A model of the long-term viability of a proposed re-introduction of white-tailed eagle *Haliaeetus albicilla* into Ireland

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1. Introduction

It is planned to begin a white-tailed eagle *Haliaeetus albicilla* re-introduction program into Ireland. This follows on from the current golden eagle *Aquila chrysaetos* program (O'Toole *et al*, 2002). The aim of this study is investigate the probable success of the proposed re-introduction strategy. Ultimately, success will depend on the creation of a self-sustaining population that eventually fills all of the available habitat. This study does not address the availability of habitat or the logistics of the release protocols, instead it examines the probable population trajectories over a range of ecologically feasible scenarios. In all population simulations the most difficult part is finding suitable, i.e. realistic, values for the various parameters that are needed to run the simulation. Fortunately we were able to draw on details derived from the Scottish re-introduction programme (Green *et al* 1996 and Bainbridge *et al*, 2003).

2. Model details

2.1 Software

Models were implemented using the ULM (Unified Life Models) software (Version 4.4, May 2006) originally developed by Legendre and Clobert (1995) and developed further by Stéphane Legendre (http://www.biologie.ens.fr/~legendre/ulm/ulm.html). The ULM software models a wide range of population dynamics using a model description text file. The parameters specified can also be modified interactively within the ULM environment. The text file for the main model used in these analyses is listed in Appendix 1. Full details of the modelling procedure have been included so that interested parties can repeat or modify them.

2.2 Model structure

There are three main parameter categories used in the model. They are outlined below and a fuller description of the implementation is given later.

1. **Release characteristics**: the number of birds released each year and the number of years over which birds are released. It is assumed that these are all birds in their first year.
2. **Survival rates**: in this model it is assumed that birds settle on ranges in their fifth year and begin, generally, to reproduce in their sixth year. Green *et al* (1996), in a study of

white-tailed eagles re-introduced into Scotland estimated an annual survival of unsettled young birds of 74% (albeit with a wide confidence interval). Once birds had settled this increased to 94%. Green *et al* (1996) acknowledge that these estimates are imprecise. They are generally lower than values reported elsewhere. For example, in Helander and Stjernberg (2002, section 2.3, page 9) survival of young birds was generally greater than 80%. Bainbridge *et al* (2003) report that a later review of the Scottish data (up to 1997) suggested higher estimated annual survival rates (75% for unsettled immatures and 97% for adults) than for the earlier period described by Green *et al* (1996).

3. **Reproductive value**: the reproductive output of the population depends on the sex ratio, the proportion of breeders and the number of young raised by successful pairs. Green *et al* (1996) report a figure of 0.465 fledged young/pair/year for birds at about 6 years old. Some younger birds breed with much reduced success and there was some evidence that older birds may do better. Bainbridge *et al* (2003) report much improved fledging between 1993 and 2000, when the mean annual productivity was 0.61 young fledged/territorial pair/year. It is unclear why this happened.

The model is expressed in a matrix format with an associated vector. *k* is the number of released individuals, *s0* to *s4* are survival rates for birds up to five years old and *v* is the adult survival rate. *fj* and *f* are measures of reproductive output while *m1* to *m5* are the numbers of individuals in each age class and *d* is used to implement releases.

Matrix

```
    1,   0,   0,   0,   0,  0
 k*s0,   0,   0,   0,  fj,  f
    0,  s1,   0,   0,   0,  0
    0,   0,  s2,   0,   0,  0
    0,   0,   0,  s3,   0,  0
    0,   0,   0,   0,  s4,  v
```

Vector

```
d, m1, m2, m3, m4, m5
```

2.3 Model parametization

The initial model (appendix 1) uses the survival and reproductive parameter values described by Green *et al* (1996) and a release rate of 20 young per year over a five year period. However, a stochastic approach is used combined with a montecarlo simulation. These are described below.

2.3.1 Release parameters

The number of years is fixed, the default being five. However, it is unlikely that the target number (20) will be achieved exactly each year. Therefore, during the montecarlo simulations, the actual number released each year is drawn from a poisson distribution. The commands associated with the release parameters are explained below. Note defvar is a ULM command to define the value of a parameter.

`defvar tr = 5`	The number of release years
`defvar yng = 20`	The number that are intended to be released each year
`defvar yngmax = yng + 2`	An upper limit is set to the randomly obtained value at two more than the target, i.e. 22 for the default value
`defvar kp = poisson(yng)`	Draw an initial release number from a poisson distribution whose mean is the target number
`defvar k0 =if(kp>yngmax, yngmax, kp)`	The number available for release (k0) in a simulation is adjusted so that the upper limit is not exceeded. There is no lower limit.
`defvar k = if(t<tr, k0, 0)`	k birds are released only if the number of release years has not been exceeded. After this no birds are released, i.e. k = 0.

As an example, the values of k0 from the first 5 simulations were: 22, 20, 13, 20 and 17 giving a total of 92 released birds.

In order to allow released individuals to enter the population a parameter d, with the constant value of 1, is included in the model vector. Without this there would be a multiplication by 0 error when t = 0.

2.3.2 Survival rates

Default survival rate (js) for unsettled birds 0.734

Standard deviation (jssd) for js used for the stochastic simulations 0.05

Upper limit for js (jsmax) is the 95% UCL in Table 4 of Green *et al* (1996) 0.865

Default adult survival rate (ads), i.e. settled birds 0.94

Upper limit for ads (asmax) is the 96% UCL in Table 4 of Green *et al* (1996) 0.998

Instances for each simulation are obtained via a two-stage process. First a value is drawn from a from a variant of the beta distribution which has a bell shape for the small standard deviations used in this study: for example: `defvar sa = beta1f(js, jssd)`, where js is the mean and jssd the standard deviation. The second stage checks to see if the random value has exceeded the maximum, if it has it is capped at the maximum: for example,
`defvar s0 = if(sa>jsmax,jsmax,sa).`
There is no lower limit to survival rate.

