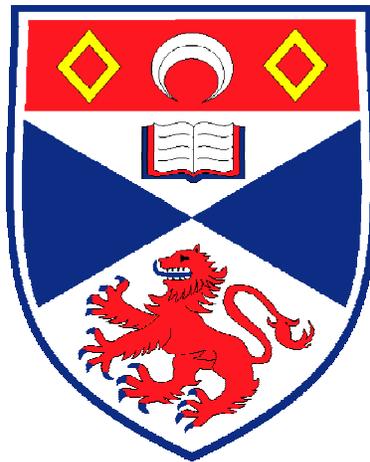


**Inter-Birth Interval Estimation for a population of Bottlenose Dolphins
(*Tursiops truncatus*): accounting for the effects of individual variation
and changes over time**

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**A Thesis Submitted for the Degree of MRes in Marine Mammal Science
to the
University of St. Andrews**



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ABSTRACT

This study presents life-history data collected from nearly two decades of field studies to allow examination of factors influencing inter-birth intervals (IBIs) and calving rates of reproductive female bottlenose dolphins (*Tursiops truncatus*). Assessment was then made of variation in IBIs over time and due to individual females. 26 females with extensive known calving histories were surveyed between 1989 and 2007 by three key research organisations studying different areas throughout the coastal range of the population known to be resident year-round in the waters along the east-coast of Scotland (56-58°N). 68 known calves were born to these females within the study period, providing 42 inter-birth intervals. 3-6 year intervals between successive births were most common (mean= 3.18 years, median= 5.5 years), a finding similar to the birth-spacing patterns of other well-studied bottlenose dolphin populations around the world. Two year intervals were present in five cases, implying an apparent high level of first year survival for these 68 calves. Variation in reproductive output due to differences between individuals was found to be low and the effect of each individual female not a significant predictor of IBIs. Within-female variation is present in 12 females known to have produced two or more calves. This allowed determination of change in IBIs through time for individual females. Variation in calving rates between individuals and between years was also present, however was found to be unimportant. IBIs were best determined by the number of years since the first known birth for each female and the previous number of calves she was known to have produced. Intervals were not predicted to change significantly through time and appear relatively constant when considered with an increase in the number of previous calves.

The data used in this project are the property of Aberdeen University, the Cetacean Research & Rescue Unit and the University of St Andrews. The data must not be used or reproduced for any purposes without prior permission from these groups.

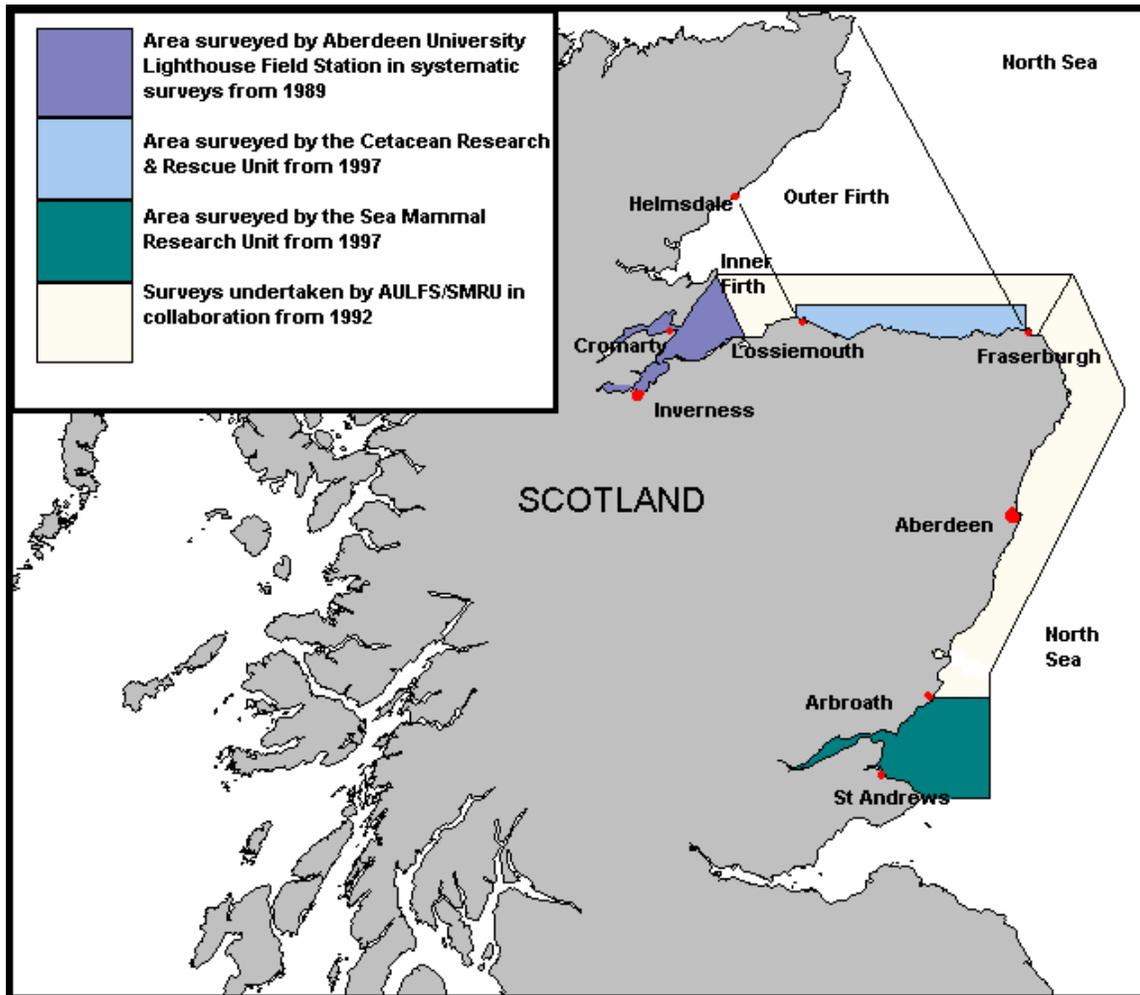


Figure 1: Map of Scotland showing the current known range of this bottlenose dolphin population and the areas covered by surveys of the Inner Moray Firth, Outer Moray Firth and the East coast of Scotland.

1. INTRODUCTION

Long term studies that monitor the lives of identified individuals have greatly expanded the opportunities to collect demographic information for wild cetacean populations (Barlow and Clapham, 1997). However, relatively few studies to date have used long-term data collection to focus primarily on inter-birth intervals (IBI) in cetaceans and use this information to determine variation in IBIs with age and with the calving histories of individual females. The spacing between births is thought to be one of the primary determinants for female reproductive success in many long-lived and slow-reproducing mammals (Fedigan and Rose, 1995).

The production and care of young is a fundamental element of mammalian societies and populations (Whitehead and Mann, 2000). For many mammalian species, including the bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), it is only the females who actively parent and who bear the costs associated with reproduction (Clutton-Brock, 1988). Each birth is dependent upon several factors including maternal age, individual fitness, the years since a previous birth (IBI), social status, and ecological factors such as food availability throughout the breeding cycle (Clutton-Brock et al. 1983). The female in her role as a mother, is the linchpin of cetacean population biology, making any understanding of the reproductive behaviour and success of females crucial for knowledge of population dynamics and related conservation implications (Whitehead and Mann, 2000). Studies of female reproduction in a small resident population of dolphins such as are present in the east coast of Scotland are thus important for the protection and conservation of the population.

Longitudinal data (long-term reproductive histories of individual females) are very revealing and, if complete, can provide the least biased type of information available in relation to reproductive output and complex patterns of variation in birth rates, both between and within individuals over time (e.g. Pomeroy et al. 1999). Between-female variation in reproductive output relates to variation in IBIs and thus calving rate, and is dependent on several interacting factors, many of which are related to individual fitness (Pomeroy et al. 1999). This variation makes some females poorer mothers, whereas others may be better and consequently able to produce more calves and rear them successfully to independence. Individual fitness is an important component of successful reproduction and is strongly dependent on resource availability and habitat quality, both of which are essential throughout the breeding cycle in relation to the timing of birth events, the ability of a female to successfully maintain a pregnancy and the successful rearing of a calf to independence. The considerations of a reproductive female have important conservation implications for coastal areas that are highly impacted by human activities.

This study aims to examine an area of cetacean natural history that is largely specific to females: the timing of reproductive events (Whitehead and Mann, 2000). In previous studies of cetacean IBIs, different methods were used for different species, for example, IBIs from longitudinal studies of identified living individuals (Barlow and Clapham, 1997), and from age and corpora analysis of dead specimens (Perrin and Reilly, 1984). The first method was used for this analysis. Two approaches were previously developed based on long-term photo-identification data to produce unbiased estimates of reproductive rates from the sightings histories of individual animals (Barlow, 1990; Payne et al. 1990). Both approaches were based on estimating the probability of giving birth at time t after a previous birth and assume that the probability of birth in a given year is dependent only on the time since an individual's most recent prior birth. This work has expanded on these studies by looking at how variation in IBIs can be attributed to change through time and the known reproductive history of individual females. Analyses were carried out using long-term data collected by several leading research organisations, enabling coverage of a wide area of the known range for the bottlenose dolphin population present year-round along the east coast of Scotland. From analysis of reproductive rate parameters and variation in IBIs for the eastern Scotland bottlenose dolphin population, stems the extreme interest in comparison with other well-studied bottlenose communities around the world.

The Bottlenose dolphin is a long-lived and slow-reproducing species. Most females produce their first calf between ages 6-15 years (Wells et al. 1987; Mann et al. 2000), following a twelve month gestation period (Perrin and Reilly, 1984; Schroeder, 1990). Females typically produce a single calf once every 3 to 6 years (Cockcroft and Ross, 1990; Mann et al. 2000; Reynolds et al. 2000; Perrin et al. 2002). Longevity of an individual is thought to range between 35 and 50 years (Scott et al. 1996; Whitehead and Mann, 2000). In many areas, including the Moray Firth (Lusseau et al. 2005), bottlenose dolphins are a free-ranging and social species, living in fission-fusion societies where individuals associate in small groups that change in composition, often on a daily or hourly basis (Wells et al. 1987; Connor et al. 2000). This group dynamic can create potential difficulties in the analyses of associations between individuals, especially in the determination of mother-calf pairs, essential for the analysis of IBIs (Grellier, 2000; Connor et al. 2000).

The bottlenose dolphin population inhabiting the coastal waters of north east Scotland (56-58°N) is the only resident population present in the North Sea, representing a population living at the highest known latitude for this species (Hammond and Thompson, 1991; Wilson, 1995). Nearly two decades of photo-identification studies show the dolphins to be resident in the area year-round (Wilson et al. 1999; Robinson et al. 2007) with strong re-sighting patterns of

individuals confined to this relatively small geographical area (Wilson et al. 1999). Studies on this population have been carried out by several central universities and institutions since the late 1980s. Aberdeen University Lighthouse Field Station (AULFS) and the Sea Mammal Research Unit (SMRU) commenced work in the inner Moray Firth in 1989, expanding their efforts to St Andrews Bay (between Arbroath and Fifeness) in the late 1990s, with new studies by the University of St Andrews commencing in 2003. In 1997, the Cetacean Research & Rescue Unit (CRRU) began working with the population along the southern coastline of the outer Moray Firth (see figure 1). The earlier studies by AULFS and SMRU led to the designation of the inner Moray Firth as a Special Area of Conservation (SAC) in 2005, with boundaries set up with the intention to include the core range of this population (Wilson et al. 1997; Wilson et al. 1999). However, research carried out in other areas of the firth and along the Aberdeenshire coastline and beyond has more recently shown that the home range of these animals extends far beyond the SAC (Wilson et. 2004; Stockin et al. 2006; Robinson et al. 2007; Culloch and Robinson, 2008).

There is a paucity of previous studies of reproductive rate parameters and variation in IBIs for cetaceans because of the many years of research required to collect such data on these long-lived and slow-reproducing mammals. In addition, obtaining robust estimates of individual birth rates for marine mammals with wide home ranges are particularly difficult, even for well-studied populations such as the bottlenose dolphins of Scotland. Analysis of IBIs for this population would not be possible without the use of long-term photo-identification and associated data provided through the collaborative effort from AULFS, the CRRU and the SMRU, to assist in the determination of the complete calving histories of as many females as possible. Through this collaborative effort, the first of its kind for this population, a unique dataset was created to resolve the absolute calving histories for 26 individual females selected based on their known production of at least two calves between 1987 and 2007. The data used includes combined sightings records for many of the selected females and the assignation of these females to a calf in any particular year (Appendix 2, tables 1, 2 and 3). Analyses of 42 IBIs are presented in this report, all determined to the nearest year of calf birth and based on the years since the birth of the previous known calf of a given female, independent of whether the calf is known to have survived or not.

Although knowledge of the birth spacing patterns for several individuals is incomplete due to the heterogeneity of recapture and the difficulties in establishing whether a birth may have been missed due to absence of animals in a limited study area and/or an imbalance of sampling effort within and between years, this study does its best to overcome these difficulties and account for them so as to ensure that the resulting analysis serves to increase our understanding of these life-history parameters for this population.

2. METHODS

2.1. Data collection

2.1.1. Field methods

Data were derived from dedicated boat surveys undertaken by each organisation throughout the ranges and years discussed in the introduction. Within the inner Moray Firth, systematic surveys (as detailed by Wilson et al. 1997) were carried out by AULFS and supplemented by opportunistic effort in the coastal waters of the outer Moray Firth and in St Andrews Bay (figure 1). Data collected by the CRRU follow the methods detailed by Robinson et al. 2007 using systematic boat-based surveys along the southern outer Moray Firth coastline between Lossiemouth and Fraserburgh. When dolphins were encountered, number of individuals was counted, group composition and age classes noted and photo-identification pictures (Wursig and Wursig, 1977) taken. Adults were defined by their large size and dark colouration, a calf by its smaller size, lighter colouration and often discernible foetal folds, usually swimming in close association with an adult. A neonate was defined as a very small, lightly coloured animal with bold foetal folds and a strong, close association with an adult, assumed to be its mother (Shane, 1990).

2.1.2. The study area

The coastal range occupied by these animals comprises the Moray Firth and the waters along the east coast of Scotland, all part of the North Sea (Figure 1). The Moray Firth is a large embayment forming an integral part of the North Sea (Harding-Hill, 1993; Wright et al. 1998) and comprises two major components. The area to the west of a line drawn from Helmsdale to Lossiemouth is identified as the “inner” Moray Firth and is sheltered from prevailing winds and is influenced by freshwater inputs, the remaining sea to the east is referred to as the “outer” firth, an area more representative of the open waters of the North Sea (Wilson et al. 1999).

2.1.3. Photo-identification

Photographs of the left and right sides of the dorsal fin were taken of as many animals as possible during an encounter. Individuals were identified from these photographs using unique natural markings such as dorsal edge marks (DEMs), fin shape, permanent scars, deformities, natural pigmentation patterns and skin lesions on the fin and flank (Hammond et al. 1990; Würsig and Jefferson, 1990; Wilson et al. 1999). Temporary marks such as scratches, scars and skin lesions, as well as permanent marks were used where possible to identify young calves and allow comparison of young animals within each year and between study sites. Using these marks was advantageous for this analysis to assist in the determination that a calf recorded by one

organisation as belonging to a known adult female was assigned correctly (appendix 2, table 1). Although temporary marks change within and between years, records made of a calf several times within a year enabled tracking of mark change throughout the year and the update of temporary identification marks in each catalogue. Individuals with obvious marks were not preferentially recorded.

2.1.4. Data processing

Photo-identification catalogues are maintained by each respective contributing organisation, each containing a unique identification number for each individual identified. Information from each catalogue was extracted for each female used in this study to create a unique dataset for the analysis which includes information telling whether the animal was sighted/recorded in a particular year (appendix 2, tables 2-3), the number of times a record was made and a photograph taken and in some instances, whether or not an identified female is thought to have calved in a given year. On some occasions, the calf itself was identified independently of the mother for instance, through a unique DEM or deformity. In this population, three female calves were continuously recorded after separation from their mother through to their own first recorded calf. This has enabled the collection of a small, but valuable sample of known age mothers. However, in the majority of cases, calves were difficult to identify in their first three years of life with resample dependent on recapture of the mother with the calf present also (Grellier, 2000).

All organisations have graded their photographs according to quality using the grading system defined by Wilson (1995) in order to minimise the number of errors associated with incorrect identifications (Wilson et al. 1999; Robinson, pers. comms). Only the highest quality photographs were useful for this analysis. Matching was carried out between the host institutions by experienced personnel using as many unique features from each individual as possible to confirm a match. Animals that could not be matched within or between catalogues were logged as individuals unique to a single catalogue. The use of photo-identification of individual animals assumes that a marked animal will be recognised with high levels of certainty in future photographs.

2.1.5. Assigning calves to females

An aspect of extreme importance in this study was confidence in the assignation of mothers to calves. For the purposes of this analysis, mothers were assigned to calves using a degree of confidence and only those with the highest confidence were maintained in the dataset used for analysis. This reduces any potential errors in the dataset that would significantly affect the results. Although association patterns can be used to determine whether a female is the likely mother of a

given calf, infant position is a more reliable indicator (Mann et al. 2000) as associations are not always 100% due to separation for brief periods, especially during foraging (Mann and Smuts, 1998). However, greater confidence was given where associations between mothers and calves were high and the calf was captured repeatedly in the echelon position with the adult female. Confidence was assigned to the mother-calf association on three levels, based on methods used in the assignation:

- Level 1: Animal recorded surfacing alongside the suspected mother in only one encounter. Supported by a single photograph.
- Level 2: Suspected mother and calf were photographed/recorded in association on greater than two occasions, with the calf photographed in the echelon position with the mother on repeated independent encounters.
- Level 3: Calf associated with mother using either level 1 or 2 by more than one of the research organizations.

