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Author(s): C. Shane Reese, James A. Calvin, John C. George and Raymond J. Tarpley

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Estimation of Fetal Growth and Gestation in Bowhead Whales

C. Shane REESE, James A. CALVIN, John C. GEORGE, and Raymond J. TARPLEY

We address estimating fetal growth and gestation for bowhead whales of the Bering, Chukchi, and Beaufort seas stock. This population is subject to a subsistence hunt by Eskimo whale hunters, which is monitored via a quota system established by the International Whaling Commission. Quota determination is assisted by biological information, such as fetal growth and gestation, which is the basis of a population dynamics model used to estimate the annual replacement yield of the stock. We developed a Bayesian hierarchical nonlinear model for fetal growth with computation carried out via Markov chain Monte Carlo techniques. Our model allows for unique conception and parturition dates and provides predictive distributions for gestation length and conception dates. These results are used to propose estimates of geographic locations for conception and parturition. A sensitivity analysis indicated caution when specifying some hyperparameters related to growth rate, conception dates, and parturition dates.

KEY WORDS: Bayes theorem; Hierarchical models; Markov chain Monte Carlo; Random curves.

1. INTRODUCTION

The bowhead whale (*Balaena mysticetus*) is a large, rotund baleen whale living year-round in close association with the ice-covered domain of circumpolar arctic seas (Moore and Reeves 1993). There are five geographically defined stocks of bowhead whales, all of which have been subject to commercial whaling at some point in the last 400 years. The largest remaining stock is the Bering, Chukchi, and Beaufort seas (BCBS) stock of the western Arctic Ocean. Commercial exploitation of the BCBS stock began in earnest in 1848, but it essentially ended in 1914 because of the increasing scarcity of whales and the decline in demand for the products they supplied. In 1946, the International Convention for the Regulation of Whaling introduced further protection with an official ban on the commercial hunting of this species. This broad restriction has continued under the auspices of the International Whaling Commission (IWC), with the exception of a limited aboriginal subsistence hunt by Eskimo whalers in Alaska (and now also in Russia) in cooperation with the Alaska Eskimo Whaling Commission (AEWC).

The most probable size of the BCBS stock is estimated to be 8,200 whales [with 95% of the posterior probability between 7,200 and 9,400 (Raftery and Zeh 1998)], and it is increasing about 3% annually. A Bayesian melding approach, used by Poole and Raftery (1998), indicated a somewhat lower rate of increase of 2%. The other stocks, however, are thought to number in the tens to the low hundreds, and data on population

trends are not available (Zeh et al. 1993; Raftery, Givens, and Zeh 1995; IWC 1997).

Raftery, Givens, and Zeh (1995) discussed the inputs used to determine replacement yield (that is, the greatest number of whales that can be taken without reducing the population). Three types of information are used: stock abundance and rates of increase, historical whaling removals, and biological information. Stock abundance and rates of increase are estimated by using ice-based visual and acoustic surveys (Zeh et al. 1993; George et al. 1995). Historians have carefully reviewed and interpreted catch records from 1848 through 1914 to assess whaling removals during the period of commercial exploitation (Bockstoe and Botkin 1983). Subsistence harvests, although monitored closely by AEWC and reported to IWC, are subject to some uncertainty as a result of strikes not captured. The determination of birth and death rates has relied, primarily, on photogrammetric surveys (Withrow and Angliss 1992), photoidentification (Miller et al. 1992), examination of dead whales (Tarpley et al. 1995; George et al. 1995), age estimates (from harvested animals) (Schell et al. 1989), and analogies with other species (Best 1991). Such information is easier to obtain for some mammals (including some cetaceans), but gathering these data for bowhead whales is difficult. The only current data that exist on fetal growth and gestation were derived entirely from pregnant whales taken unintentionally during subsistence hunts.

Historically, much of the reproductive data for baleen whales were obtained from animals taken in the course of commercial hunts conducted largely during the summer (Laws 1959; Horwood 1987). Seasonal hunts restrict collection of reproductive information from bowhead whales, with hunts occurring during spring and autumn. As a result, it is difficult to accurately estimate fetal growth curves because fetuses cannot be collected throughout the entire gestation period. Most analyses use extrapolation to estimate conception date (Laws 1959; Nerini et al. 1984; Rice 1983). Further, only one observation can be made on a given fetus. With only a cross-sectional view of fetal growth, it is difficult to distinguish within and between fetus variation, and so such studies may