Similar calculations are used to obtain values for s1, s2 and s3.

Green *et al* (1996) showed that the annual survival rate increases once a bird was settled on home range. Since the mean age for settled birds was 3.4 yrs, the annual survival rate for the next age class uses the default adult survival rate as a starting value. The randomly generated value is tested to see if it exceeds the upper limit.

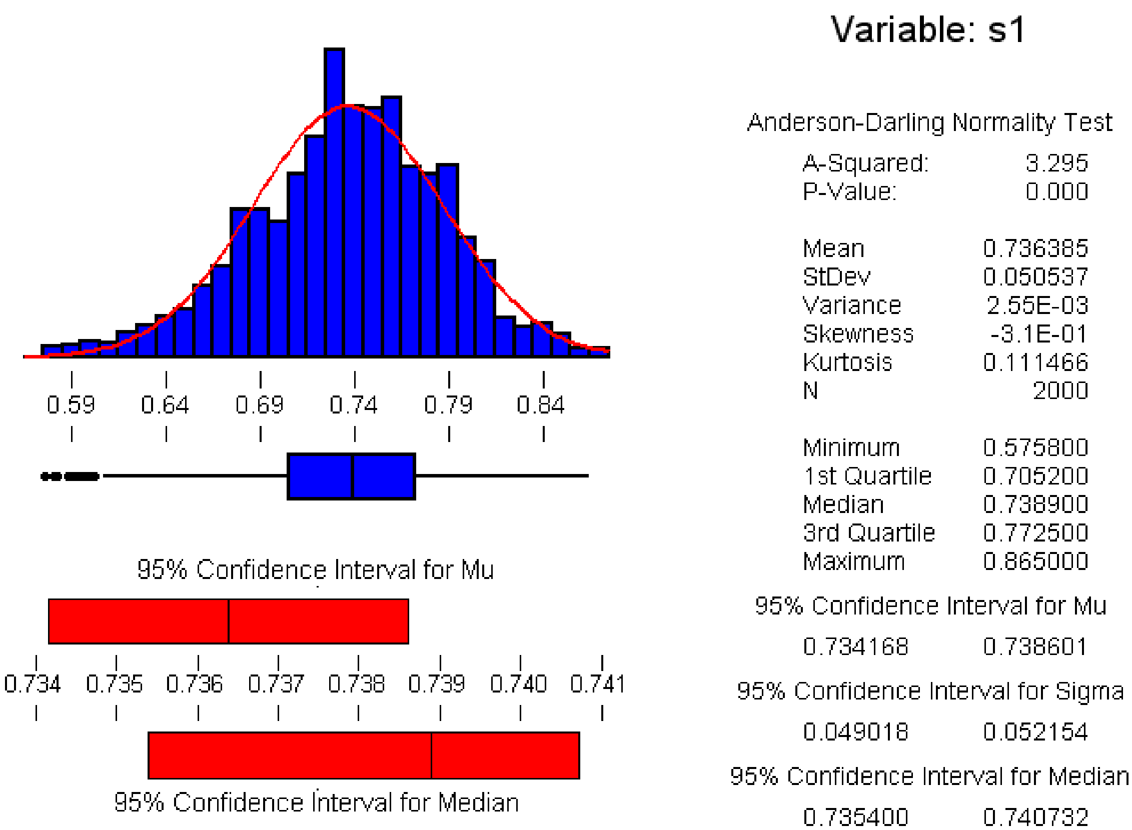
```
defvar se = beta1f(ads, 0.05)
defvar s4 = if(se>asmax,asmax,se)
```

Adults are treated as one class and their annual survival (v) is calculated in a similar way to the s4 value.

```
defvar v0 = beta1f(ads, 0.05)
defvar v  = if(v0>asmax, asmax, v0)
```

2.3.3 Illustration of the effectiveness of the random sampling scheme

The following details are drawn for the simulated values used for the default model (1000 simulated trajectories). They illustrate the range of values generated for s1. Note that the target value was 0.734 and the upper limit was 0.865.



2.3.4 Reproductive characteristics

The proportion of breeders, gamma, is obtained as a random value from a modified beta distribution with a mean of 0.87 (87% breeders) and a standard deviation of 0.05:

```
defvar gamma  = beta1f(0.87,0.05)
```

Two values are used for the number of young fledged per pair per year. The first is the early value (mpp1) described by Green *et al* (1996).

```
defvar mpp1 = 0.465
```

The second (mpp2), which comes into play 20 years into the reintroduction, is the higher value from Bainbridge *et al* (2003).

```
defvar mpp2 = 0.6
```

This is set by comparing the current year with 20

```
defvar mpp = if(t>20, mpp2, mpp1)
```

The value used in a particular simulation is drawn randomly from a beta distribution with a mean of mpp and a standard deviation of 0.05.

```
defvar fn = beta1f(mpp,0.05)
```

Similarly, the sex ratio used in a particular simulation is drawn randomly from a beta distribution with a mean of 0.5 (equality) and a standard deviation of 0.05.

```
defvar sigma = beta1f(0.5,0.05)
```

The fertility of birds aged six or more is a product of the proportion of females multiplied by the number fledged per pair and the s0 survival rate.

```
defvar f  = sigma*fn*gamma*s0
```

Some allowance is made earlier reproduction by setting the rate for five year old birds at a fifth of that for adults. Younger birds are not considered to reproduce.

```
defvar fj=f/5
```

2.4 Monte Carlo simulations

Models were run for 50 years with 1000 population trajectories. Populations were deemed to have gone extinct if the population fell below 2.

2.5 Model modifications

2.5.1 Model 1

The model was run with the default parameter values described above.

2.5.2 Model series 2

These models investigate the effect of varying the release conditions. In the first model the planned release is increased to 25 per year for 5 years. The second series keeps the total released at approximately 100, but varies the number of release years.

a. Keep the period fixed at five years but increase the releases to 25 per year.
b. 17 over 6 years;
c. 14 over 7 years;
d. 13 over 8 years;
e. 11 over 9 years and
f. 10 over 10 years.