All contributors have assigned reproductive females to known calves based on their extensive knowledge of the study animals and the use of photo-identification data.

26 individual females were known to have had more than a single calf (assigned to them with a high level of confidence) throughout 1989-2007. These 26 females and 68 respective calves were used to make up the data set for use in this study (appendix 2, table 1).

2.1.6. Determination of calf year of birth

Birth in a given year was assumed based on a neonate recorded in repeat observations in the echelon position with a known adult female, thought to be the mother. In addition, mother/calf pairs observed together on more than one occasion further confirmed these assignments. Where a female was not seen in a given year, but sighted repeatedly in subsequent years with an older calf, the birth year of the calf was determined by its relative size and the prominence of foetal folds. Calves were only extracted back as far as two years as studies suggest that a calf is likely to become independent of its mother around its third year (Mann et al. 2000).

2.2. Data Analysis

Statistical models were created to determine the probability of IBIs and calving depending on several fixed effect covariates: year of calf birth, the number of years since a females previous known birth, the number of previous known calves to a given female, the number of years since the first birth of an individual female and the variation associated with each individual female. Results show whether certain variables have a significant impact in the determination of IBI and

birth and best-fitting models were used to predict the probability of calving at a given interval and the probability of calving dependent on several fixed-effect covariates.

2.2.1. Selection of the data for use in this study

Repeat-measure data were collected to study change over time in IBIs and calving rates for females sampled with or without a calf between 1989 and 2007. Only well-marked and recapturable females known to have produced more than a single calf were used for this analysis. Investigations were carried out using only data where females were known to have reached reproductive maturity, determined through the presence of a known calf. Due to their gestation period of 12 months (Perrin and Reilly, 1984), females are known to be reproductively mature for at least one year before their first known calf, thus, only sightings in the year immediately before the year of first known birth and all those after were used in analysis. This was a measure to prevent the incorporation of non-reproductively mature females in the study. An assumption based on previous studies was that a female was unlikely to give birth in the years immediately pre- and post- a known birth event (Bearzi et al. 1997; Connor et al. 2000), thus a female was recorded without a new calf in these years. Taking this approach allows the best determination of individual calving rates for known mature individuals.

2.2.2. Variation in observed calving rates between females and between years

To determine individual calving rates (table 1, appendix 1), the number of known calves for each female was taken as a proportion of the number of years that the female was sighted. To determine annual calving rates, the number of known calves born each year to sample females was taken as a proportion of the known reproductively mature females sighted in that year (table 3, appendix 1). Individual calving rates were compared between females and between years using the Analysis of Variance test.

2.2.3. Variation in observed Inter-birth intervals

The IBIs determined for this analysis are irrespective of whether the calf was known to have survived to weaning or not as this could not be accurately ascertained for the calves in this study population. Two categories of IBI were analysed, one containing all of the known IBIs (n=42 intervals) and the other containing only IBIs where a female was sighted in every year between known calves (n=31 intervals) (table 5, appendix 1). An average was taken of IBI between each successive calf (table 6, appendix 1) and a single factor anova test carried out to determine whether there was any significant variation through time, based on known IBIs between successive calves.

2.2.4. Determination of between-female variation in Inter-birth Intervals

In this multi-female study, the overall female variation in IBIs was broken down into within- and between- female variation, reflecting variation at the individual and aggregate levels respectively. This similarity was expressed by the Intra-class Correlation Coefficient (ICC), which compared the within-female variance with the between-female variance. The ICC was calculated using equation (1) where S^2A is the mean square between individuals, and S^2E is that within. Equation (1) estimates the amount of variation between females over the total variability (within and between females).

$$(1) \quad ICC = S^2A / (S^2A + S^2E)$$

ICC was determined through two analyses; one containing all of the individuals (n=26 females), the other containing only those with a complete sighting history between each successive birth (n=12 females), appendix 1 (tables 7-10) and equations 2-5 show calculation of ICC values.

Equations 2-3 were used to calculate the **within** female error rate:

$$(2) \quad \text{Sum of squares} = \frac{\sum((SX^2/ni)/ni) - \sum(SX)^2/ni}{ni}$$

$$(3) \quad S^2E = \text{Sum of squares} / \text{Degrees of Freedom (DF)}.$$

Equations 4-5 were used to calculate the **between** female error rate:

$$(4) \quad No. = 1 / DF(MSA) * \sum(ABI^2) / DF(MSE)$$

$$(5) \quad S^2A = (MSA - MSE) / no$$

Where: n = the total number of individual females

ni = the total number of intervals

SX = the sum of all the intervals for each individual

SX^2 = the square of the sum of all intervals for each individual

SX^2/ni = the square of the sum of all intervals for each individual divided by the total number of intervals for each individual

DF = degrees of freedom

From the results of equations 2-5, the ICC was determined using equation (1).

2.2.5. Determination of effects related to the duration of each female in the trial

The number of years since a females first known birth was used as a proxy for change occurring with age. 'Survival' in this study was taken to represent the number of years that the female continued to be sampled. Where a female was not sampled in a given year, but sampled in later years, she was still counted as present as she was still known to be alive.

Estimation of the survival curve was used to determine the number of initial animals remaining in the trial through time. 'Survival' through time was determined by taking the number

of females known to be present in each age class as a proportion of the total entering the trial initially (n=26). A decrease in sample size with time can lead to an increase in variability which, may decrease the precision of results obtained from statistical analyses (table 11, appendix 1).

The Kaplan-Meier estimate of survival was used to determine how female 'survival' fluctuates from one year to the next. Table 12, appendix 1 shows calculations for the Kaplan-Meier estimate.

To Determine whether there was a change in calf production with increasing years since first birth, the calving rate each year after first birth was calculated as the proportion of known calves born in each time (year) of the number of females known to be present in that time (table 13, appendix 1).

2.3. Generalised Additive Models (GAMs)

The 'Minimalist Generalised Cross Validation' (mgcv) library in the statistical software package R was utilised for the construction of Generalised Additive Models (Wood, 2006). GAM was employed as the most appropriate statistical model due to the need to incorporate flexible non-linear functional relationships in the regression analysis (Ruppert et al. 2003; Wood, 2006). GAMs were created incorporating both fixed effects (parameters with repeatable levels: year of calf birth, IBI, the number of years since a first known birth and the previous number of calves), as well as random effects (individual females). The GAMs employed a non-parametric function to account for the relation of non-linear coefficients to the predicted response value. The non-linear function of predictor variables was estimated via the Thin Plate Regression Spline (Wood, 2006). GAMs were employed to model the relationship between predictor variables and response in two analyses:

- 1) Birth event (1) or not (0) as a binary response.
- 2) IBI as a Gaussian response.

Residual plots were used to evaluate the nature of the relationship between the predictor and the residualised dependent variable values and the nature of the influence of the respective predictor in the overall model. Residuals plots (appendix 1, figs 1-2) show the smoothed predictor variable values plotted against the partial residuals. The solid line/curve represents the spline (the estimated effect), the dashed lines represent 95% confidence bands, points represent observed values. The best-fitting models show the partial residuals evenly scattered around the curve to which they relate.

2.3.1. Model selection and interpretation

The best fitting models were selected using manual stepwise-selection, based on the significance of variables in predicting the model outcome as determined by the AIC value (Akaike, 1973). When selected, the best-fitting model was interpreted using the p-values for each linear model term and the estimated degrees of freedom and p-value for each of the smooth terms. The Generalised cross-validation score (GCV) determined the significance of the smooth terms where the Gaussian family was used, and the Unbiased Risk Estimator (UBRE) value where the binomial family was used. Low values of GCV and UBRE indicate the most appropriate model smoothness. The adjusted R^2 value (coefficient of determination) and the percentage deviance explained were used to determine the goodness of the model fit, and thus the extent to which probabilities based on the model would reflect the truth (tables 14 and 16, appendix 1).

2.3.2. Making predictions based on the best-fitting models

Predictions were made for the probability of calving and IBIs dependent on combinations of the covariates from the best-fitting models. Although year of birth appeared as a significant covariate in predicting the response in both models, to predict out-with the survey period, the year of birth was omitted from the predictions. A predictive framework was subsequently constructed using the significant covariates in the best fitting GAMs, and predictions were made using combinations of the model terms accompanied by associated standard error estimates of uncertainty (tables 15 and 17, appendix 1).

2.3.2. Fixed-effects and mixed-effects models

A mixed-effects model was employed to determine the contribution of the individual females as a random-effect in the determination of the response. Generalised Additive Mixed Models (GAMM) were chosen as an extension of GAM to account for individual variation within and between females. GAMM incorporates smoothed and parametric fixed-effect covariates also. The best-fitting GAMM was determined using the R^2 value.

3. RESULTS:

3.1. Individual variation in observed calving rate

Individual calving rates for the 26 females are shown in (table 1, appendix 1) and figure 2. Figure 2 shows that there was a level of variability in the number of calves produced throughout the study period, ranging from 2-5 calves per known individual female, however, no significant variation between any two of the individual calving rates was found (Anova, $p=0.105$; table 2, appendix 1). The number of times that a female was sampled in the years after she was known to be reproductively mature ranged from 4-20 years. This may account for some of the variation in apparent reproductive rates, with some females being sampled more than others. Variation may also arise due to heterogeneity of recapture of individual females and females not being sighted in given years, leading to uncertainty in whether she has calved in those years. If she did calf in those years, this can lead to underestimation of the calving rate, if she did not, this can lead to overestimation of the rate.

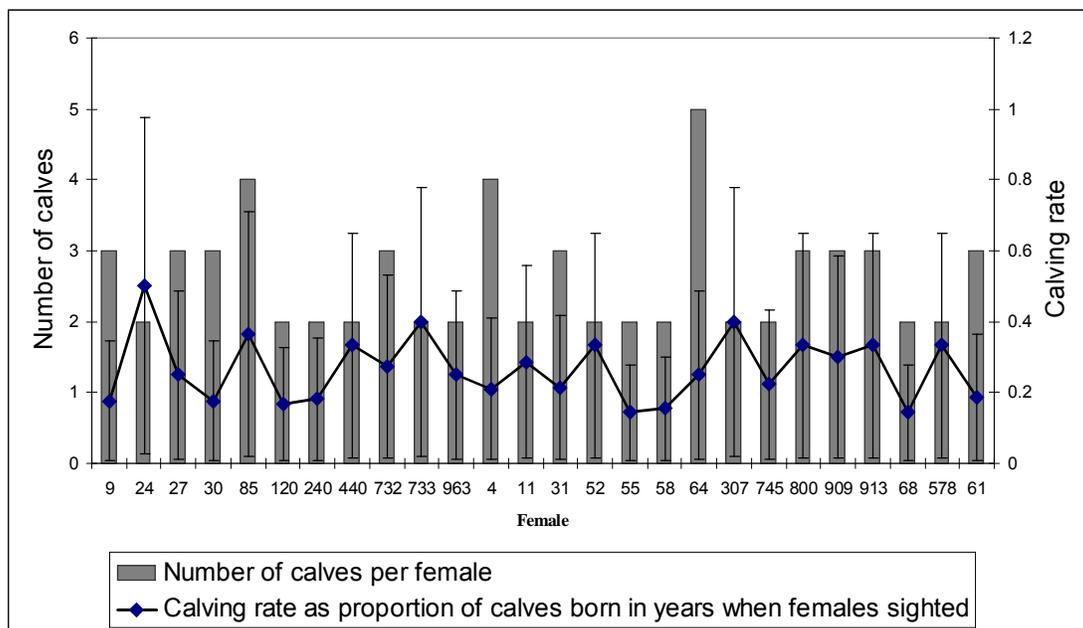


Figure 2: Individual calving rate of reproductively mature females with 95% confidence intervals.

3.2. Annual Variation in observed calving rate

No significant variation between any two of the annual calving rates was found (Anova, $p=0.29$; table 4, appendix 1). Figure 3 and table 3 in appendix 1 show that between 1989 and 2007, there was variability in the number of known calves born per year for the 26 females (1-7 calves born per year) with lower numbers of calves and lower calving rates in 1993, 1998 and 1999. These

appear to be low calf years as the number of females sighted were not lower than in other years. The number of sample females sighted in each year range between 8 in 1989 and 21 in 2003 and 2004.

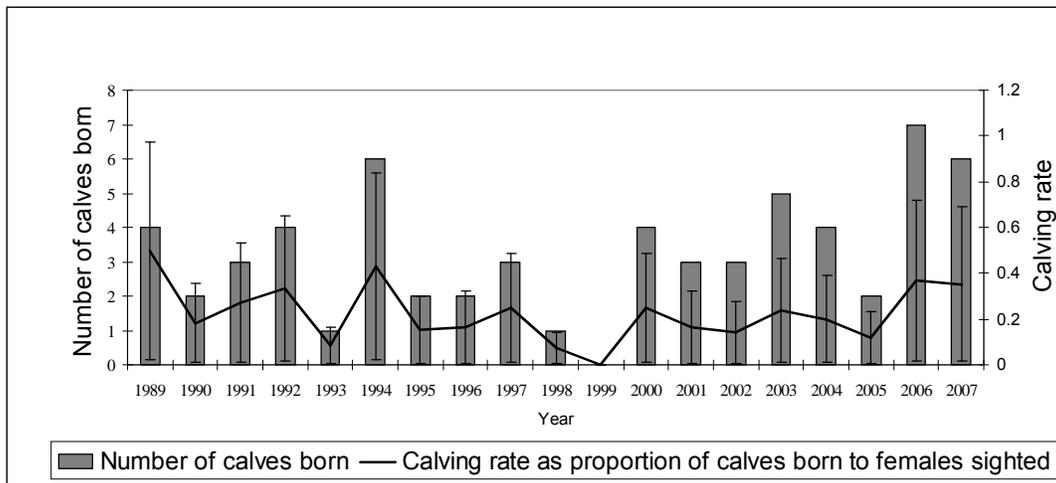


Figure 3: Annual calving rate for known reproductively mature females with 95% confidence intervals.

3.3. Observed Inter-Birth Intervals

No calves were born in the first year after a known birth, with IBIs for calves found to occur most commonly between 3 and 6 years (figure 4; table 5, appendix 1). Intervals of 2 years (n=5) also occurred, as did 8-9 year intervals (n=3-4), however, these longer intervals may be due to missed births if a female was sampled on few occasions between successive births, thus making an interval appear longer than it truly is. When all of the IBIs (n=42) were taken into account, 3 and 4 year intervals were most typical, but when using only the intervals where the female was sighted every year between successive calves, then 4 year intervals appear most common. When all of the intervals were included in the analysis, irrespective of whether a birth may have been missed in between, then the mean IBI for the selected females is 3.18 years (n=42 intervals, range = 2-12 years, median=5.5 years), when only intervals where the female was sighted in every year between successive births were included, the mean interval is 2.81 years (n=31 intervals, range= 2-9 years, median=5 years). The probability of calving at a given interval following the previous calf increases up to 4 years and declines again after 6 years (figure 5). The estimated birth-interval probabilities (conditional on the animal not having calved at a shorter interval) are 0.119, 0.214, 0.214, 0.167 and 0.167 for birth intervals of 2 through 6 years respectively. The probabilities of each interval are shown in table 5, appendix 1.

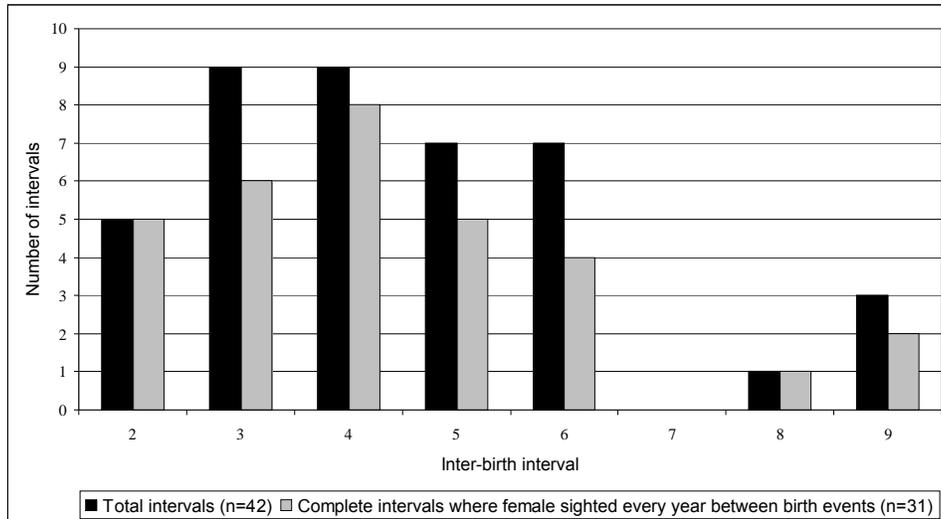


Figure 4: Number of IBIs accounted for using the study sample of 26 females.

