Review "Adaptive Harvest Management for the Svalbard Population of Pink‑Footed Geese;

Progress Summary"; Fred A. Johnson, Gitte H. Jensen & Jesper Madsen; February 1, 2013.

Reviewers: Hans Baveco[1], Paul Goedhart[2] and Dick Melman[1], April 2013.

1. Introduction

At the request of Theo de Gelder (Dutch Ministry of Economic Affairs), we performed a review of the progress summary describing Adaptive Harvest Management for Pink-Footed Geese, written by Johnson, Jensen and Madsen (February 2013).

Our findings are reported below. We start with a summary and discussion of our main findings (section 2). Then we give a brief description (section 3) of the work presented in the progress summary (in the following referred to as "the report"), using mostly our own wording. Next, we present in section 4 more detailed comments. Finally, a short bibliography is added and an appendix describing an application of state-space modeling to the data presented in the report. The latter should not be interpreted as criticism of the approach followed in the report. Rather, one of the reviewers had just applied the method to ungulate population data with a structurally identical underlying population model, and enjoyed testing the method on Pink-Foot Geese.

We realized from the beginning that the objective of the method described in the report is to "maximize sustainable harvest, but avoid harvest decisions that are expected to result in a subsequent population size different than the population goal." Choosing an optimization approach has many implications. It implies among others that population size is allowed to fluctuate within a certain bandwidth, as long as the harvest rate is maximized. This is thus different from a harvest strategy that tries to keep the population close to a desired level irrespective of the size of the harvest. It is outside the scope of this review to discuss the pros and cons of an optimization method. Nonetheless, we were quite interested in the question 'when and where does it really make a difference?". The research presented in the report has a large potential to shed some light on this question – we hope some of our comments will motivate the authors to do so.

The harvest required to obtain a stable population depends on the survival rate and the reproduction rate. The authors use three models for the survival rate, assuming that the observed annual mortality can be split into natural mortality and hunting mortality such that hunting mortality is one-half of total annual mortality. Also, three models were used for reproduction without distinguishing adults from sub-adults. Combining the survival and reproduction models results into 9 different models for which an (optimal) harvest strategy can be derived. These nine models varied form a harvest of 500 to 17000 to stabilize current population size. In addition the authors derived optimal harvest strategies employing stochastic dynamic programming,.

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2. Key Comments and Discussion

First of all, we conclude that the authors are developing a very promising approach to determine harvest rates for use in adaptive management of the Pink-Footed geese, based on harvest maximization. They succeed in striking a good balance between simplicity and realism of models, as well as in exploiting all of the empirical data sources.

The report provides information on 3 aspects of the adaptive harvest management for Pink-Footed geese, a) the selection of models with their structural definition, the determination of model coefficients and their goodness of fit on the monitoring data; b) the calculation of optimal harvest rates for each possible state of the system (population and important environmental variables); c) the application and integration of the calculated optimal harvest rates in an adaptive harvest management cycle of e.g., three years.

Models

The authors are bound to use a two stage population model, because their statistical methodology does not allow to estimate parameters of a three stage model. We suggest a possible alternative way (state-space modeling, see Schaub and Abadi, 2011; Buckland et al., 2004) to estimate model coefficients for each of the 9 models discussed in the report, and thus enabling the use a three stage model. The state-space modeling approach would allow estimation of natural survival rates and avoid the a-priori assumption that harvest mortality amounts to one-half of total mortality. It also provides a structured way to incorporate additional data becoming available with continued monitoring. Also the capture-recapture based data used in the report, could be incorporated in the suggested approach.

Optimal harvest rates

For the determination of optimal harvest rates we trust that the implementation of the method (stochastic dynamic programming) is correct (in theory, this could be checked from the source-code, by a person with hands-on experience with the program).

From the text in the report we find it hard to grasp the exact meaning/definition of optimal harvest rates (see some of our comments to section V). A precise definition in words would help, in particular to understand the implications the choice of specific options/settings in the optimization method will have for application of the results in an adaptive harvest management cycle. Our current understanding is that optimal harvest rate depends on current state of the system (population and environment) and is the rate of harvesting that maximizes – when exerted over a long period (infinity?) with stochastic fluctuations in demographic rates and some environmental variables – harvest under the condition that the total population stays around a target level (e.g. 60k with standard deviation 10k, which seems rather large to us).

Regarding the weighting of the models, the text suggests that weights are adjusted during the optimization process. On the other hand, it is stated everywhere that results apply to the situation with equal weights assigned to models. This brings us to the more theoretical question whether it is more clear/insightful to calculate a weighted average harvest rate over 9 models in every step of the optimization program, or to compare optimal harvest rates calculated for each model separately. As an alternative an uncertainty analysis using a simple single model, e.g. with a single survival and reproduction parameter and no density dependence, could be performed.

Adaptive harvest management

Missing from the report is a proposal for the way to integrate optimal harvest rates in a three-year management cycle. In the end, it is this aspect that will allow us to judge the usefulness of the

optimization approach, and to evaluate whether its clear advantages outweigh its drawbacks (complexity of the methodology). To us, it is not immediately clear whether this is the case. Optimal harvest rates given a current state of the system are (if understood correctly) based on a kind of expected/average/uncertain future (accounting for environmental stochasticity like the number of warm days in May and for random variation in demographic rates). The realization in the three years of the management cycle following the choice of an optimal harvest rate will always be a particular sequence, of e.g., 2 warm May months and 1 cold. In hindsight, the adopted management action (a particular harvest rate) will not be optimal at all. Of course, AHM is adaptive, and designed to handle this situation by adjusting the harvest rate to one that is considered optimal for the updated system state, and also by updating the weight given to each model (if more than one) by a new fit of models on the extended set of monitoring data. But it also begs the question whether the proposed harvest rate really needs to be the long term optimal one and cannot be replaced by a harvest rate obtained from a simpler, non-optimizing modeling approach, e.g., 3 year stochastic simulations projecting population size and structure for a range of harvest rates, with each of the nine models.

In general it would be interesting to get a feeling for the added value of the optimization approach. Comparison of results for the nine models in a stable state at 70k (discussed in the upper part of page 14) with Monte Carlo simulation results of optimal harvest rates (Table 2 on page 19) could be enlightening in this respect. However, a systematic comparison is not possible based on the information provided in the report.