2.5.3 Model series 3

These models investigate the effect of varying the survival rates (release conditions are the default of 20 per year over 5 years).

a. Increase sub-adult survival to the Bainbridge *et al* (2003) value of 0.75, leave adult survival unchanged.
b. Increase adult survival to the Bainbridge *et al* (2003) value of 0.97, leaving sub-adult survival unchanged at 0.73.
c. Increase both adult and sub-adult survival to the Bainbridge *et al* (2003) values of 0.75 and 0.97.

Models were run from a batch files (see Appendix 2). For example, the first model was described by:

ulm.exe wte3.ulm wtemodel1.in wtemodel1_out.txt

ulm.exe is model program (a path is not required if the batch file is in the same directory)
wte3.ulm is the file which describes the model (see Appendix 1)
wtemodel1.in is an input model (see below)
wtemodel1_out.txt is a text output files which is copy of everything that appears in the ULM text window.

wtemodel1.in file contents

```
{command file for wte3.ulm model file
{default model
file wtemodel1a.txt k0 s0 s1 s2 s3 s4 v
file wtemodel1b.txt m1 m2 m3 m4 m5
montecarlo 50 1000 2 100
```

wtemodel2a.in file contents

```
{change release parameters
change yng 25
file wtemodel2aa.txt k0 s0 s1 s2 s3 s4 v
file wtemodel2ab.txt m1 m2 m3 m4 m5
montecarlo 50 1000 2 100
```

Each input file runs one simulation. The first is the default model (Model 1). Because there is a limit to the number of variables that can be written to single text file two output files are specified and values for the 12 variables are written to the two files, with one line per simulation, i.e. the files have 1000 lines, 1 line per simulated trajectory.

The montecarlo simulations are run for 50 years with 1000 trajectories using an extinction threshold of 2 and an ‘escape’ threshold of 100. A population escapes when its population exceeds the threshold.

In the second model the conditions specified in the wte3.ulm file are modified and the number of young released for each of 5 years is increased from 20 to 25 (change yng 25). Results are written to separate text files.

3. Results and Interpretation

3.1 How models are assessed

Models are assessed by four criteria.

1. The value of lambda (rate of population growth). Values greater than one indicate that a population that will increase. If the confidence limits for lambda include 0 it is possible that the population will begin to decline.
2. Probability of extinction: in the montecarlo simulations this is the percentage of simulated trajectories where the population size dropped below two during the 50 year simulation.
3. The final population size at t=50, larger populations are suggestive of greater stability and a reduction for the detrimental effects of stochastic events.
4. The parameter elasticity values are used to identify the parameters that the model trajectory is most sensitive to.

3.2 Results

The results of the models are summarised in tables and figures. The individual models are described and interpreted in the next section.

Tables 1a and 1b summarise the results from all ten models, while Figure 1 shows the final values, at t=50, for each trajectory in each model. Figures 2 and 3 show the mean population trajectories for the ten models.

Table 1a Summary of model conditions, changes from the default conditions (Model 1) are highlighted in bold.

	Survival rates		Release details		
Model	**sub-adults**	**adults**	**Duration**	**per year**	**Released**
1	0.734	0.94	5	20	100
2a	0.734	0.94	5	**25**	**125**
2b	0.734	0.94	**6**	**17**	**102**
2c	0.734	0.94	**7**	**14**	**98**
2d	0.734	0.94	**8**	**13**	**104**
2e	0.734	0.94	**9**	**11**	**99**
2f	0.734	0.94	**10**	**10**	**100**
3a	**0.750**	0.94	5	20	100
3b	0.734	**0.97**	5	20	100
3c	**0.750**	**0.97**	5	20	100

Table 1b: Summary of population trajectories (t=50 over 1000 trajectories). m1 – m5 are the five age classes. The population values refer to the population at t = 50. The growth rate (l) is measured over all 50 time intervals (years).

		Vector means and standard errors					Population min, max and mean			Growth rate	Extinction probability %
Model		**m1**	**m2**	**m3**	**m4**	**m5**	**min**	**max**	**mean**		
1	mean	4.95	3.62	2.6	1.91	25.74	16.2	79.7	39.8	1.0757	0.0
	se	0.052	0.038	0.027	0.020	0.232			0.35	0.0002	
2a	mean	6.17	4.5	3.24	2.38	32.18	18.9	114.4	49.5	1.0800	0.0
	se	0.065	0.049	0.034	0.025	0.293			0.44	0.0002	
2b	mean	5.029	3.66	2.66	1.94	26.31	16.1	89.3	40.6	1.0761	0.0
	se	0.053	0.038	0.029	0.021	0.241			0.36	0.0002	
2c	mean	4.865	3.553	2.564	1.862	25.38	11.4	95.2	39.2	1.0753	0.0
	se	0.051	0.038	0.026	0.019	0.227			0.34	0.0002	
2d	mean	5.122	3.761	2.723	1.981	26.82	14.1	97.3	41.4	1.0765	0.0
	se	0.053	0.038	0.028	0.021	0.236			0.35	0.0002	
2e	mean	4.921	3.586	2.615	1.901	25.64	15.2	78.8	39.7	1.0756	0.1
	se	0.049	0.036	0.028	0.020	0.226			0.34	0.0002	
2f	mean	4.938	3.604	2.624	1.882	25.72	15.2	75.4	39.8	1.0764	0.1
	se	0.049	0.037	0.027	0.020	0.229			0.34	0.0002	
3a	mean	6.615	4.885	3.588	2.636	33.71	22.2	105.4	52.4	1.0816	0.0
	se	0.068	0.049	0.037	0.026	0.299			0.45	0.0002	
3b	mean	14.758	10.509	7.431	5.258	78.32	36.9	251.4	117.3	1.0991	0.0
	se	0.157	0.115	0.082	0.058	0.733			1.08	0.0002	
3c	mean	19.479	14.117	10.222	7.342	102.07	50.2	313.8	154.2	1.1051	0.0
	se	0.197	0.151	0.108	0.081	0.914			1.36	0.0002	

Figure 1. Number of class 5 individuals at t = 50 from each of the 1000 simulated population trajectories. Three reference lines are shown: green = 100 individuals, dashed orange = 20 individuals, solid red line = 10 individuals.