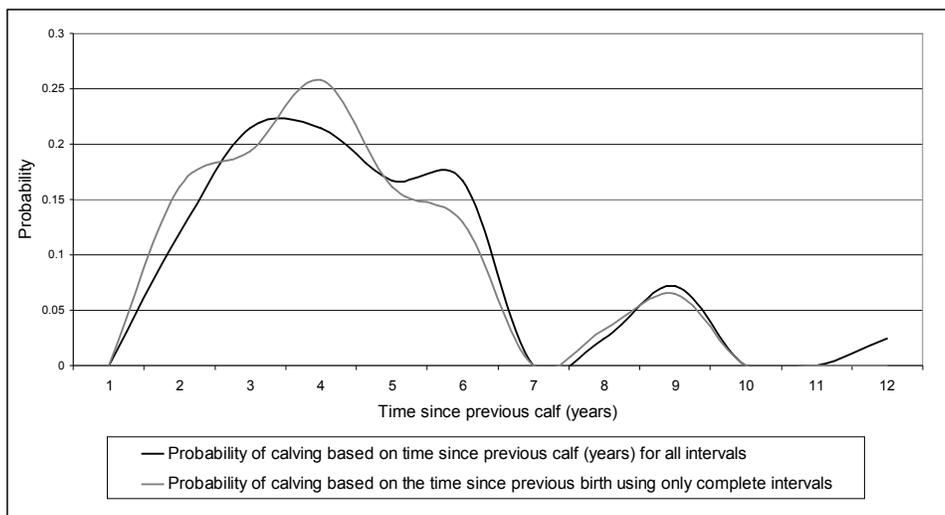


Figure 5: Curve showing the proportion of known births at a given interval.

3.4. Variation in Inter-birth Intervals

Within female variation in IBIs is apparent between successive calves for females in this study. However, the level of variation was difficult to quantify due to the small sample of females with greater than 2 calves and thus more than 1 IBI (n=12 females). Only three females were known to have produced 4 calves or more and thus have 3 IBIs. Again, although within-female variation was apparent in these IBIs, a significant change through time was not determined. Only 2 of these females could be used as the 2nd and 3rd calves of AU#85 were known to have died in their first year (AULFS, unpublished data).

There were 25 IBIs between 1st and 2nd known calves, 12 IBIs between 2nd and 3rd known calves, 3 IBIs between 3rd and 4th known calves and 1 IBI between a 3rd and 4th known calf. The average

interval length was calculated between successive calves and a single-factor anova test (table 6, appendix 1) found there to be no significant differences in IBI length attributable to previous number of calves ($p=0.611$). However, the sample size for the IBIs between 3rd and 4th, and 4th and 5th calves are very low, thus, there is uncertainty associated with the results from the analysis which implies no significant variation in IBIs with increased number of calves.

3.4.1. Within- and Between-Female variation in Inter-birth Intervals

The Intra-class Correlation Coefficient (ICC) for individual females indicates that the between group variation is relatively low (ICC=0.35), suggesting that variability in the response is driven mainly by fixed-effect covariates and within-female variation, rather than between-female variation. The within-female error rates, calculated using equations (2) and (3) were determined to be 84.762 for only the females with complete sightings ($n=12$), and 153.83 for the total females ($n=26$). The among-female error rates, calculated using equations (4) and (5) were determined to be 1.84 for the only the females with complete sightings, and 1.79 for the total females (appendix 1, tables 7-10). From these values, equation (1) was used to determine values for the ICC of 0.35 for both analyses, indicating that the total intervals for all of the females appear to be a good representation of what is known to be correct, based on the value determined from the smaller sample using only females with a complete sighting record between each known calf. The relatively low value of 0.35 suggests that there is little variation between individual females, however, ICC is not so low as to suggest that individual variation may not have some impact on the response. Within-female variation in IBIs was also found to be insignificant shown by the apparent lack of significant variation in IBI between successive calves (section 3.4). This implies that variability in IBIs is not significantly affected by individual females, thus the significant predictor variables for IBI are likely due to fixed-effect covariates.

3.5. Effect of the length of data available for each female after her first known birth

Fig 6 and table 11 in appendix 1 show that all individuals ($n=26$) entered the study in the year after their first known birth. The survival curve finds survival (the number of females remaining through time $S(t)$) to decline as time increases. Observations for each individual were only obtained until a certain point in time, after which there were no more measurements. An issue resulting from this is the depletion of study subjects in higher age classes which leads to reduced confidence in inferences made from this small number of data points. The Kaplan-Meier estimate of 'survival' between years is shown in figure 7 (table 12, appendix 1) and shows that individuals have a higher probability of dropping out of the trial in the later age classes. This likely reflects the lower numbers of animals remaining in the trial in these years, thus exaggerating the effect of

dropout later in the trial. There appears to be no significant variation in the calving rate through time for the females in this trial, figure 8 and table 13 (appendix 1), shown by greatly overlapping 95% confidence intervals associated with the variability surrounding each calving rate. The calving rate of each age class was determined based on the number of animals known to be present in each age class and the number of calves born to animals in each. Based on this sample of females, it appears that individuals reproduce consistently and do not change their reproductive output and IBIs significantly over time when one accounts for the number of calves produced in each year after known first birth.



Figure 6: Survival curve showing the proportion of total females (n=26) present in the trial in each subsequent year after first known birth

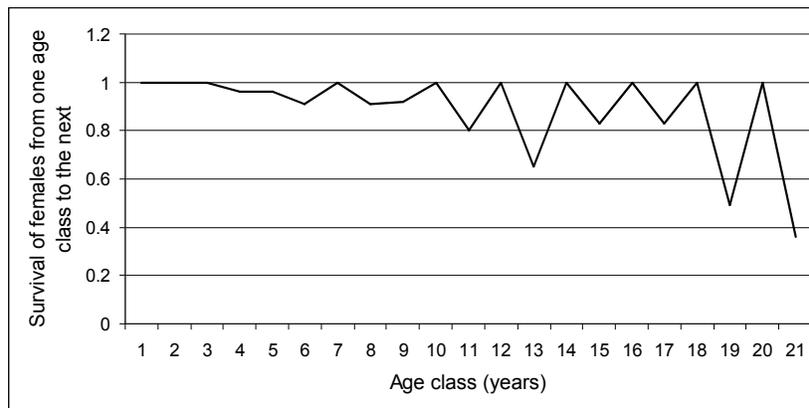


Figure 7: Kaplan-Meier estimate of survival for females into their next year, calculated as the number of animals present in age class $t+1$ as the proportion of those present in age class t .

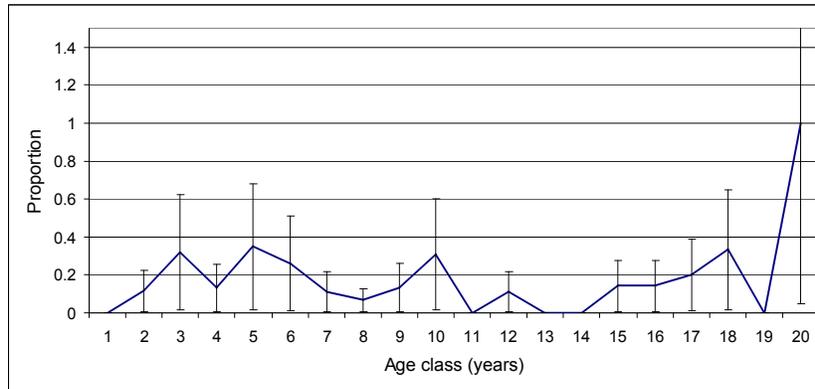


Figure 8: Proportion of calves born to females known to be present in each year after their first known birth.

3.6. Results from statistical models

3.6.1. Modelling calving as the response

The best fitting GAM contains the covariates: year of calf birth, years since previous birth and previous known calves as smoothed terms with female as a factor variable (table 16, appendix 1). This model has the most appropriate model smoothness (UBRE=-0.3741). The adjusted R^2 value of 0.6 implies that over half of the variability in the data is explained/captured by the regression and the model has an appropriate fit for the data. In addition, 65.3% of the residual deviance was explained by the fitted model. The model suggests a significant regression between all of the smoother covariates and calf births ($p < 0.05$ for the covariates year of birth, IBI and previous known calves). Curves corresponding to 4.2 degrees of freedom (df) were estimated for the effect of year, 1.9df for previous calves and 4.7df for years since previous calf. The total degrees of freedom (TDF) is the sum of individual df plus one df for the model intercept (TDF=36.78). The residual plots (figure 9) highlight the possibility of a threshold between 3.5 and 5 years since previous birth in the relationship between a calf being born and years since previous birth and a decline in the probability of a calf being born with an increase in the number of previous known calves. The residual plots also highlight the variability around the smoothed terms, for instance, in the residual plot for previous calves (figure 9), there is a high level of variability associated with the spline at 4 calves due to the low amount of data available for this point. Visualisation of the GAM (figure 10) shows the response regressed against the terms previous number of calves and IBI.

3.6.2. Predictions made based on the best-fitting model

The predicted probability of calving, associated standard error and odds of calving versus not calving, dependent on combinations of variables are shown in table 17 (appendix 1) and the

predictions are plotted in figure 11. The probability of calving is best predicted by the number of previous calves and IBIs. A calving threshold is suggested between 3 and 6 years since the previous known birth before decreasing. There appears to be a decline in the probability of calving with increased calves, however, this is subjective due to the wide 95% confidence intervals surrounding the residual line which represents the very small sample size used to determine the effect of 3 and 4 previous calves (n=2 and n=1 intervals respectively).

Model specification of the best assumed relationship between IBI and predictor covariates is:

$$Y_i = \beta_0 + f_1(\text{Year}_i) + f_2(\text{IBI}_i) + f_3(\text{previous_calves}_i) + \text{Female} + \varepsilon_i (Y_i \sim \text{Binomial}(n_i, p))$$

Where: ε_i represents the random component, the Gaussian or binomial family error term

β_0 is the intercept parameter

f_j are smooth functions, the degree of smoothness (within certain limits) of f_j is estimated by the UBRE score (GCV for Gaussian). f_j represents the change in the expected response $E[Y_i]$ when each explanatory variable (x_i) increases by 1 unit.

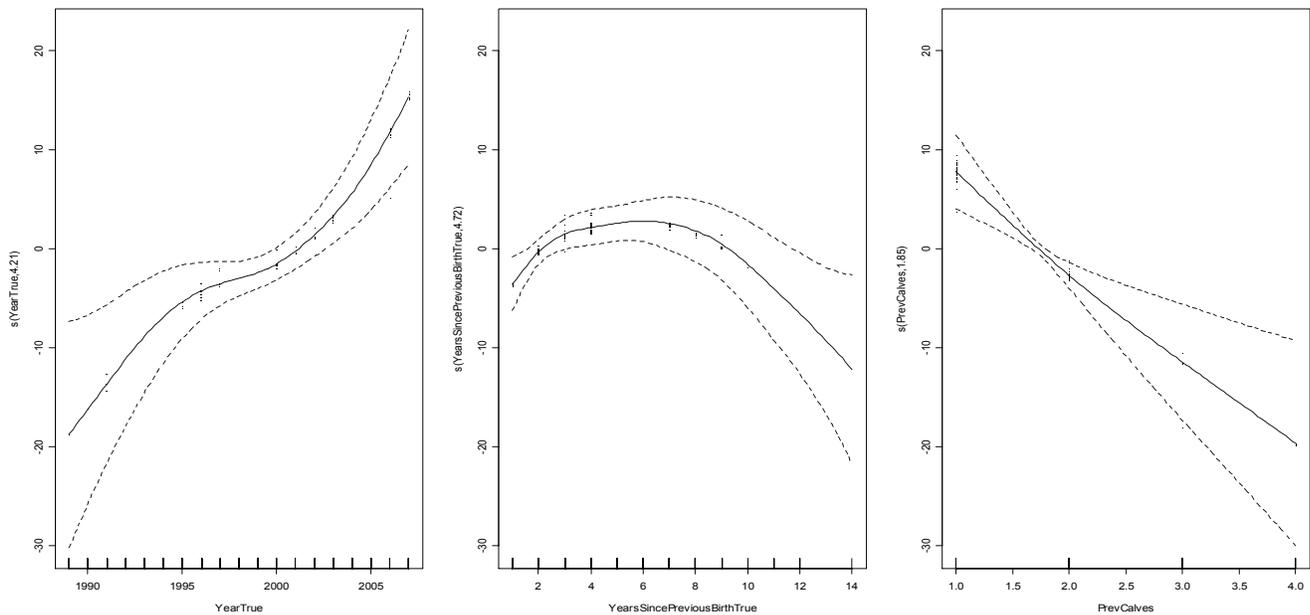


Figure 9: Residual plots for the smoothed terms in the model with birth as the response, from left to right: Year of calf birth, the number of years since previous birth and the previous number of calves

Changes in IBI with previous number of calves and years since first birth

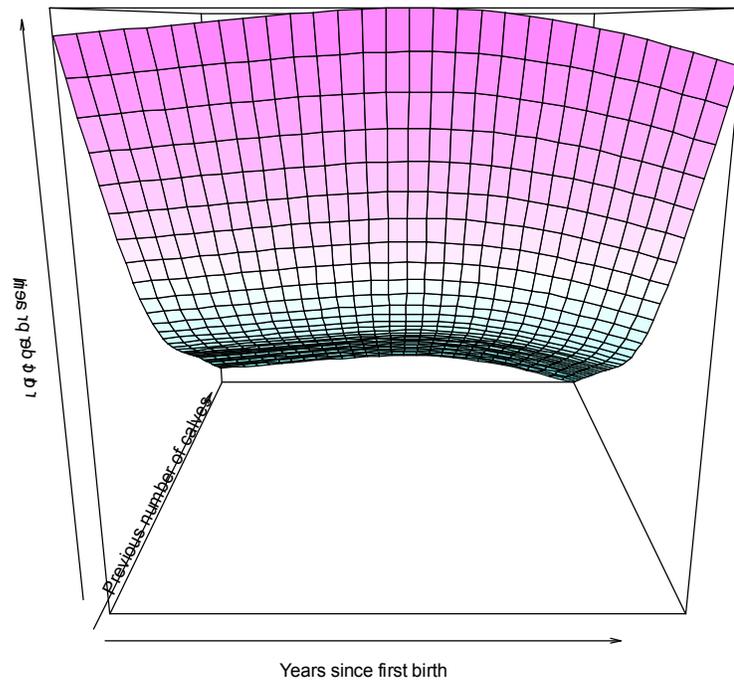


Figure 10: 3d visual plot showing the change in the birth response regressed against the previous number of calves and IBI with the linear predictor on the z-axis.

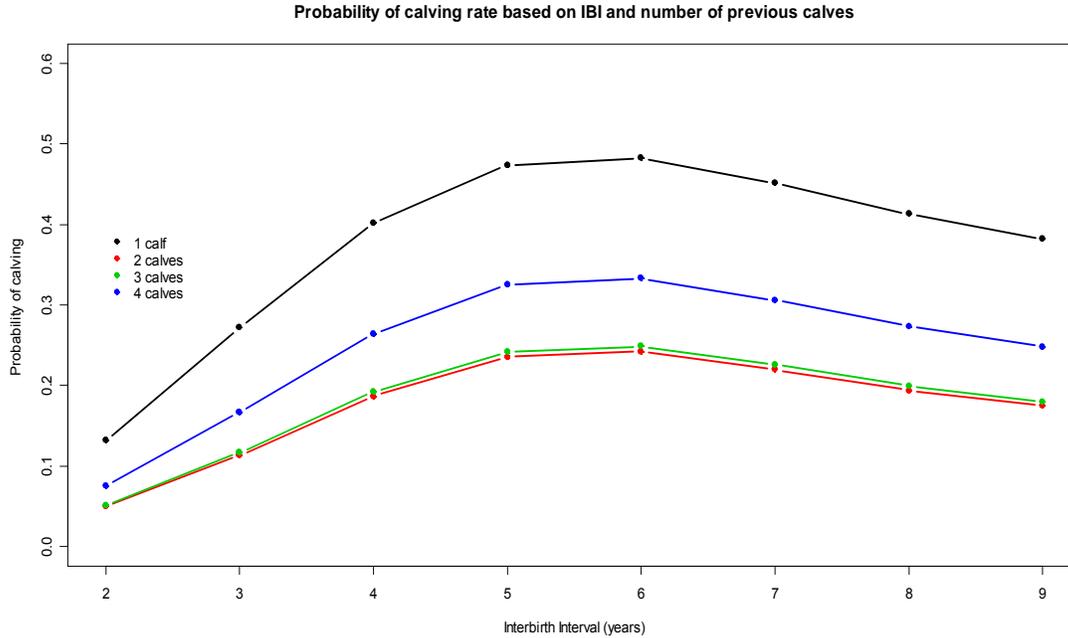


Figure 11: Predicted probability of calving based on IBI and previous number of calves born.

3.6.3. Mixed-effects models

The best-fitting GAM has captured some between-female variance and accounted for this in determination of the response, however, only 65.3% of the deviance is explained. Mixed-effects models were employed to try and capture more of the between-female variance through the incorporation of female as a random-effect. The best-fitting GAMM determined using R^2 was found to contain the smoothed effects Years since previous birth and year of birth, the linear term previous number of calves and individual females as the random effect. The model returns the smooth terms year of birth and the number of years since a previous birth and the parametric coefficient, the previous number of calves as significant predictors of the response variable, however, R^2 is very low (0.29) suggesting the model does not fit the data closely. The estimated model terms were plotted in the residual plots (figure 12) showing an estimated long-term trend appearing to decline in the late 1990s before increasing again. The humped relationship between years since previous birth and birth highlights the possibility of a threshold between 4 and 7 years since a previous birth in the prediction of the response.