Shane Reese is a Technical Staff Member at Los Alamos National Laboratory, Los Alamos, NM. James Calvin is Professor of Statistics at Texas A&M University, College Station. John George is a wildlife biologist at the North Slope Borough, Department of Wildlife Management, Barrow, AK. Raymond Tarpley is Associate Professor of Veterinary Anatomy and Public Health at Texas A&M University, College Station. The authors thank the Eskimo whaling captains and hunters, in cooperation with the Alaska Eskimo Whaling Commission, for permitting the use of data from subsistence-taken whales. The authors appreciate the logistic support provided by the North Slope Borough, Department of Wildlife Management, in the collection of data. The authors thank Scott Berry, Texas A&M University, Sue Moore of the National Marine Mammal Laboratory, and Judy Zeh, University of Washington, for many useful discussions. The authors thank the referees, the associate editor, and the editor for their helpful comments, which improved the content and exposition of this paper. Partial support for this project was supplied by the Texas A&M University Center for Environmental and Rural Health, which is funded by the National Institutes of Environmental Health Science through grant ES09106.

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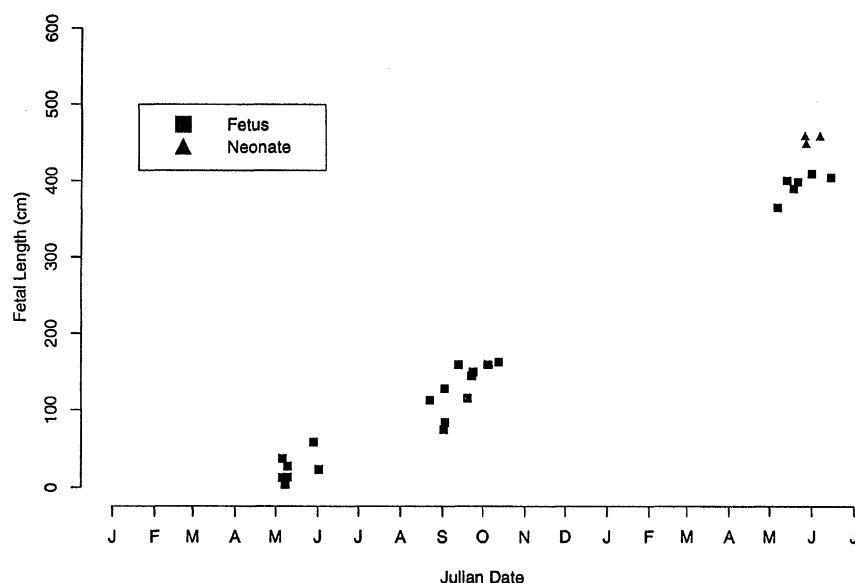


Figure 1. Bowhead Whale Data. The horizontal axis represents date on which the fetuses were taken, and the vertical axis represents fetal length.

offer less power than longitudinal alternatives (Diggle, Liang, and Zeger 1994). Reproductive studies for bowhead whales are further compromised by small sample sizes due to the relatively small number of animals taken in the subsistence hunt. Data relevant to fetal growth in the bowhead whale can be collected only on the even less frequent occasions when a pregnant female is taken and a wildlife biologist is present to gather the proper measurements and specimens. The resulting small sample sizes lead to wide interval estimates.

Despite such difficulties, researchers have presented several analyses of fetal growth in baleen whales. On the basis of commercial whaling data, Laws (1959) presented a linear statistical model for the latter stages of fetal growth in the fin whale. Rice (1983) modeled fetal growth of the gray whale by using a nonlinear growth equation based on commercial harvests and stranded newborn calves.

Our goal is to estimate a function representative of fetal growth in bowhead whales and to obtain both point and interval estimates of the length of gestation. We use data collected in northernmost Alaska. In Section 2, we describe the data on which our analyses are based. Section 3 presents some possible models for describing fetal growth and the Bayesian framework we use in modeling the data. Model assessment and posterior distributions of the important parameters are discussed in Section 4. Section 5 contains concluding remarks.

2. DATA

The North Slope Borough Department of Wildlife Management and the U.S. National Marine Mammal Laboratory provided the data for our current analysis. Fetal length data used in our study date to 1969, and the majority of the data were collected since 1986. Also included in the data is a small group of neonates (newly born whales identified by a unique layer of skin), to more accurately model the latter stages of growth (Durham 1980; Nerini et al. 1984).

Each fetus was measured rectilinearly, in centimeters, and the Julian date on which the whale was killed was recorded.

For larger fetuses, the Julian date plus 365 was recorded (indicating they are more than 1 year old). The data are shown in Figure 1.