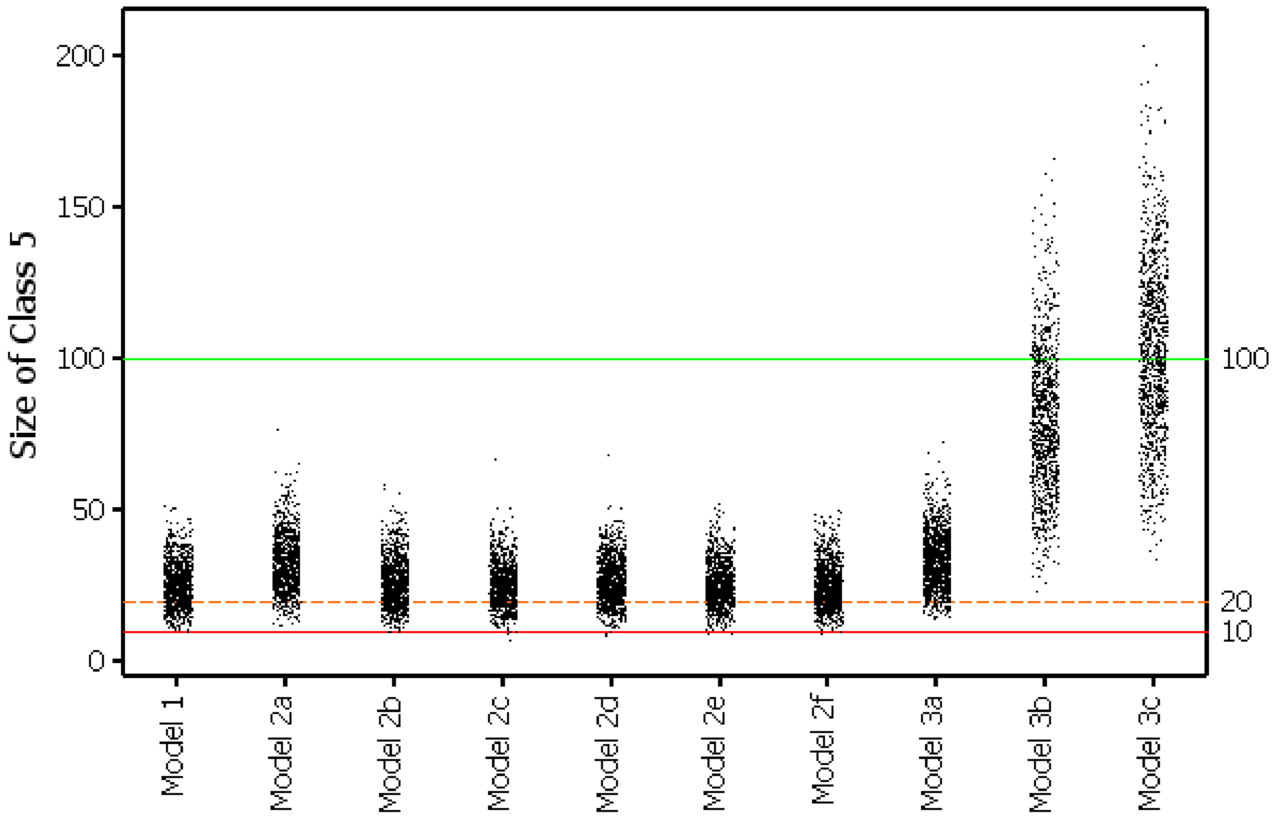


Figure 2 Mean population trajectories for Model 1 and Model 2. Because they are so narrow 95% confidence limits are shown only for Model 2a (release 25 birds per year over 5 years). The first vertical bar marks the end of the default five-year release period. The second vertical line at t=20 is the point at which reproductive output increases.