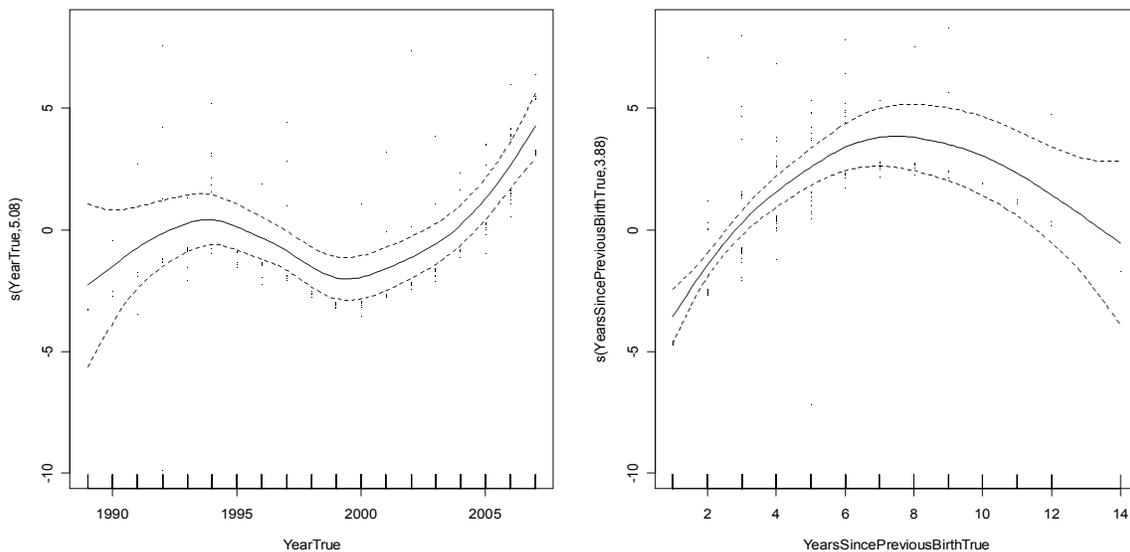


Figure 12: Residual plots for the smoothed terms in the mixed-effects model with birth as the response. From left to right: Year of birth and years since previous birth.

Both the GAM and GAMM suggest an increase in the number of calves being born in the later study years and a humped relationship between years since previous birth reaching an apparent threshold between 3 and 7 years (figures 9 and 12)

3.7. Modelling Inter-birth Interval as the response

The best-fitting GAM with IBI as the response variable returns the smoothed terms year of calf birth, previous number of calves and the number of years since first birth as significant predictors of the IBI (table 14, appendix 1). R^2 is very high ($R^2= 0.939$) suggesting a very close fit to the data, thus predictions made based on this model can be interpreted with a high level of confidence. The estimated model terms are plotted in the residual plots (figure 13). Curves corresponding to 1.8 df are estimated for the effect of year, 2.9 df for previous calves and 10.3 df for years since first calf. The TDF is 16.04. The degree of smoothness is estimated by the GCV score, which is low (GCV=0.45), indicating an appropriate model smoothness. The approximate p-values suggest significant predictors for the IBI are the number of previous calves ($p=1.5e-12$) and years since first birth ($p=2.86e-7$). Residual plots suggest an estimated trend in IBI which fluctuates with time. Given that the smoothed term 'Year of birth' is estimated to be a straight line, the model was also fitted with year as a parametric covariate without a smoothing function. The AIC value returned for the model containing year as a smoothed term (AIC=79.3) suggests a better model fit than that with year as a parametric coefficient (AIC= 82.2). Visualisation of the GAM is shown in figure 14, showing IBI regressed against the terms, previous number of calves and years since first birth.

3.7.1. Predictions made based on the best-fitting model

The predicted probability of giving birth after a specific interval and the associated standard error, based on combinations of the variables previous number of known calves and the number of years since a females first birth are shown in table 15 (appendix 1) and the predictions are shown in figure 15.

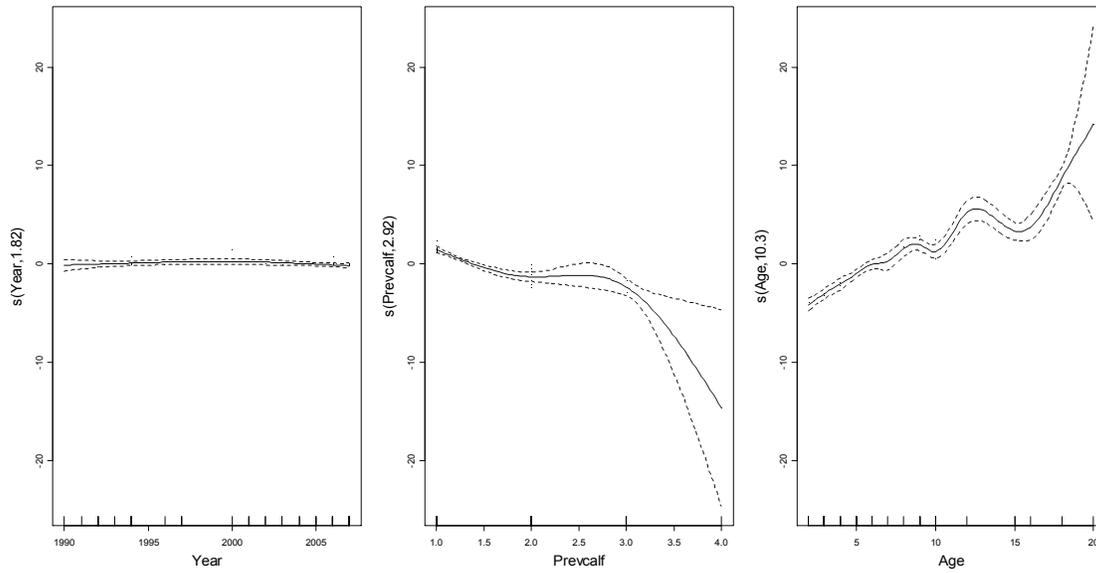


Figure 13: Residual plots for the smoothed terms in the model with IBI as the response. From left to right: Year of birth, the previous number of calves and the number of years since first birth.

Changes in IBI with previous number of calves and years since first birth

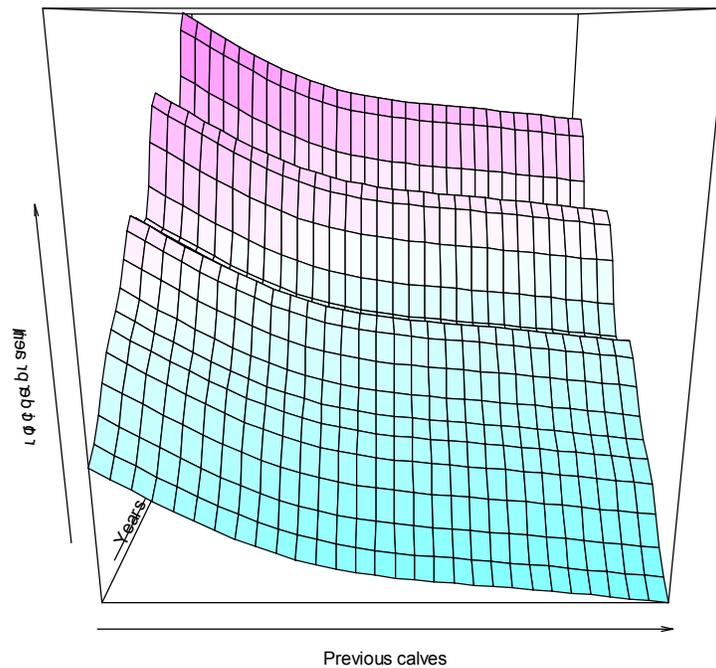


Figure 14: 3d visual plot showing the response regressed against the two main effect terms, previous number of calves and years since first birth.

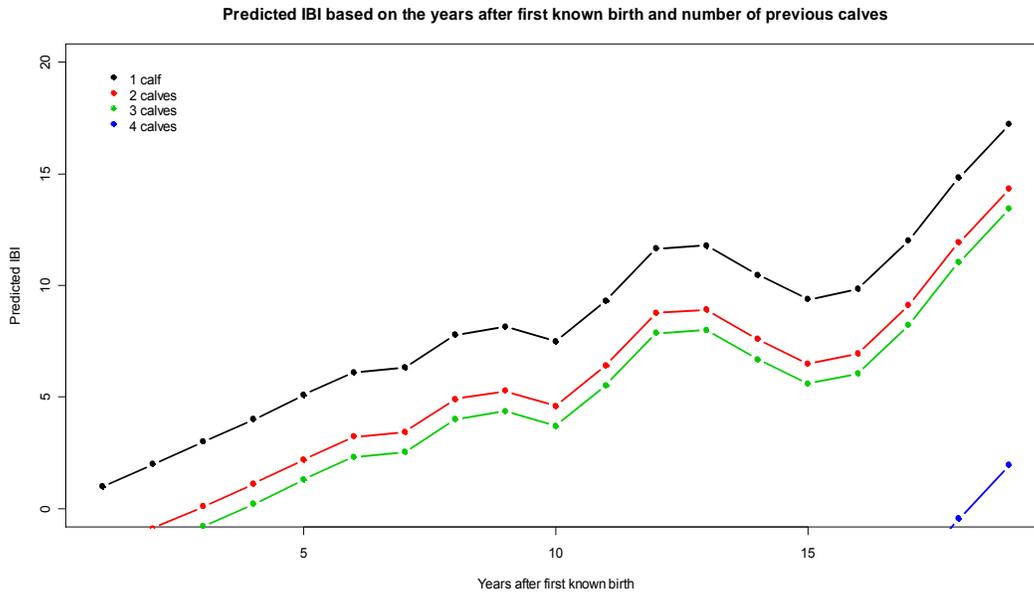


Figure 15: Predicted IBIs based on the years after first known birth and previous number of calves.

The best-fitting GAM with IBI as the response suggests that IBIs are best predicted by the number of previous known calves and years since first known birth. IBIs are predicted to be relatively constant, provided that the calf survives its first year (figure 15).

Model specification of the best assumed relationship between IBI and predictor covariates is:

$$Y_i = \beta_0 + f_1(\text{Year}_i) + f_2(\text{previous_Calves}_i) + f_3(\text{Years_after_first_birth}_i) + \varepsilon_i (Y_i \sim \text{Gaussian})$$

4. DISCUSSION

4.1. The benefits of long-term studies and collaborative effort between organisations

Primary interests of this study were to assess whether there was any variation in IBIs over time and due to individual females in the east coast of Scotland population of bottlenose dolphins, and to determine factors that were likely to be significant predictors for a calf being born. Two important and unique components essential in determining answers to the above questions relate to the use of long-term datasets and the collaboration between three important research organisations studying the population throughout different areas of their home range.

The use of long-term data from several research organisations has enabled more information on IBIs and calving histories of individual animals over time to be taken into consideration. The collaborative effort from several leading organisations with extensive long-term study histories of these animals was the first of its kind for this population and has benefitted this work greatly in several ways. It has allowed data-sparse animals in one region to be included in

the analysis when the data was complemented from another area. Collaboration has also enabled matching to be carried out between organisations for both mothers and calves, allowing a high degree of confidence in the assignment of a mother to a calf. The same individuals have also been sighted throughout a more extensive portion of their range, thus a greater level of information is available for individuals who are more transient, allowing their involvement in this analysis along with individuals who appear to be more resident in a particular area, such as the inner Moray Firth.

Long-term studies are important for the accurate determination and interpretation of IBIs and reproductive-related parameters for long-lived and slow-reproducing mammals such as the bottlenose dolphin, as well as other cetacean species (Hammond et al. 1990; Wells and Scott, 1990; Barlow and Clapham, 1997; Mann et al. 2000; Grellier et al. 2003; Steiner and Bossley, 2008). Throughout the waters of north-east Scotland, a combination of the strong residency patterns of the animals and the extensive survey effort and continued work of AULFS, CRRU and SMRU has enabled the production of detailed sighting histories for individually identified females and a great expansion in the collection of demographic information for this population. This has enabled the use of nearly 20 years of quality data-collection over a wide area of the species home range to determine reliable estimates of 42 IBIs for 26 individual females. There does however, remain a small amount of missing information where some females were not seen in a given year, leading to potential overestimation of 9 intervals (Baker et al, 1987).

Two key assumptions hold for the study of this population using photo-identification: the probability of observing an individual in a given year was independent of her reproductive status (Barlow, 1990) and the probability of observing a mother with a new calf was independent of whether the prior calf was observed (Payne et al. 1990).

4.2. Determination of adult females and assignment of mothers to calves

When studying the reproductive success of wild female dolphins, an issue of extreme importance is the identification of which individuals were female, and which of these females were reproductively mature (Grellier, 2000). Determination of the gender of wild bottlenose dolphins is difficult as the genital and mammary slits are not always easy to observe (Connor et al. 2000). In addition, adult bottlenose dolphins show a lack of obvious and recognisable sexual dimorphism (Read et al. 1993). The determination of gender for individuals in this population did include the observation of genital areas when the opportunity presented (Cheney, pers. comms), however, more commonly, repeat field observations of an individual consistently seen in association with a young calf were used (Grellier et al. 2003; Cheney, pers. comms; Robinson, pers. comms).

Knowledge of calving histories for individual females also required information on which of these females produced offspring in a given year (Grellier, 2000). Bottlenose dolphin calves depend on their mothers for an extended period, with the bond between the mother and calf strongest in the first year of life (Scott et al. 1990), thus the consistent presence of a young calf surfacing in the echelon position with a known female was used to assist in sex determination of an identifiable adult as a female and provide information on her reproductive status (Grellier, 2000; Cheney, pers. comms; Robinson, pers. comms). This technique worked well when the assumed mother was well-marked, sighted regularly, and sighted/recorded in small groups. However, problems arose when the converse situations occurred (Grellier, 2000; Robinson, pers. comms). 'Babysitting' of young calves is also known to occur in wild cetaceans (Whitehead, 1996). The occurrence of babysitting can reduce the number of observed associations between a mother and her calf and in some circumstances result in false pairings. This was minimised in this study by ensuring that at least two photographic frames showing the calf surfacing in the echelon position alongside the suspected mother were taken by each respective organisation (Cheney, pers. comms).

4.3. Inter-birth Intervals and implications for calf survival

This study expands on the results of Barlow (1990) and Payne et al. (1990) both of whom based the probability of giving birth solely on the time since a previous known birth. Variability in IBIs can potentially be attributed to several factors relating to an individual female including years since first birth, previous number of calves produced, year of calf birth, female age, female age at first birth, parity of the mother, body mass, survival of the previous infant (Mann et al. 2000) and whether the previous calf was known to be deformed or not, an issue of increasing concern in this population (Haskins and Robinson, 2007). There are also social factors including female dominance, group size, group composition and associations with other animals, both male and female. Other considerations that may have an effect on the above factors include spatial and temporal variation in resource availability, conditions for calf rearing, temperature and seasonality.

IBIs for this study were found to occur most commonly between 3 and 6 years (n=32 intervals) with few at only 2 years (n=5) and few greater than 6 years (n=4). Similar findings come from studies of bottlenose dolphin demographics in New Zealand (3 years, Haase and Schneider, 2001), South Africa (3 years, Cockcroft and Ross, 1989) and Japan (3-3.5 years, Kasuya et al. 1997; Kogi et al. 2004). Mann et al. (2000) report 4.1 year birth cycles for *Tursiops sp.* in Shark Bay, Australia, however, Mann et al. (2000) only calculated IBIs where successful weaning was known to have occurred, using the years between the birth of a surviving calf and another birth to determine IBI. This study looked at the years between the birth of one calf and the birth of the

next to determine IBI, irrespective of whether the previous calf survived. This was due to high levels of uncertainty relating to the determination of whether a calf was deemed to have survived to be successfully weaned and independent from its mother, for instance, there were difficulties in determining whether a calf sighted in association with its mother in year two, but not three has died or successfully become independent. Mann et al. (2000) determined IBIs for surviving/successfully weaned calves to be between 3.0 and 6.2 years, with 4 year intervals the most typical. The intervals present in this study imply that should weaning age be the same for this population as that of the Shark Bay population, then calf survival for the sample of mothers used in this study is high.

As observed for other cetaceans, calf death in the first year can lower the mean calving interval (Perrin and Reilly, 1984; Cockcroft and Ross, 1990; Bearzi et al. 1997), resulting in a lower mean IBI. Female AU#85 is an example of a mother for whom two calves were known to have died in their first years (AU calves #84 and #251 respectively). IBIs for #85 following these deaths were reported as 2 years, suggesting that #85 conceived again in the breeding season immediately following the death of her calves. The only report listing IBIs of 2 years with a surviving calf was for *T. truncatus* in Sarasota, Florida (Connor et al. 2000), however, intervals of 3-6 years were found to be more common. Based on the above literature, it is likely that if a calf survived beyond Year 1, IBI increases to 3-6 years, thus giving a good indication of the level of calf survival past first year for this sample. The estimates of IBIs for bottlenose dolphins in eastern Scottish waters are comparable to other populations worldwide and are suggestive that IBIs do not appear to be affected by latitude and/or water temperature. There may however, be some underestimation of mortality for young calves, given that some calves likely died before being sighted. Although infancy, and the first year in particular, is the period of greatest mortality risk (Mann et al. 2000), juveniles also die before weaning, which may lead to the mothers resumption of cycling in the year immediately after a juvenile death.

