Estimation of Age Specific Pupping Probabilities of the Grey Seal (*Halichoerus grypus*)

by

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Abstract

The population of the Grey Seal (*Halichoerus grypus*) has increased dramatically since the 1960's. Along with the rapid change in population density has come concern for the seals and their impact upon the surrounding environment. Hammill and Gosselin (1995) investigated the impact of these changes upon population parameters for a dataset collected from the Northwest Atlantic.

Their study used bootstrapping techniques to estimate the percentage of seals that begin pupping at each specific age and estimate a mean age of first birth for each of six sample periods. Variance estimates of the mean age of first birth were also calculated. The goal of this project is to re-estimate these parameters without using the bootstrap. Instead, maximum likelihood techniques are used with binomial models.

Theory is worked through for three different cases. The first is a straightforward case of non-decreasing observed pregnancy rates. More complicated is the case with some decreasing observed pregnancy rates for which isotonic regression is used to pool data and get new estimates. Contour plots are used to illustrate this concept. Finally, a new restriction of unimodality of the estimates is introduced and Gompertz models are fit to the data. A Taylor series expansion is used to calculate variance estimates for this case.

Lastly, likelihood ratio and Wald tests are used to test if parameters have changed across time. A simulation study is used to estimate degrees of freedom and evaluate p-value of the tests. A comparison of estimates with those of Hammill and Gosselin is presented.

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Contents

List of Tables

List of Figures

Chapter 1

Introduction

Grey Seals (*Halichoerus grypus*) are found along the Atlantic coasts of Canada and northeastern United States as well as in the Baltic Sea. In the western Atlantic, Grey Seal whelping occurs primarily on Sable Island, off the coast of Nova Scotia, with smaller groups on Amet, Anticosti, Deadman and White Islands in the Gulf of St. Lawrence. Figure 1.1 shows the study area in the Northwest Atlantic. Pupping takes place throughout December to January, with new breeding commencing a few weeks after birth. Pregnancy lasts almost a whole year and pregnancy rates are high for mature females, resulting in animals that are pregnant almost every year of their adult life. Seals also almost always give birth to only 1 young.

Grey Seals have been reported to be abundant in Canadian waters in the mid-1800's but their numbers appear to have been extensively reduced since then, possibly through hunting. The population of the animal was not properly enumerated until the 1960's, when Mansfield (1966) estimated the population to be approximately 5600 Grey seals. Since then, the population has increased dramatically despite a government sponsored cull from 1967-84. Mohn and Bowen (1994) estimated the population to be 143,000 in 1993 and the Sable Island component was estimated to be increasing at a rate of 13% annually.

The rapid population growth of the Grey Seal has created interest in the impact of this expansion in at least two ways. Mammalian populations often exhibit changes in reproductive parameters following dramatic increases in population size (Bowen et al. 1981). These changes can often appear in the mean age of sexual maturity and age specific pupping rates as a result of a change in the density of the population. Age specific pupping rates are defined as probability of giving birth for the first time for each specific age.

A further concern is a negative impact upon the commercial fishing industry. The Grey Seal is thought to be the definitive host of the Sealworm (*Pseudoterranova decipiens*) parasite which is passed from the seal to the ocean through feces. Sealworm larvae hatch from these feces and are consumed by passing fish, infecting them and making the fish unpleasant for the consumer. This larva can be removed from the flesh of the fish but at an increased processing cost.

An examination of reproductive parameters to estimate age-specific pupping rates and mean age of first birth for female Grey Seals will assess the impact of a density change in the population. This information could be used to help control future growth if another government sponsored cull is warranted.

1.1 Data Collection

The data for this project is taken from Hammill and Gosselin (1995). Reproductive tracts and lower jaws from females aged greater than one year were collected by trained hunters from the eastern shore of Nova Scotia, during May-September 1968-70. Further samples were obtained during June-September 1982, 1986, 1987, 1988 and 1992. The total number of females in the sample was 526.

1.2 Age and Pregnancy Determination

The age of individual seals was determined from taking a cross-section of a lower canine tooth just below the gum line and examining it under a microscope. The reproductive condition was determined from whole reproductive tracts preserved in 10% formalin. There were two methods used to determine state of pregnancy. The first method was the presence or absence of a fetus at time of capture. The second method was through dissection of collected ovaries into slices which were examined for

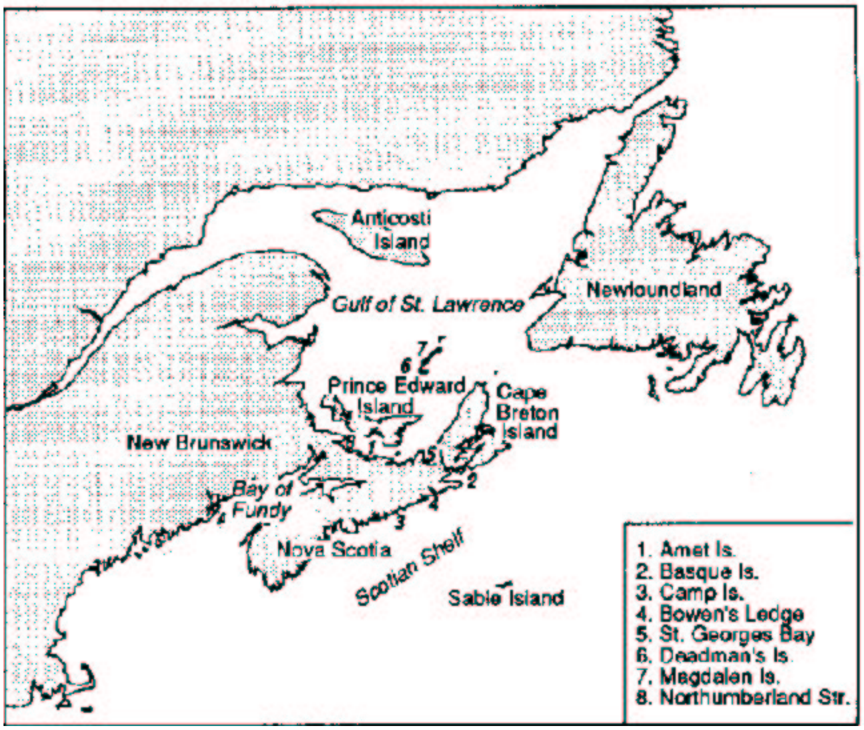


Figure 1.1: Map of the study area in the Northwest Atlantic

corpora lutea. The corpus luteum is a yellow glandular mass in the ovary formed by an ovarian follicle that has matured and discharged its ovum. Immature females have small ovaries containing no corpus luteum. Thus ovaries in which a corpus luteum was present were considered evidence that females were pregnant.

Data from collection by these methods over the six time periods appear in Table 1.1. Note that the first age listed in the table is age at the time of capture. The age at the time of pupping would be the following year, and thus 1 year older.

Note that some data for samples 1986 and 1992 were not available. The ratio $\frac{0}{0}$ was treated as 100% in the methodology that follows, as this was a typical value at those ages across the samples.

1.3 Problem and Previous Methodology

Hammill and Gosselin (1995) examined this data and found estimates of age-specific pupping rates and mean age of first birth. The procedure they used is as follows.

They defined reproductive rate as percentage of mature females in each age class that were deemed pregnant (by presence of a corpus luteum or a fetus). To estimate age of first birth, age was increased to the age the female would have been during the subsequent pupping period (January). Mean age of first birth was determined as follows.

1. $$\tilde{P}_{a,t} = n_{a,t}/N_{a,t}$$

where $\tilde{P}_{a,t}$ is estimated proportion of females pregnant at age a in sample t
$n_{a,t}$ is number of females with fetus or corpus luteum at age a in sample t
$N_{a,t}$ is total number of females at age a in sample t

2. $$\tilde{f}_{a,t} = \tilde{P}_{a,t} - \tilde{P}_{a-1,t}$$

where $\tilde{f}_{a,t}$ is estimated proportion of females pregnant for the first time at age a, time t

This probability was used to calculate the average age of first birth and variance by bootstrapping with replacement. If each age class had k_a pregnant and non-pregnant individuals, k_a draws with replacement were made at random from this pool and $\tilde{f}_{a,t}$ recalculated. The estimated mean age of first birth was then calculated as

3. $$\widehat{\text{age}}_t = \sum_{a=2}^{11} a \times (\tilde{f}_{a,t})$$

This was repeated 500 times and mean age at first birth and variance of $\widehat{\text{age}}_t$ was estimated.

The difficulty with this approach is in step 2. It is possible through sampling fluctuation, that samples can lead to negative estimates of probabilities. If a sample at age 5 has 100% pregnant seals followed by only 70% at the next age, the estimate would be -30%. This does not make sense. One method to bypass this problem is to use normal smoothing in cases where proportions dip from one year to another.

The objective of this project is to use maximum likelihood theory to approach the estimation problem in the straightforward cases where there are no drops between years, and to use isotonic regression in cases that lead to negative estimates of parameters and probabilities.

This approach avoids the use of the bootstrap. We will also use likelihood ratio tests to investigate if there have been changes to the parameters over time, and compare estimates to earlier results of Hammill and Gosselin.

Table 1.1: Total Number (N) of female Grey Seals collected between 1968 and 1992 and numbers of those showing presence of a corpus luteum (CL) or a fetus.

	Age (yr)										
Sampling	Capture →	≤2	3	4	5	6	7	8	9	10	≥11
Period	Birth →	≤3	4	5	6	7	8	9	10	11	≥12
1968-1970	N	20	12	7	9	6	6	4	4	2	20
	CL	0	7	7	9	6	6	4	4	2	20
	Fetus	0	3	5	9	6	6	4	4	1	14
1982	N	7	4	4	8	1	4	3	3	3	35
	CL	0	2	4	8	1	4	3	3	3	35
	Fetus	0	0	3	7	1	3	3	3	3	31
1986	N	16	4	2	4	7	4	3	4	0*	23
	CL	0	2	2	4	7	4	3	4	0*	23
	Fetus	0	0	2	3	6	4	3	4	0*	22
1987	N	5	7	10	8	9	6	8	3	5	49
	CL	1	4	10	8	9	6	8	3	5	49
	Fetus	0	1	5	5	6	6	8	2	4	47
1988	N	3	4	10	9	3	2	3	1	3	38
	CL	0	4	8	9	3	2	3	1	3	38
	Fetus	0	2	7	8	2	2	2	1	3	35
1992	N	24	16	16	15	5	1	4	0*	3	26
	CL	0	2	13	15	5	1	4	0*	3	26
	Fetus	0	1	12	13	4	1	4	0*	2	25

Note: Age of first birth one year greater than age at capture
*Missing Data. See text for discussion.

Chapter 2

Methodology

This chapter uses maximum likelihood theory to get estimates for age specific pupping rates in three different ways. The first is when there are no drops in observed pregnancy rates from one year to the next, that is the estimated proportion of females thought to be pregnant increases monotonically over time. The second case relaxes this restriction and allows decreases in the observed pregnancy rates. This leads to negative estimates of age-specific pupping rates and a solution is explored using isotonic regression. The third case adds a restriction of unimodality to the estimates of pupping rates.

2.1 Notation and General Likelihood Methodology

Referring to Table 1.1, we see that data was collected for 10 age classes, and we define the first group to be ≤ 2 years and the last group to be ≥ 11 years old at age of capture (or one year greater for age at pupping). There are two methods to measure pregnancy, by presence of either a corpus luteum or a fetus, denoted by CL and Fet respectively. There are six samples denoted by year of collection.