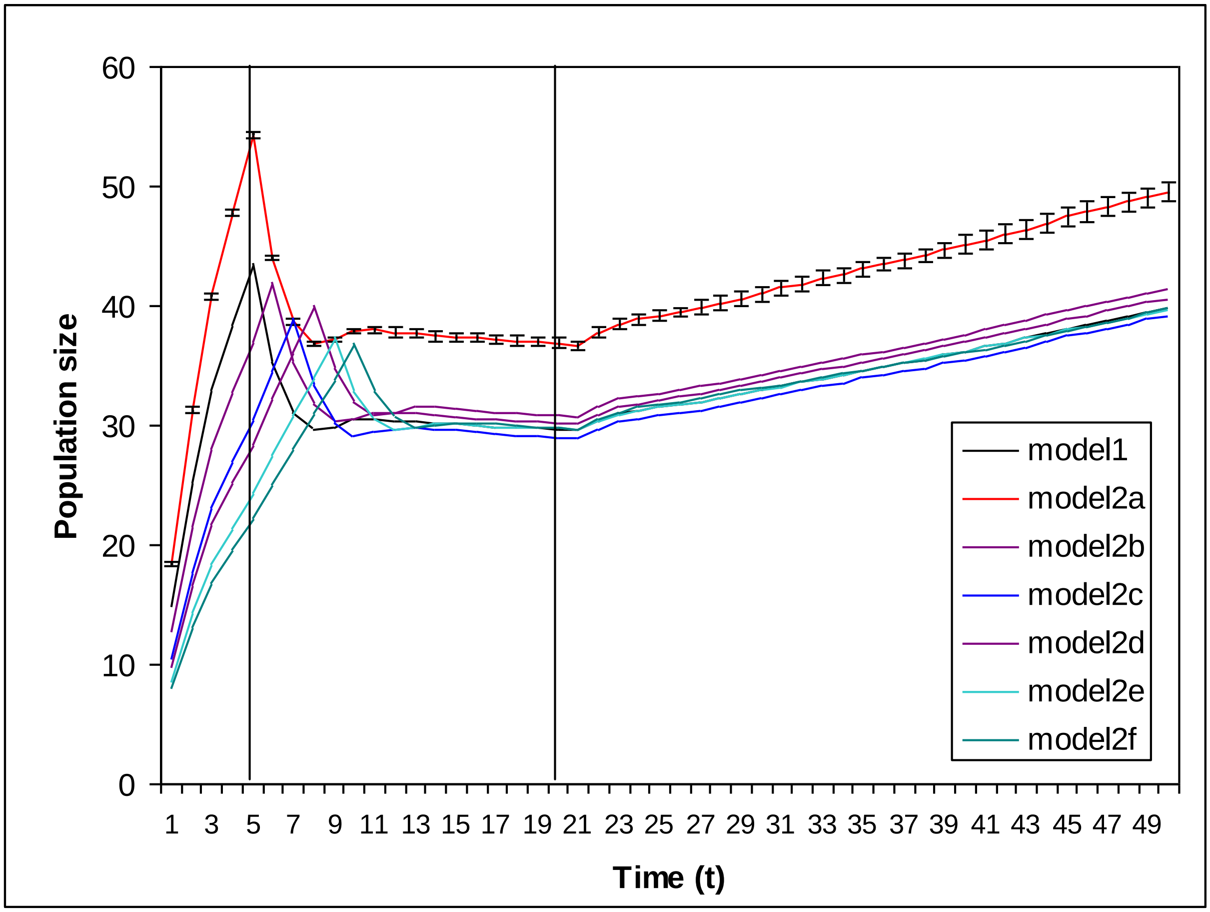
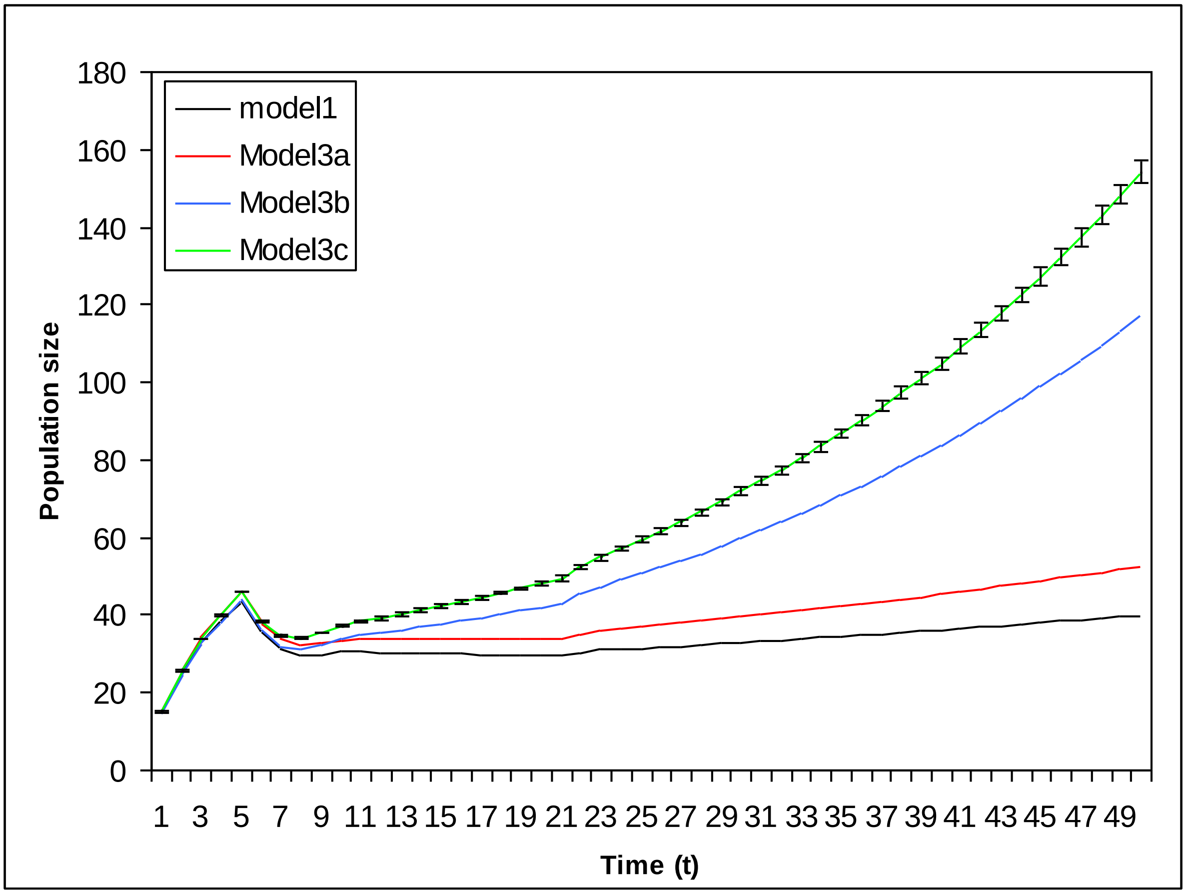


Figure 3 Mean population trajectories for Model 1 and Model 3. Because they are so narrow 95% confidence limits are shown only for Model 3c.