The importance/relevance of applying an optimization approach could be tested by comparing the results for harvest maximization, as described in the report, with results for harvest minimization. This would give us direct information on the range of outcomes using an optimization approach. When the bandwidth between maximized and minimized harvest is small, optimization is not really worth the trouble. In addition it would make the methodology useful for the management of e.g., more numerous species, like the steadily increasing breeding population of Greylag geese in the Netherlands, where managing the population with minimal hunting effort appears to be more of an issue.

3. Summary of the Work

We go through the 6 main sections of the document and briefly describe the analyses performed by authors (in the following referred to as JJM) and the results that were obtained.

I. Data

JJM give an overview of the compiled relevant demographic and weather data. These refer to

- **Abundance**. Estimates based on counts (around November 1; from 1965; DK, NL and B) and on capture-recapture (neck-banding during spring migration, re-sighting during migration and wintering periods; 1991-2003). Both estimates highly correlated (r=0.68); capture-recapture estimates on average 6 % higher.
- **Survival**. From capture-recapture data (neck-banding; survival first 10 months; 1990-2002), scaled to annual survival. Partitioned into Nov-Jan en Feb-Oct periods. Important assumptions: harvest mortality additive to natural mortality & harvest mortality representing one-half of total mortality. JJM note that this might not be the case for recent years (harvest pressure likely increased in N and DK). No mention of age-dependent survival.
- **Harvest**. Estimates from DK (1990-2010) and N (2001-2010). No discussion of reliability here.
- **Reproduction**. Proportion of juveniles in the population and observations of average brood size in autumn (DK and NL, from 1980). Proportion is used as an indicator of reproductive success in the preceding breeding season.
- **Weather Covariates**. Snow cover in late May is expected to have an impact on breeding effort. Proxies (highly correlated with snow cover) are: number of days in May with mean temperature above 0 C (TempDays) & cumulative mean daily temperature sum above 0 C (TempSum).

II. The Annual Cycle of Pink-Footed Geese

In this section JJM formulate a simple 3-stage model, with age-classes juveniles (Y), sub-adults (SA) and adults (A), and investigate whether the available estimates of annual survival (1990-2002) and reproduction more or less reproduce the changes in population size observed in the population census. The one-step ahead predictions of total population size for these 13 years are compared to observed (census) population size, in Figure 3. The observation that the slope of a line fit through the points in the graph is not significantly different from 1, suggests that survival and reproductive estimates were unbiased.

The 3-stage model is simplified to a 2-stage model, with the age-classes juveniles (Y) and sub-adults + adults (A), for use in the calculations of state-dependent harvest strategy (optimal harvest rate depending on extant population size and environmental conditions). The model is defined in two equations

$$A_{t+1} = (A_t + Y_t)\theta_t(1 - h_t)$$

$$Y_{t+1} = (A_t + Y_t)\theta_t(1 - h_t)R_t$$

With $R_t = \frac{p_{t+1}}{1-p_{t+1}}$ (p is the fraction of juveniles in the November population), θ_t the survival rate, and h_t the hazard rate at time t. From the transition equations, the harvest of adults and of young can be calculated as

$$H_t^A = (A_t + Y_t)\theta_t h_t$$

$$H_t^Y = \left[\frac{(A_t + Y_t)\theta_t(1 - h_t)R_t}{(1 - dh_t)} \right] dh_t$$

Note that in the harvest of the young equation the coefficient *d* represents the differential vulnerability of young to harvest. JJM derive the value of *d* to be approximately 2, but acknowledge that it may likely vary over time, space and with population structure. The term between brackets represents the population of young <u>before</u> the harvest.

III. Models of Survival and Reproduction

Goal is "to develop a suite of models that fit the data but that also make different predictions of demographic rates outside the realm of experience". Three models for survival and three models for reproduction are (separately) fitted on the data (Survival 1990-2002 in appendix 1).

Survival (from non-hunting related sources)

Random variation. Beta-distribution parameterized from mean and standard deviation of estimated survival from natural causes $\widehat{\theta}_t$. The continuous distribution is transformed in a discrete distribution, with 5 classes between 0.90 and 0.98.

$$\widehat{\theta}_t \sim Beta(125.16, 6.46)$$

Annual survival varies depending on weather conditions. Logit($\widehat{\theta}_t$) fit on various weather variables (least-squares regression). Fit compared with Akaike Information Criterium (AIC). Of all fit models, the ones with TempDays and TempSum have a comparable good score (low AIC). With TempDays as X_t, the model is:

$$Ln\left(\frac{\widehat{\theta}_t}{1 - \widehat{\theta}_t} \right) = 2.738 + 0.049X_t$$

Annual survival varies depending on weather conditions and on population size at the start of the year (November 1). Same procedure, N_t in thousands, X_t as TempDays, resulting in the model:

$$Ln\left(\frac{\widehat{\theta}_t}{1 - \widehat{\theta}_t} \right) = 4.293 + 0.053X_t - 0.044N_t$$

The last model has the lowest AIC of all. It predicts a dramatic reduction in survival when population size exceeds 60 thousand. However, as JJM state, this conclusion involves extrapolating beyond the limits of the data.

JJM discuss the assumptions of additive mortality and harvest mortality being one-half of total mortality, and conclude that there is no substantive conflict between estimates of harvest and an additive mortality hypothesis.

Reproduction

Three models, with random variation, dependence on weather conditions and density-dependence, are fitted on the data of the census (fraction juveniles) from 1980-2011. A generalized linear model with *logit* link is fitted:

$$Ln\left(\frac{\hat{p}_t}{1 - \hat{p}_t}\right) = \beta_0 + \beta_1 X_t + \beta_2 A_t$$

Because in the 2-stage model there is no distinction between sub-adults and adults, the number of sub-adults plus adults of the previous year is used for A_t. the counts of the young are assumed to be binomial or beta-binomial trials of N_t.

Random variation. Beta-binomial model with no covariates. The distribution is discretized (5 classes).

Model with dependence on TempDays

$$Ln\left(\frac{\hat{p}_t}{1 - \hat{p}_t}\right) = -1.989 + 0.027X_t$$

Model with density-dependence and TempDays. The model with the lowest AIC:

$$Ln\left(\frac{\hat{p}_t}{1 - \hat{p}_t}\right) = -1.687 + 0.048X_t - 0.014A_t$$

In the last model, with the lowest AIC, the coefficient for adult population size is only marginally significant, presumably because there is a lack of evidence for density dependence in the period after 2002. JJM suggest that, in a period of above-average temperature days, reproduction may have been released from density-dependent mechanisms.