The average IBI when accounting for only births where the female was sighted at least twice in every year between successive calves (n=31 intervals) is 2.8 years, median=5yrs, however, the average for all of the intervals (n=42 intervals) is 3.8 years, median=5.5yrs (a little higher than the above estimates). This may represent an overestimation of IBIs due to missed birth events, or the need for mothers in this high latitude, temperate population to invest more energy and time into the successful rearing of her calf.

The best-fitting GAM suggests that IBIs are predicted by the number of previous known calves and years since a females first known birth. IBIs were predicted to be relatively constant, provided that a given calf survives its first year (figure 15). Between female variation in IBI is

relatively low suggesting that there is a higher level of variation within each female, however, within-female variation in IBIs was difficult to determine for this sample as most females have only 1 or 2 intervals to assess. A lot of the variation in IBIs is also likely due to fixed-effect covariates, for instance, associated with the years since first birth and previous number of calves for a given female. There also appears no significant variation between individual females in their calving rates and there is no apparent significant variation in annual calving rate. There was an apparent increase in the number of calves produced in the later years of the study. This likely reflects an increase in effort and increased survey work by some or all of the organisations, as there is no significant variation in the calving rate between years shown by increased numbers of females being sighted in the later survey years also. However, this could reflect an actual trend whereby there is a true increase in the number of calves being produced.

4.4. The effects of age on Inter-birth Intervals

This study found that there were no significant differences in IBI lengths that were attributable to age for each individual with more than one IBI (n=12 females). This could suggest that individuals do not appear to change their reproductive output and IBIs significantly with time, and that age, often identified in the literature as a causal factor for IBI length (Whitehead and Mann, 2000), was not operating in the life histories of this sample of females. However, it is possible that despite the nearly two-decade length of the study, there was not a sufficient sample size of females with long enough sighting records after their first birth to allow discrimination of individual differences brought about by age. It is thus difficult to conclude with confidence any lack of significant change in IBIs with age.

There is a decline in the number of females remaining in the trial through time when the female enters the trial in the year after her first birth, resulting in 'incompleteness' or 'dropout' (Verbeke and Molenberghs, 2000). This refers to cases where all observations on an individual were obtained until a certain point in time, after which, all measurements were missing. An issue resulting from 'dropout' is depletion of study subjects in higher age classes (Verbeke and Molenberghs, 2000). This decreasing sample size leads to an increase in variability, which in turn, may decrease the precision of analyses carried out to determine whether there is any significant variation with time. The survival curve shows that there is dropout of the subjects through time in this analysis, with a higher proportion of dropout in the later age classes (as shown in the Kaplan-Meier estimate). The higher proportion of dropout in the later age classes is likely due to the smaller number of individuals present in these age classes, making the effect of dropout of one individual appear greater. This does however, lead to the scenario where few females are present in the later times since first birth. Factors affecting the dropout rate have not been determined for

the subjects in this study, although it is known that female AU#85 died in 1997 (AULFS, unpublished records). Of the 26 females present in the study, 17 were sampled in 2007, indicating that 'dropout' in the large majority of cases was due to termination of the trial and not due to factors such as death or migration.

Although 17 IBIs are not completed due to termination of the study in 2007, two females show an extended period after the birth of their last known calf where no further calves are born. This could be indicative of reproductive senescence, or merely an artefact of the data collection due to missed sightings. Although most female mammals show an age-specific fertility decline, few species show clear evidence of menopause, the termination of reproductive function before expected age of death (eg. Dunbar, 1987). Physiological and demographic data indicate menopause for short-finned pilot whales (Marsh and Kasuya, 1984) and killer whales (Olesiuk et al. 1990) and reduced fertility with age for other odontocete species, including *Tursiops*. (Marsh and Kasuya, 1986). The decline in pregnancy rate with age can be explained by life history theory predicting that as female age, they should allocate a greater proportion of resources to each offspring by increasing IBIs and nursing offspring longer (Clutton-Brock, 1984, Whitehead and Mann, 2000).

AU#85 was known to have died in 1997, however, she continued to reproduce into her final years, producing calf #433 in 1994 and rearing her successfully to independence (#433 is a known-age female). Female #85 was with a calf when the study began in 1989 and was known to have produced 3 calves within the study period. The cause of death and the age of #85 at the time of death however, was not determined by post-mortem examination (Thompson, pers. comms).

4.5. Determination of age-at-first-birth

The sighting of 17 animals in 2007 and the relatively short sightings histories of these animals, suggest that the females were missed in surveys carried out in earlier years, or that these females are all relatively young and were previously reproductively immature, thus the calves recorded are probable first calves.

Past studies suggest that first-time mothers are more likely to lose their first calf than experienced mothers (Clutton-Brock, 1988). There are three known-age mothers for this population, two of which are known to have produced multiple calves, thus allowing discussion of whether first calf survival is present here. The age-at first birth for the three females are: AU#433= 12 years old, AU#733= 6 years old, and AU#11= 13 years old. Of these known-age females, #11 and #733 are known to have had two calves, born at intervals of 5 and 3 years after the first known calf respectively, indicating that it is likely that the first calf survived beyond its first

year. #433 was recorded with her calf in 2008 (Cheney pers. comms) thus, this calf has survived its first year also.

The reported ages at first birth (6-12 years) are within the ranges reported for other *Tursiops* (Shark Bay, 12-15 years, Mann et al. 2000; 6-7 year old female births known to have occurred in Sarasota, Wells et al. 1987). Age at first birth in the east coast of Scotland must enable females to grow to a size where they are large and fit enough to produce a calf that the female can successfully nurse. The exclusive use of known-age animals to estimate reproductive parameters would help in the long-term determination of the effects of age on IBI, however, would severely restrict the sample size (n=3 animals) and not be useful for the analyses carried out in this study.

4.6. Social factors affecting Inter-birth Intervals

There are factors known to affect IBIs which are related to the social behaviour of females (Whitehead and Mann 2000), these include grouping behaviour and dominance. The general costs and benefits of group living among cetaceans are discussed by Connor et al. (2000). Females in different stages of their reproductive cycles may segregate on account of different food requirements (Bernard and Hohn, 1989) or other behavioural differences related to the presence or absence of a calf (Mann and Smuts, 1999). Calf protection may be another function for grouping in females (Mann and Smuts, 1998). Newborn calves are thought to be the most vulnerable in their first year of life and (Mann et al. 2000), found that this was when mothers stayed in the largest groups.

Dominance has not been systematically studied in wild bottlenose dolphins, only in captivity (Samuels and Gifford, 1997). Agonistic interactions involving female bottlenose dolphins are rarely observed, either in captivity (Samuels and Gifford, 1997), or in the wild (Mann and Smuts, 1998) making it difficult to assess dominance relationships and whether they are of biological significance (Whitehead and Mann, 2000). Reproductive suppression may be a form of female-female competition in which dominant females, either through harassment or other forms of social competition, cause subordinate females to suppress or delay cycling (Whitehead and Mann, 2000). Reproductive suppression has been documented in a variety of mammals, including wolves (*Canis lupus* eg. Derix et al. 1993), rodents (eg. Wolff, 1992), and primates (eg. Snowdon, 1996). For social animals, the benefits of group living are not equal for all members of the group. If there is an optimal group size, or resource competition favours fewer group members, reproductive suppression is one way that dominant females can favour their own reproduction at the cost of that of other females in the group (Whitehead and Mann, 2000). Reproductive suppression is most likely in species in which females form long-term cooperative groups

(Snowdon, 1996), so it might be most expected in sperm whales or killer whales but not likely for bottlenose dolphins (Whitehead and Mann, 2000; Mann et al. 2000). However, there has been no systematic search for evidence of reproductive suppression in bottlenose dolphins (Whitehead and Mann, 2000).

Another variable that could potentially be identified as a causal factor in affecting the fecundity of female mammals are known associations with other females. This may allow co-operative breeding strategies amongst females whereby females will help another to nurse her calf, while at the same time, potentially practising her own parenting. Analysis of known female-female associations and the IBIs and year of calf births can be used to determine the level, if any, of co-operative breeding strategies in this population.

4.7. Accounting for the effect of individual females and between-female variation

There appears to be little evidence for variation resulting from differences amongst the 26 individual females in this study. However, the primary concern was not the individual status of each particular individual in this study; if 26 different individual females had been used, these effects would have taken slightly different values. Without determining the level of between-female variation, ignoring the effect of individual females could have induced a level of dependence between the response observations for IBI and calving, thus it was deemed appropriate to model the distribution of female effects across the population and to suppose that the particular female effects in the study were independent observations from this distribution. This was done through the modelling of the female effect as the random component of a mixed-effect GAM, with other significant covariates modelled as fixed effects in determining the response.

GAM incorporating females as a fixed-effect term would not be appropriate to predict the effect of a female other than for the 26 in the study if there was significant between-female variation. Incorporating female as a fixed-effect would make the model too flexible by implying that each female was completely different to every other. Thus, having the results for 26 females would suggest nothing about those outside the sample. Treating individuals, not as completely unique, but as a random sample from the target population would allow estimation of the effects of the other variables, and generalise beyond only the females in the study, were female to be returned as a significant determinant of IBI or calving.

The best predictors of IBI and calving rate as determined from the use of GAMs did not include the individual female when she was present in the model as a fixed effect term. The inclusion of the female as a fixed-effect term in the model cannot determine the effect of individuals unless the individual effect is negligible, which it does not appear wholly to be

($R=0.35$), thus the incorporation of the female as a random term in the mixed-effects model was employed to determine whether the response is in part determined by the effect of individuals. This confirmed that there appears to be little, if any between-female variation responsible for determining the IBI or calving rate and that the inclusion of female in the model as a random-effect yields the same significant predictors and effects on the response variables for calving and IBI, however, with poorer model fit, determined by the low R^2 score.

4.8. Summary

The bottlenose dolphin can have a reproductive lifespan of around 40 years, thus despite almost two decades of data collection, only a snapshot of the reproductive status of a few individual females in the population has been captured. Female bottlenose dolphins invest heavily in their calves, and show a prolonged period of nursing and maternal investment. The breeding cycle is a lengthy process incorporating a 12 month gestation period, and a nursing period, which can last up to six years if the calf survives its first year and juvenile period (Mann et al. 2000; Grellier et al. 2003). Getting an extensive reproductive history for a large sample of individual females with multiple calves is thus difficult. The determination of effects of maternal age and previous number of calves on IBI length and reproductive success will require many more years of dedicated survey effort and accurate assignation of known mothers to calves. This will build on the strong dataset that has been used for this analysis and will also require continued research and an increased collaborative effort between all parties involved in the study of this population throughout its range.

Within this sample, individual females show variation in the length of their IBIs, both between and within females. Continued study of this population over time will help explain the relevance of any variability between- and within- females and help determine any change through time in IBIs and the reproductive success of females in this unique population of bottlenose dolphins. IBI change through time could form an essential component of a population growth model. In this study, predictions were made of IBIs and the probability of calving dependent on known parameters related to individual females. These estimates could potentially be combined with survival rates for animals in this population to assist in the development of an age-structured model for the population. The estimates could then form an essential component for the estimation of the asymptotic rate of growth for the population (see Barlow and Clapham, 1997). The approach used in this study is also applicable to other populations and species for which there is a long-term data series available.

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7. Appendix 1: Results and output

Table 1: Calving rate of individual females in the sample: Female ID number (AULFS), number of known calves, number of years sighted after the attainment of sexual maturity, and calving rate as the number of known calves as a proportion of the years sighted.

Female	No. calves	Number of years each female was sighted	Calving rate
4	4	18	0.22
9	3	17	0.176
11	2	7	0.286
24	2	4	0.5
27	3	12	0.25
30	3	17	0.176
31	3	14	0.214
52	2	6	0.33
55	2	14	0.143
58	2	12	0.167
61	3	17	0.176
64	5	20	0.25
68	2	12	0.167
85	4	9	0.44
120	2	17	0.118
240	2	11	0.182
307	2	5	0.4
440	2	5	0.4
578	2	6	0.33
732	3	10	0.3
733	2	5	0.4
745	2	9	0.22
800	3	9	0.33
909	3	11	0.273
913	3	9	0.33
963	2	7	0.286

Table 2: Probability values for the single-factor analysis of variance test carried out to determine whether there appears to be any significant difference between the calving rates of individual females. The between group variability is indexed by Female and SumSq (sum of the squares). The within group variability is indexed by residuals and SumSq.

	DF	Sum Sq	Mean Sq	F-value	Pr(>F)
Female	1	0.485	0.485	2.6523	0.1045
Residuals	279	51.059	0.183		

Table 3: Annual calving rate for the females in this study, based on the number of known sexually mature females sighted in a given year: number of known calves, number of known mature females sighted in each year, and calving rate as the number of known calves as a proportion of the females sighted in each year.

Year	Calves born	Females sighted in each year	Calving rate
1989	4	8	0.5
1990	2	10	0.2
1991	3	9	0.33
1992	4	12	0.33
1993	1	11	0.091
1994	6	14	0.429
1995	2	12	0.167
1996	2	12	0.167
1997	3	12	0.250
1998	1	14	0.071
1999	0	17	0.00
2000	4	15	0.267
2001	3	17	0.176
2002	3	19	0.158
2003	5	21	0.238
2004	4	21	0.190
2005	3	16	0.186
2006	8	20	0.400
2007	6	17	0.353

Table 4: Probability values for the single-factor analysis of variance test carried out to determine whether there appears to be any significant difference between annual calving rates. The between group variability is indexed by Year and SumSq (sum of the squares). The within group variability is indexed by residuals and SumSq.

	DF	Sum Sq	Mean Sq	F-value	Pr(>F)
Year	1	0.205	0.205	1.1162	0.2917
Residuals	279	51.339	0.184		

Table 5: Number of each IBI present in the sample: total number of intervals (n=42) and number of intervals where there is a complete female sighting history between subsequent birth events (n=26). The proportion of intervals was calculated. Mean interval length (years), standard deviation and median are shown.

Inter-birth interval (years)	Total intervals	Proportion of total intervals	Complete intervals	Proportion of complete intervals
2	5	0.119	5	0.161
3	9	0.214	6	0.194
4	9	0.214	8	0.267
5	7	0.167	5	0.133
6	7	0.167	4	0.133
7	0	0	0	0
8	1	0.0238	1	0.033
9	3	0.0714	2	0.067
10	0	0	0	0
11	0	0	0	0
12	1	0.024	0	0
Mean	3.818		2.818	
Standard deviation	14.349		5.935	
Median	5.5		5	

Table 6: Single factor anova test showing variation in IBIs between successive calves

Groups	Count of IBIs	Sum of IBIs	Average Interval for each calf	Variance
IBI calf 1 and 2	25	108	4.32	3.39
IBI calf 2 and 3	12	64	5.3	8.24
IBI calf 3 and 4	3	13	4.33	4.33
IBI calf 4 and 5	1	4	4	

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	8.983	3	2.99	0.613	0.611	2.859
Within Groups	180.8	37	4.886			
Total	189.8	40				

Calculation of ICC:

Table 7: Numbers used in the derivation of the Intra-class correlation coefficient for the females with a complete sighting history in the sample (n=12 females).

Female	IBI 1	IBI 2	IBI 3	IBI 4	ni	SX	SX^2	(SX^2)/ni	IBI1^2	IBI2^2	IBI3^2	IBI4^2
27	3	6			2	9	81	40.5	9	36	0	0
30	3	9			2	12	144	72	9	81	0	0
85	3	2	2		3	7	49	16.333333	9	4	4	0
732	4	3			2	7	49	24.5	16	9	0	0
4	4	6	5		3	15	225	75	16	36	25	0
31	6	4			2	10	100	50	36	16	0	0
64	6	4	6	4	4	20	400	100	36	16	36	16
800	2	4			2	6	36	18	4	16	0	0
909	6	4			2	10	100	50	36	16	0	0
913	4	3			2	7	49	24.5	16	9	0	0
61	6	12			2	18	324	162	36	144	0	0
9	8	7			2	15	225	112.5	64	49	0	0
Total	12				28	136		745.33333				

Table 8: Anova showing the determination of the coefficient of repeatability for the complete sightings sample (n=12 females).

	DF	Sum of squares	Mean of Squares
Among female (MSA)	11	84.761905	7.7056277
Between females error (MSE) (S^2E)	16	54.666667	3.4166667
No.		2.3311688	
Among female error (S^2A)		1.8398329	
R=S^2A/(S^2A+S^2E)=		0.350011	

Table 9: Numbers used in the derivation of the value for the repeatability coefficient for all the females in the sample (n=26 females).

Female	IBI 1	IBI 2	IBI 3	IBI 4	ni	SX	SX^2	(SX^2)/ni	IBI1^2	IBI2^2	IBI3^2	IBI4^2
24	2				1	2	4	4	4	0	0	0
27	3	6			2	9	81	40.5	9	36	0	0
30	3	9			2	12	144	72	9	81	0	0
85	3	2	2		3	7	49	16.3	9	4	4	0
120	5				1	5	25	25	25	0	0	0
240	9				1	9	81	81	81	0	0	0
440	3				1	3	9	9	9	0	0	0
732	4	3			2	7	49	24.5	16	9	0	0
963	5				1	5	25	25	25	0	0	0
4	4	6	5		3	15	225	75	16	36	25	0
11	5				1	5	25	25	25	0	0	0
31	6	4			2	10	100	50	36	16	0	0
52	2				2	2	4	2	4	0	0	0
55	3				1	3	9	9	9	0	0	0
58	5				1	5	25	25	25	0	0	0
64	6	4	6	4	4	20	400	100	36	16	36	16
307	2				1	2	4	4	4	0	0	0
745	5				1	5	25	25	25	0	0	0
800	2	4			2	6	36	18	4	16	0	0
909	6	4			2	10	100	50	36	16	0	0
913	4	3			2	7	49	24.5	16	9	0	0
68	3				1	3	9	9	9	0	0	0
578	4				1	4	16	16	16	0	0	0
61	6	12			2	18	324	162	36	144	0	0
9	8	7			2	15	225	112.5	64	49	0	0
Total	25				42	189		1004.3				

Table 10: Anova showing the determination of the coefficient of repeatability for all of the females in the sample (n=42 females).

