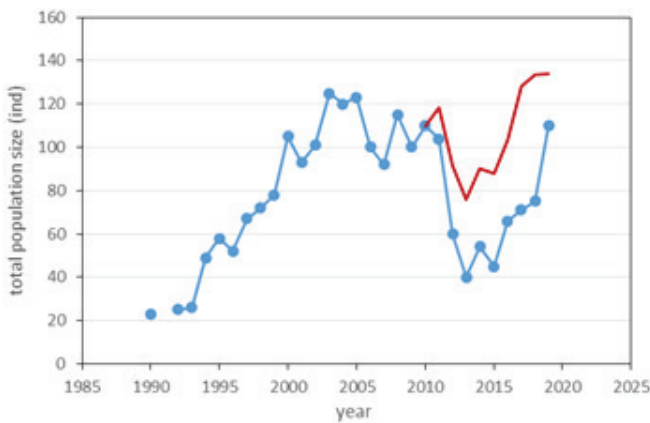
Figure 6. Development of the Swedish LWfG population based on autumn counts (blue), and the population trajectory predicted by the model including released birds and year-specific reproduction estimates, from 2010 onwards (red).

Population trajectory with releases

The effect of augmentation was explored using a second version of the model, in which the annual numbers of fledglings and yearlings released in each year since 2010 are added at the corresponding time steps. In addition, we used the year-specific values for reproduction (table 3), as reproduction varied strongly between years. For survival we used the mean values (table 2). The resulting population trajectory reproduces the recovery in recent years fairly closely, but the decline in 2011-2013 is predicted markedly less deep than observed (figure 6). This may suggest that either survival or reproduction at that time were lower than assumed in the model. Other explanations, i.e. an incomplete autumn count or emigration of birds out of this population to some place where they are no longer observed, seem unlikely.

With respect to reproduction, the number of juveniles actually observed in the autumn of 2011 (35, leading to 1.13 juveniles per adult pair) was the highest in this 10-year series, and the second highest recorded since 1993. Densities of lemmings were very high in the Swedish mountains in 2011 (M. Svensson, *pers. comm.*), which may have reduced predation by foxes on alternative prey like eggs and young geese. With respect to survival however, during the breeding/moulting period of 2012 many indications of high predation pressure were found in the breeding area. A total of six carcasses of predated LWfG were noted during field work not explicitly done to search for dead birds. I addition, direct observations of White-tailed Eagles hunting for (several cases) and taking (one case) LWfG were reported (N. Liljebäck *in litt.* 2020). A good match of the model prediction with the count in 2013 is reached

if survival of wild birds of all ages is set to 0.35 for 2012 or 0.4 for both 2011 and 2012. The year-specific mark-resight estimate of adult survival for 2012 is low (0.56, from model 4 in table 1) and due to a still small sample of marked birds its 95% confidence interval (0.24-0.84) is wide and does include 0.35. For 2011, a resighting-based survival estimate is not available, but from observations at staging sites in the spring and the autumn, the absolute numbers of adults were estimated at about 100 and 61 respectively, suggesting a summer mortality of about 40%. It therefore seems likely that predation was significant already in 2011 but many pairs bred successfully, hiding the losses of adults (N. Liljebäck *in litt.*). These observations taken together indicate that low survival caused by predation on the breeding grounds was the primary cause of the strong decline in 2011-2013.

In a second run with a model including releases, we looked at the predicted population trajectory since 1994, i.e. including the first, 'old' period of introductions using foster parents. For the years up to 2010, we used mean survival values obtained for 1993-2003 (S_j=0.74, S_1=0.87 in wild-borns and 0.34 in released yearlings, S_a=0.79; Schekkerman & Koffijberg 2019), and annual count-based estimates of reproduction. The predictions capture the observed development quite well until 2001, are obviously too low in 2003-2012, but again fairly close to the counts in 2013-2019 (figure 7). The greatest discrepancies between predicted and observed numbers arise in 2003 and in 2013; equalising the prediction with the counts in those years results in a fairly good overall fit (figure 7). As discussed above, survival may have been lower than assumed in 2012. What
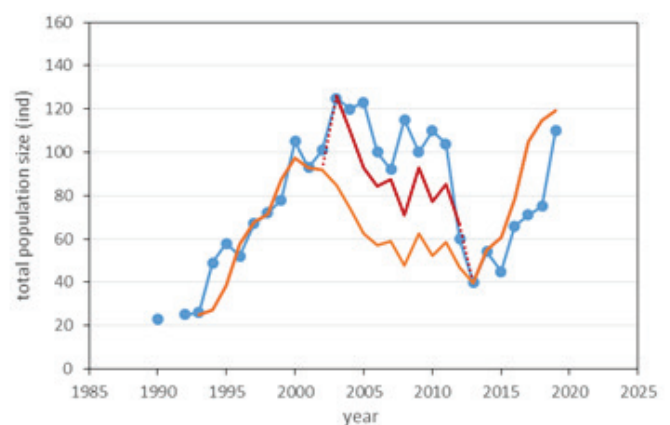

Figure 7. Development of the Swedish LWfG population based on autumn counts (blue line and dots), and the population trajectories predicted by the model including released birds and year-specific reproduction estimates (orange line). The red line shows the predictions from this same model, but with predictions reset to the observed numbers in 2003 and 2013.

caused the difference in 2003 is an open question. It cannot have been survival alone (even assuming zero deaths does not remove it completely) and reproduction in 2003 would have to be severely underestimated and exceptionally high (1.77 instead of 0.41), suggesting that there might be a problem with the autumn count (e.g. biased high due to duplicate counts). During the period without introductions (2000-2009), the model seems to predict slightly less well than during the preceding and following years (figure 7). A factor contributing to this is that the numbers of birds released are an important component of annual changes in population size in those two periods, and are known exactly.