Dynamics of Temperature Days

The authors analyze the dynamics of temperature days in May (1969-2011). No autocorrelation was observed. JJM specify a beta-binomial distribution for the proportion of warm days out of the possible 31 days in May. Mean value is 7.3 days, so for the beta-binomial = 7.3/31= 0.23. JJM also specify a distribution for a warmer environment (assumption: mean number of days increased by one standard deviation) with mean of 12 warm days.

IV.   Annual-Cycle Models and Their Implications for Harvest Management

JJM combine the 3 survival models with the 3 models for reproduction into 9 alternative "annual-cycle" models. By simulation they estimate the carrying capacity K: the population size resulting in absence of any harvest. Clearly, only in the models with density-dependence in survival and/or reproduction such a carrying capacity exists; the other models lead to exponential growth.

The models with density dependent survival lead to unrealistically low carrying capacity of 59k to 66k (lower than the current population size). The models with density dependent reproduction predict higher K (120k to 129k). JJM remark that with higher temperatures in May a higher K will result.

For each of these models the harvest rate can be calculated that is needed to make the population stabilize at a fixed level. From the harvest rate the harvest can be derived. For a population with the size at

November 2010 (N = 70k; Y = 15.4k and A = 54.6k) and with temperature days as in May 2011 (10 days) JJM calculate the following harvest:

0 – 500 in the models with density dependent survival (the ones leading to $K < 70k$!)

Approximately 17k for two of the models without density dependence.

5 – 11k for the other models

With a harvest of approximately 11k (estimated for DK and N) the population increased from 70k to 80k; therefore JJM conclude that a larger harvest is needed for stabilization of the population.

V.   Harvest Management Implications

JJM give a detailed description of the followed optimization approach, using the method of Stochastic Dynamic Programming.

Optimal is defined as a maximization of harvest while keeping the population size close to a target level. Stochastic dynamic programming model optimizes harvest rates (not harvest). It integrates over the 9 different models. Each model is assigned a weight. Weights are assumed to be equal here (at least, results are only given for the situation with equal weights).

The result of the optimization calculations is big table defining for each state of the system (defined by 3 variables here: number of adults (plus sub-adults), number of young birds, number of temperature days in May) the optimal harvest rate.

From the optimal harvest rate the associated harvest can be calculated (this is not the optimal harvest as harvest was not maximized), for each model separately. By averaging these harvests, again assuming equal weights for the different models, JJM can provide and present the results for harvest in the same way as for harvest rates.

Monte Carlo simulations of the optimal harvest rate for each model produce the result presented in Table 2 (reproduced below, numbers in thousands, except for harvest rate).

Performance metric	System model								
	M0	M1	M2	M3	M4	M5	M6	M7	M8
Young (sd)	6.7 (1.4)	6.7 (1.5)	6.6 (1.6)	8.6 (0.9)	8.7 (1.0)	8.1 (1.0)	8.7 (3.6)	8.8 (3.6)	8.04 (3.3)
Adults (sd)	51.3 (2.2)	51.8 (1.6)	47.8 (1.1)	51.4 (2.1)	51.7 (1.6)	48.0 (1.1)	51.6 (2.5)	52.2 (2.2)	47.7 (1.3)
Harvest rate (sd)	0.07 (0.04)	0.07 (0.04)	0.03 (0.03)	0.10 (0.04)	0.10 (0.03)	0.05 (0.03)	0.10 (0.05)	0.10 (0.05)	0.05 (0.05)
Harvest (sd)	5.0 (3.0)	5.4 (3.0)	2.1 (2.3)	7.8 (3.4)	8.4 (3.2)	3.5 (2.4)	8.0 (5.0)	8.6 (4.9)	3.5 (3.6)
Objective value (sd)	4.8 (2.8)	5.3 (3.0)	1.8 (2.1)	7.7 (3.3)	8.3 (3.1)	3.3 (2.2)	7.1 (4.3)	7.7 (4.3)	3.1 (3.2)

VI.   Future Needs

The authors discuss the need to:

1. Continue the monitoring of number of birds and the proportion of young
2. Record and improve the estimates of harvest: total harvest, age-structure of harvest, number of harvest banded birds
3. Obtain estimates of current rates of survival for the different stages (age-specific survival)

ad 1) counts in November are problematic because they provide information on the post-harvest age structure, while the pre-harvest age structure is needed for the model. Also from a management point of

view it is better to be able to base decisions on recent counts (e.g., directly before the hunting season) than on counts 9-10 months before the start of the hunting season.

ad 3) JJM propose a comprehensive analysis of all mark-recapture data since 1990. In addition it is important to know whether there are (big) age-dependent differences in survival, as these can lead to transient dynamics (damped oscillations) and time delays in the response of the system to harvest.

JJM discuss the application of the approach in an adaptive harvest management cycle of three years. This would imply that the (optimal) harvest rate is set for a period of 3 years. After 3 years the population state is assessed and an adjusted harvest rate is selected. According to JJM a three-year cycle introduces additional uncertainty in the projections of harvest and population size, that are required to optimize a harvest strategy. The framework described in the report is a "preliminary framework" and not yet operational for a three-year cycle.

4. Detailed Comments

Page 5. For survival the assumption that harvest mortality is one-half of total mortality seems quite drastic. A first check could be to compare the harvest numbers in DK (1990-2002) (assuming no harvest in N) to estimated survival of the monitored population (HarvDen, Survival and censusN in the table of Appendix 1). The results indicate that at the first half of this period the (minimum) estimate of harvest mortality is higher than one-half of total mortality, while in the second half it is approximately equal to one-half. Is this check too simple, e.g. because harvest estimates are too unreliable for this period?

Year	censusN	Annual Survival	Annual Mortality	Harvest Denmark	Natural Mortality	Fraction Natural Mortality
1990	26000	0.9201	2077	1800	277	0.011
1991	32500	0.9672	1066	3000	-1934	-0.060
1992	32000	0.9321	2173	2500	-327	-0.010
1993	34000	0.9328	2285	2300	-15	0.000
1994	33000	0.9256	2455	2600	-145	-0.004
1995	35000	0.9171	2901	2800	101	0.003
1996	33000	0.8531	4848	2000	2848	0.086
1997	37500	0.8917	4061	2500	1561	0.042
1998	44800	0.9149	3812	1414	2398	0.054
1999	38500	0.9315	2637	1973	664	0.017
2000	43100	0.8639	5866	2567	3299	0.077
2001	45000	0.8671	5981	2353	3628	0.081
2002	42000	0.8743	5279	2611	2668	0.064

It seems quite unfortunate that no age-dependent survival estimates are available. In our appendix A we show that with a state-space model, all available data (in appendix 1) can be used to estimate survival for sub-adults and adults separately, assuming the 3-stage model described in the next section.