	DF	Sum of squares	Mean of squares
Among female error (MSA)	24	153.83333	6.4097222
Between female error (MSE) (S^2E)	17	56.666667	3.3333333
No		1.7103175	
Among female error (S^2A)		1.7987239	
R=S^2A/(S^2A+S^2E)=		0.350488	

Table 11: Number of females present each age class following the year after her first known birth, and the subsequent survival into future age classes as the proportion of those present in age class one.

Age class	Number	Proportion remaining
1	26	1
2	26	1
3	25	0.96
4	23	0.88
5	20	0.77
6	19	0.73
7	18	0.69
8	15	0.58
9	15	0.58
10	13	0.5
11	12	0.46
12	9	0.35
13	7	0.27
14	7	0.27
15	7	0.27
16	7	0.27
17	6	0.23
18	3	0.12
19	2	0.08
20	1	0.04

Table 12: calculations for Kaplan-Meier estimator of $S(t)$. Column 1 contains the number of years after an animals first known birth. Column 2 indicates failures ie. how many females present in the previous age class are not present in the current age class. Column 3 contains the number that could have been present in the corresponding time. Column 4 is calculated using the equation $1-d/n$ and Column 5 is the value in the previous row of column 5 multiplied by the value in the present row of column 4.

Age class	No. females not present in age class who were present in previous (d)	No. females (n)	$1- d/n$	$S(t)$
1	-	26	-	1
2	0	26	1	1
3	0	26	1	1
4	1	25	0.96	0.96
5	2	23	0.92	0.96
6	3	20	0.87	0.91
7	1	19	0.95	1
8	1	18	0.95	0.91
9	3	15	0.83	0.92
10	0	15	1	1
11	2	13	0.87	0.8
12	1	12	0.92	1
13	3	9	0.75	0.65
14	2	7	0.78	1
15	0	7	1	0.83
16	0	7	1	1
17	0	7	1	0.83
18	1	6	0.86	1
19	3	3	0.5	0.49
20	1	2	0.67	1
21	1	1	0.5	0.36

Table 13: number of females in each age class, number of calves born to females in each class and the calving rate of each class, where age class 1 is the year after first birth.

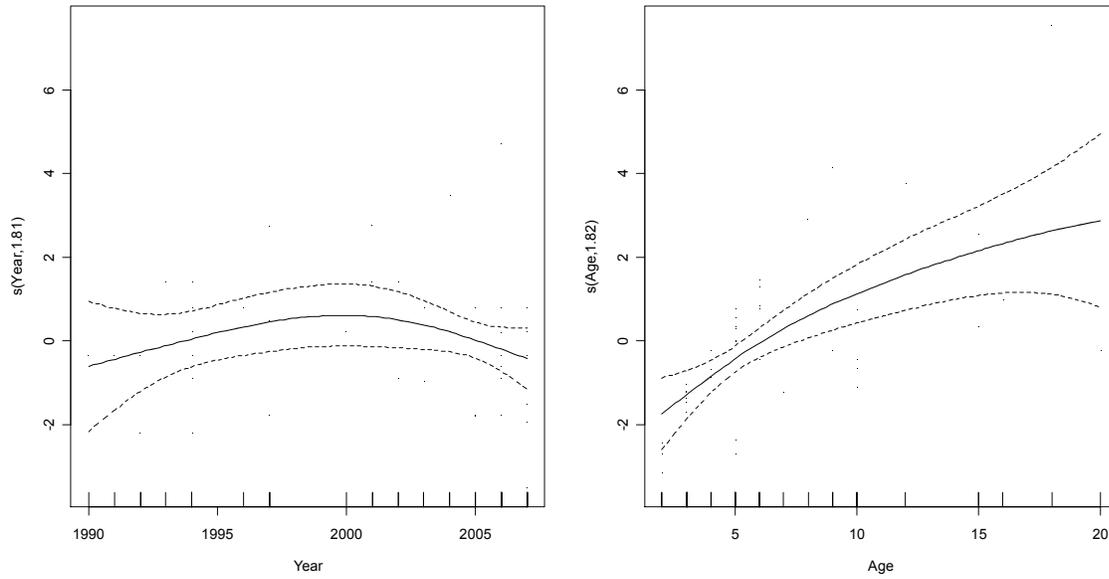
Age Class	Number of females	Number of calves	Calving rate
1	26	0	0
2	26	3	0.12
3	25	8	0.32
4	23	3	0.13
5	20	7	0.35
6	19	5	0.26
7	18	2	0.11
8	15	1	0.07
9	15	2	0.13
10	13	4	0.31
11	12	0	0
12	9	1	0.11
13	7	0	0
14	7	0	0
15	7	1	0.14
16	7	1	0.14
17	5	1	0.2
18	3	1	0.33
19	2	0	0
20	1	1	1

Model output and predictions for all intervals

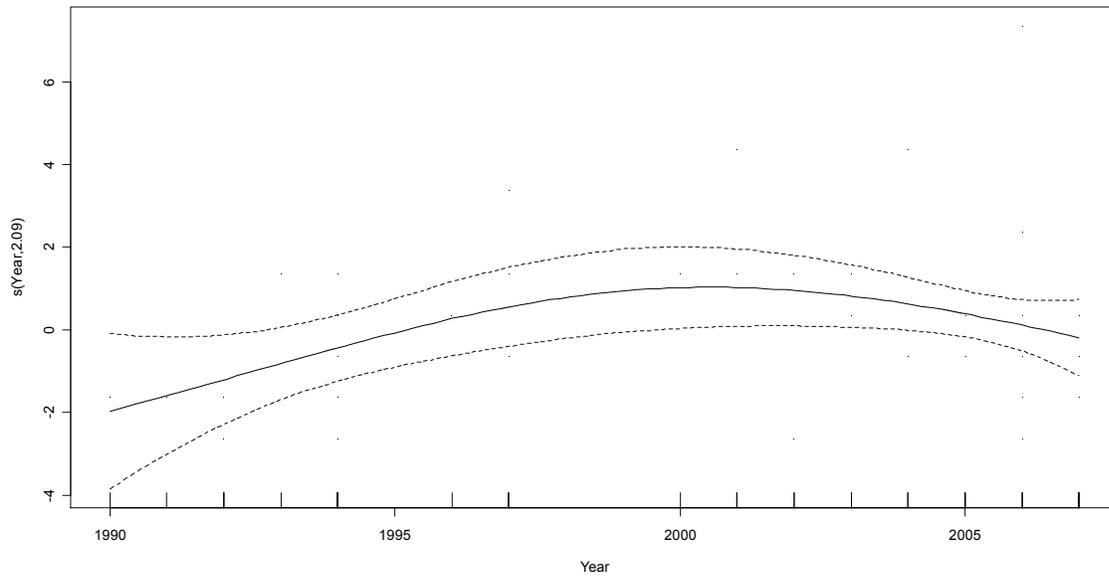
Table 14: Output from GAMs for the dataset containing all the intervals between births (n=42). Each model is shown with its respective parametric and smooth covariates. For each covariate, the slope estimate is given, along with the p-value representing the significance of the covariate in the model response, the standard error, the estimated and total degrees of freedom (EDF) and (TDF), the adjusted R², generalized cross-validation (GCV) value, % deviance explained and the AIC value representing the best fitting model.

<u>Model</u>	<u>Covariates</u>	<u>Estimate</u>	<u>SE</u>	<u>P</u>	<u>EDF</u>	<u>TDF</u>	<u>Adj R²</u>	<u>GCV</u>	<u>Dev explained</u>	<u>AIC</u>		
Model 2	Parametric coefficients	Intercept	4.643	0.304	2e-16		0.14	4.202	18.4%	181.25		
	Smooth terms	Year (k=9)			0.0885	2.09	3.09					
Model 3	Parametric coefficients	Intercept	4.643	0.191	2e-16							
	Smooth terms	Age (k=10)			4.2e-7	8.69	9.69	0.662	1.989	73.4%	147.432	
Model 4	Parametric coefficients	Intercept	4.643	0.329	2e-16		-	4.813	3.03%			
	Smooth terms	Previous calves (k=4)			0.531	1.37	2.37	0.0032	4.813		187.053	
Model 5	Parametric coefficients	Intercept	4.643	0.081	2e-16							
	Smooth terms	Year (k=15)			0.166	1.82		0.939	0.4498	96.1%	79.299	
		Prev Calves (k=4)				1.05e-12	2.92					
		Age (k=14)				2.86e-7	10.3					
Model 7	Parametric coefficients	Intercept	29.871	32.79	0.371			15.3	0.934	0.472	95.7%	82.17
		Year	-0.0126	0.0164	0.448	1						
	Smooth terms	Previous calves (k=4)				1.1e-12	2.91					
		Age (k=14)			3.77e-7	10.4						
Model 6	Parametric coefficients	Intercept	4.643	0.083	2e-16			14.5	0.963	0.444	95.7%	80.592
	Smooth terms	Prev Calves (k=4)			6.16e-13	2.85						
		Age (k=14)				2.49e-7	10.6					
Model 1	Parametric coefficients	Intercept	4.643	0.248	2e-16			4.63	0.428	2.909	47.9%	165.48
	Smooth terms	Year (k=4)			0.189	1.8						
		Age (k=14)				0.079	1.8					

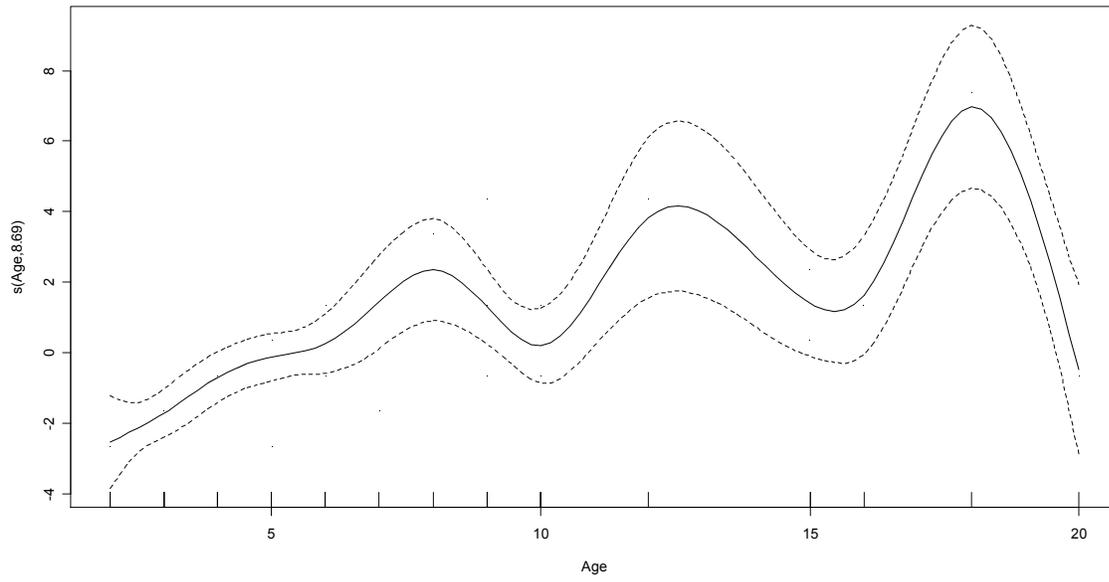
Figure 1: Residual plots for the smoothed terms in each model:



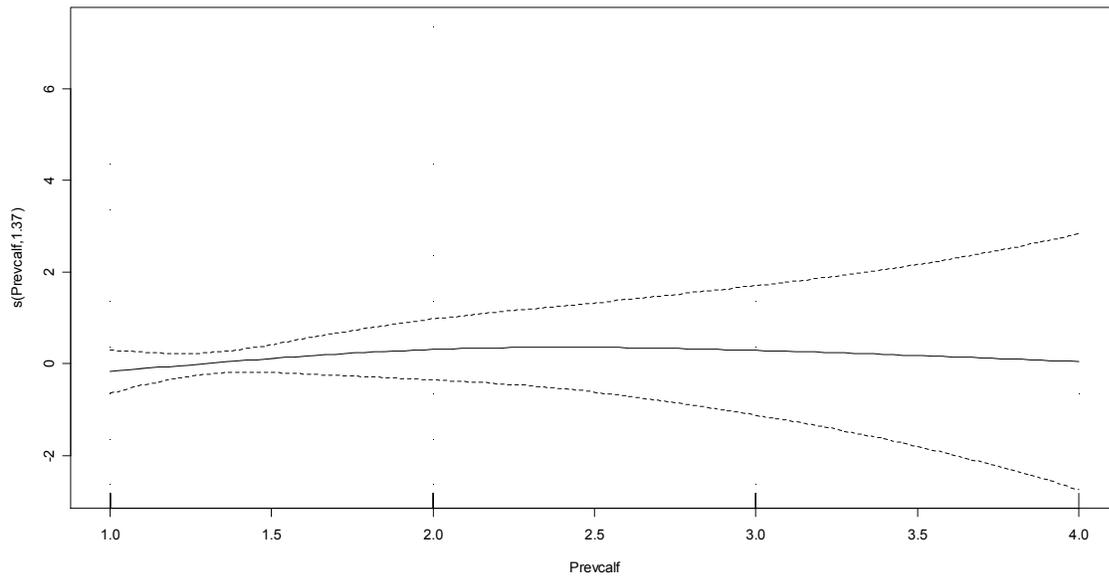
1.1. Model 1



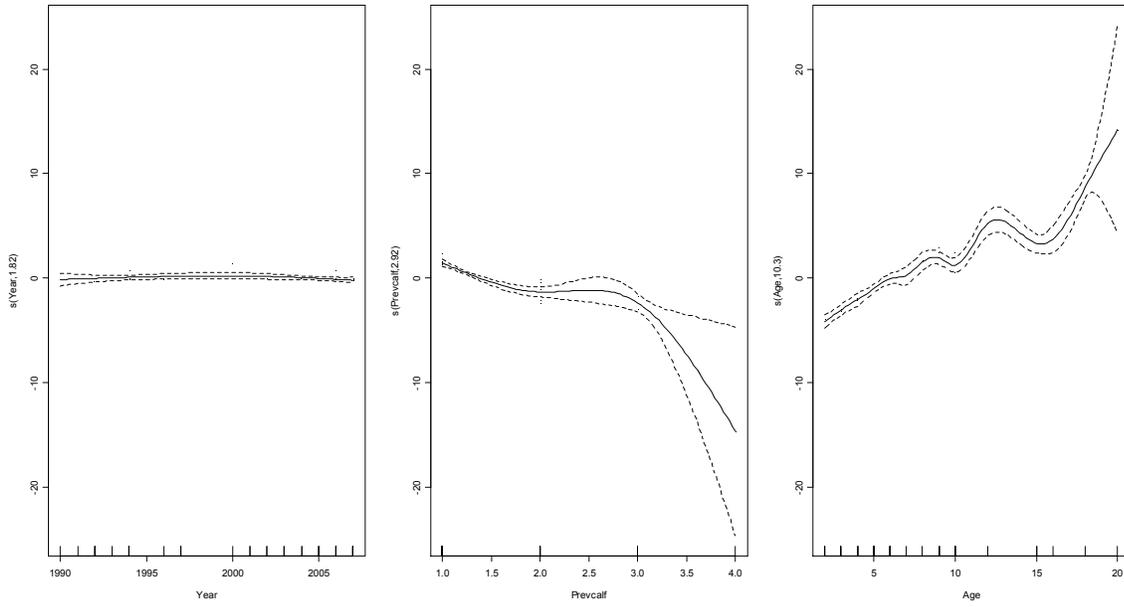
1.2. Model 2



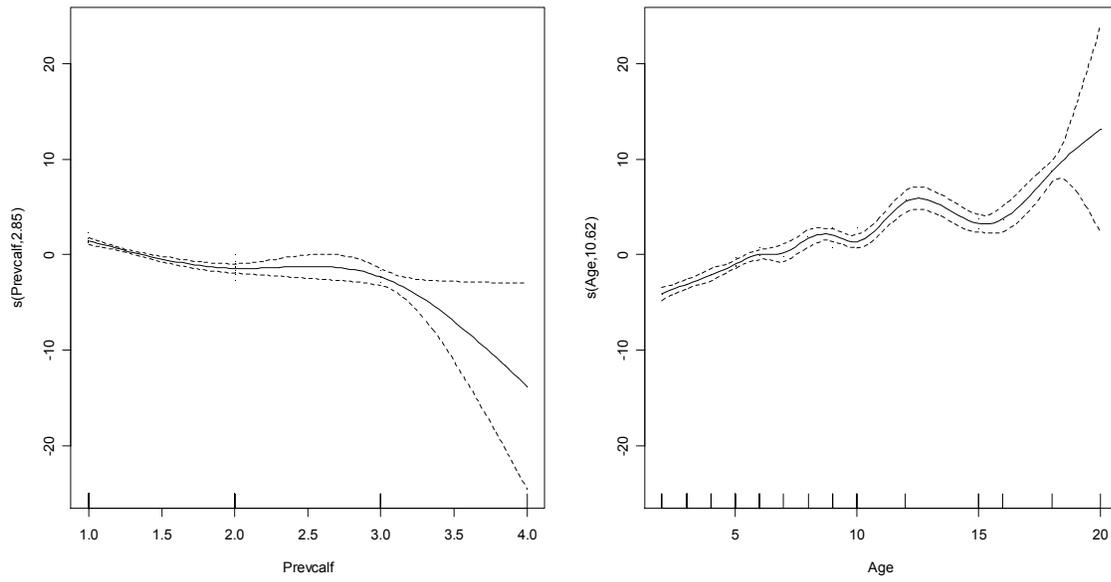
1.3. Model 3



1.4. Model 4



1.5. Model 5



1.6. Model 6

Table 15: Predicted IBIs (with se limits) based on the predictor variables; number of previous calves and years since first known birth derived from the model using all of the intervals (n=42).