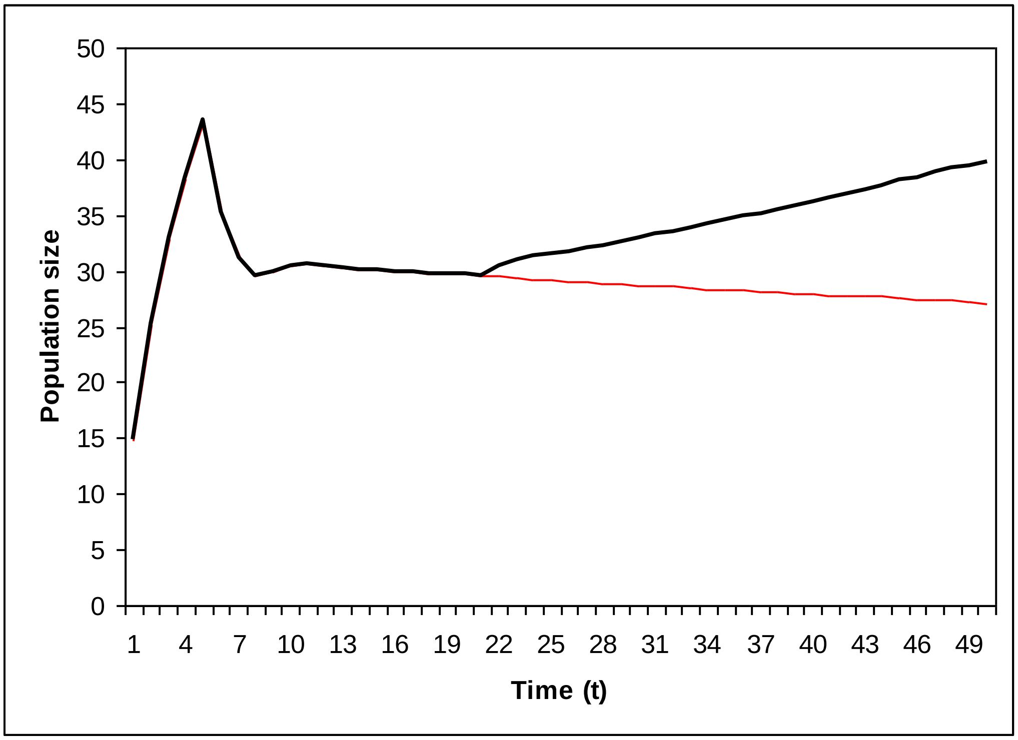
3.3 Model Interpretation

3.3.1 Model 1: default values

There is an initial peak and decline n the predicted population associated with the ending of the introductions. After this the population is static, and possibly declining slightly until the extra production begins at t = 20. In the absence of this extra production the population is not predicted to go extinct but there is some evidence of a long term slow decline. Figure 4 compares the default model 1 with a revised model (1b) in which there is no increased productivity after 20 years.

The productivity, and survival, of the birds could be monitored and if it seems that there is no increase in either, over those modelled in scenario 1b, it may be necessary to consider bringing in more birds, as was the case for Scotland. However, if either the rate of reproduction or survival are greater than those used in these simulations a further re-introduction seems unnecessary to achieve the required population growth and stability.

Figure 4. Comparison of mean population trajectories with enhanced production at t = 20 (thick black line) and no enhanced production (solid red line). The summary statistics for model b are a mean population of 27.1 at t = 50 (min = 9.9, max = 57.6, se = 0.24).



3.3.2 Model series 2: vary release conditions

Changing the release protocol has little effect on the predicted trajectories (Figure 2), although increasing the total to 125 does produce an enhanced, but parallel trajectory. However, these models suggest that, if released numbers are below the target at year five, it is probably worth extending the release period to achieve the desired total releases.

3.3.3 Model series 3: vary survival rates

Increasing sub-adult survival has a small positive effect (Figure 3) but the most obvious impact comes when adult survival is increased, either with or without an increased sub-adult survival (Models 3b and 3c). It is apparent from the early trajectories of models 3b and 3c that extra productivity at t=20 is not needed to ensure an healthy population. Since the most likely impact of adult mortality is likely to the result of the actions of people it is essential that this is monitored and any interference is dealt with quickly, probably with the maximum publicity to reduce further risks.

3.3.4 Sensitivities and elasticity

It is possible to estimate the effect of various parameters on the predicted population trajectories by calculating parameter sensitivity and elasticity values. Sensitivity measures how a change in a parameter's value alters the population growth rate, sensitivity is large if a small change produces a large change to the population growth. However, absolute size changes have to be mediated against the magnitude of the parameter, i.e. proportional change is important. This is measured by the elasticity. Only one parameter, v, has a large elasticity in all models. v is the adult survival rate and this has been identified by others as one of the most important factors affecting the population dynamics of many raptors, especially those such as the current species which are large with a low reproductive rate and delayed maturity. Many studies have shown that in such populations growth is most influenced by adult survival, followed by sub-adult survival and finally productivity (e.g., Ferrer and Calderón, 1990; Bowman *et al*., 1995; Green *et al*, 1996; Hiraldo *et al*, 1996; Real and Mañosa, 1997). Real and Mañosa (1997), for example, found that population growth rate in Bonelli's eagle *Hieraaetus fasciatus* was four times less sensitive to changes in sub-adult survival than to changes in adult survival and about ten times less sensitive to changes in fecundity.

4. Overall conclusions and recommendations

The proposed re-introduction strategy of releasing 100 young birds over five years seems to be adequate to produce a growing population that is unlikely to go extinct. These predictions are valid even though the parameters used are at the lower ends of the values found elsewhere. The model 3 series demonstrate how even small increases in adult and sub-adult survival increase the population's growth rate. However, given the importance of the additional production after 20 years it is important that productivity is monitored and appropriate actions planned should this not happen. Fortunately, there appears to be a wide time window over which action could be taken to remedy the situation.

5. References

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Ferrer, M. and Calderón, J. 1990. The Spanish Imperial Eagle *Aquila adalberti* C.L. Brehm 1861 in Doñana National Park (south west Spain): a study of population dynamics. *Biological Conservation*, **51**: 151–161.