Page 6. TempDays and TempSum are considered as the only weather covariates. The correlation between these two variables equals 0.86. It is therefore not surprising that TempDays and TempSum do equally well in regression models for survival and reproduction.

Page 8. The 3-stage model is used only to make one-year ahead predictions for the period 1990-2002. We were able to reproduce Figure 3 using the data in Appendix 1. The table below shows the quantities used; the first 4 columns are taken from Appendix 1, and the remaining columns are calculated according to the formulae at the bottom of page 7 and the top of page 8.

Year	censusN	censusNjuv	Survival	θ_t	$\theta_t^{0.25}\theta_{t+1}^{0.75}$	$1-h_t$	p_t	$\widehat{N_t}$
1990	26000	3224	0.9201	0.9584	0.9770	0.9601	0.1240	-
1991	32500	7215	0.9672	0.9833	0.9694	0.9836	0.2220	32116
1992	32000	1984	0.9321	0.9649	0.9651	0.9661	0.0620	32449
1993	34000	6154	0.9328	0.9652	0.9623	0.9664	0.1810	36443
1994	33000	4092	0.9256	0.9614	0.9579	0.9628	0.1240	35961
1995	35000	8260	0.9171	0.9568	0.9296	0.9586	0.2360	39661
1996	33000	6072	0.8531	0.9207	0.9372	0.9265	0.1840	36944
1997	37500	5400	0.8917	0.9427	0.9523	0.9459	0.1440	34174
1998	44800	5466	0.9149	0.9556	0.9623	0.9575	0.1220	38945
1999	38500	4736	0.9315	0.9645	0.9362	0.9657	0.1230	47474
2000	43100	2112	0.8639	0.9270	0.9284	0.9320	0.0490	35323
2001	45000	4905	0.8671	0.9288	0.9319	0.9335	0.1090	41923

| 2002 | 42000 | 4452 | 0.8743 | 0.9329 | - | 0.9371 | 0.1060 | 43960 |

These values can be used to check whether the assumption holds that hunting mortality is one-half of total annual mortality. The assumed amount of hunting equals $h_{t+1}N_t$ and this can be compared with the sum of HarvDen and HarvNor taken from Appendix 1. In doing so, the missing values for HarvNor are replaced by 250. It appears that the assumption does not hold too good for the years 1991-1997 and for the year 1999 (compare last two columns of the table below). This could imply that natural survival is larger than assumed in this report.

Year	censusN	HarvDen	HarvNor	h_t	HarvDen+HarvNor	$h_{t+1}N_t$
1990	26000	1800	250	0.0399	2050	-
1991	32500	3000	250	0.0164	3250	426
1992	32000	2500	250	0.0339	2750	1103
1993	34000	2300	250	0.0336	2550	1075
1994	33000	2600	250	0.0372	2850	1265
1995	35000	2800	250	0.0414	3050	1368
1996	33000	2000	250	0.0735	2250	2571
1997	37500	2500	250	0.0541	2750	1787
1998	44800	1414	250	0.0425	1664	1596
1999	38500	1973	250	0.0343	2223	1534
2000	43100	2567	250	0.0680	2817	2620
2001	45000	2353	400	0.0665	2753	2864
2002	42000	2611	500	0.0629	3111	2828

The authors state that Figure 3 suggests "that survival and reproductive estimates were unbiased". Although stated cautiously this is a rather strong statement.
Note also that different partitions of Survival into natural mortality and harvest rate may all more or less reproduce Figure 3. The formulae on top of page 8 all have the same multiplication factor $\theta_t^{0.25} \theta_{t+1}^{0.75} (1 - h_{t+1})$. This factor is more or less the same for every partition of Survival into natural mortality and harvest rate. Taking different values for this partition, i.e. different values of δ in $h_t = (1 - S_t)/\delta$, the multiplication factors below are obtained. Note that small values of δ imply large hunting rates, and large values of δ imply small hunting rates.

Year	$\delta = 1.1$	$\delta = 1.5$	$\delta = 2$	$\delta = 4$	$\delta = 8$
1990	0.966	0.963	0.961	0.958	0.957
1991	0.933	0.935	0.937	0.939	0.940
1992	0.933	0.933	0.933	0.933	0.933
1993	0.926	0.926	0.927	0.927	0.927
1994	0.917	0.918	0.918	0.919	0.919
1995	0.855	0.859	0.861	0.865	0.867
1996	0.891	0.888	0.886	0.884	0.883
1997	0.914	0.913	0.912	0.910	0.910
1998	0.931	0.930	0.929	0.928	0.928
1999	0.866	0.870	0.873	0.877	0.878
2000	0.867	0.867	0.867	0.866	0.866
2001	0.874	0.874	0.873	0.873	0.873
2002	-	-	-	-	-

This implies that something very similar to Figure 3 can be obtained for a large range of δ values.

Page 8. JJM discard the 3-stage model and replace it by a 2-stage model, mainly because there are no survival estimates and no census data available distinguishing between sub-adults and adults. JJM state that "Pink-footed geese may not be sexually mature until age three". Assuming sub-adults and adults to reproduce equally, thus seems like an undesirable simplification, leading to under-estimates of per-capita reproduction. JJM also assume that "Hunting mortality was additive to natural mortality and a constant one half of total annual mortality". This is an important assumption since, see page 21, "survival is the most critical rate determining an appropriate harvest strategy", that should – if possible – not be made a-priori. We show that it is possible to fit a three stage model, to disentangle natural mortality from mortality through hunting and to estimate survival, using the whole time-series of census and harvest (appendix A).

Page 9. The authors state that "the behavior of models outside the range of experience is often more important than that for which data are available". This is the rationale for fitting different models for both survival and reproduction. An alternative could be to use a single model but with different parameter values which cover the range of plausible values.