Years since first birth	Number of previous calves	Predicted IBI	SE of prediction
2	1	2.0003	0.3083
3	1	2.9994	0.1865
4	1	3.9971	0.2859
5	1	5.0986	0.1996
6	1	6.1129	0.2433
4	2	1.1093	0.4215
5	2	2.2109	0.3248
6	2	3.2252	0.3319
7	2	3.4283	0.4571
8	2	4.9117	0.5054
9	2	5.2756	0.3139
10	2	4.6086	0.2629
11	2	6.4278	0.3641
12	2	8.7684	0.5260
9	3	4.3803	0.5381
10	3	3.7133	0.5467
11	3	5.5325	0.6100
12	3	7.8731	0.7131

Table 16. Model output and predictions using GAMs with calving as the response

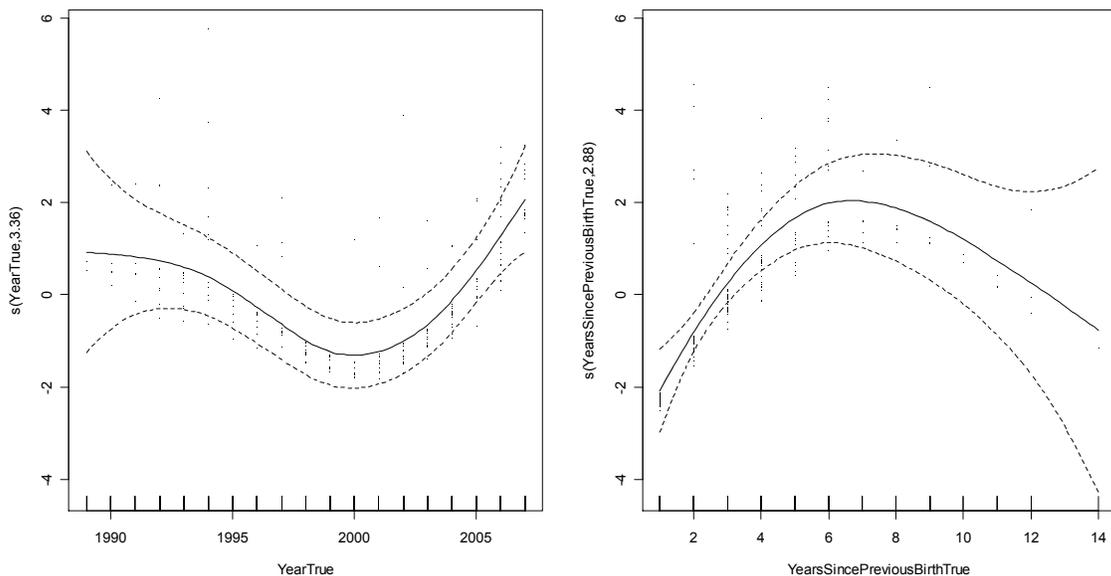
<u>Model</u>		<u>Covariates</u>	<u>Estimate</u>	<u>SE</u>	<u>P</u>	<u>Chi Sq</u>	<u>EDF</u>	<u>TDF</u>	<u>Adj R²</u>	<u>% Dev exp</u>	<u>AIC</u>	<u>UBRE</u>
Model 1	Parametric coefficients	intercept	-1.41e+1	3.87e+7	1						152.6	-0.364
		As.factor(female)			0.91	16.2						
		As.factor(year)			1.00	1.6e-7						
		Previous calves	-2.21e+1	5.99	0.000	13.5						
	Smooth terms	Years since previous birth			0.022	17.9	7.32		0.779	78.1		
Model 2	Parametric coefficients	Intercept	-1.504	0.7256	0.038			9.23	0.276	29.4	175.8	-0.271
		Previous calves	-0.500	0.347	0.15			7				
		Female	0.0008	0.0008	0.341							
	Smooth terms	Year			0.000	26.2	3.36					
		Years since previous birth			1.51e-5	32.2	2.89					
Model 3	Parametric coefficients	Intercept	-2.24e+1	7.38e+4	1							
		As.factor (Year)			1	1.6e-6						
		Previous calves	-5.47e-1	3.74e-1	0.143	2.15						
		Female	1.00e-3	9.420e-4	0.287	1.13						
	Smooth terms	Years since previous birth			1.72e-5	31.9	2.75	23.7	0.31	38.8	183.9	-0.237
Model 4	Parametric coefficients	Intercept	-2489.5	647.5	0.000							
		As.factor(female)			1							
		Year	1.25	0.326	0.132	32.9						
		Year			0.000	14.8						
		Previous Calves	-7.84	1.799	1							

	Smooth terms	Years since previous birth			0.001 92	24.5	5.41	33.4 1	0.428	50.8	176.5	-0.268
Model 5	Parametric coefficients	Intercept	18.43	5.21	0.000 41			37.2 0	0.607	64.9	152.6	-0.367
		Previous calves	-10.1	2.44	3.68e -5	17.0						
	Smooth terms	As.factor(female) Year			0.20 0.000 31	30.7 30.9	4.37					
		Years since previous birth			0.001 1	25.9	5.83					
Model 8	Parametric coefficients	Intercept	0.785	1.35	0.56			36.7 8	0.616	65.3	150.8 4	-0.374
	Smooth terms	As.factor (female) Year true (k=10)			0.129 0.000 17	33.08 32.47	4.20 8					
		Years since previous birth (k=9)			0.000 83	26.59	4.72 2					
		Previous Calves (k=4)			7.21e -5	21.79	1.85 2					
Model 6	Parametric coefficients	Intercept	-1.08	0.556	0.051			8.17 4	0.276	28.9	174.8	-0.275
		Previous calves	-0.632	0.314	0.044	4.06						
	Smooth terms	Year			0.000 17	28.6	3.28					
		Years since previous birth			1.83e -5	31.7	2.89					
Model 7	Parametric coefficients	Intercept	-0.826	0.501	0.09				0.117	15.6	198.5	-0.176
		Previous calves	0.641	0.295	0.029	4.7						
	Smooth terms	Years since previous birth			0.001	24.2	3.13	5.12 5				

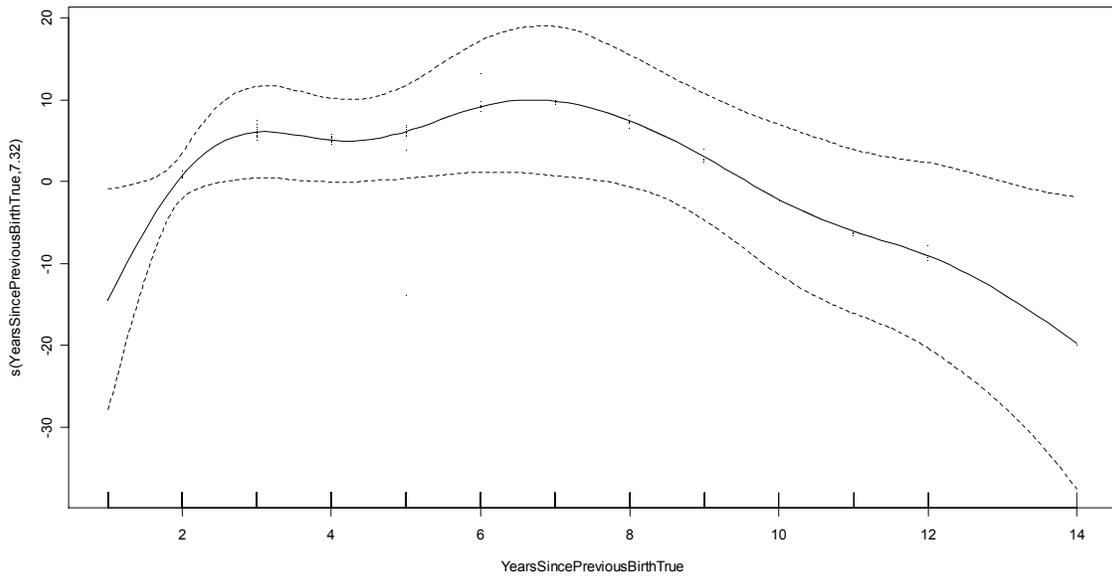
Table 17: Covariate values for years since previous birth and number of previous calves that predictions have been made from, the probability of calving and associated standard error based on these values, and the odds of calving (vs not calving) based on these values.

Years since previous birth	Previous calves	Probability of calving	SE of probability	Odds of calving (vs not calving)
2	1	0.1316	0.0407	0.152
3	1	0.2718	0.0572	0.373
4	1	0.4019	0.0702	0.672
5	1	0.4738	0.0792	0.900
6	1	0.4828	0.0916	0.934
3	2	0.1332	0.0359	0.128
4	2	0.1869	0.0518	0.229
5	2	0.2355	0.0608	0.308
6	2	0.2420	0.0656	0.319
7	2	0.2198	0.0686	0.282
8	2	0.1939	0.0711	0.241
9	2	0.1744	0.0759	0.211
10	2	0.1592	0.0834	0.189
11	2	0.1483	0.0961	0.174
12	2	0.1398	0.1186	0.163
9	3	0.1795	0.1030	0.219
10	3	0.1640	0.1067	0.196
11	3	0.1528	0.1158	0.180
12	3	0.1441	0.1350	0.168

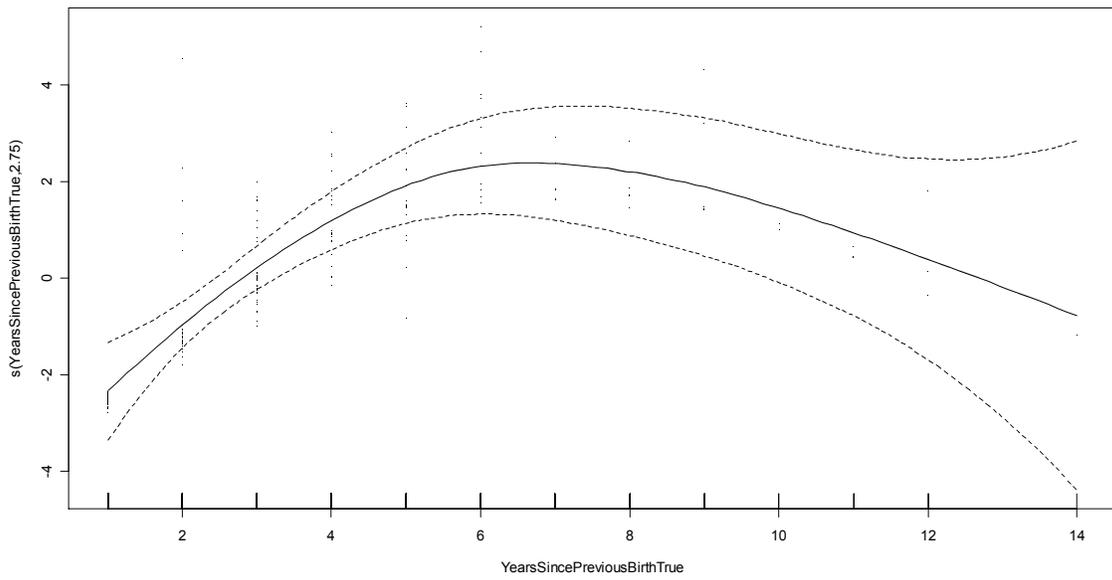
Figure 2. Residual plots for the smoothed covariates of each model



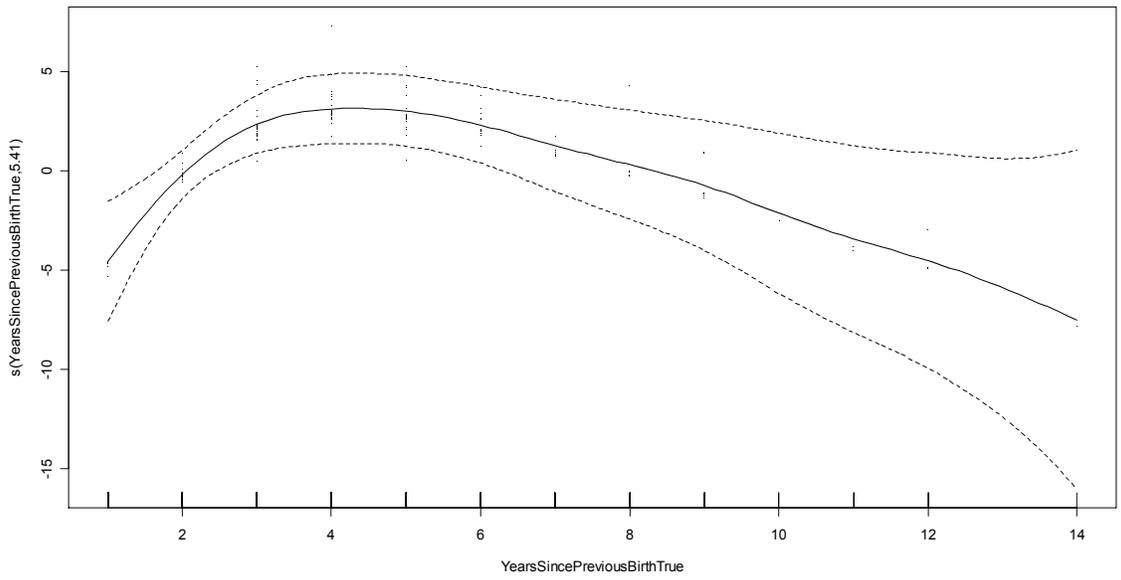
2.1. Model 2



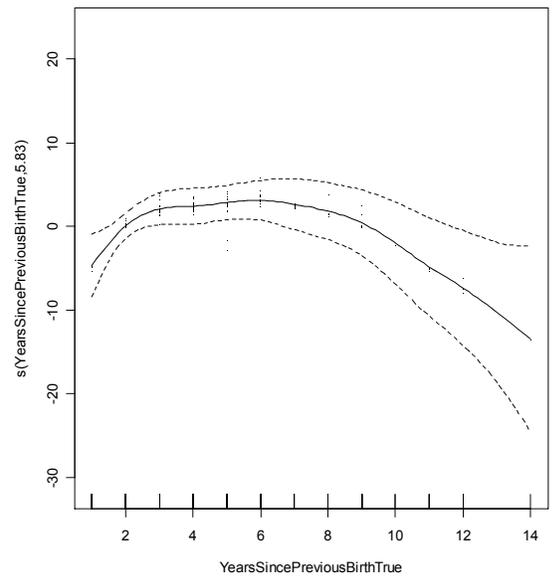
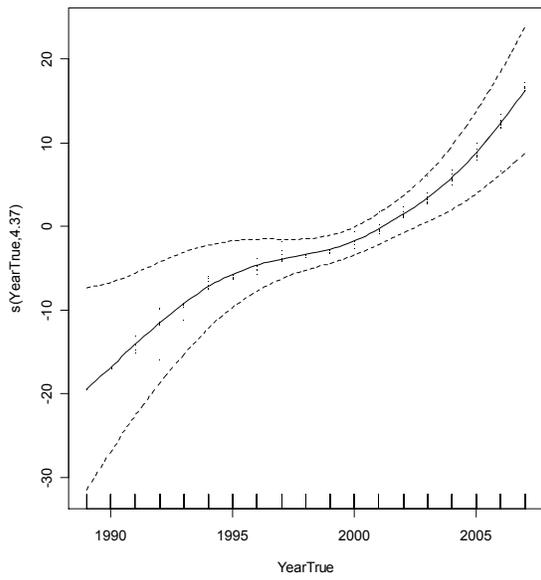
2.2. Model 1