Let

$N_{a,t}$ be the total number of female seals captured at age a in the sample taken at time t

$X_{a,t}$ be number showing presence of a CL or a Fetus captured at age a in sample taken at time t

and define

$b_{3,t}$ = Probability of first birth at age 3 (or less) for seals taken in sample t
$b_{4,t}$ = Probability of first birth at age 4 for seals taken in sample t
$b_{5,t}$ = Probability of first birth at age 5 for seals taken in sample t
$\vdots$
$b_{11,t}$ = Probability of first birth at age 11 for seals taken in sample t
$b_{12,t}$ = Probability of first birth at age 12 (or more) for seals taken in sample t

$\sum_{3}^{12} b_{i,t} = 1$, and $0 \leq b_{i,t} \leq 1 \quad \forall i$ as they are probabilities. Note that the age of birth is 1 year greater than year of capture.

Denote

$p_{2,t}$ = Probability of being pregnant at age 2 (or less) in sample t
$p_{3,t}$ = Probability of being pregnant at age 3 in sample t
$\vdots$
$p_{i,t}$ = Probability of being pregnant at age i in sample t
$\vdots$
$p_{11,t}$ = Probability of being pregnant at age 11 (or more) in sample t

Using the above definitions, it seems reasonable to model each $X_{i,t}$ as independent binomial random variables as follows.

$$X_{i,t} \sim \text{Bin}(N_{i,t}, p_{i,t}) \qquad i= 2,\cdots,11$$

A further relationship between the b's and the p's can be derived. If a female is pregnant at age a, then she will give birth at age a+1. If a female has a pup at age a+1, then first birth must be at age a+1 or less. We have

$$p_{i,t} = b_{3,t} + b_{4,t} + b_{5,t} + \cdots + b_{i,t} + b_{i+1,t} \qquad i = 2, \cdots, 11$$

Thus

$$X_{i,t} \sim \text{Bin}(N_{i,t},\, b_{3,t} + b_{4,t} + \cdots + b_{i+1,t})$$

For a specified sample t, a single binomial likelihood is

$$\begin{pmatrix} N_i \\ X_i \end{pmatrix} (p_i)^{X_i}(1 - p_i)^{N_i - X_i}$$

or

$$\begin{pmatrix} N_i \\ X_i \end{pmatrix} (b_3 + b_4 + \cdots + b_{i+1})^{X_i}(1 - (b_3 + b_4 + \cdots + b_{i+1}))^{N_i - X_i}$$

We would like to get the maximum likelihood estimates for the b's as we are interested in age-specific pupping probabilities.

The likelihood for a general case is then the product of all the separate binomials

$$\begin{aligned} \mathcal{L} &= K \times (b_3)^{X_2}(1 - b_3)^{N_2 - X_2}(b_3 + b_4)^{X_3}(1 - (b_3 + b_4))^{N_3 - X_3} \cdots \\ &\quad (b_3 + b_4 + \cdots + b_{11} + b_{12})^{X_{11}}(1 - (b_3 + b_4 + \cdots + b_{11} + b_{12}))^{N_{11} - X_{11}} \end{aligned}$$

where K is the product of the binomial coefficients.

The log-likelihood then becomes

$$\begin{aligned} l &= \log(K) + X_2 \log(b_3) + (N_2 - X_2)\log(1 - b_3) + X_3 \log(b_3 + b_4) + \\ &\quad (N_3 - X_3)\log(1 - (b_3 + b_4)) + \cdots + X_{11}\log(b_3 + b_4 + \cdots + b_{11} + b_{12}) \\ &\quad + (N_{11} - X_{11})\log(1 - (b_3 + b_4 + \cdots + b_{11} + b_{12})) \end{aligned}$$

$$= \log(K) + \sum_{2}^{11}\{X_i \log(b_3 + b_4 + \cdots + b_{i+1}) + (N_i - X_i)\log(1 - (b_3 + b_4 + \cdots + b_{i+1}))\}$$

The score equations are found as

$$\begin{aligned}
\frac{\partial l}{\partial b_3} &= \frac{X_2}{b_3} - \frac{N_2 - X_2}{1 - b_3} + \frac{X_3}{b_3 + b_4} - \frac{N_3 - X_3}{1 - (b_3 + b_4)} + \cdots \\
&\quad + \frac{X_{11}}{b_3 + b_4 + \cdots + b_{11} + b_{12}} - \frac{N_{11} - X_{11}}{1 - (b_3 + b_4 + \cdots + b_{11} + b_{12})} \\
\frac{\partial l}{\partial b_4} &= \frac{X_3}{b_3 + b_4} - \frac{N_3 - X_3}{1 - (b_3 + b_4)} + \cdots \\
&\quad + \frac{X_{11}}{b_3 + b_4 + \cdots + b_{11} + b_{12}} - \frac{N_{11} - X_{11}}{1 - (b_3 + b_4 + \cdots + b_{11} + b_{12})} \\
&\vdots \\
\frac{\partial l}{\partial b_{12}} &= \frac{X_{11}}{b_3 + b_4 + \cdots + b_{11} + b_{12}} - \frac{N_{11} - X_{11}}{1 - (b_3 + b_4 + \cdots + b_{11} + b_{12})}
\end{aligned}$$

Setting the above equations equal to zero yields a system of equations. Looking at the last equation we solve for $(b_3 + b_4 + \cdots + b_{11} + b_{12})$ to get

$$\begin{aligned}
&\frac{X_{11}}{b_3 + b_4 + \cdots + b_{11} + b_{12}} = \frac{N_{11} - X_{11}}{1 - (b_3 + b_4 + \cdots + b_{11} + b_{12})} \\
&\Rightarrow\ X_{11}(1 - (b_3 + b_4 + \cdots + b_{11} + b_{12})) = N_{11} - X_{11}(b_3 + b_4 + \cdots + b_{11} + b_{12}) \\
&\Rightarrow\ X_{11} - X_{11}(b_3 + b_4 + \cdots + b_{11} + b_{12}) = N_{11}(b_3 + b_4 + \cdots + b_{11} + b_{12}) \\
&\qquad\qquad\qquad\qquad\qquad\qquad\qquad -X_{11}(b_3 + b_4 + \cdots + b_{11} + b_{12}) \\
&\Rightarrow\ b_3 + b_4 + \cdots + b_{11} + b_{12} = \frac{X_{11}}{N_{11}}.
\end{aligned}$$

Taking this, we substitute into the equation before it

$$\frac{\partial l}{\partial b_{11}} = \frac{X_{10}}{b_3 + b_4 + \cdots + b_{11}} - \frac{N_{10} - X_{10}}{1 - (b_3 + b_4 + \cdots + b_{11})} + \frac{X_{11}}{b_3 + b_4 + \cdots + b_{11} + b_{12}} - \frac{N_{11} - X_{11}}{1 - (b_3 + b_4 + \cdots + b_{11} + b_{12})} = 0$$

to get

$$\frac{\partial l}{\partial b_{11}} = \frac{X_{10}}{b_3 + b_4 + \cdots + b_{11}} - \frac{N_{10} - X_{10}}{1 - (b_3 + b_4 + \cdots + b_{11})} + \frac{X_{11}}{X_{11}/N_{11}} - \frac{N_{11} - X_{11}}{1 - (X_{11}/N_{11})} = 0$$

The last two terms cancel, and we solve to get

$$b_3 + b_4 + \cdots + b_{11} = \frac{X_{10}}{N_{10}}$$

This continues for all derivatives, plugging each solution into the equation before it until we finally get a system of equations

$$\begin{aligned} b_3 &= \frac{X_2}{N_2} \\ b_3 + b_4 &= \frac{X_3}{N_3} \\ b_3 + b_4 + b_5 &= \frac{X_4}{N_4} \\ &\vdots \\ b_3 + b_4 + \cdots + b_{11} + b_{12} &= \frac{X_{11}}{N_{11}} \end{aligned}$$

Solving for individual b's in the equations above yields following estimates

$$\begin{aligned} \hat{b}_3 &= \frac{X_2}{N_2} \\ \hat{b}_4 &= \frac{X_3}{N_3} - \frac{X_2}{N_2} \end{aligned}$$

$$\begin{aligned} \hat{b}_5 &= \frac{X_4}{N_4} - \frac{X_3}{N_3} \\ &\vdots \\ \hat{b}_{12} &= \frac{X_{11}}{N_{11}} - \frac{X_{10}}{N_{10}} \end{aligned} \tag{2.1}$$

These are the same estimates used by Hammill & Gosselin. We see our estimate for probability of first birth at an age is found by the difference of the sample pregnancy rates at the age of conception and the age before it. Intuitively, this would be our first guess, and it turns out to be the maximum likelihood estimates as well. So for a given year if 80% are pregnant at age x and 90% are pregnant at age x+1, we conclude 10% got pregnant for the first time at age x+1, and thus 10% gave birth for the first time at age x+2.

There are some problems with the above though. First, there is the possibility of negative estimates, which is not biologically reasonable. This occurs when there is a "drop" in the observed pregnancy rates from one year to the next. The second problem is that we have a restriction that $\sum_{3}^{12} b_i = 1$, ie the first birth must occur at some age (we assume all females get pregnant at some point). However, if you add up all the estimates, you get $\sum_{3}^{12} \hat{b}_i = \frac{X_{11}}{N_{11}}$, which in some cases is not equal to 1. This can be easily fixed, by forcing $b_{12} = 1 - (b_3 + b_4 + \cdots + b_{11})$ to ensure the equality. This is justified when you consider we defined b_{12} to be probability of first birth at age 12 or greater. All leftover probability is lumped in with this parameter since we assume a seal must eventually have a birth. If barren females were to be considered, you could modify this approach to add up to a number slightly less than one.

We can also work out the general theory to calculate the mean and variance of age of first birth using these maximum likelihood estimates.

To calculate mean age of first birth using either a corpus luteum or fetus to indicate pregnancy, we use the females age at the time of pupping during the following January. That is, we add a year to the age of the seal when captured as gestation takes 1 year. To do this we use the following vector (3,4,5,6,7,8,9,10,11,12) to indicate age of pupping and calculate mean age of first birth by multiplying this vector with estimates of probability of first birth for specific ages.

$\widehat{\text{age}} = \sum_{i=3}^{12} i \cdot \hat{b}_i$ or in vector format

$$\widehat{\text{age}} = (3, 4, 5, 6, 7, 8, 9, 10, 11, 12) * \begin{pmatrix} \hat{b}_3 \\ \hat{b}_4 \\ \vdots \\ \hat{b}_{12} \end{pmatrix}$$

The variance of this mean age is found by first constructing the variance-covariance matrix for the $\hat{b}$'s and using the above vector to find variance for the linear combination of the $\hat{b}$'s we are interested in, $\sum_{i=3}^{12} i \cdot \hat{b}_i$.