Ferrière, R., Sarrazin, F., Legendre, S. and Baron, J-P. (1996). Matrix population models applied to viability analysis and conservation: Theory and practice with ULM software. *Acta Oecologica*,**17**:629-656.

Green, R. E., Pienkowski, M. W. and Love, J. A. 1996. Long-Term Viability of the Re-Introduced Population of the White-Tailed Eagle *Haliaeetus albicilla* in Scotland . *Journal of Applied Ecology*, **33(2)**: 357-368.

Helander, B. and Stjernberg, T. 2002. Action Plan for the conservation of White-tailed Sea Eagle (*Haliaeetus albicilla*). Report of the SEA EAGLE 2000 workshop, Björkö, Sweden, September 2000. http://www.coe.int/t/e/cultural_co-operation/environment/nature_and_biological_diversity/nature_protection/sc22_inf02erev.pdf

Legendre, S and Clobert, J. 1995. ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics*, **22:**817-834. (Version 4.4. downloaded from http://www.biologie.ens.fr/~legendre/ulm/ulm.html).

O'Toole, L., Fielding, A. H. and Haworth, P. F. 2002. Re-introduction of the Golden Eagle *Aquila chrysaetos* into the Republic of Ireland. *Biological Conservation*, **103**: 303-312.

Real, J. and Mañosa, S. 1997. Demography and conservation of western European Bonelli's eagle populations. *Biological Conservation* **79:** 59–66.

Appendix 1 ULM model description file

```
{Model predicted population trajectory for Irish White-tailed
{eagle reintroduction

{References:
{RE Green, MW Pienkowski, JA Love
{1996  Long-Term Viability of the Re-Introduced Population of
{the White-Tailed Eagle Haliaeetus albicilla in Scotland
{Journal of Applied Ecology, Vol. 33, No. 2 (Apr., 1996), pp. 357-368

defmod wte(6)
mat : wm
vec : wt

{SURVIVAL RATES, randomly sampled but capped at a maximum value
{sub-adult survival - upto 5 years, 0.73 is low value from Green et al

defvar js = 0.734

{and a sd for random sampling
defvar jssd = 0.05

{upper cap for sub-adult survival, UCL 95% in Table 4 of Green et al
defvar jsmax = 0.865

{adult survival, 0.94 is mean value in Table 4 of Green et al
defvar ads = 0.94

{upper cap for adult survival, UCL 95% in Table 4 of Green et al
defvar asmax = 0.998

{now set rates for each year
defvar sa = beta1f(js, jssd)

defvar s0 = if(sa>jsmax,jsmax,sa)

defvar sb = beta1f(js, jssd)

defvar s1 = if(sb>jsmax,jsmax,sb)

defvar sc = beta1f(js, jssd)

defvar s2 = if(sc>jsmax,jsmax,sc)

defvar sd = beta1f(js, jssd)

defvar s3 = if(sd>jsmax,jsmax,sd)

{survival rate increases once settled on home range, mean age 3.4 yrs
{Green et al
defvar se = beta1f(ads, 0.05)

defvar s4 = if(se>asmax,asmax,se)
```

```
{adults
defvar v0 = beta1f(ads, 0.05)

defvar v  = if(v0>asmax, asmax, v0)

{REPRODUCTION
{proportion of breeders,note could adjust to take account of popn size
defvar gamma  = beta1f(0.87,0.05)

{female fecundity, mean figure from Green et al is 0.465
{But, Bainbridge at al, found that etween 1993 and 2000, there were 48
{successful breeding attempts (compared with 18 for 1985-1992)
{mean annual nest success was 48% (Table 2;Figure 3),71 young fledged,
{mean fledged brood size was 1.48 and mean annual productivity was 0.61
{young fledged/territorial pair/year (Table 2; Figure 4).

{earlier rate
defvar mpp1 = 0.465

{later rate, use 20 years into the reintroduction
defvar mpp2 = 0.6

defvar mpp = if(t>20, mpp2,mpp1)

defvar fn = beta1f(mpp,0.05)

{sex ratio
defvar sigma = beta1f(0.5,0.05)

{fertility = prop females x yng per pair * prop breeding * yr0 survival
defvar f  = sigma*fn*gamma*s0

{some birds can reproduce earlier, but rate is low
defvar fj=f/5

{RELEASE PARAMETERS
{duration of releases in years
defvar tr = 5

{number released each year
defvar yng = 20

{set a maximum overflow for released
defvar yngmax = yng + 2

{number of individuals released yearly is derived from a poisson
{distribution capped at yngmax
defvar kp = poisson(yng)

{but with a cap that is +2 > target number

defvar k0 =if(kp>yngmax, yngmax, kp)

{ number of individuals released yearly
{ according to duration of releases
defvar k = if(t<tr, k0, 0)
```

```
{ MATRIX MODEL

defvec wt(6)
d, m1, m2, m3, m4, m5

defmat wm(6)
    1,   0,   0,   0,  0,  0
 k*s0,   0,   0,   0, fj,  f
    0,  s1,   0,   0,  0,  0
    0,   0,  s2,   0,  0,  0
    0,   0,   0,  s3,  0,  0
    0,   0,   0,   0, s4,  v

{wild born individuals: starts at 0 at start of programme
defvar m1 = 0

defvar m2 = 0

defvar m3 = 0

defvar m4 = 0

defvar m5 = 0

{needed to avoid multiplication by 0 at start of model
defvar d  = 1.00

{population size
defvar m = m1 + m2 + m3 + m4 + m5
```