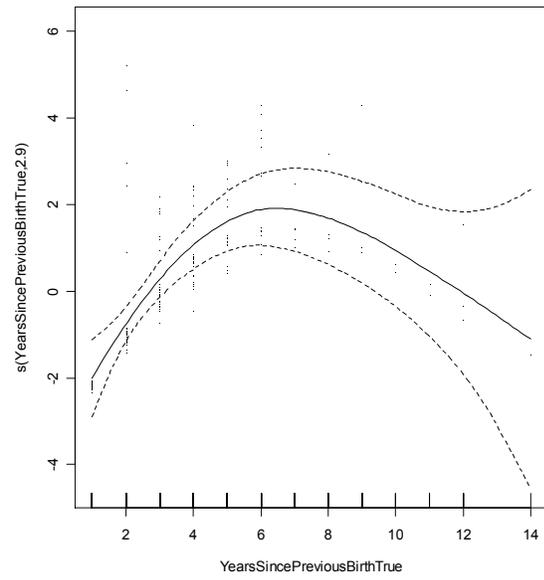
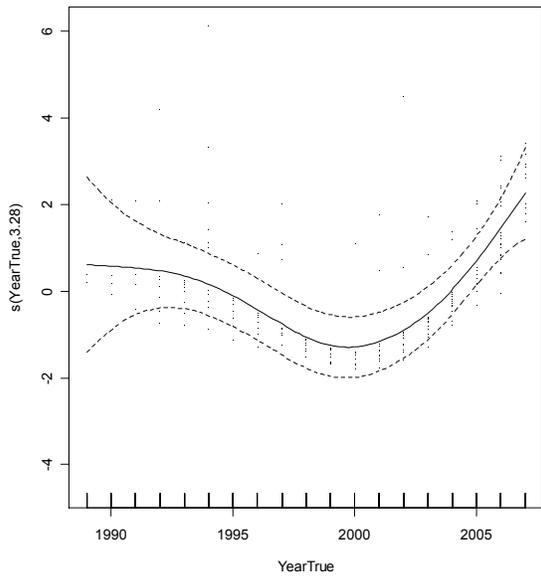
2.3. Model 3



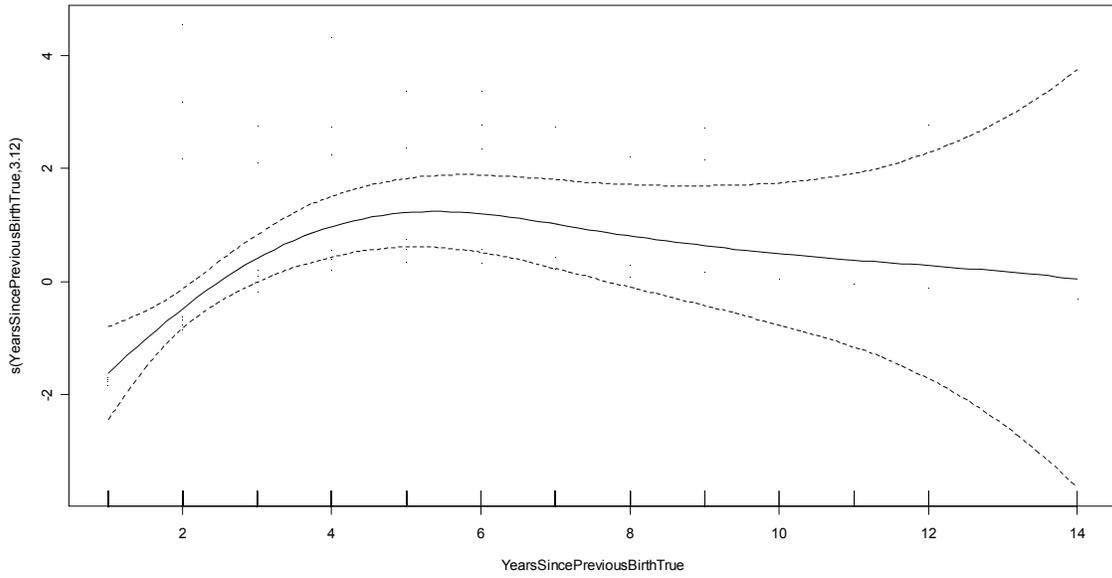
2.4. Model 4



2.5. Model 5



2.6. Model 6



2.7. Model 7

8. Appendix 2: Data

Table 1: Mothers assigned to calves using photo-identification data from AULFS, CRRU and SMRU. Table 1 shows mother and calf ID number where present from the relevant organization(s). Where several organizations have recorded the mother and/or calf, photographic evidence has been used to confirm that these are the same animals and that there is a true match. Mothers were assigned to calves with varying levels of confidence based on the methods used to allocate a mother to a calf.

Level 1: Animal recorded with mother in echelon position on only 1 occasion

Level 2: Photographed in greater than 2 encounters in the echelon position with mother by AULFS, CRRU or SMRU

Level 3: Calf assigned to mother by two or more of AU, SMRU and CRRU

Mother ID AU	Mother ID CRRU	Calf	Year of calf birth	Confidence level of association	
24		C1 (AU#301)	1992	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
		C2 (AU#463)	1994	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
27		C1 (AU#095)	1988	2	Calf recorded and photographed in 1989 at one year old.
		C2 (AU#217)	1991	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
		C3 (AU#645)	1997	2	Photographed in greater than 2 encounters in the echelon position with 27
30		C1 (AU#070)	1989	2	Photographed in greater than 2 encounters in the echelon position with 30
		C2 (AU#302)	1992	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
		C3 (AU#814)	2001	2	Photographed in greater than 2 encounters in the echelon position with 30
68	402	C1 (AU#067)	1989	2	Photographed in greater than 2 encounters in the echelon position with 68
		C2 (AU#329)	1992	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
85		C1 (AU#084)	1987	2	84 recorded and photographed as a three year old in 1990.
		C2 (AU#184)	1990	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>

		C3 (AU#251)	1992	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
		C4 (AU#433)	1994	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
120		C1 (AU#139)	1989	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
		C2 (AU#432)	1994	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
240		C1 (AU#506)	1995	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
		C2 (AU#988)	2004	2	Photographed in greater than 2 encounters in the echelon position with 240
440		C1 (AU#979)	2003	2	Photographed in greater than 2 encounters in the echelon position with 440
		C2 (AU#1014)	2006	2	Photographed in greater than 2 encounters in the echelon position with 440
578	<i>80</i>	C1 (AU#980),(CRRU#361)	2003	2	Photographed in greater than 2 encounters in the echelon position with 578
		C2 (AU#1022)	2007	2	Photographed in greater than 2 encounters in the echelon position with 578
732		C1 (AU#733)	1998	2	Photographed in greater than 2 encounters in the echelon position with 732
		C2 (AU#989)	2003	2	Photographed in greater than 2 encounters in the echelon position with 732
		C3 (AU#1018)	2007	2	Photographed in greater than 2 encounters in the echelon position with 732
733		C1 (AU#991)	2004	2	Photographed in greater than 2 encounters in the echelon position with 733
		C2 (AU#1017)	2007	2	Photographed in greater than 2 encounters in the echelon position with 733
963	<i>434</i>	C1 (AU#923)	2001	2	Photographed in greater than 2 encounters in the echelon position with 963
		C2 (AU#1009), (CRRU#435)	2006	3	Photographed in greater than 2 encounters in the echelon position with 963. <i>Calf only recorded once by CRRU in 2007, photographed surfacing alongside 434 in the photo</i>
4	<i>26</i>	C1 (AU#259)	1990	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
		C2 (AU#459)	1994	2	Photographed in greater than 2 encounters in the echelon position with 4,
		C3 (AU#813), (CRRU#218)	2000	3	<i>Calf 218 only recorded on once occasion in 2001, when it was recorded surfacing alongside female 26</i>
		C4 (ABZ553)	2005	2	Calf recorded by ABZ(ACC 2008)

9	78	C1 (AU#11), (CRRU#65) C2 (CRRU#108)	1988	2	Photographed in greater than two encounters with 9 by AU Calf 108 recorded on three occasions, each time in association with mother, supported by photographic evidence Calf recorded by SMRU
			1997	2	
			2006	2	
11	65	C1 (AU#970), (CRRU#297)	2002	3	AU verification level 1, <i>calf 297 recorded in association with female 65 on 36 occasions by CRRU, supported by photographic evidence.</i>
		C2 (AU#1024)	2007	3	Photographed in greater than 2 encounters in the echelon position with 11. Recorded by CRRU in 2008
61	374	C1 (AU#452)	1994	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
			2006	2	Calf encountered with mother by CRRU, ACC and SMRU in 2006.
31	362	C1 (AU#569)	1995	2	Photographed in greater than 2 encounters in the echelon position with 31 Photographed in greater than 2 encounters in the echelon position with 31. <i>Calf 332 only recorded on one occasion by CRRU, calf only ever seen with a single animal, female 362, however, not photographed in the same frame as suspected mother.</i> Photographed in greater than 2 encounters in the echelon position with 31. <i>Calf 406 only photographed on one occasion by CRRU in association with female 362.</i>
		C2 (AU#815), (CRRU#332)	2001	3	
		C3 (AU#998), (CRRU#406)	2005	3	
52	119	C1 (CRRU#365)	2003	2	<i>Calf 365 recorded in association with female 119 on 16 occasions. Supported by photographic evidence.</i>
		C2 (AU#1008), (CRRU#395)	2006	3	AU verification level 1, <i>Calf 395 recorded in association with female 119 on 16 occasions. Supported by photographic evidence.</i>
55	46	C1 (AU#216)	1991	2	Mother assigned to calf using technique of <i>Grellier (2000)</i>
		C2 (AU#493)	1994	2	Photographed in greater than 2 encounters in the echelon position with 31

58	5	C1 (AU#250), (CRRU#043) C2 (CRRU#092)	1991 1996	2 2	Mother assigned to calf using technique of <i>Grellier (2000)</i> <i>Calf 92 recorded in association with female 5 on 17 occasions, supported by photographic evidence.</i>
64	89	C1 (AU#065) C2 (AU#456) C3 (AU#676) C4 (AU#981), (CRRU#419) C5 (AU#1020), (CRRU#428)	1987 1993 1997 2003 2007	2 2 1 3 3	Photographed in greater than 2 encounters in the echelon position with 64 Photographed in greater than 2 encounters in the echelon position with 64 Photographed several times in association with 64, only on one trip though. Photographed in greater than 2 encounters in the echelon position with 64 Photographed in greater than 2 encounters in the echelon position with 64. <i>Calf 428 only recorded on one occasion by the CRRU where it was photographed in the surfacing position alongside female 89.</i>
307	187	C1 (AU#355) C2 (AU#1010), (CRRU#390)	2004 2006	2 3	<i>Calf 355 recorded in association with female 187 on 18 occasions, Photographs showing calf in breaching position.</i> Photographed in greater than 2 encounters in the echelon position with 307. <i>Calf 390 shows spinal deformity and is easily recapturable. Recorded in association with female 187 on 19 occasions, supported by photographic evidence of the calf in the breaching position with the mother.</i>
745	118	C1 (AU#973), (CRRU#253) C2 (AU#1000), (CRRU#377)	2000 2005	3 3	Photographed in greater than 2 encounters in the echelon position with 745. <i>Calf 253 recorded in association with female 118 on 12 occasions. Photographic evidence of calf in breaching position with 118 in one photo.</i> Photographed in greater than 2 encounters in the echelon position with 745, <i>Calf 377 recorded in association with female 118 on 28 occasions. Supported by photographic evidence of this deformed calf in the surfacing position alongside mother 118.</i>
800	3	C1 (CRRU#277)	2000	2	<i>Calf 277 recorded in association with female 3 on 8 occasions, supported</i>

		C2 (CRRU#329)	2002	2	<i>by photographic evidence.</i> Calf 329 recorded in association with female 3 on 14 occasions, supported by photographic evidence.
		C3 (AU#1012), (CRRU#421)	2006	3	Photographed in greater than 2 encounters in the echelon position with 800. Calf 421 recorded in association with female 3 on 6 occasions, supported by photographic evidence of breaching position.
909	67	C1 (CRRU#68)	1996	2	<i>Calf 68 recorded in association with female 68 on 7 occasions. Supported by photographic evidence of calf in breaching position.</i>
		C2 (CRRU#328)	2002	2	<i>Calf 328 recorded in association with female 67 on 13 occasions. Supported by photographic evidence.</i>
		C3 (AU#1011), (CRRU#392)	2006	3	Photographed in greater than 2 encounters in the echelon position with 909. Calf 392 recorded in association with female 67 on 17 occasions. Supported by photographic evidence.
913	225	C1 (CRRU#204)	2000	2	<i>Calf 204 recorded in association with female 225 on 18 occasions. Supported by photographic evidence.</i>
		C2 (AU#1006), (CRRU#359)	2004	3	Photographed in greater than 2 encounters in the echelon position with 913. Calf 359 recorded in association with female 225 on 33 occasions. Supported by photographic evidence.
		C3 (AU#1021), (CRRU#431)	2007	3	Photographed in greater than 2 encounters in the echelon position with 913. Calf 431 recorded on five occasions with female, photographic evidence shows calf in breaching position with female.

Table 2: Mother's Id and number of sightings each year by AULFS, SMRU and CRRU for females in the sample between 1989 and 2007. Shaded boxes represent the years that the identified female is thought to have given birth to a calf.

<u>AUSMRU ID</u>	<u>CRRU ID</u>	<u>1987</u>	<u>1988</u>	<u>1989</u>	<u>1990</u>	<u>1991</u>	<u>1992</u>	<u>1993</u>	<u>1994</u>	<u>1995</u>	<u>1996</u>	<u>1997</u>	<u>1998</u>	<u>1999</u>	<u>2000</u>	<u>2001</u>	<u>2002</u>	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>	
24				1	15	8	12	4	3														
27				1	7	12	10	5	2	4	8	2	5	3									
30				1	11	14	13	9	8	13	10	6	10	5	4	7	2	3	5		4		
61	374			1	2		3	2	4	4		4	2	2	1	2	6		5	2	3	2	
85					6	17	18	6	9	8	10	10											
9				5	1	8	2	1	6	2	2	3	2	2	2	3		1	4		5	1	
120					4	6	4	4	10	8	7		7	3	4	8	5	13	5	7	5		
240					1	5	12	5	1	7	11	3	8	2	6	7	7	6	3				
440									3	3	10	3					10	6	10	5		3	24
732													5	3	7	9	9	9	10	14	12	17	
733													5	2	8	10	6	14	2	6	15	20	
963	434																	8	2	9	9	8	
4	26			3	3		5	2	5	4	1	3	4	2	2	8	1	1	3		3	1	
11	65			3	2	5	6	2	5	5		18	1	2	3	12	2	10	8	15	15	15	
31	362			2	15	15	11	6	9	6	12	3	6	3	8	10	7	11	7	14	22	33	
52	119			1			3	1	1				4	7	2	9		3	1	17	13	18	
55	46			1	4	3	7	1	7	5	1	2	2	5	1	3	2	1					
58	5			1		9	8	3	3	10	3	21	1	1	1	2	1						
64	89			3	13	5	10	5	5	8	3	6	1	2	3	9	7	2	2	3	14	12	
307	187						2	2	1	2	2			1	2	5	5	1	9	15	5	22	
745	118												1	1		11	8	4	5	17	15	17	
800	3											3	4		3	1	48	8	10	12	4	9	
909	67											5	8	1			2	7	7	19	6	21	
913	225														1	5	9	10	7	27	20	14	
68	402			2	2		2		3				1	1	3	2	2	5	3		6		
578	80										11	9	5	5	2	9	7	7	8	13	15	18	

Table 3: Mother's Id and number of sightings each year by AULFS, CRRU and SMRU for known females, CRRU sightings are in italic font, SMRU are in bold font.

<u>AU/ SMRU ID</u>	<u>CRRU ID</u>	<u>1989</u>	<u>1990</u>	<u>1991</u>	<u>1992</u>	<u>1993</u>	<u>1994</u>	<u>1995</u>	<u>1996</u>	<u>1997</u>	<u>1998</u>	<u>1999</u>	<u>2000</u>	<u>2001</u>	<u>2002</u>	<u>2003</u>	<u>2004</u>	<u>2005</u>	<u>2006</u>	<u>2007</u>
24		1	15	8	12	4	3													
27		1	7	12	10	5	2	4	8	2	5	3								
30		1	11	14	13	9	8	13	10	6	10	5	4	7	2	3	5		4	
85			6	17	18	6	9	8	10	10										
120			4	6	4	4	10	8	7		7	3	4	8	5	13	5	7	5	
240			1	5	12	5	1	7	11	3	8	2	6	7	7	5,1	3			
440							3	3	10	3				10	6	10	5		3	24
732											5	3	7	9	9	9	10	14	12	17
733											5	2	8	10	6	14	2	6	15	20
963	434															8	2	9	9	7,1
4	26	3	3		5	2	5	4	1	3	1,3	1,1	1,1	7,1	1	1	3		2,1	1
11	65	3	2	5	6	2	5	5		9,9	1	2	3	9,3	2	3,7	3,5	10,14	5,10	13,2
31	362	2	15	15	11	6	9	6	12	3	6	3	8	10	7	9,1,1	6,1	12,2	21,1	33
52	119	1			3	1	1				4	7	1,1	7,2		2,1	1	5,12	7,6	6,12
55	46	1	4	3	7	1	7	5	1	2	1,1	4,1	1	3	2	1				
58	5	1		9	8	3	3	10	3	21	1	1	1	2	1					
64	89	3	13	5	10	5	5	8	3	3,3	1	2	3	8,1	6,1	2	2	2,1	10,4	11,1
307	187				2	2	1	2	2			1	1,1	4,1	5	1	5,4	10,14	2,3	6,16
745	118										1	1		5,6	6,2	1,3	4,1	6,11	4,11	8,9
800	3									3	4		3	1	4,4	3,5	6,4	4,8	3,1	3,6
909	67									5	8	1			1,1	7	4,3	10,9	1,5	7,14
913	225												1	5	5,4	10	7	8,19	12,8	10,4
68	402	2	2		2		3				1	1	3	2	2	5	3		1,3,2	
578	80								11	4,5	5	4,1	2	7,2	7	7	4,4	13	13,2	18