The variance-covariance matrix for the $\hat{b}$'s is found by remembering that we modeled X's as independent binomials, and that $\hat{b}$'s are linear functions of $\frac{X}{N}$'s. Thus if $X \sim \text{Bin}(N,\, p)$ with mean Np and variance $Np(1-p)$, then $\frac{X}{N}$ has mean p and variance $\frac{p(1-p)}{N}$. A variance covariance for these new independent random variables is:

$$\mathbf{V_1} = \begin{pmatrix} \frac{p_2(1-p_2)}{N2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{p_3(1-p_3)}{N3} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{p_4(1-p_4)}{N4} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{p_5(1-p_5)}{N5} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{p_6(1-p_6)}{N6} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \frac{p_7(1-p_7)}{N7} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{p_8(1-p_8)}{N8} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{p_9(1-p_9)}{N9} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{p_{10}(1-p_{10})}{N10} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{p_{11}(1-p_{11})}{N11} \end{pmatrix}$$

Now we have the variance-covariance matrix for the $\frac{X}{N}$'s, and to get the variance-covariance matrix for the $\hat{b}$'s we need only look at the linear relationship between the $\hat{b}$'s and $\frac{X}{N}$'s. (2.1) tells us this relationship, which can be rewritten in vector format as

$$\hat{\mathbf{b}} = \mathbf{C}\frac{\mathbf{X}}{\mathbf{N}}$$

where $\frac{\mathbf{X}}{\mathbf{N}}$ is vector of $\frac{X}{N}$'s and $\hat{\mathbf{b}}$ is vector of $\hat{b}$'s and $\mathbf{C}$ is the following contrast matrix:

$$\mathbf{C} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & -1 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & -1 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & -1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 1 \end{pmatrix}$$

Using the above notation we get estimates of $\mathbf{b}$

$$\hat{\mathbf{b}} = \mathbf{C}\frac{\mathbf{X}}{\mathbf{N}} = \mathbf{C}\hat{\mathbf{p}}$$

and mean age of first birth is found as

$$\widehat{\text{age}} = (3, 4, 5, 6, 7, 8, 9, 10, 11, 12)\,\hat{\mathbf{b}} = (3, 4, 5, 6, 7, 8, 9, 10, 11, 12)\,\mathbf{C}\hat{\mathbf{p}}$$

and variance of mean age of first birth is then

$$\mathrm{V}(\widehat{\text{age}}) = (3, 4, 5, 6, 7, 8, 9, 10, 11, 12)\,\mathbf{C}\mathbf{V_1}\mathbf{C^t}\,(3, 4, 5, 6, 7, 8, 9, 10, 11, 12)^t$$

2.2 Case 1: Non-Decreasing Pregnancy Rates $\hat{p}$'s

The above theory applies straightforwardly when the estimated pregnancy rates are non-decreasing. We will illustrate the work in Section 2.1 by using the 1968-70 sample from Table 1.1 for pregnancy indicated by presence of a corpus luteum. The data for this period are:

	Age (yr) at Capture									
	<2	3	4	5	6	7	8	9	10	>11
N	20	12	7	9	6	6	4	4	2	20
CL	0	7	7	9	6	6	4	4	2	20

Note that after a certain age (4 and above) all seals in the sample were observed to be pregnant. This is not unusual as typically pregnancy rates are very high after maturity.

The likelihood in this case reduces to:

$$\begin{aligned}\mathcal{L} &= K \times (1-b_3)^{20}(b_3+b_4)^7(1-(b_3+b_4))^5(b_3+b_4+b_5)^7(b_3+b_4+b_5+b_6)^9\\ &\quad (b_3+b_4+b_5+b_6+b_7)^6(b_3+b_4+b_5+b_6+b_7+b_8)^6(b_3+b_4+b_5+b_6+b_7+b_8+b_9)^4\\ &\quad (b_3+b_4+b_5+b_6+b_7+b_8+b_9+b_{10})^4(b_3+b_4+b_5+b_6+b_7+b_8+b_9+b_{10}+b_{11})^2\\ &\quad (b_3+b_4+b_5+b_6+b_7+b_8+b_9+b_{10}+b_{11}+b_{12})^{20}\end{aligned}$$

with log-likelihood

$$\begin{aligned}l &= \log(K)+20\log(1-b_3)+7\log(b_3+b_4)+5\log(1-(b_3+b_4))+7\log(b_3+b_4+b_5)\\ &\quad +9\log(b_3+b_4+b_5+b_6)+6\log(b_3+b_4+b_5+b_6+b_7)+6\log(b_3+b_4+b_5+b_6+b_7+b_8)\\ &\quad +4\log(b_3+b_4+b_5+b_6+b_7+b_8+b_9)+4\log(b_3+b_4+b_5+b_6+b_7+b_8+b_9+b_{10})\\ &\quad +2\log(b_3+b_4+b_5+b_6+b_7+b_8+b_9+b_{10}+b_{11})\\ &\quad +20\log(b_3+b_4+b_5+b_6+b_7+b_8+b_9+b_{10}+b_{11}+b_{12})\end{aligned}$$

As in Section 2.1, the solutions reduce to

$$\hat{b}_3 = \frac{0}{20} = 0$$

$$\begin{aligned}
\hat{b}_4 &= \frac{7}{12} - 0 = .5833 \\
\hat{b}_5 &= \frac{7}{7} - \frac{7}{12} = .4167 \\
\hat{b}_6 &= \hat{b}_7 = \hat{b}_8 = \hat{b}_9 = \hat{b}_{10} = \hat{b}_{11} = \hat{b}_{12} = 0
\end{aligned}$$

The estimated variance-covariance matrix $\hat{\mathbf{V}}_{CL_{1968}}$ is

$$\hat{\mathbf{V}}_{CL_{1968}} = \begin{pmatrix}
\frac{0(1-0))}{20} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \frac{\frac{7}{12}(1-\frac{7}{12})}{12} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \frac{0(1-0)}{7} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \frac{0(1-0)}{9} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \frac{0(1-0)}{6} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \frac{0(1-0)}{6} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{0(1-0)}{4} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{0(1-0)}{4} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{0(1-0)}{2} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{0(1-0)}{20}
\end{pmatrix}$$

$$= \begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.02025 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}$$

The estimated mean age of first birth is

$$\widehat{\text{age}}_{CL_{1968}} = (3,4,5,6,7,8,9,10,11,12)\,\hat{\mathbf{b}} = 3 \times 0 + 4 \times \tfrac{7}{12} + 5 \times \tfrac{5}{12} = 4.417$$

and the estimated variance of mean age is found

$$\hat{\mathbf{V}}(\widehat{\text{age}}_{CL_{1968}}) = (3,4,5,6,7,8,9,10,11,12)\,\mathbf{C}\hat{\mathbf{V}}_{\mathbf{CL_{1968}}}\mathbf{C^t}\,(3,4,5,6,7,8,9,10,11,12)^t$$
$$= 0.020$$

Thus using the theory we get a mean age of first birth of 4.42 years and standard error of 0.142 years for the 1968 sample when pregnancy was indicated by the presence of a CL.

2.3 Case 2: Presence of Decreasing Pregnancy Rates

At the start of the chapter, we mentioned problems if there is a drop in pregnancy rates over consecutive years, leading to negative estimates of b's. Since these values are not biologically reasonable, we need to find new restricted MLE's, with restrictions of $\sum_{3}^{12} b_i = 1$, and $0 \leq b_i \leq 1 \quad \forall i$. From Table 1.1, this problem occurs for all years where pregnancy is indicated by presence of a Fetus. This method of determining pregnancy seems to lead to more variable sample proportions which leads to the drops versus the CL method which seems to have more stability.

For example, the following is the data for indication of pregnancy by a corpus luteum for the 1988 sample:

	Age (yr) at Capture									
	<2	3	4	5	6	7	8	9	10	>11
N	3	4	10	9	3	2	3	1	3	38
CL	0	4	8	9	3	2	3	1	3	38

In the above example notice there is a drop in the observed pregnancy rate from age 3 to age 4. There is 0% observed pregnancy rate at age 2, a 100% observed pregnancy rate at age 3, followed by a drop to an observed pregnancy rate of only

80% again at age 4 before returning to a 100% observed pregnancy rate. This would lead to an estimate of $\hat{b}_4 = \frac{8}{10} - \frac{4}{4} = -.20$ if we followed earlier MLE theory.

Barlow, Bartholomew, Bremner and Brunk (1972) investigated order restrictions. In this case, we desire to restrict $\hat{p}_2 \leq \hat{p}_3 \leq \cdots \leq \hat{p}_{11}$ so that $\hat{b}$'s will all be positive and be between 0 and 1.

This is an example where isotonic regression can be used. Barlow et al (1972) provided the following algorithm, called "Pooled-Adjacent-Violators" Algorithm to find the restricted MLE's.

Let Y be a finite set $\{Y_1, Y_2, \cdots, Y_k\}$ with simple ordering $Y_1 \leq Y_2 \leq \cdots \leq Y_k$. A real valued function f on Y is isotonic if $Y_1, Y_2 \in \mathbf{Y}, Y_1 \leq Y_2$ implies $f(Y_1) \leq f(Y_2)$. Associated with each value of Y is a function $g(Y)$ with weight function w, and $g*$ is an isotonic function of g with weights w with respect to the simple ordering $Y_1 \leq Y_2 \leq \cdots \leq Y_k$ if it minimizes in the class of isotonic functions f on Y the sum

$$\sum_{y \in \mathbf{Y}} [g(y) - f(y)]^2 w(y)$$

In terms of our problem , we want to take $g(y)$ and find a new isotonic function, but one that decreases the likelihood the least.

The algorithm for finding $g*$ is as follows: define an arbitrary set of consecutive elements of Y to be a block. The algorithm starts with the finest possible partition into blocks, namely the individual points of Y, and joins blocks together step by step until a final partition is reached.

1. If $g(Y_1) \leq g(Y_2) \leq \cdots \leq g(Y_k)$ the initial is also the final partition, $g^*(Y_i) = g(Y_i) \quad i = 1 \cdots k$.

2. If not, select any of the pairs of violators of the ordering, where a violator is defined as any pair Y_{i-1}, Y_i such that $g(Y_{i-1}) > g(Y_i)$. Pool the two values of g; i.e. join two points Y_i and Y_{i+1} in a block $\{Y_i, Y_{i+1}\}$ ordered between $\{Y_{i-1}\}$ and $\{Y_{i+2}\}$ with associated average value

$$\frac{[w(Y_i)g(Y_i) + w(Y_{i+1})g(Y_{i+1})]}{[w(Y_i) + w(Y_{i+1})]}$$

and associated weight $w(Y_i) + w(Y_{i+1})$.

3. Check to see if desired isotonic order is reached. If not choose another pair of violators and return to 2.

4. Stop when ordering is achieved. This is g^*.

A decision must be made as to how pairs are chosen to pool. Barlow et al (1972) suggested two methods as follows.

1. Start at the lowest blocks and move to the higher blocks until violators are found.

2. Identify monotonically non-increasing runs of values of g and pool them in the first pass through the data. Do the same for a second pass and continue until there are no more violators.

We apply this algorithm to the Example at the start of the section.

	Age (yr) at Capture									
	<2	3	4	5	6	7	8	9	10	>11
N	3	4	10	9	3	2	3	1	3	38
CL	0	4	8	9	3	2	3	1	3	38

Let $\mathbf{Y} = \{2, 3, 4, 5, 6, 7, 8, 9, 10, 11\}$, k=10,
g is equal to $\frac{X}{N}$, the proportion of seals that are deemed pregnant at age i, and $w(Y_i) = N_i$.

Following the algorithm for this data, there is clearly a violator between ages 3 and 4. This is then pooled

$$\frac{\frac{4}{4} \cdot 4 + \frac{8}{10} \cdot 10}{4 + 10} = \frac{12}{14}$$

.

Thus we re-pool the fourth year into the third year, and rewrite our table as:

	Age (yr) at Capture									
	<2	3	4	5	6	7	8	9	10	>11
N	3	4	10	9	3	2	3	1	3	38
CL	0	4	8	9	3	2	3	1	3	38
		$\underbrace{4 \quad 8}_{14}$								
		12								

We stop as there are no more violators and new estimates of b are then calculated as

$$
\begin{aligned}
\hat{b}_3 &= \frac{0}{3} = 0 \\
\hat{b}_4 &= \frac{12}{14} - 0 = 0.857 \\
\hat{b}_5 &= 0 \\
\hat{b}_6 &= \frac{9}{9} - \frac{12}{14} = 0.143 \\
\hat{b}_7 &= \hat{b}_8 = \hat{b}_9 = \hat{b}_{10} = \hat{b}_{11} = \hat{b}_{12} = 0
\end{aligned}
$$

Notice that for $\hat{b}_6$, we go back and subtract $\frac{12}{14}$ as age 3 and 4 have been pooled into 3. The above $\hat{b}$'s are the restricted MLE's, with all estimates between 0 and 1 and add up to 1 as desired.