Appendix 2 Batch file to run models

The format of the batch file is program_name model_file input_file output_file

```
ulm.exe wte3.ulm wtemodel1.in wtemodel1_out.txt
ulm.exe wte3.ulm wtemodel2a.in wtemodel2a_out.txt
ulm.exe wte3.ulm wtemodel2b.in wtemodel2b_out.txt
ulm.exe wte3.ulm wtemodel2c.in wtemodel2c_out.txt
ulm.exe wte3.ulm wtemodel2d.in wtemodel2d_out.txt
ulm.exe wte3.ulm wtemodel2e.in wtemodel2e_out.txt
ulm.exe wte3.ulm wtemodel2f.in wtemodel2f_out.txt
ulm.exe wte3.ulm wtemodel3a.in wtemodel3a_out.txt
ulm.exe wte3.ulm wtemodel3b.in wtemodel3b_out.txt
ulm.exe wte3.ulm wtemodel3c.in wtemodel3c_out.txt
```

Input file examples

Sample input files (Model 1, wtemodel1.in)

```
{ command file for wte3.ulm model file
{ default model
file wtemodel1a.txt k0 s0 s1 s2 s3 s4 v
file wtemodel1b.txt m1 m2 m3 m4 m5
montecarlo 50 1000 2 100
```

(Model 2a, wtemodel2a.in)

```
{ command file for wte3.ulm model file
{ change release parameters
change yng 25
file wtemodel2a.txt k0 s0 s1 s2 s3 s4 v
file wtemodel2b.txt m1 m2 m3 m4 m5
montecarlo 50 1000 2 100
```

Output file example (model 1)

Contents of wtemodel1_out.txt

```
> Init 1
> {command file for wte3.ulm model file
command file for wte3.ulm model file
> {default model
default model
> file wtemodel1a.txt k0 s0 s1 s2 s3 s4 v
File wtemodel1a.txt opened
> file wtemodel1b.txt m1 m2 m3 m4 m5 mpp
File wtemodel1b.txt opened
> montecarlo 50 1000 2 100
> Montecarlo 50 1000
Mean value [SE]:
d =     1.0000 [0.0000]
m1 =     4.9531 [0.0520]
m2 =     3.6171 [0.0377]
```

```
m3 =     2.5951 [0.0273]
m4 =     1.9082 [0.0203]
m5 =    25.7475 [0.2322]
Mean value over non extinct trajectories [SE]:
d* =     1.0000 [0.0000]
m1* =     4.9531 [0.0520]
m2* =     3.6171 [0.0377]
m3* =     2.5951 [0.0273]
m4* =     1.9082 [0.0203]
m5* =    25.7475 [0.2322]
Model wte (extinction threshold = 2.00; escape threshold = 100.00))
  Non extinct population size (pop*):
    min = 16.17
    max = 79.70
    mean = 39.82
      sigma = 10.9532
      SE = 0.3464
  Probability of escape: 0.0000
  Probability of extinction: 0.0000
  Mean growth rate [SE]: 1.075661 [0.0002]
  Growth rate of the mean pop: 1.076471
  Mean growth rate2 [SE]: 1.023658 [0.000119]
  Growth rate2 of the mean pop: 1.023987
  Mean scaled population structure:
  0.0272  0.1236  0.0907  0.0652  0.0481  0.6452
```

t	pe(t)	pop(t)	SE	pop*(t)	SE
1	0.0000	14.9	0.1	14.9	0.1
2	0.0000	25.2	0.1	25.2	0.1
3	0.0000	32.9	0.1	32.9	0.1
4	0.0000	38.4	0.1	38.4	0.1
5	0.0000	43.5	0.1	43.5	0.1
6	0.0000	35.3	0.1	35.3	0.1
7	0.0000	31.1	0.1	31.1	0.1
8	0.0000	29.6	0.1	29.6	0.1
9	0.0000	29.9	0.1	29.9	0.1
10	0.0000	30.5	0.1	30.5	0.1
11	0.0000	30.6	0.1	30.6	0.1
12	0.0000	30.4	0.1	30.4	0.1
13	0.0000	30.3	0.1	30.3	0.1
14	0.0000	30.1	0.1	30.1	0.1
15	0.0000	30.1	0.1	30.1	0.1
16	0.0000	30.0	0.1	30.0	0.1
17	0.0000	29.9	0.2	29.9	0.2
18	0.0000	29.8	0.2	29.8	0.2
19	0.0000	29.8	0.2	29.8	0.2
20	0.0000	29.7	0.2	29.7	0.2
21	0.0000	29.6	0.2	29.6	0.2
22	0.0000	30.4	0.2	30.4	0.2
23	0.0000	31.0	0.2	31.0	0.2
24	0.0000	31.3	0.2	31.3	0.2
25	0.0000	31.5	0.2	31.5	0.2
26	0.0000	31.8	0.2	31.8	0.2
27	0.0000	32.0	0.2	32.0	0.2
28	0.0000	32.3	0.2	32.3	0.2
29	0.0000	32.6	0.2	32.6	0.2
30	0.0000	33.0	0.2	33.0	0.2
31	0.0000	33.3	0.2	33.3	0.2

32	0.0000	33.6	0.2	33.6	0.2
33	0.0000	33.9	0.2	33.9	0.2
34	0.0000	34.2	0.2	34.2	0.2
35	0.0000	34.6	0.3	34.6	0.3
36	0.0000	34.9	0.3	34.9	0.3
37	0.0000	35.2	0.3	35.2	0.3
38	0.0000	35.5	0.3	35.5	0.3
39	0.0000	35.9	0.3	35.9	0.3
40	0.0000	36.2	0.3	36.2	0.3
41	0.0000	36.6	0.3	36.6	0.3
42	0.0000	36.9	0.3	36.9	0.3
43	0.0000	37.3	0.3	37.3	0.3
44	0.0000	37.7	0.3	37.7	0.3
45	0.0000	38.1	0.3	38.1	0.3
46	0.0000	38.4	0.3	38.4	0.3
47	0.0000	38.8	0.3	38.8	0.3
48	0.0000	39.2	0.3	39.2	0.3
49	0.0000	39.5	0.3	39.5	0.3
50	0.0000	39.8	0.3	39.8	0.3