Page 10. Survival model (1). All survival models were fitted using the important assumption that hunting mortality is one-half of total annual mortality. Moreover these models are fitted using data in the years 1990-2002 only. This is a period in which the population is growing slowly, in contrast to the larger growth in later years. The first model employs a Beta distribution. We were able to reproduce the parameter estimates 125.16 and 6.46 (we used maximum likelihood instead of the method of moments to obtain estimates 124.50 and 6.42). The Beta distribution is then discretized to a coarse grid. This seems unnecessary since drawing from a Beta distribution is rather simple.

Page 10. Survival model (2). We were almost able to reproduce the parameter estimates at the top of page 11. Using data for the years 1990-2002 we obtained $\text{logit}(\theta) = 2.770 + 0.0495\, X_t$

Page 11. Survival model (3). Ordinary regression is applied to transformed observations. This assumes that the variance of the transformed values is constant. It is better to use logistic regression to fit this model. We were unable to reproduce the parameter estimates at the bottom of page 10. Using data for the years 1990-2002 we obtained $\text{logit}(\theta) = 4.114 + 0.0488\, X_t - 0.0366\, N_t$. JJM state about this model that it "involves extrapolating beyond the limits of the data and thus lacks empirical evidence". It may be hazardous to apply this model to later years with larger population sizes, since there does not appear to be a strong density dependence in the data (see Appendix 1). Of course possible density dependence in later years could be masked by warmer springs.

Page 11-12. Reproduction models. Data from 1980 onwards were used to fit the three models. We obtained approximately the same parameter estimates for all three models. The last model, i.e. the beta binomial model with no covariates was again discretized. Again this seems unnecessary.

Page 12. We were able to reproduce the estimates of the beta-binomial model for temperature days. Discretization of this distribution seems unnecessary.

Page 13. The three models for survival and reproduction are then combined into 9 different models. Using the equation at the top of page 14 (which can be derived from the 2 equations at the bottom of page 8) the required harvest rate can be calculated. Using Y=15.4k, A=54.6, X=10, and applying the fitted models we obtained the values in the table below.

model	θ_i	p_i	R_i	h_i^*	Harvest

					h_i^* x 70k
M0	0.9510	0.1222	0.1393	0.0770	5391
M1	0.9619	0.1222	0.1393	0.0874	6121
M2	0.8511	0.1222	0.1393	-0.0314	-2196
M3	0.9510	0.1520	0.1792	0.1083	7581
M4	0.9619	0.1520	0.1792	0.1184	8287
M5	0.8511	0.1520	0.1792	0.0036	252
M6	0.9510	0.1400	0.1628	0.0957	6698
M7	0.9619	0.1400	0.1628	0.1059	7414
M8	0.8511	0.1400	0.1628	-0.0105	-735

Note that the models do not differ much in their value of R_i, but do differ considerably in their value of θ_i. Especially the value for the density dependent survival model does seem to produce a rather low value of natural survival . For the observed population size in 2011 (80k) the survival rate of this model is even as low as 0.786. This is due to extrapolation (which the authors noted on page 10).
The authors state that for models M6 and M7 a harvest of approximately 17k is required. We arrive at a required harvest of 7k for these models.

Page 14. The equation at the top of page 14 can be used to derive the required harvest rate to obtain a stable population of 60k under various parameter values θ and R. This will give a range of required harvest rates. These parameter values can be assigned prior probabilities by using data, models and/or expert opinion, resulting in a mean harvest rate along with a standard error. This simple and robust approach can be also used for a population of 80k to see what has to be done extra to arrive at a population of 60k.

Page 14. The likelihood at the bottom of page 14 employs a model specific prediction of population size. This is, as we assume, given the observed population size in the previous year. If this is correct, the comparison of the models is based on the one-year ahead predictions. This a rather limited comparison of the models since the starting point is always "correct". The difference between the models becomes especially apparent after repeatedly applying the same model, as can be seen in the table at the bottom of page 13. Given this limited comparison the authors conclude that the 9 models should be assigned equal prior probability. However there seems scope to assign a (much) lower probability to the density dependent survival model.

Page 16-18. Some aspects of the applied method (optimization, Stochastic Dynamic Programming) are not completely clear from the text. The description of the method suggests that model weights are updated *inside* the optimization procedures. However, it is also stated at many locations in the text that results apply to the case of equal weights assigned to the models. The optimal harvest rate is calculated for the period t=0 to t=T. Is T in this case infinity, or just a sufficiently large value, or related to a much shorter period? Which sources of stochasticity are accounted for in the optimization? The demographic rates and, for the models with weather variables, the number of temperature days in May? Or are there more?

page 18. Harvest utility is given a mean value of 60k and a standard error of 10k. The standard error seems rather large. Does the value of the standard error affect the conclusions in any way?

page 19. The table shows that under models M2, M5 and M8 (the density dependent survival models) the population size is approx. 56k instead of 60k as required. Is this due to the discrete values for harvest rate which are used in the simulation?

page 20. I would be very nice indeed to have more data on the age structure of the population, either in spring (after reproduction) or in the autumn. Moreover the age structure of the harvest is also valuable information. Note that in our alternative model there is less need to have a census at another time as long as (1) harvest can be partitioned into pre/post census and (2) it can be assumed that natural mortality mainly is in winter and after harvesting.
.

page 20. We agree with the authors that it is more suitable to maximize harvest instead of harvest rate, when following an optimization method. As the authors show in appendix 2, this requires a pre-harvest census instead of post-harvest census.

5. References

Schaub M & Abadi F (2011). Integrated population models: a novel analysis framework for deeper insights into population dynamics. A review. J. Ornithol. (2011) 152 (Suppl 1): S227–S237.

Buckland ST, Newman KB, Thomas L & Koesters NB (2004). State-space models for the dynamics of wild animal populations. Ecological Modelling, 171: 157–175.

Appendix A. State-Space model

The alternative model is a so-called state-space model which describes the population dynamics of the underlying process for three stages: juveniles, sub-adults and adults. The model assumes that

1. natural mortality θ occurs in winter after the census in November but before reproduction in spring.
2. natural mortality is the same for juveniles, sub-adults and adults.
3. only adults, i.e. starting at age three, reproduce with reproduction parameter r
4. harvest H is solely after reproduction in spring and fully before the census in November.
5. the harvest data are without error and it is assumed that there was no harvest in Norway before 2001.
6. The differential harvest vulnerability of young equals 2. This implies that percentage young which are harvested is twice as large as the percentage sub-adults and adults. For instance suppose that the population size in spring equal 10000 juveniles, 10000 sub-adults and 5000 adults. A harvest of 5000 individuals is then partitioned into H_0=1250 juveniles, H_1=625 sub-adults and H_2=3125 adults.