The likelihood can also be maximized numerically with keeping all $\hat{b}_i$'s between 0 and 1. Splus was used to solve for estimates using a minimization function nlminb. The negative log-likelihood function was entered with a penalty added to force the parameters to sum to 1 as desired. The MLE's were as follows:

```
0.0000000 0.8571429 0.0000000 0.1428572 0.0000000 0.0000000 0.0000000
0.0000000 0.0000000 0.0000000
```

These results exactly matched those produced theoretically.

A contour plot of the log-likelihood was constructed by substituting in all the values of the estimates into the likelihood except for the violators b_4 and b_5. The likelihood was plotted at various values of these variables (Figure 2.1). The circle represents the unrestricted MLE of $b_4 = 1$ and $b_5 =$ -.2 while the triangle is the restricted MLE found above. The horizontal line is at b_5 =0, and a restricted estimate needs to be found on or above this line that maximizes the likelihood. We can see that the values $b_4 = 12/14$ and $b_5 = 0$ are clearly on a contour (with value -5.74163) and closest to the unrestricted MLE as it touches the line b_5 =0 only once. Other contour lines would either be farther from the MLE's or have negative estimates.

A more interesting example with more than one drop is the data from the 1982 sample, where a pregnancy is indicated by the presence of a fetus.

Age (yr) at Capture

	<2	3	4	5	6	7	8	9	10	>11
N	7	4	4	8	1	4	3	3	3	35
Fetus	0	0	3	7	1	3	3	3	3	31

The observed pregnancy rate increases until age 7 when it drops from 100% to 75% and again at year 11 when it drops from 100% to 89%. These years are pooled with previous years

Age (yr) at Capture

	<2	3	4	5	6	7	8	9	10	>11
N	7	4	4	8	1	4	3	3	3	35
Fetus	0	0	3	7	1	3	3	3	3	31
					5				38	
					4				34	

After the first pooling, there are still violators. There is now a drop in the observed pregnancy rate from 87.5% to 80% from age 5 to 6 as the re-pooling value at age 6 is now lower than before. There is also a drop between age 9 and 10 now. We re-pool again.

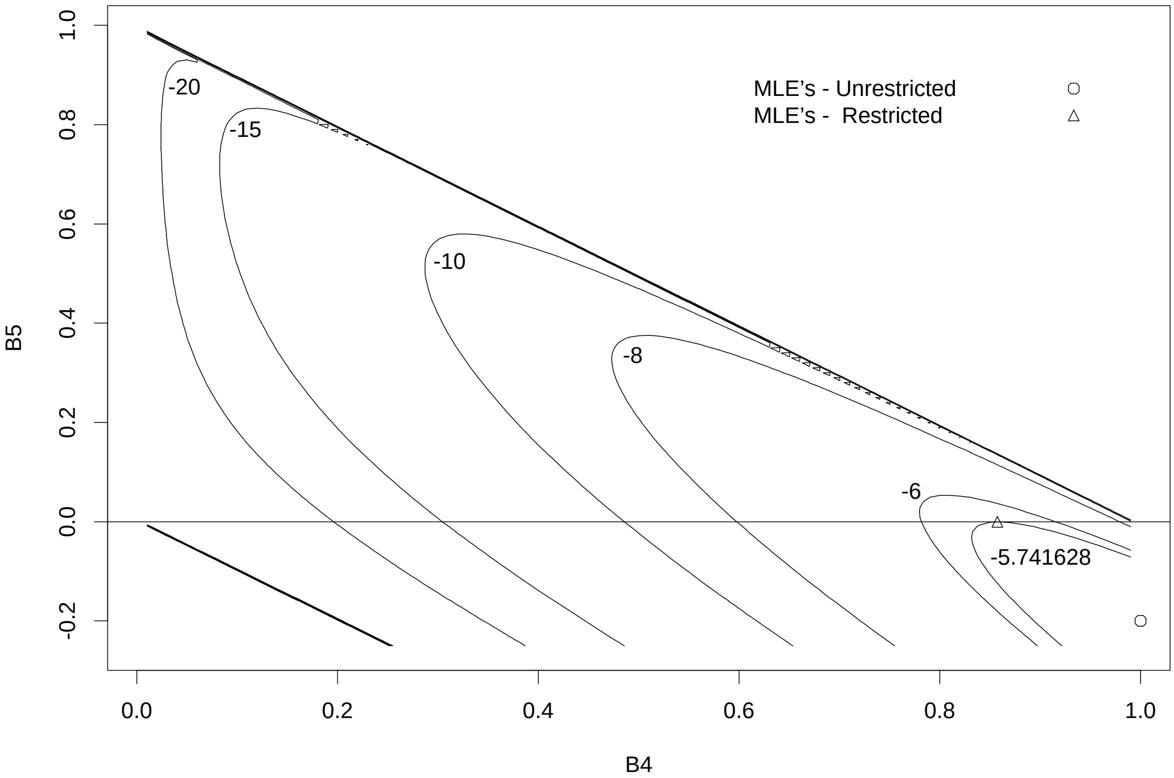


Figure 2.1: Contour Plot for the 1988 sample - pregnancy indicated by a corpus luteum

Age (yr) at Capture

	<2	3	4	5	6	7	8	9	10	>11
N	7	4	4	8	5		3	3	38	
Fetus	0	0	3	7	4		3	3	34	
				⏟				⏟		
				13				41		
				11				37		

The first violation is now eliminated but there is still a drop in the observed pregnancy rate from ages 8 to 9, from 100% to 90%. Re-pooling

Age (yr) at Capture

	<2	3	4	5	6	7	8	9	10	>11
N	7	4	4	13			3	41		
Fetus	0	0	3	11			3	37		
							⏟			
							44			
							40			

There are now no more drops in the observed pregnancy rate and we stop the algorithm and have achieved the desired ordering, of non-decreasing probabilities. The final ordering is:

Age (yr) at Capture

	<2	3	4	5	6	7	8	9	10	>11
N	7	4	4	13			44			
Fetus	0	0	3	11			40			

To find $\hat{b}$'s we proceed as usual but note the final non-zero value will always be changed to 1 since we assume all $\hat{b}$'s add up to 1. Estimates are:

$$\begin{aligned}\hat{b}_3 &= \frac{0}{7} = 0,\ \hat{b}_4 = \frac{0}{4} = 0 \\ \hat{b}_5 &= \frac{3}{4} - 0 = .75\end{aligned}$$

$$\begin{aligned}
\hat{b}_6 &= \frac{11}{13} - \frac{3}{4} = .096 \\
\hat{b}_7 &= \hat{b}_8 = 0 \\
\hat{b}_9 &= 1 - \frac{11}{13} = 0.154 \\
\hat{b}_{10} &= \hat{b}_{11} = \hat{b}_{12} = 0
\end{aligned}$$

This was again run through Splus to verify results and the MLE's were:

```
0.00000000 0.00000000 0.74999269 0.09615992 0.00000000 0.00000000
0.15380268 0.00000000 0.00000000 0.00000000
```

A contour plot for the first drop in the observed pregnancy rate (years 5 and 6) is in Figure 2.2.

Now that we have estimates of the b's , we can find estimates for the mean age of first birth and variances using same theory from Section 2.1 with some modifications. We still need a contrast matrix **C** so that

$$\hat{\mathbf{b}} = \mathbf{C}\frac{\mathbf{X}}{\mathbf{N}}$$

but the **C** cannot be the one used in section 2.3 as that will give the unrestricted estimates. We construct a **C** matrix that pools the data to get our new estimates. In our first example for the 1988 CL sample, we pooled ages 2 and 3 together. This can essentially be reproduced by eliminating the denominator for each year, adding the numerators together and dividing by the new pooled denominator.

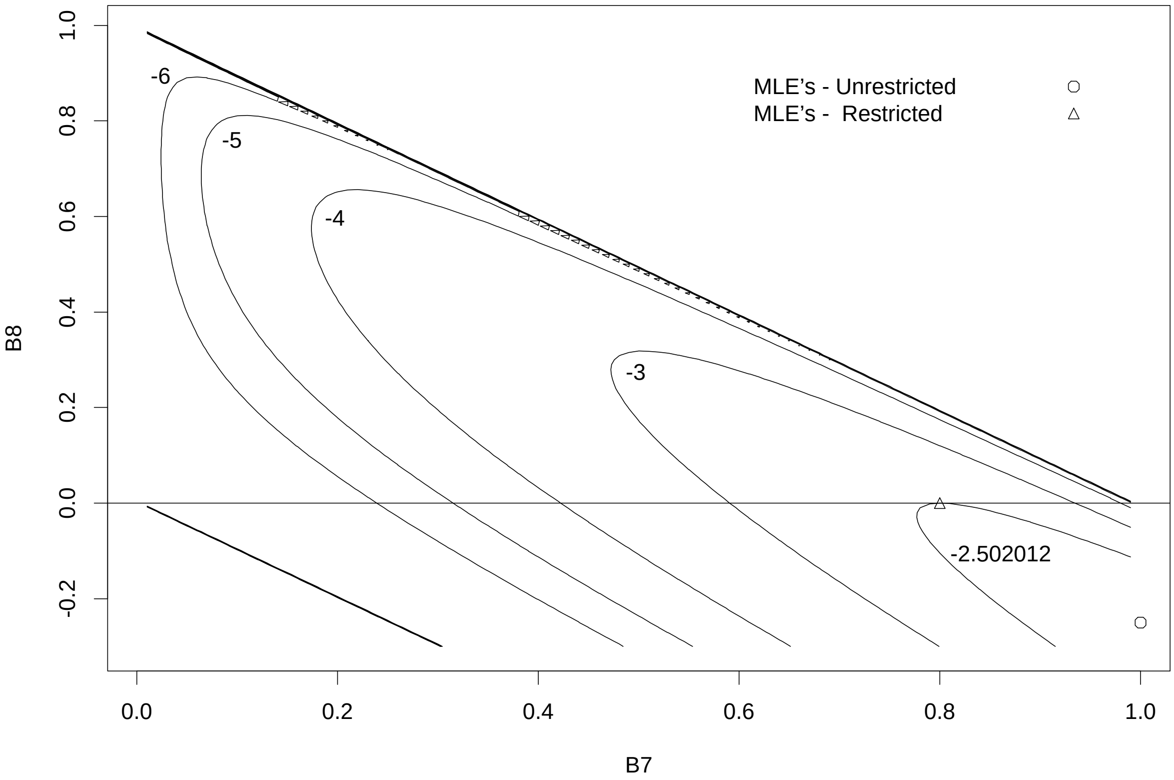


Figure 2.2: Contour Plot for year 1982 - pregnancy indicated by a Fetus

<table>
<tr><th></th><th colspan="10">Age (yr) at Capture</th></tr>
<tr><th></th><th><2</th><th>3</th><th>4</th><th>5</th><th>6</th><th>7</th><th>8</th><th>9</th><th>10</th><th>>11</th></tr>
<tr><td>N</td><td>3</td><td>4</td><td>10</td><td>9</td><td>3</td><td>2</td><td>3</td><td>1</td><td>3</td><td>38</td></tr>
<tr><td>CL</td><td>0</td><td>4</td><td>8</td><td>9</td><td>3</td><td>2</td><td>3</td><td>1</td><td>3</td><td>38</td></tr>
<tr><td></td><td></td><td colspan="2">$\underbrace{\qquad}_{14}$</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td colspan="2">12</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
</table>

The **C** that achieves this is:

$$\mathbf{C}_{CL_{1988}} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ -1 & \frac{4}{14} & \frac{10}{14} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -\frac{4}{14} & -\frac{10}{14} & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & -1 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & -1 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & -1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 1 \end{pmatrix}$$

The fractions on the second line create the correct values after pooling while the fractions on the fourth line make sure that pooled value is subtracted from the next value. This contrast matrix is then used as in Section 2.1 to estimate the mean age of first birth and its variance estimates. First the estimated variance-covariance matrix $\hat{\mathbf{V}}_{CL_{1988}}$ is constructed as before:

$$\hat{\mathbf{V}}_{CL_{1988}} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{\frac{8}{10}(1-\frac{2}{10})}{10} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

Mean age of first birth equals

$$\widehat{\text{age}}_{CL_{1988}} = (3,4,5,6,7,8,9,10,11,12)\,\hat{\mathbf{b}} = (3,4,5,6,7,8,9,10,11,12)\,\mathbf{C}_{CL_{1988}}\frac{\mathbf{X}}{\mathbf{N}}$$

and the estimated variance of mean age of first birth is then

$$\text{V}(\widehat{\text{age}}_{CL_{1988}}) = (3,4,5,6,7,8,9,10,11,12)\,\mathbf{C}_{CL_{1988}}\hat{\mathbf{V}}_{CL_{1988}}\mathbf{C}^t_{CL_{1988}}\,(3,4,5,6,7,8,9,10,11,12)^t$$

giving $\widehat{\text{age}}_{CL_{1988}}$ equal to 4.29 years with estimated standard error of 0.18 years.