3.4 Sensitivity to demographic parameter values

Table 5 presents sensitivity and elasticity values for the basic model. Sensitivity is the absolute change in λ given a certain absolute change in a demographic parameter, and elasticity is the proportional change in λ given a certain proportional change in that parameter. The elasticity values in table 5 show that in theory, the population growth rate of LWfG is most sensitive to changes in adult survival, and markedly less so to changes in first- or second-year survival or in reproductive success. (Note that effects of variation in the B parameters are absorbed by R in this particular model, because of the way in which R is estimated from the count data). However, the relative contributions of each parameter to actually observed (short-term) changes in population growth does not depend only on these elasticities, but also on the magnitude of the variation occurring in each variable in real life. This combined effect can be quantified by multiplying the elasticity by the coefficient of variation (CV) of the yearly estimates of each variable. The resulting LTRE (Life Table Response Experiment) values indicate that over the past 10 years, variation in reproductive output has had as much influence on

the population dynamics as variation in survival, due to its larger annual variability.

3.5 Inference from the model

Overall, the (despite some exceptions) reasonably good general agreement between model predictions and counts indicates that the model captures important population processes acceptably, and can be used to make inferences about the Swedish LWfG population.

Viability of the wild population
The model results indicate that currently reproduction does not balance mortality in the Swedish LWfG population, and that the release of captive-bred individuals has been essential in avoiding a further steep decline and in the recovery in the past six years. With respect to the demographic imbalance, a relevant question is whether it is caused mainly by insufficient reproduction or by low survival. The survival estimates for the recent 'new' period are somewhat lower than reported for the 'old' release period 1983-2003 (Schekkerman & Koffijberg 2019, means: Sa~0.74, S1~0.85), and perhaps also on the low side compared to natural survival in other goose species. However, inserting these older survival values in the basic model yields λ=0.92, still a substantial decline of 8% per year. To achieve a stable population at the current mean reproductive output, both second-year and adult survival should increase to 0.86, or adult survival alone to 0.88. On the other hand, at the mean survival rates estimated for the current period, reproduction should increase to a mean of 1.2 fledglings per adult pair to achieve λ=1, which corresponds to ~30% juveniles in the autumn population. Values of this magnitude have been observed only twice in 27 years of monitoring this population (in 2009 and 2011). At the survival values observed in the 'old' release period, this required reproductive output is 0.83 fledglings/pair, which was also ex-

Table 5. Sensitivity and elasticity of λ to demographic parameter values in the basic model, the relative variability (CV) of these variables in the past 10 years (taken from model 4 in table 1 for S, and from table 3 for R), and the resulting LTRE indicating the relative influence of each on the realised population development. See main text for explanation.

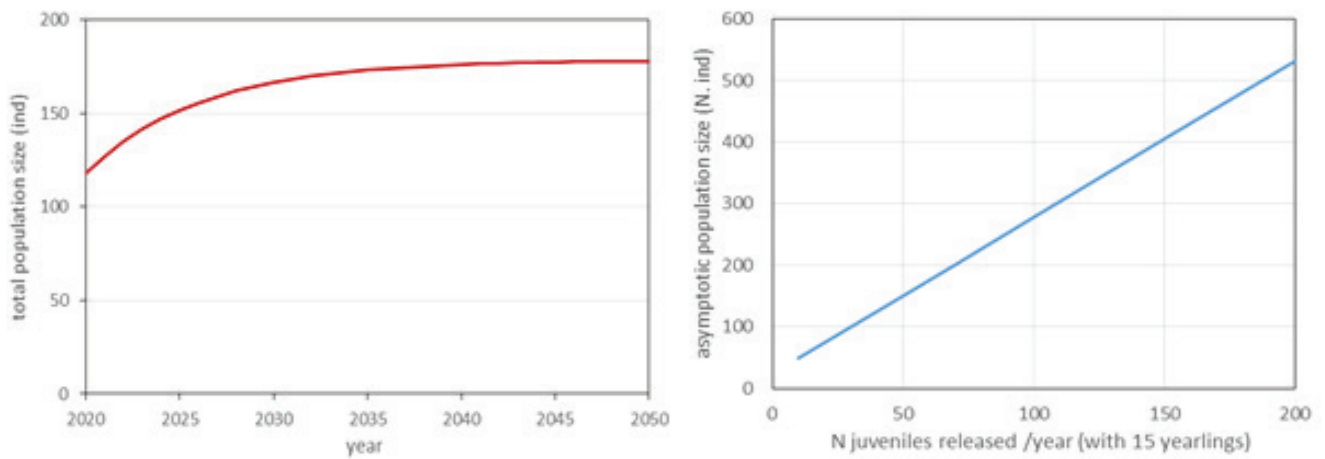| parameter	symbol	sensitivity	elasticity	CVobs	LTRE
fraction of 2cy breeding	B1	0.018	0.000		
fraction of 3cy breeding	B2	0.020	0.024		
fraction of >3cy breeding	Ba	0.100	0.118	0.694	0.104
fledged young / adult pair	R	0.260	0.150		
survival 1st year (1-2cy)	Sj	0.188	0.150	0.088	0.013
survival 2nd year (2-3cy)	S1	0.180	0.150	0.148	0.022
survival adults (from 3cy)	Sa	0.717	0.607	0.161	0.098