The process model, distinguishing between autumn and spring numbers, is then given by
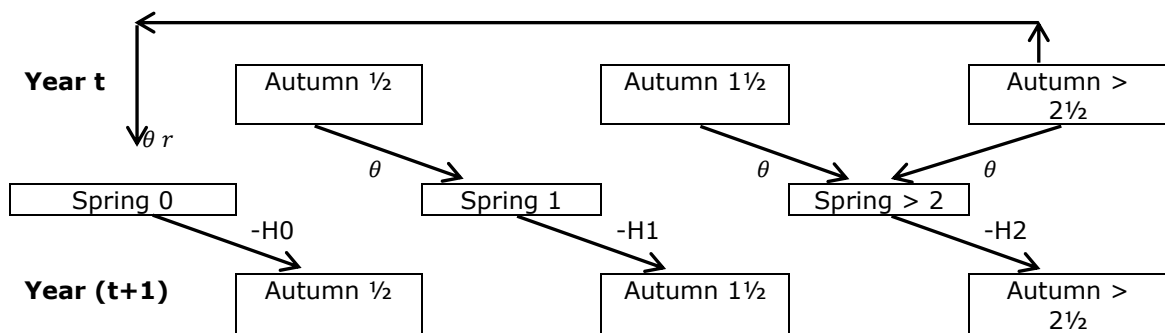
So from autumn to spring there is survival at a rate θ, and reproduction by 3-year olds at a rate $\theta\,r$. From spring to autumn there is no natural mortality but the numbers are decreased by subtracting the partitioned harvesting. The partitioning is according to the spring numbers.

This model is deterministic. To introduce stochasticity the survived numbers in spring are assumed to follow a binomial distribution with binomial total the corresponding population size in autumn and binomial probability θ. Moreover the number of offspring in spring is assumed to follow a Poisson distribution with rate parameter $\theta\,r$. So

$\quad$ Spring0 $\quad\sim$ Poisson($\theta\,r$ (Autumn > 2½))
$\quad$ Spring1 $\quad\sim$ Binomial(Autumn ½, θ)
$\quad$ Spring>2 $\quad\sim$ Binomial(Autumn 1½ + Autumn 2½, θ)

The population sizes in autumn are then simply obtained by subtracting the partitioned harvest:

$\quad$ Autumn ½ $\;=$ Spring0 $\quad - H_0$
$\quad$ Autumn 1½ $=$ Spring1 $\quad - H_1$
$\quad$ Autumn 2½ $=$ Spring>2 $\;- H_2$

The parameters of this model, i.e. θ and r, can be estimated using Bayesian techniques by imposing a so-called observation process which links the observed counts Y to the underlying process given above. We assumed a Poisson distribution for this observation process, i.e.

$Y\frac{1}{2}$ ~ Poisson($N\frac{1}{2}$)

$Y1\frac{1}{2} + Y2\frac{1}{2}$ ~ Poisson($N1\frac{1}{2} + N2\frac{1}{2}$)

in which Y denotes the observation in autumn and N the underlying process value in autumn. Note that this model does not require that observations are required for all stages. The program OpenBugs called from the R package was used to fit this model to the data for the years 1990-2011. The R code and necessary data files are given below.

Three models were fitted:

1. constant survival and reproduction
2. survival and reproduction depend linearly on TempDays using a logistic link. In the R code the lines used are given by, with rr0, rr1, ss0 and ss1 the regression parameters

   ```
   logit(rr[tt-1])  <- rr0 + rr1*(TempDays[tt]-8)
   logit(s12[tt-1]) <- ss0 + ss1*(TempDays[tt]-8)
   ```

3. survival depends on TempDays number of population size in the Autumn, and reproduction depends on TempDays and number of adults in Autumn, again using a logistic link. The R code for this model is given by:

   ```
   logit(rr[tt-1])  <- rr0 + rr1*(TempDays[tt]-8) + rr2*(Autumn2[tt-1]-30000)/1000
   logit(s12[tt-1]) <- ss0 + ss1*(TempDays[tt]-8) +
                   ss2*(Autumn0[tt-1] + Autumn12[tt-1]-45000)/1000
   ```