For the second example (Fetus, year 2) with more drops we get

$$\mathbf{C}_{Fet_{1982}} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & \frac{8}{13} & \frac{1}{13} & \frac{4}{13} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -\frac{8}{13} & -\frac{1}{13} & -\frac{4}{13} & \frac{3}{40} & \frac{3}{40} & \frac{3}{40} & \frac{35}{40} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

The numbers in the seventh row ensure total of the $\hat{b}$'s sum to 1. This results in mean age of 4.98 years and estimated standard error of 0.37 years.

2.4 Case 3: Unimodality Restriction on the $\hat{b}$'s

In Section 2.2, it was shown that multiple drops could be handled by pooling on a pair by pair basis until we got to a solution that met our restrictions. However, it may not seem reasonable that age-specific pupping rates would have multiple modes. We would expect a rise and drop around the mean age of first birth, but there is no reason to believe that there would be a second increase a few years later.

For example, the pooled values from Fetus Period 2 derived in section 2.3 are

$\hat{b}_3$	$\hat{b}_4$	$\hat{b}_5$	$\hat{b}_6$	$\hat{b}_7$	$\hat{b}_8$	$\hat{b}_9$	$\hat{b}_{10}$	$\hat{b}_{11}$	$\hat{b}_{12}$
0	0	.75	.096	0	0	.154	0	0	0

We can re-estimate $\hat{b}$'s in the cases where the $\hat{b}$'s themselves are not unimodal by fitting a smooth curve to the cumulative proportion of pregnant seals.

A Gompertz curve is a versatile model that has the form $Y = \exp[-\exp(\beta - \gamma X)]$ and has asymptotes at Y=0 and Y=1 and is asymmetric about its inflection point which occurs at $\frac{\beta}{\gamma}$. The curve is monotonically increasing, which we find desirable for our purpose. This curve can be fit to the raw probabilities $\frac{X}{N}$ for each time period. Then for each age, the value on the curve can be found, and b estimates can again be estimated by subtraction between pairs of ages.

To fit the Gompertz model, we let

$$\begin{aligned}
p_2 &= \exp(-\exp(\beta - \gamma \cdot 2)) \\
p_3 &= \exp(-\exp(\beta - \gamma \cdot 3)) \\
p_4 &= \exp(-\exp(\beta - \gamma \cdot 4)) \qquad (2.2) \\
&\vdots \\
p_{11} &= \exp(-\exp(\beta - \gamma \cdot 11))
\end{aligned}$$

These expressions are substituted into the generic log-likelihood

$$\begin{aligned} l &= \log(K) + X_2 \log(\exp(-\exp(\beta - \gamma \cdot 2))) + (N_2 - X_2) \log(1 - \exp(-\exp(\beta - \gamma \cdot 2))) \\ &\quad + X_3 \log(\exp(-\exp(\beta - \gamma \cdot 3))) + (N_3 - X_3) \log(1 - (\exp(-\exp(\beta - \gamma \cdot 3)))) + \cdots \\ &\quad + X_{11} \log(\exp(-\exp(\beta - \gamma \cdot 11))) + (N_{11} - X_{11}) \log(1 - (\exp(-\exp(\beta - \gamma \cdot 11)))) \\ &= \sum_{i=2}^{11} X_i(-\exp(\beta - \gamma \cdot i)) + (N_i - X_i) \log(1 - (\exp(-\exp(\beta - \gamma \cdot i)))) \qquad (2.3) \end{aligned}$$

Now instead of 11 b parameters, there are only 2 parameters to estimate, β and γ. These can be estimated using the usual maximum likelihood theory.

For example, the likelihood for the 1982 sample using the presence of a fetus to indicate pregnancy,

$$\begin{aligned} l &= \log(K) + 7 \log(1 - \exp(-\exp(\beta - \gamma \cdot 2))) + 4 \log(1 - \exp(-\exp(\beta - \gamma \cdot 3))) \\ &\quad + 3 \log(\exp(-\exp(\beta - \gamma \cdot 4))) + \log(1 - \exp(-\exp(\beta - \gamma \cdot 4))) \\ &\quad + 7 \log(\exp(-\exp(\beta - \gamma \cdot 5))) + \log(1 - \exp(-\exp(\beta - \gamma \cdot 5))) \\ &\quad + \log(\exp(-\exp(\beta - \gamma \cdot 6))) + 3 \log(\exp(-\exp(\beta - \gamma \cdot 7))) \\ &\quad + \log(1 - \exp(-\exp(\beta - \gamma \cdot 7))) + 3 \log(\exp(-\exp(\beta - \gamma \cdot 8))) \\ &\quad + 3 \log(\exp(-\exp(\beta - \gamma \cdot 9))) + 3 \log(\exp(-\exp(\beta - \gamma \cdot 10))) \\ &\quad + 31 \log(\exp(-\exp(\beta - \gamma \cdot 11))) + 4 \log(1 - \exp(-\exp(\beta - \gamma \cdot 11))) \end{aligned}$$

The MLE's of β and γ are

```
5.048409 1.366823
```

respectively, and the fitted curve is in Figure 2.3 .

Estimates of the b's are found by taking the value on the Gompertz line at each age and subtracting the one before it (the first value b_3 is value on the curve alone). Using the MLE's from above, we get the following values for points on the line:

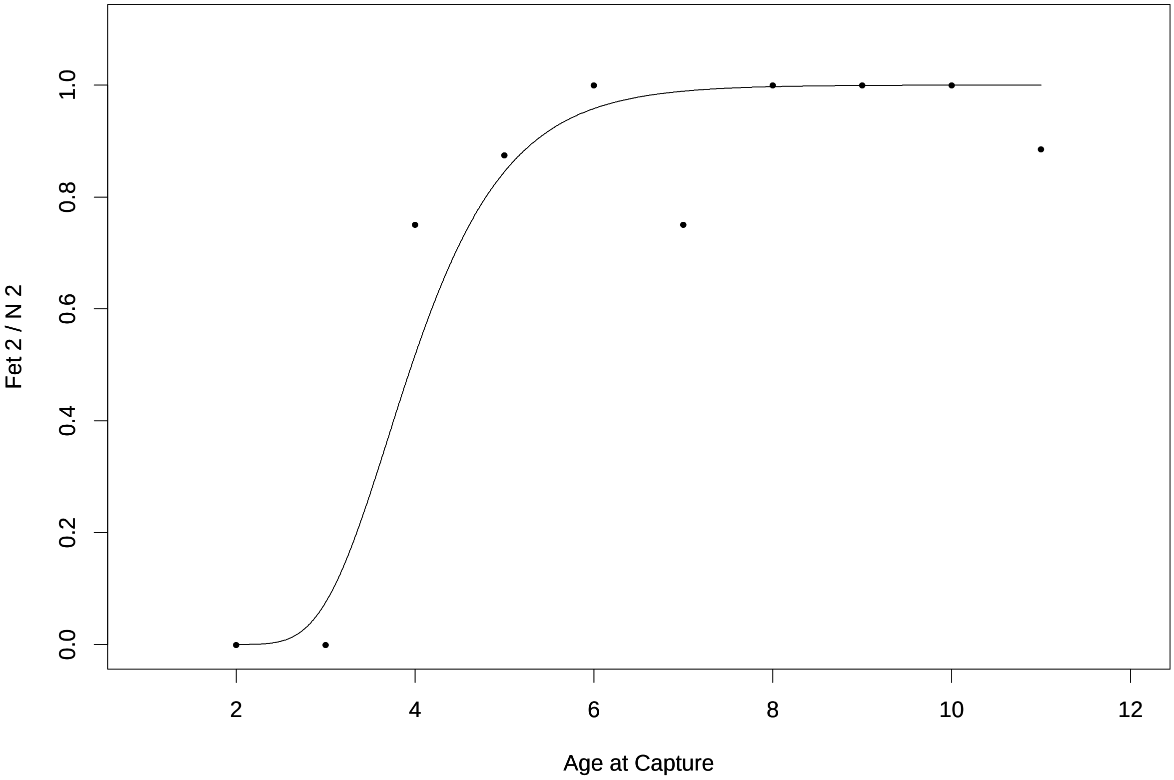


Figure 2.3: Gompertz model for year 1982 sample - pregnancy indicated by a Fetus

$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$	$\hat{p}_6$	$\hat{p}_7$	$\hat{p}_8$	$\hat{p}_9$	$\hat{p}_{10}$	$\hat{p}_{11}$
0.000	0.076	0.518	0.846	0.958	0.989	0.997	0.999	1.000	1.000

which gives estimates of:

$\hat{b}_3$	$\hat{b}_4$	$\hat{b}_5$	$\hat{b}_6$	$\hat{b}_7$	$\hat{b}_8$	$\hat{b}_9$	$\hat{b}_{10}$	$\hat{b}_{11}$	$\hat{b}_{12}$
0.000	0.076	0.442	0.328	0.113	0.031	0.008	0.002	0.001	0.000

Mean age is calculated as before, and was found to be 5.616.