These data consist of sparsely observed, cross-sectional observations ($n = 26$). In addition, it is likely that very small fetuses were missed during biological examination, making estimation in the early stages of gestation purely extrapolation. In the next section, we summarize other approaches and present our approach to modeling fetal growth and the length of gestation in the face of these limitations.

3. BAYESIAN MODELING

3.1 Models

Fetal growth and gestation length for Fin whales were analyzed by Laws (1959). In his approach, Laws separated the total gestation period, t_g , into an initial growth period, t_0 , and a remaining period, $t_g - t_0$. Growth during the second period was modeled linearly as a function of time. Laws (p. 286) noted that t_0 increases with t_g but "forms a decreasing fraction of the total gestation time." The fraction was determined arbitrarily, and Laws suggested that an appropriate value for gestation periods greater than 400 days is .09. Thus, for our case, the initial growth period, t_0 , can be considered to be approximated by $.09t_g$, or

$$t_0 = .09t_g = .09(t_g - t_0)/.91. \quad (1)$$

Finally, the latter growth phase ($t_g - t_0$) was determined by calibration using the fitted linear model.

For most species, a linear growth model is an appropriate approximation for only a small portion of the gestational period. More realistic growth models have nonlinear components. Rice (1983) utilized a nonlinear logistic growth equation to model fetal growth in gray whales. A general model provided by Schnute (1981) has as special cases many of the most commonly used growth models. Letting Y_i represent size

and x_i represent the Julian date, we can express these models as

$$Y_i = \left[\delta_1^\gamma + (\delta_2^\gamma - \delta_1^\gamma) \frac{1 - \exp[-\beta(x_i - \tau_1)]}{1 - \exp[-\beta(\tau_2 - \tau_1)]} \right]^{1/\gamma} + \epsilon_i, \quad i = 1, \dots, n, \quad (2)$$

where β is the relative rate of growth, δ_1 is the size at time τ_1 , δ_2 is the size at time τ_2 , γ is the incremental growth acceleration, and ϵ_i are iid $N(0, \delta^2)$ errors.

When the size variable is length, the specialized von Bertalanffy (or Pütter No. 1) form is frequently used (Ricker 1979),

$$Y_i = \frac{\delta_2[\exp\{\beta(x_i - \theta)\} - 1]}{[\exp\{\beta(x_{\delta_2} - \theta)\} - 1]} + \epsilon_i, \quad i = 1, \dots, n, \quad (3)$$

where θ is the mean conception date and x_{δ_2} is the date of parturition. It is easy to show that (3) is a special case of (2) with $\gamma = 1$ and $\delta_1 = 0$.

Figure 2 shows three special cases of (3), the logistic ($\gamma = -1, \beta > 0$), Gompertz ($\gamma = 0, \beta > 0$), and von Bertalanffy growth curves, fit to our data, where the parameters were estimated using maximum likelihood estimation under the assumption of iid normal errors. A limiting factor for the Gompertz model is that the slow rate of increase at the early stages of growth and the asymptote at the late stages of growth make the fit at those stages inadequate. The logistic model has some of the same problems, although not to the same extent. Additionally, the logistic model parameter for conception date, θ , is estimated at day -147.45 which is clearly nonsensical. The specialized von Bertalanffy model has more desirable features for both the early and the late stages of fetal development, and parameter interpretability is maintained with the model given by (3). In addition, $E(Y_i|X_i = \theta) = 0$, so that fetal length at conception is zero, a biologically essential result.

An implication of the parameterization in the von Bertalanffy model is that θ represents the mean conception

date. Summarizing the results in terms of days since conception, we would be forced to assume that all whales were conceived on the same day. Biologically, it makes more sense to allow for different conception and parturition dates for each fetus. Thus, we use the basic form given by (3) with two modifications. We let each fetus have its own conception date, θ_i , and its own parturition date, x_{FBL_i} . That is,

$$Y_i = \frac{FBL_i[\exp\{\beta(x_i - \theta_i)\} - 1]}{[\exp\{\beta(x_{FBL_i} - \theta_i)\} - 1]} + \epsilon_i, \quad i = 1, \dots, n, \quad (4)$$

where FBL_i is the fetal birth length at date x_{FBL_i} for whale i , β is the growth rate, and θ_i is the conception date for whale i . Using this parameterization, the gestation period, given a fetal birth length, is calculated as $x_{FBL_i} - \theta_i$.

Given estimates of x_{FBL_i} and θ_i , $(\hat{x}_{FBL_i} - \hat{\theta}_i)$ provides an estimate of length of gestation. Unfortunately, parameter estimation in (4) is not possible using maximum likelihood methods. There are $3n + 2$ parameters but only n observations. Our solution to this problem is to recast the model in a Bayesian framework. This can be done by using a multistage hierarchical modeling approach (Draper et al. 1992).