Figure 8. A (left panel): Predicted development of total population size assuming that current demo-graphic para-meters and annual numbers of releases (61 fledglings, 14 yearlings) remain unchanged. B (right panel): Asymptotic stable population size as a function of the number of fledglings released annually, assuming 14 yearlings also being released.

ceeded just two times. It thus seems that both poor reproduction and relatively low survival contribute to the (projected) decline of the wild LWfG population. Recent genetic studies have shown that the wild LWfG population shows a high degree of inbreeding and low genetic variation, which might negatively affect reproduction or/and survival. This issue is currently being mediated by releasing LWfG with a different genetic set-up (Díez-del-Molino *et al.* 2020).

Effects of introductions
As the Swedish LWfG population is not self-sustaining yet, augmentation by releasing captive-bred birds is at present an essential factor in its conservation. The model can be used to explore the effects of choices with respect to these introductions on expected population development.

If releases are continued at the current level (i.e. 61 fledglings and 14 yearlings annually), the population count (excluding birds released in the same year) is expected to grow initially but then stabilise around 180 birds after *c.* 25 years (figure 8). This stabilisation occurs because whereas the absolute number of releases remains the same, its relative contribution to the population diminishes as the total goose numbers grow. One may see this as if the releases elevate 'reproduction' above the threshold needed for population growth, but over time the resulting *per capita*

'reproduction' declines until it just balances mortality, after which it stabilises together with population size. This will occur irrespective of the numbers released, as long as these are large enough to increase R over the value required for growth in the current situation. However, the population size at which this will happen (figure 8b) does increase with the annual numbers released. Note that these predictions assume that recruitment of released birds is independent on the size of the wild population, whereas in reality it may show either a positive ('Allee effect', Odum 1953) or a negative (density dependence mediated by e.g. saturation of the breeding habitat) association with population size (or both, sequentially). The effect of deviations from this assumption will however generally be limited.

For the interpretation of models like this it is important to keep in mind that other factors, not accounted for in the model, may change and influence the validity of its assumptions and predictions. For instance, the recent attempts to increase genetic variability in the population by releasing LWfG with a different genetic set-up might over time lead to higher reproductive success and/or survival. And if the population would start to colonize new breeding sites, the risk of negative density dependent effects will diminish.

4. Conclusions

The key findings of this study are:

- In the recent 'new' period of releases (2012-2019), annual (apparent) survival of adult Lesser White-fronted Geese, and that of 1-year old geese previously released as captive-reared fledglings, have fluctuated around a value of ~0.71. There is some indication that survival in the most recent years was somewhat higher than early in this period.

- Survival in the year directly after release of captive-reared birds is markedly lower than that of adults, ~0.37 in birds released as fledglings and ~0.21 in those released as yearlings. These low values seem to reflect a survival cost of releasing young birds without parents.

- In the past 10 years, reproductive output of the wild LWfG population, estimated from juvenile proportions assessed in autumn counts, has fluctuated between 0.07 and 1.13 fledged young per potentially breeding adult (≥2 years old), with a mean of 0.49 (and SD of 0.34).

- Based on the above estimates, reproduction does currently not balance mortality in the Swedish LWfG population. This means that without further augmentation, the population would show a continued decline, of about 15% per year.

- Both relatively low survival and poor breeding success seem to contribute to this imbalance. In order to achieve a stable, self-sustaining population, reproduction should increase to 1.2 fledglings/pair (corresponding to ~30% juveniles in the autumn population), or adult and second-year survival to ~0.86.

- The long-term growth rate of this population is more sensitive to variation in (adult) survival than to similarly large changes in reproduction, but short-term changes in population growth during the past years have been influenced as much by the large annual variations in reproductive success as by survival.

- The wild population has undergone a severe decline between 2011 and 2013. Although these early years of the 'new' introduction period are not covered well by the mark-resight data, several lines of evidence point to poor survival due to predation on the breeding grounds as the primary cause of this 'crash'.

- The release of captive-bred individuals has been essential in avoiding a further steep decline after the crash and for the recovery observed since 2013.

- If releases are continued above some minimum level, the population will initially grow further but then stabilise at a certain size affected by the numbers released. At the current numbers of releases and values of demographic parameters, this stabilisation will occur around a total population of roughly 180 birds.

5. Acknowledgements

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