The variances of the estimates are found using the information matrix for β and γ and a Taylor series expansion. To do this we define the linear equation used above to find mean age estimates.

$$\begin{aligned} f &= 3\hat{b}_3 + 4\hat{b}_4 + 5\hat{b}_5 + 6\hat{b}_6 + 7\hat{b}_7 + 8\hat{b}_8 + 9\hat{b}_9 + 10\hat{b}_10 + 11\hat{b}_{11} + 12\hat{b}_{12} \\ &= 3\hat{p}_2 + 4(\hat{p}_3 - \hat{p}_2) + 5(\hat{p}_4 - \hat{p}_3) + 6(\hat{p}_5 - \hat{p}_4) + 7(\hat{p}_6 - \hat{p}_5) + 8(\hat{p}_7 - \hat{p}_6) + 9(\hat{p}_8 - \hat{p}_7) \\ &\quad +10(\hat{p}_9 - \hat{p}_8) + 11(\hat{p}_{10} - \hat{p}_9) + 12(\hat{p}_{11} - \hat{p}_{10}) \\ &= -\hat{p}_2 - \hat{p}_3 - \hat{p}_4 - \hat{p}_5 - \hat{p}_6 - \hat{p}_7 - \hat{p}_8 - \hat{p}_9 - \hat{p}_{10} + 12\hat{p}_{11} \end{aligned}$$

The variance for the mean age can now be found by taylor expansion as

$$\mathrm{V}(\widehat{\mathrm{age}}) = \mathrm{V}(f(\hat{\beta}, \hat{\gamma})) \approx \partial f(\hat{\beta}, \hat{\gamma})\ \mathrm{V}(\hat{\beta}, \hat{\gamma})\ \partial f(\hat{\beta}, \hat{\gamma})^t$$

The Variance-Covariance matrix of $\hat{\beta}$ and $\hat{\gamma}$ are needed along with the gradient of f. The latter is found by substitution of (2.2) into f above and differentiation.

$$\begin{aligned} f &= -\exp(-\exp(\hat{\beta} - \hat{\gamma} \cdot 2)) - \exp(-\exp(\hat{\beta} - \hat{\gamma} \cdot 3)) - \exp(-\exp(\hat{\beta} - \hat{\gamma} \cdot 4)) \\ &\quad - \exp(-\exp(\hat{\beta} - \hat{\gamma} \cdot 5)) - \cdots + 12\exp(-\exp(\hat{\beta} - \hat{\gamma} \cdot 11)) \end{aligned}$$

$$\begin{aligned}\frac{\partial f(\hat{\beta},\hat{\gamma})}{\partial\hat{\beta}} &= \exp(\hat{\beta}-\hat{\gamma}\cdot 2)\exp(-\exp(\hat{\beta}-\hat{\gamma}\cdot 2)) + \exp(\hat{\beta}-\hat{\gamma}\cdot 3)\exp(-\exp(\hat{\beta}-\hat{\gamma}\cdot 3)) \\ &\quad + \exp(\hat{\beta}-\hat{\gamma}\cdot 4)\exp(-\exp(\hat{\beta}-\hat{\gamma}\cdot 4)) + \cdots \\ &\qquad\qquad -12\exp(\hat{\beta}-\hat{\gamma}\cdot 11)\exp(-\exp(\hat{\beta}-\hat{\gamma}\cdot 11))\end{aligned}$$

$$\begin{aligned}\frac{\partial f(\hat{\beta},\hat{\gamma})}{\partial\hat{\gamma}} &= -2\exp(\hat{\beta}-\hat{\gamma}\cdot 2)\exp(-\exp(\hat{\beta}-\hat{\gamma}\cdot 2)) - 3\exp(\hat{\beta}-\hat{\gamma}\cdot 3)\exp(-\exp(\hat{\beta}-\hat{\gamma}\cdot 3)) \\ &\quad -4\exp(\hat{\beta}-\hat{\gamma}\cdot 4)\exp(-\exp(\hat{\beta}-\hat{\gamma}\cdot 4)) - \cdots \\ &\qquad\qquad +132\exp(\hat{\beta}-\hat{\gamma}\cdot 11)\exp(-\exp(\hat{\beta}-\hat{\gamma}\cdot 11))\end{aligned}$$

The $\mathrm{V}(\hat{\beta},\hat{\gamma})$ is calculated by taking general log-likelihood (2.3), taking the second derivatives, forming the information matrix, substituting the MLE's and then inverting as in Appendix A.

For our continuing example of the 1982 sample, Fetus data, MLE's were $\hat{\beta} = 5.048409$ and $\hat{\gamma} = 1.366823$ with $\partial\mathbf{f}(\hat{\beta},\hat{\gamma}) = (0.7332197, -3.004489)$ and

$$\hat{\mathrm{V}}(\hat{\beta},\hat{\gamma}) = \begin{pmatrix} 4.535310 & 1.088022 \\ 1.088022 & 0.272765 \end{pmatrix}$$

giving

$$\hat{\mathrm{V}}(\widehat{\mathrm{age}}) = (0.7332197, -3.004489)\begin{pmatrix} 4.535310 & 1.088022 \\ 1.088022 & 0.272765 \end{pmatrix}\begin{pmatrix} 0.7332197 \\ -3.004489 \end{pmatrix} = 0.106753$$

Thus we obtained a mean age of first birth of 5.616 years and an estimated standard error of 0.327 years.

Chapter 3

Results

As reported in Hammill and Gosselin (1995), corpora lutea were first observed in animals age 2+ yr but there were no indications of pregnancy before age 3+ year (pupping at age 4). The theory presented is Sections 2.2 and 2.3 were applied to all 12 samples. Notice from Table 1.1 that 5 time periods(corpus luteum 1968-70, 1982, 1986, 1987 and 1992) fell into the category of nondecreasing pregnancy rates, while the other 7 periods used the pooling technique of Section 2.3 as there were drops in the observed pregnancy rates. The results and Hammill and Gosselin's estimates are in Table 3.1.

Table 3.1: Age of first birth in Northwest Atlantic Grey Seals.

	Mean Age From Corpora Lutea			Mean Age From Fetus		
Sample	H & G	MLE	Gompertz	H & G	MLE	Gompertz
1968-1970	4.42±.14	4.42±.14	4.42±.00*	5.03±.22	5.23±.25	5.20±.25
1982	4.48±.24	4.50±.25	4.50±.00*	5.39±.24	4.98±.37	5.62±.37
1986	4.49±.24	4.50±.25	4.50±.00*	5.40±.25	5.84±.45	5.72±.33
1987	3.61±.76	4.23±.26	4.19±.24	6.08±.32	6.43±.38	6.10±.39
1988	4.19±.12	4.29±.18	4.37±.32	5.22±.42	4.86±.45	5.11±.29
1992	5.06±.12	5.06±.13	5.06±.15	5.52±.24	5.99±.46	5.46±.19

Note: Values are given as mean ± standard error.
H & G are Hammill and Gosselin estimates.
*See text for explanation.

The mean age of first birth, calculated using presence of a corpus luteum to indicate pregnancy and using female age at time of pupping during the subsequent January, ranged from 4.23 to 5.06 yr. The mean age of first birth calculated from reproductive tracts with a fetus varied between 4.86 and 6.43 .

If we compare these numbers to those found in Hammill and Gosselin using the bootstrap method, we see similar results. Our calculated estimates for CL using the MLE approach and Hammill and Gosselin's estimates are almost identical with the exception of 1987, where their value of 3.61 ± .76 stands out from all other estimates. The data for 1987 is not markedly different from any other sample and no reason was given for this anomaly. The fetus estimates are much less similar between the H&G and MLE methods, which could be expected as the drops in the observed pregnancy rate that were present in all fetus samples was handled differently between methods.

Also, mean age and variances were re-estimated for all time periods using the Gompertz curves. Figures 3.1–3.2 display these graphs. Estimates are in Table 3.1.

The Gompertz mean estimates vary from 4.19 to 5.06 for pregnancy indicated by a corpus luteum and from 5.11 to 6.10 for pregnancy indicated by a fetus. Note that no variance calculation was possible for the first 3 years using CL data as ironically, the Gompertz line fit perfectly through all the points. This is similar to the phenomenon in regression where a perfect fit will give SSE equal to 0 and no variance estimate exists for the estimate. For CL, the Gompertz estimates were very similar to the other methods estimates, due to the close fit of the curve. For Fetus, the estimates of the standard error were observed to be smaller for the Gompertz estimates. The raw b estimates can be found in Tables 3.2–3.3.

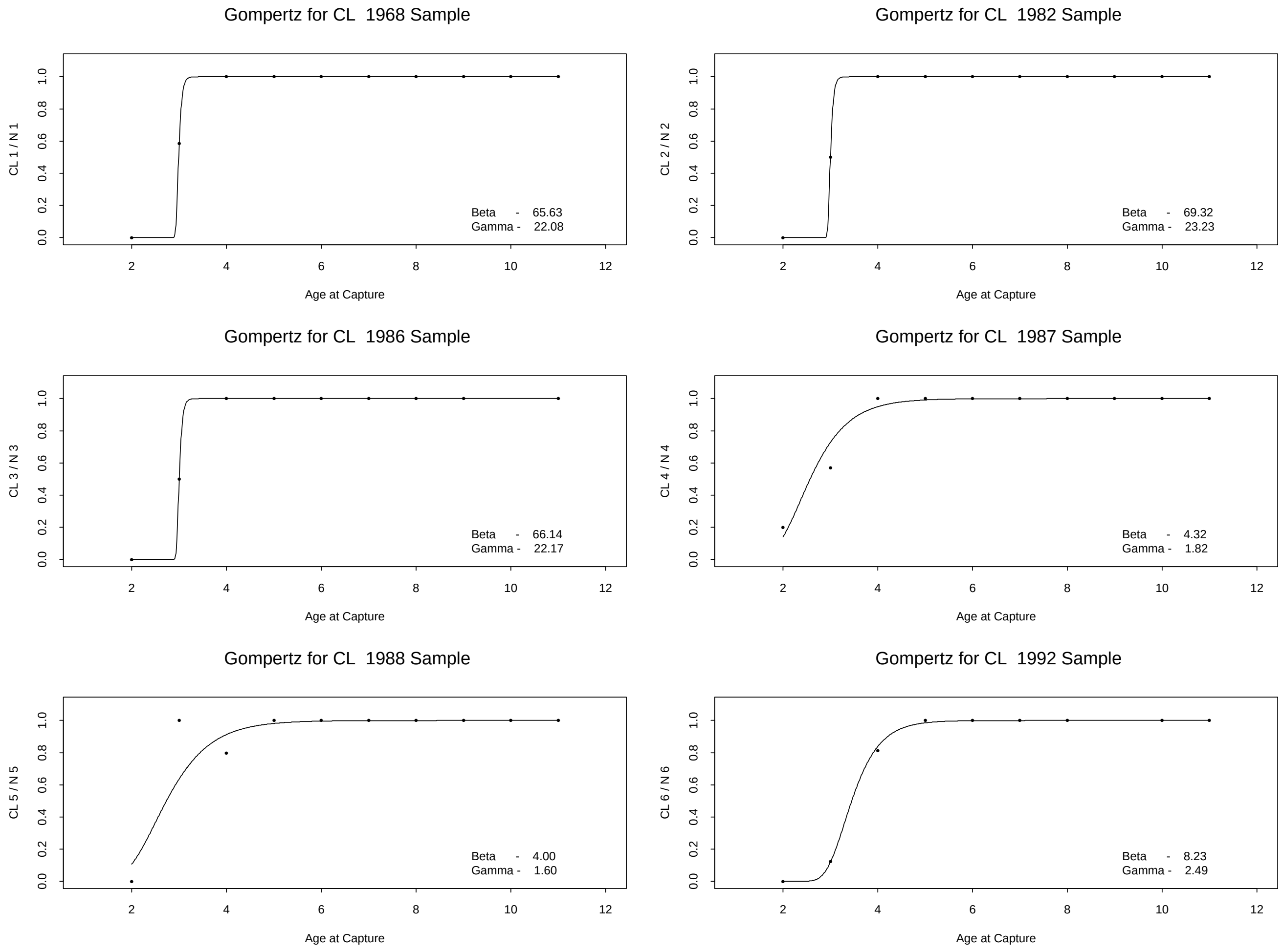
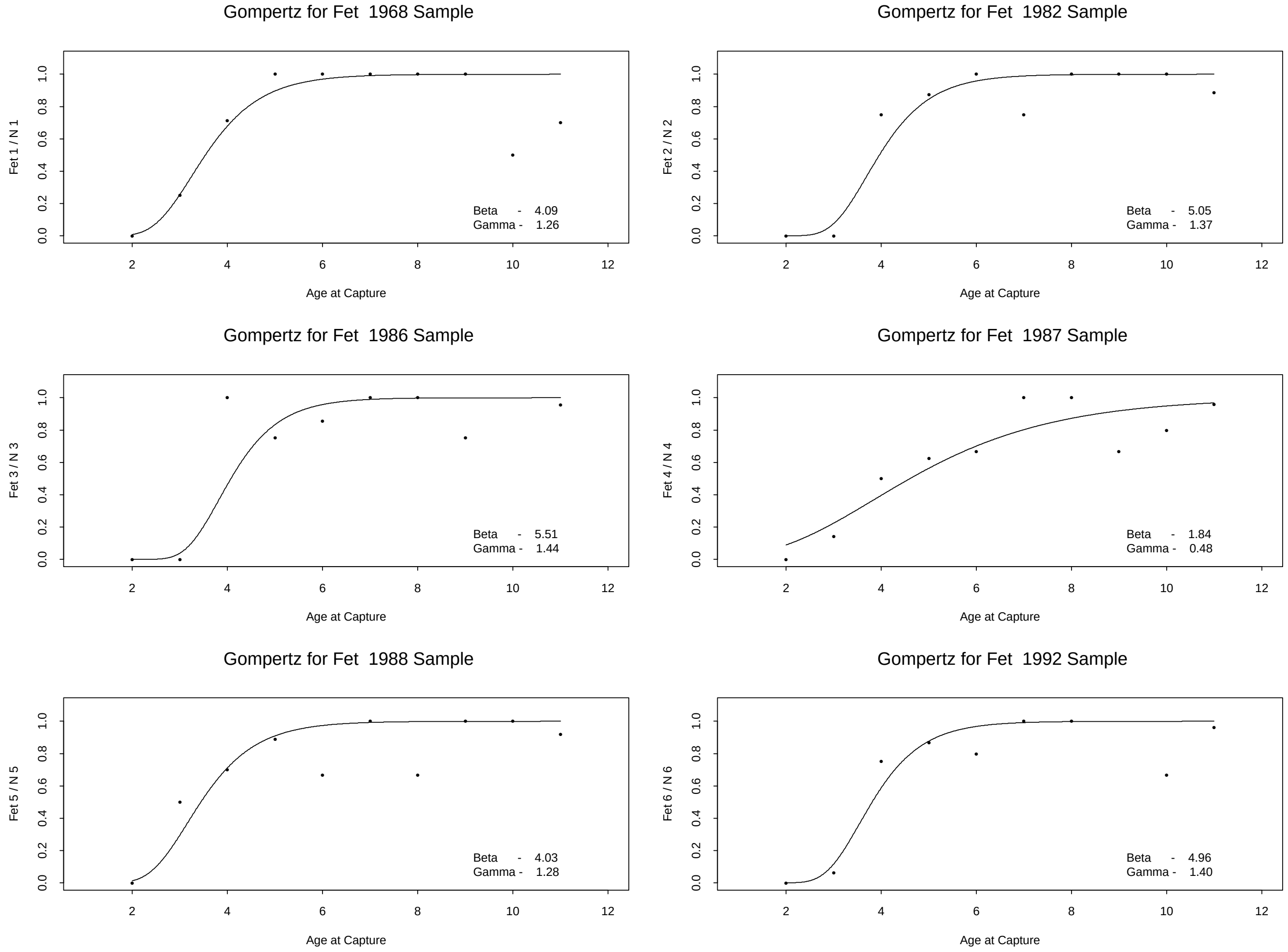