This results in posterior distributions for the parameters as well as for the fitted values, i.e. the underlying population sizes $N\frac{1}{2}$, $N1\frac{1}{2}$ and $N2\frac{1}{2}$. The figure below displays the data and the mean of the posteriors of the fitted values for the three models.
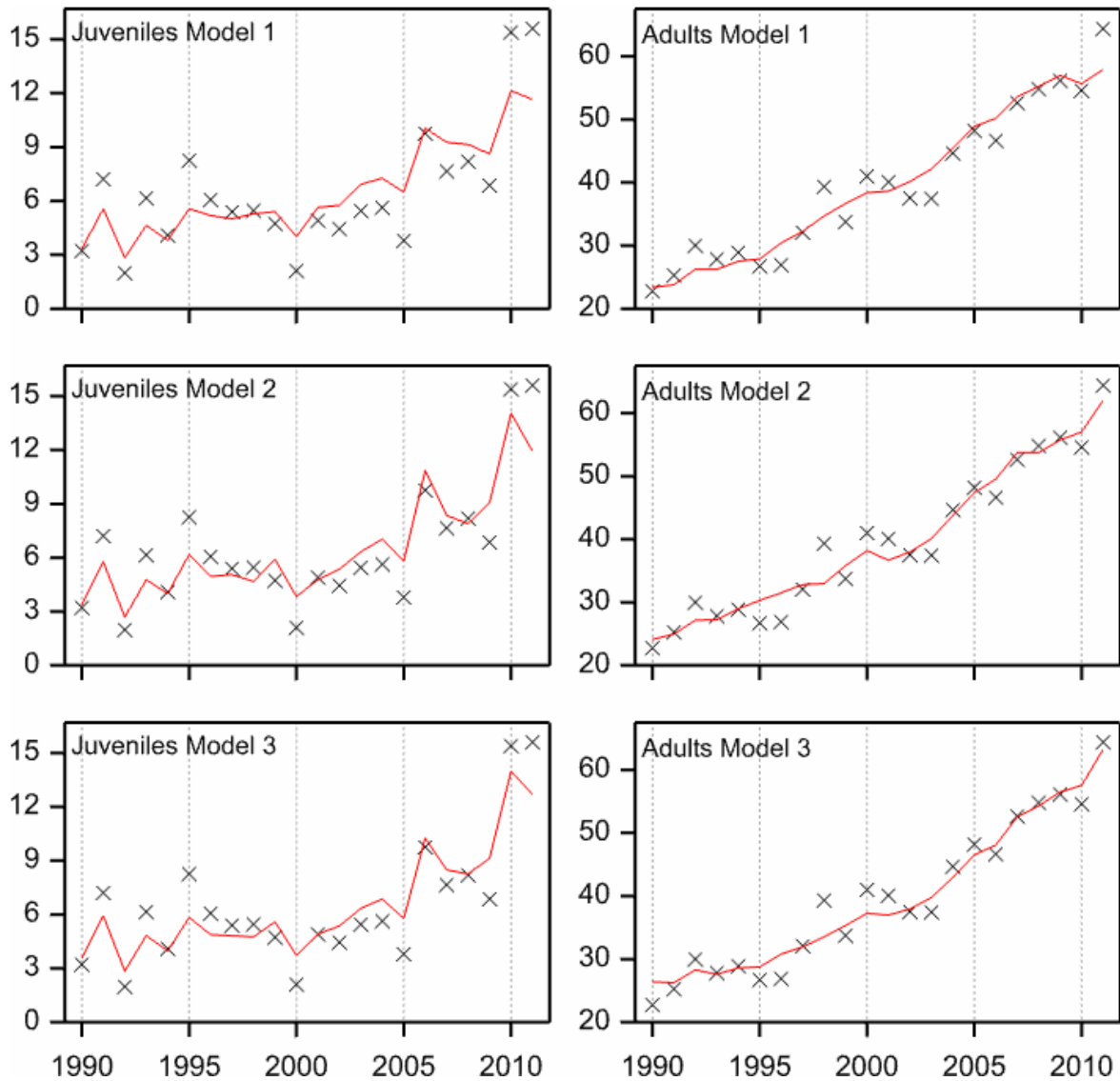
It is clear that models 2 and 3 provide a better fit than model 1, and also that there is not much difference between model 2 and model 3. The mean of the posteriors of the parameters, along with a 95% posterior interval, are given in the table below. Note that for models 2 and 3 the estimates are on the logit scale

Model 1	Intercept	Slope TempDays	Slope PopSize
Reproduction	0.2420 (0.2400, 0.2427)	-	-
Survival	0.9651 (0.9642, 0.9654)	-	-
Model 2	Intercept	Slope TempDays	Slope PopSize
Reproduction	-1.2089 (-1.2210, -1.2050)	0.0426 (0.0409, 0.0432)	-
Survival	3.7195 (3.6630, 3.7390)	0.1957 (0.1838, 0.1998)	-
Model 3	Intercept	Slope TempDays	Slope PopSize
Reproduction	-1.2543 (-1.2690, -1.2490)	0.0304 (0.0281, 0.0312)	0.0105 (0.0090, 0.0111)
Survival	3.5364 (3.4930, 3.5520)	0.0362 (0.0172, 0.0426)	0.0551 (0.0499, 0.0569)

For model 1 a survival rate of 0.965 is obtained with a very coarse 95% posterior interval. This is somewhat larger than the estimate of 0.951 given at page 10 of the report. The reproduction parameter equals 0.242, also with a small interval, which is much larger than $0.163 = 0.14/(1-0.14)$ where 0.14 is the estimate given on page 12 of the report. This is of course due to the fcat that in our model only adults are reproductive.

For models 2 and 3 the 95% posterior intervals for the regression parameters do not include 0, indicating that the covariates are "significant". Moreover the effect of population size on both reproduction and survival is positive! This is opposite to the more usual density dependence. A graph of the fitted reproduction and survival parameters across time for the two models (black for model 2, red for model 3) is given below.
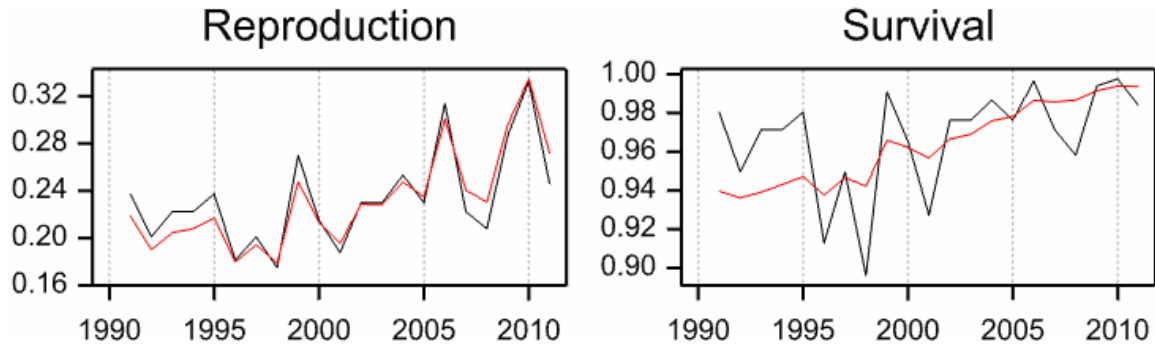
It is clear that the models for reproduction are more or less equivalent, while the models for survival are not. The density dependence model (model 3 in red) shows a more or less steady increase throughout the last two decades.

We consider model 2, with TempDays as covariate, as the more plausible model and used that to examine which harvest rate should be used to stabilize the population at 60k. Three scenarios were used:
1. using the estimates for model 1:   reproduction = 0.2420 and survival = 0.9651
2. model 2 with TempDays = 7:   reproduction = 0.2224 and survival = 0.9714
3. model 3 with TempDays = 12:   reproduction = 0.2614 and survival = 0.9890

Two initial situations were examined
A. We started with a population of 15k Juveniles, 11k sub-adults and 54k adults (80k in total) and used our now deterministic model with different harvest rates to determine the harvest rate at which the population is reduced to approximately 60k in 4 years. Note that the actual harvest rate is larger because of the larger vulnerability of juveniles.
B. Secondly an initial population of 8k juveniles, 7k sub-adult and 45 adults (totalling 60k) was used to determine in the same way the harvest rate at which the population remains more or less stable.

In the table below the required harvest rates are given with the actual harvest rates in parenthesis. Also the resulting numbers that need to be harvested are given.