Figure 3.1: Gompertz models for all years - pregnancy indicated by a corpus luteum



Gompertz for Fet 1968 Sample

Gompertz for Fet 1982 Sample

Gompertz for Fet 1986 Sample

Gompertz for Fet 1987 Sample

Gompertz for Fet 1988 Sample

Gompertz for Fet 1992 Sample

Figure 3.2: Gompertz models for all years - pregnancy indicated by a Fetus

		Estimates									
Sampling Period		$\hat{b}_3$	$\hat{b}_4$	$\hat{b}_5$	$\hat{b}_6$	$\hat{b}_7$	$\hat{b}_8$	$\hat{b}_9$	$\hat{b}_{10}$	$\hat{b}_{11}$	$\hat{b}_{12}$
1968-1970	CL	0	0.58	0.42	0	0	0	0	0	0	0
	Fet	0	0.25	0.46	0.25	0	0	0	0	0	0.03
1982	CL	0	0.50	0.50	0	0	0	0	0	0	0
	Fet	0	0	0.75	0.10	0	0	0.15	0	0	0
1986	CL	0	0.50	0.50	0	0	0	0	0	0	0
	Fet	0	0	0.83	0	0.02	0.05	0	0	0	0.09
1987	CL	0.20	0.37	0.43	0	0	0	0	0	0	0
	Fet	0	0.14	0.36	0.13	0.04	0.24	0	0	0	0.09
1988	CL	0	0.86	0	0.14	0	0	0	0	0	0
	Fet	0	0.50	0.20	0.12	0	0	0	0.18	0	0
1992	CL	0	0.13	0.69	0.19	0	0	0	0	0	0
	Fet	0	0.06	0.69	0.10	0	0.03	0	0	0	0.13

Table 3.2: b estimates for all years using methods of Sections 2.2 and 2.3

Sampling Period		Gompertz Estimates									
		$\hat{b}_3$	$\hat{b}_4$	$\hat{b}_5$	$\hat{b}_6$	$\hat{b}_7$	$\hat{b}_8$	$\hat{b}_9$	$\hat{b}_{10}$	$\hat{b}_{11}$	$\hat{b}_{12}$
1968-1970	CL	0	0.58	0.42	0	0	0	0	0	0	0
	Fet	0.01	0.25	0.42	0.22	0.07	0.02	0.01	0	0	0
1982	CL	0	0.50	0.50	0	0	0	0	0	0	0
	Fet	0	0.08	0.44	0.33	0.11	0.03	0.01	0	0	0
1986	CL	0	0.50	0.50	0	0	0	0	0	0	0
	Fet	0	0.04	0.43	0.37	0.12	0.03	0.01	0	0	0
1987	CL	0.14	0.59	0.22	0.04	0.01	0	0	0	0	0
	Fet	0.09	0.14	0.17	0.17	0.14	0.10	0.07	0.05	0.03	0.02
1988	CL	0.11	0.53	0.28	0.07	0.02	0	0	0	0	0
	Fet	0.01	0.28	0.42	0.20	0.06	0.02	0.01	0	0	0
1992	CL	0	0.12	0.72	0.15	0.01	0	0	0	0	0
	Fet	0	0.12	0.47	0.29	0.09	0.02	0.01	0	0	0

Table 3.3: b estimates for all years using methods of Section 2.4

Chapter 4

Testing if Parameters Have Changed over Time

We saw in the last chapter that the estimated mean age of first birth using a corpus luteum ranged from 4.22 to 5.06 years. To test if there is a true difference in mean age of first birth over the samples, we test if the b parameters change over time. This is achieved via a likelihood ratio test. For this test, we have a null hypothesis that the b's are the same and an alternative that are not all the same over the samples. Under the null hypothesis, the data may be pooled over all 6 samples of data:

	Age (yr) at Capture									
	<2	3	4	5	6	7	8	9	10	>11
Total N	75	47	49	53	31	23	25	15	16	191
Total CL	1	21	44	53	31	23	25	15	16	191

The b estimates can now be computed for the pooled data using theory of Chapter 2. There are no drops in the observed pregnancy rate, so the method of Section 2.2 applies to give

$\hat{b}_3$	$\hat{b}_4$	$\hat{b}_5$	$\hat{b}_6$	$\hat{b}_7$	$\hat{b}_8$	$\hat{b}_9$	$\hat{b}_{10}$	$\hat{b}_{11}$	$\hat{b}_{12}$
0.01333	0.43348	0.45115	0.10204	0	0	0	0	0	0

The log likelihood under this reduced model is -53.76991.

The full model uses b estimates already derived in chapter 3, substitutes each into their respective log-likelihoods, and adds all 6 values together, giving the value -40.46906. The reduced model has only 10 b parameters while the full has 60, for a difference of 50 parameters. A likelihood ratio test is now constructed

LRT = -2(-53.76991) + 2(-40.46906) = 26.6017

To interpret this value, the degrees of freedom are needed so the test statistic can be compared to a chi-squared distribution. As stated, 50 parameters are lost from the full model to the reduced model so we might consider degrees of freedom equals 50. However, Table 3.2 shows that some parameters like $\hat{b}_7$, $\hat{b}_8$ to $\hat{b}_{12}$ do not vary at all over the samples. It is possible that these should not be considered parameters and should not be counted in the degrees of freedom.

To calculate degrees of freedom and a p-value, a simulation study was used. A new dataset (similar to Table 1.1) was constructed by generating from a binomial distribution using

$X_{i,t} \sim \text{Bin}(N_{i,t}, \hat{p}_{i,t}) \qquad i = 2, \cdots, 11$

The observed probabilities of being pregnant is used to generate a new number of pregnant seals for each age group in each sample. After each dataset was generated, methods from Sections 2.2 and 2.3 were used to find estimates of b and new likelihood ratio statistics were formed. This was repeated 100 times and the number of likelihood ratio statistics that exceeded the observed value of 26.6017 were counted. In our simulation, 73 likelihood ratio statistics exceeded this value, giving an estimate of a p-value of .73.

The values of the likelihood ratio statistics can also be used to get an estimate of degrees of freedom as well. First, the 100 likelihood ratio statistics are ordered into $\text{LRT}_1, \text{LRT}_2 \cdots \text{LRT}_{100}$. Next, quantiles are found for a chi-squared distribution with varying degrees of freedom for 100 different probabilities, $\frac{1}{101}$, $\frac{2}{101} \cdots \frac{100}{101}$, corresponding to the observed percentiles from the simulation. These quantiles are then plotted against the ordered values of the likelihood ratio statistics. This plot is in Figure 4.1.

If the data follows a chi-squared distribution with x degrees of freedom, then we expect the plotted line of quantiles from that chi-squared with x degrees of freedom against ordered likelihood ratio statistics cluster around the line through the origin with slope 1. From Figure 4.1 we conclude degrees of freedom for the data is between 30 and 35 (perhaps 32). A calculated p-value for statistic 26.6017 from chi-squared distribution with 32 degrees of freedom is 0.7364, which matches the previous estimate. It is unclear from looking at Table 3.2 where 32 degrees of freedom comes from since only the parameters b_3 to b_6 have nonzero values across the 6 samples, and the pooled estimates had only 4 nonzero estimates, giving an expected degrees of freedom of around 20.

From this, we cannot reject the null hypothesis that the b's are the same over all years. If we consider the b's to be the same, the 6 samples can be pooled and we calculate a pooled estimated mean age of first birth of 4.642 with standard error of 0.085.

A separate method uses an assumption of multivariate normality to test if the mean age of first birth of the 6 samples are equal. This method is known as a Wald test. We model

$\widehat{\mathbf{age}} \sim \mathrm{MVN}(\mu, \mathbf{\Sigma})$

And we want to test if $\mathbf{C}\mu = 0$ where

$$\mathbf{C} = \begin{pmatrix} 1 & -1 & 0 & 0 & 0 & 0 \\ 0 & 1 & -1 & 0 & 0 & 0 \\ 0 & 0 & 1 & -1 & 0 & 0 \\ 0 & 0 & 0 & 1 & -1 & 0 \\ 0 & 0 & 0 & 0 & 1 & -1 \end{pmatrix}$$

To test this we look at $\mathbf{C} \cdot \widehat{\mathbf{age}} \sim \mathrm{MVN}(\mathbf{C}\mu, \mathbf{C\Sigma C}^t)$

$$\widehat{\mathbf{age}} = \begin{pmatrix} 4.42 \\ 4.50 \\ 4.50 \\ 4.23 \\ 4.29 \\ 5.06 \end{pmatrix} \qquad \mathbf{\Sigma} = \begin{pmatrix} 0.02025 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.0625 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.0625 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.0670 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.0327 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.0164 \end{pmatrix}$$

with the above values coming from our earlier calculations.

A chi-squared test statistic with 5 degrees of freedom is

$$\widehat{\mathbf{age}}^t \mathbf{C}^t \left[\mathbf{C}\mathbf{\Sigma}\mathbf{C}^t\right]^{-1} \mathbf{C} \cdot \widehat{\mathbf{age}}$$

$=20.137$ for our simulation data with a p-value of .001. Using this test we conclude the 6 population means are not the same.

This is not too surprising given the large difference in the mean age for the 6th sample from the other samples. Removing the 6th sample, the same type of test results in a statistic of 1.140 with a p-value of 0.888, from which we would conclude there is no evidence that the first 5 sample years have different mean ages of first birth.

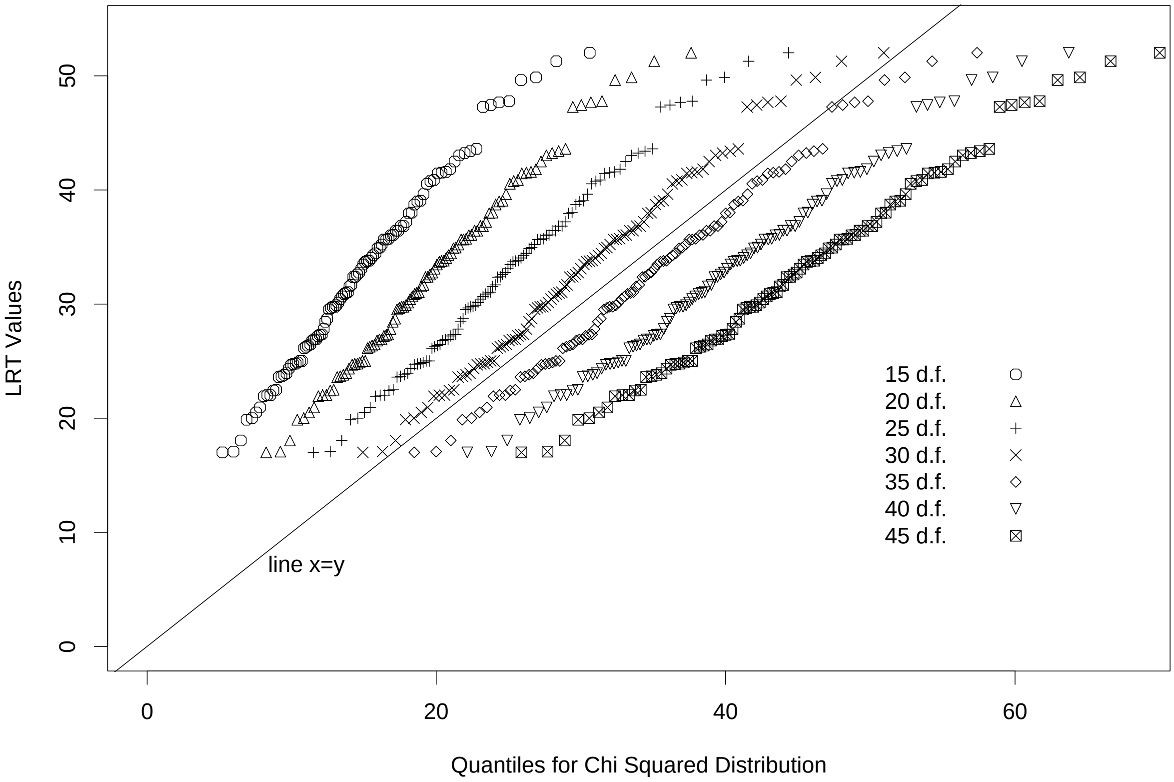


Figure 4.1: Estimation of degrees of freedom for LRT

Chapter 5

Summary and Discussion

In general, Grey Seal pregnancies begin to occur at age 3+ years old and continue with high rates of pregnancy throughout most of their lives. Females are pregnant for almost 1 year and usually give birth to only 1 young.

The population of Grey Seals in the Northwest Atlantic has increased roughly seven times since the 1960's. It is desirable to know estimates of population parameters for these seals to test if this expansion has influenced their breeding behaviour over time, and for future decisions about rate of population growth.

Hammill and Gosselin (1995) were able to estimate age specific pupping probabilities and mean age of first birth using bootstrap techniques. We were able to produce similar and reasonable estimates without the bootstrap, instead using available information with maximum likelihood theory and isotonic regression.

Estimates based on the presence of a corpus luteum to indicate pregnancy may overestimate pregnancy rates owing to early mortality of the embryo. Alternatively, estimates using the fetus to estimate pregnancy may underestimate true pregnancy rate, owing to the spread in implantation rates, which may extend into June.

Despite this large increase since the 1960's, our likelihood ratio test did not detect a difference of the b estimates. This is likely due to such a large number of parameters and a small sample size, it would be unlikely to detect a difference. The Wald test also supports that there has been no change in the mean age of first birth over the years after removing the last sample.

Ironically, although bootstrapping has been shown to have been not necessary, a parametric bootstrap was still necessary to estimate the p-value and the degrees of freedom for our likelihood ratio test.

Appendix A

Calculation of $\mathbf{V}(\beta, \gamma)$

In section 2.4, we deferred the variance calculations for the Gompertz estimates. The general log-likelihood is:

$$\begin{aligned} l &= X_2 \log(\exp(-\exp(\beta - \gamma \cdot 2))) + (N_2 - X_2) \log(1 - \exp(-\exp(\beta - \gamma \cdot 2))) \\ &\quad + X_3 \log(\exp(-\exp(\beta - \gamma \cdot 3))) + (N_3 - X_3) \log(1 - (\exp(-\exp(\beta - \gamma \cdot 3)))) + \cdots \\ &\quad + X_{11} \log(\exp(-\exp(\beta - \gamma \cdot 11))) + (N_{11} - X_{11}) \log(1 - (\exp(-\exp(\beta - \gamma \cdot 11)))) \\ &= \sum_{i=2}^{11} X_i(-\exp(\beta - \gamma \cdot i)) + (N_i - X_i) \log(1 - (\exp(-\exp(\beta - \gamma \cdot i)))) \end{aligned}$$

$$\begin{aligned} \frac{\partial l}{\partial \beta} &= \sum_{i=2}^{11} X_i(-\exp(\beta - \gamma \cdot i)) + (N_i - X_i) \frac{\exp(\beta - \gamma \cdot i)(\exp(-\exp(\beta - \gamma \cdot i))}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))} \\ \frac{\partial l}{\partial \gamma} &= \sum_{i=2}^{11} -i \cdot X_i(-\exp(\beta - \gamma \cdot i)) + -i \cdot (N_i - X_i) \frac{\exp(\beta - \gamma \cdot i)(\exp(-\exp(\beta - \gamma \cdot i))}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))} \\ \frac{\partial^2 l}{\partial \beta^2} &= \sum_{i=2}^{11} X_i(-\exp(\beta - \gamma \cdot i)) + (N_i - X_i) \left[\frac{\exp(\beta - \gamma \cdot i)(\exp(-\exp(\beta - \gamma \cdot i))}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))} \right. \\ &\quad \left. - \frac{\exp(\beta - \gamma \cdot i)^2(\exp(-\exp(\beta - \gamma \cdot i))}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))} - \frac{\exp(\beta - \gamma \cdot i)^2(\exp(-\exp(\beta - \gamma \cdot i))^2}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))^2} \right] \end{aligned}$$

$$\begin{aligned}\frac{\partial^2 l}{\partial \gamma^2} &= \sum_{i=2}^{11} i^2 X_i(-\exp(\beta - \gamma \cdot i)) + i^2(N_i - X_i)\left[\frac{\exp(\beta - \gamma \cdot i)(\exp(-\exp(\beta - \gamma \cdot i))}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))}\right. \\ &\quad \left. - \frac{\exp(\beta - \gamma \cdot i)^2(\exp(-\exp(\beta - \gamma \cdot i))}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))} - \frac{\exp(\beta - \gamma \cdot i)^2(\exp(-\exp(\beta - \gamma \cdot i))^2}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))^2}\right]\end{aligned}$$

$$\begin{aligned}\frac{\partial^2 l}{\partial \beta \partial \gamma} &= \sum_{i=2}^{11} -i \cdot X_i(-\exp(\beta - \gamma \cdot i)) - i \cdot (N_i - X_i)\left[\frac{\exp(\beta - \gamma \cdot i)(\exp(-\exp(\beta - \gamma \cdot i))}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))}\right. \\ &\quad \left. - \frac{\exp(\beta - \gamma \cdot i)^2(\exp(-\exp(\beta - \gamma \cdot i))}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))} - \frac{\exp(\beta - \gamma \cdot i)^2(\exp(-\exp(\beta - \gamma \cdot i))^2}{(1 - (\exp(-\exp(\beta - \gamma \cdot i))))^2}\right]\end{aligned}$$

The observed information is then formed

$$\mathrm{V}(\beta, \gamma) = \begin{pmatrix} -\frac{\partial^2 l}{\partial \beta^2} & -\frac{\partial^2 l}{\partial \beta \partial \gamma} \\ -\frac{\partial^2 l}{\partial \beta \partial \gamma} & -\frac{\partial^2 l}{\partial \gamma^2} \end{pmatrix}$$

and maximum likelihood estimates are substituted in the above to form the observed information matrix which is inverted to give V(β, γ).

Bibliography

Barlow, R.E., Bartholomew, D.J., Bremner, J.M. and Brunk, H.D. (1972). *Statistical Inference under Order Restrictions.* New York: Wiley.

Boness, D.J. and James, H. (1979). Reproductive Behaviour of the Grey Seal (Halichoerus grypus) on Sable Island, Nova Scotia. *Journal of Zoology. Series A. Proceedings of the Zoological Society of London* **188** 477-500.

Bowen, W.D., Capstick, C.K. and Sergeant, D.E. (1981). Temporal Changes in Reproductive Potential of Female Harp Seals (Pagophilus groenlandicus). *Canadian Journal of Fisheries and Aquatic Sciences* **38** 495-503.

Boyd, I.L. (1985). Pregnancy and Ovulation Rates in Grey Seals (Halichoerus grypus) on the British Coast. *Journal of Zoology. Series A. Proceedings of the Zoological Society of London* **205** 265-272.

Hammill, M.O. and Gosselin, J.F. (1995). Grey Seal (Halichoerus grypus) from the Northwest Atlantic: female reproductive rates, age of first birth, and age of maturity in males. *Canadian Journal of Fisheries and Aquatic Sciences* **52** 2757-2761.

Hammill, M.O., Kingsley M.C.S., Beck G.G. and Smith, T.G. (1995). Growth and Condition in the Northwest Atlantic Harp Seal. *Canadian Journal of Fisheries and Aquatic Sciences* **52** 478-488.

Lavigueur, L. and Hammill, M.O. (1993). Distribution and Seasonal Movements of Grey Seals, Halichoerus grypus, born in the Gulf of St. Lawrence and Eastern Nova Scotia shore. *Canadian Field-Naturalist* **107** 329-340.

Mansfield, A.W. (1966). The Grey Seal in Eastern Canadian Waters. *Canadian Audubon Magazine* **28** 161-166.

Ratkowsky, D.A. (1990). *Handbook of Nonlinear Regression Models*. New York: Dekker.

Stobo, W.T. and Zwanenburg, K.C.T. (1990). Grey Seal (Halichoerus grypus) Pup Production on Sable Island and Estimates of Recent Production in the Northwest Atlantic. *Canadian Bulletin of Fisheries and Aquatic Sciences* **222** 171-184.

Zwanenburg, K.C.T. and Bowen, W.D. (1990). Population Trends of the Grey Seal (Halichoerus grypus) in Eastern Canada. *Canadian Bulletin of Fisheries and Aquatic Sciences* **222** 185-197.