Scenario	Rate for A	Rate for B	Harvest for A	Harvest for B
1	15.5 (17.8)	10.6 (12.2)	15877 - 13241	8350
2	15.5 (17.7)	10.4 (11.9)	15662 – 12996	8090
3	18.0 (20.9)	13.1 (15.2)	19269 - 15873	10800

The required numbers that need to harvested according to this approach are comparable, maybe somewhat larger, to those that are reported at page 20 of the report.

For scenario 1 a yearly harvest of 8350 would keep the population stable at 60k. This could be compared to a more optimal 4-year strategy (in terms of numbers harvested) in which the population is allowed to grow during two years without harvesting after which two years are taken to return to a population size of 60k, admittedly a rather extreme strategy. This strategy requires yearly harvests of 0, 0, 20k and 17k giving a total harvest of 37k. This is approximately 4k more than 4 years with a harvest of 8350, i.e.

approximately 1k per year. Also for scenario 2 the difference between the two strategies is 1k per year, while for scenario 3 it is 2k per year. These difference are rather small given the uncertainty about the state-space model and its parameters.

Discussion

1. The alternative model can be used to estimate important population parameters without making the assumption that hunting mortality is some fixed fraction of total annual mortality. Moreover a three stage model, distinguishing sub-adults from adults, could be used. It must be stressed that the alternative model assumes that all natural mortality occurs during the winter, and that harvest only occurs before the census in November.
2. The model further assumes that natural survival is constant across juveniles, sub-adults and adults. Trying to fit a model with a different survival for juveniles failed because there is no information in the data to estimate such a parameter. This could be remedied in case there is some information about the age structure of the population.
3. The alternative model is a good start for an integrated population model (IPM). Such a model would require external data about reproduction (e.g. estimates of reproduction success) and/or external data about survival (e.g. using re-sighting of coloured bands), and/or information about the age structure of the population. One idea now is to supplement our model with the total annual survival rates which are available for the years 1990-2002. Setting up a full IPM model can however be a time-consuming task.
4. A combination of the alternative model (and their variants) and the adaptive harvest management approach in the report would be most welcome.
5. The question is whether a rather complicated (at least for us) adaptive system dynamics approach is necessary given the uncertainty about the model and its parameters. It seems that a simple approach with some different parameter values, as outlined above, is sufficient to get a quantitative idea of the harvest needed to reduce or to stabilize the population.

R code and datasets

```
## Define Settings
library(R2OpenBUGS)
ntimes    = 100000
n.burnin  = ntimes
n.iter    = ntimes
n.chains  = 2
seed      = 3
debug     = TRUE

## Nodes to monitor
monitor = c("Autumn0", "Autumn1", "Autumn2", "reproduction", "theta")

## Define OpenBugs model
model = function()
{ # Priors for the parameters
  reproduction  ~ dunif(0,1)
```

```
    theta ~ dunif(0,1)
    # Spring
    Spring0[1] ~ dnorm( 3000, 0.000001) %_% I(1000,)
    Spring1[1] ~ dnorm( 3000, 0.000001) %_% I(1000,)
    Spring2[1] ~ dnorm(20000, 0.000001) %_% I(10000,)
    # Distribute harvest
    Fraction[1] <- harvest[1]/(2*Spring0[1] + Spring1[1] + Spring2[1])
    Harvest0[1] <- 2*Fraction[1]*Spring0[1]
    Harvest1[1] <- 1*Fraction[1]*Spring1[1]
    Harvest2[1] <- 1*Fraction[1]*Spring2[1]
    # Autumn
    Autumn0[1] <- round(max(Spring0[1] - Harvest0[1], 1000))
    Autumn1[1] <- round(max(Spring1[1] - Harvest1[1], 1000))
    Autumn2[1] <- round(max(Spring2[1] - Harvest2[1], 10000))
    Autumn12[1] <- Autumn1[1] + Autumn2[1]

    for (tt in 2:nt){ # System process
      # Spring
      birthrate[tt] <- (reproduction * theta * Autumn2[tt-1])
      Spring0[tt] ~ dpois(birthrate[tt])
      Spring1[tt] ~ dbin(theta, Autumn0[tt-1])
      Spring2[tt] ~ dbin(theta, Autumn12[tt-1])
      # Distribute harvest
      Fraction[tt] <- harvest[tt]/(2*Spring0[tt] + Spring1[tt] + Spring2[tt])
      Harvest0[tt] <- 2*Fraction[tt]*Spring0[tt]
      Harvest1[tt] <- 1*Fraction[tt]*Spring1[tt]
      Harvest2[tt] <- 1*Fraction[tt]*Spring2[tt]
      # Autumn
      Autumn0[tt] <- round(max(Spring0[tt] - Harvest0[tt], 1000))
      Autumn1[tt] <- round(max(Spring1[tt] - Harvest1[tt], 1000))
      Autumn2[tt] <- round(max(Spring2[tt] - Harvest2[tt], 10000))
      Autumn12[tt] <- Autumn1[tt] + Autumn2[tt]
      }

    for (tt in 1:nt) { # Observation process
      y0[tt]  ~ dpois(Autumn0[tt])
      y12[tt] ~ dpois(Autumn12[tt])
      }
}




## Write model to text file
write.model(model, "z.txt")

## Read Data and Inits from files
data = as.list(read.table("z.dat", header=T))
```

```
data$nt = length(data[[1]])
init = as.list(read.table("z.ini", header=T))
inits = function() { init }

## Run OpenBugs
bugsout = bugs(data, inits, monitor, "z.txt",
    n.chains=n.chains, n.iter=n.iter+n.burnin, n.burnin=n.burnin, digits=8,
    debug=debug, codaPkg=FALSE, bugs.seed=seed)
bugsout
write.csv(bugsout$summary, "z.csv")
q()
```

File model.dat

y0	y12	harvest
3224	22776	1800
7215	25285	3000
1984	30016	2500
6154	27846	2300
4092	28908	2600
8260	26740	2800
6072	26928	2000
5400	32100	2500
5466	39334	1414
4736	33764	1973
2112	40988	2567
4905	40095	2753
4452	37548	3111
5448	37452	2849
5634	44666	2756
3796	48204	2894
9757	46643	5118
7658	52642	6797
8190	54810	8016
6867	56133	7546
15400	54600	12041
15600	64400	11429

File model.ini

theta	reproduction
0.90	0.30