In the first stage, we condition on $(x_{FBL_i}, \beta, \theta_i, \sigma^2, x_i, FBL_i)$ and model Y_i as

$$(Y_i | x_{FBL_i}, \beta, \theta_i, \sigma^2, x_i, FBL_i) \sim N\left(\frac{FBL_i[\exp\{\beta(x_i - \theta_i)\} - 1]}{[\exp\{\beta(x_{FBL_i} - \theta_i)\} - 1]}, \sigma^2\right), \quad i = 1, \dots, n.$$

Again, this model is an extension of (4), allowing for unique fetal birth lengths (and, thus, unique parturition dates) and unique conception dates. In the next subsection, we discuss prior specification.

3.2 Priors

The second stage of our hierarchical model involves specification of prior distributions for each of the parameters

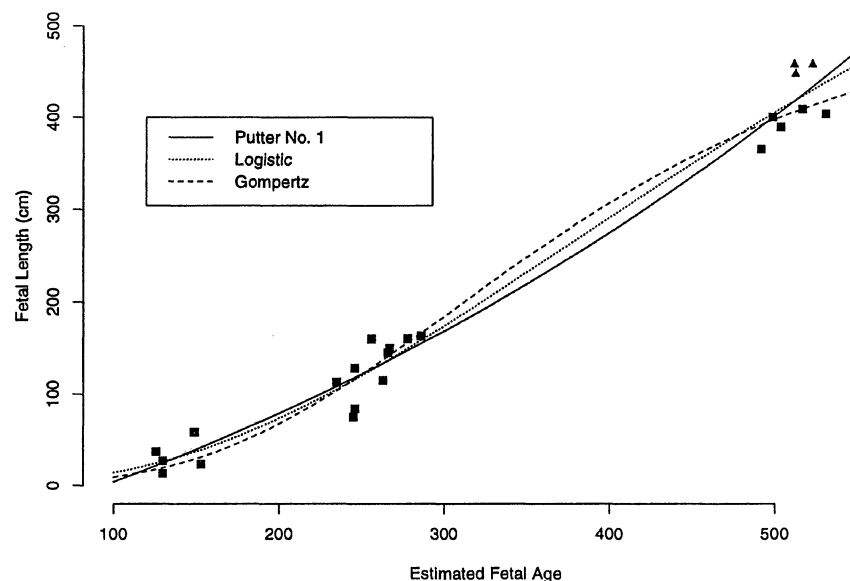


Figure 2. Estimated Growth Curve Using Three Underlying Models. Each model uses a common conception date.

$\beta, \theta_i, FBL_i, x_{FBL_i}$, and σ^2 . The choice of both the distributional family and the values of the yet-to-be-discussed hyperparameters was based on a series of discussions involving statisticians and wildlife biologists. On the basis of these discussions, which are summarized below, we chose the following prior distributions:

$$\begin{aligned} \pi(FBL_i|v, \kappa) &\sim N(v, \kappa^2), \quad i = 1, \dots, n, \\ \pi(x_{FBL_i}|\chi, \omega) &\sim N(\chi, \omega^2), \quad i = 1, \dots, n, \\ \pi(\theta_i|\mu, \tau^2) &\sim N(\mu, \tau^2), \quad i = 1, \dots, n, \\ \pi(\beta|\gamma, \lambda^2) &\sim LN(\gamma, \lambda^2) \quad \text{and} \quad \pi(\sigma^2|\zeta, \eta) \sim IG(\zeta, \eta) \end{aligned} \quad (5)$$

where LN is the log normal distribution and $IG(a, b)$ is the inverse gamma distribution, where if $y \sim IG(a, b)$, then the pdf of y is proportional to

$$f(y) \propto y^{-(a+1)} \exp\{-(by)^{-1}\}, \quad y > 0,$$

with mean $\{b(a-1)\}^{-1}$ and variance $\{b^2(a-1)^2(a-2)\}^{-1}$.

The choice of the normal prior for FBL_i was based on the belief that the birth lengths are symmetrically distributed and that a large percentage of the birth lengths would fall within 20 to 30 cm of the center. To accommodate this belief, and to reflect the fact that the birth lengths represent a sample from a population of lengths, a hierarchical structure was used. Symmetry about a mean with no large deviations suggests that parturition dates, x_{FBL_i} , are normally distributed, also in a hierarchical manner. The specification (5) indicates that there is a population of conception dates, θ_i , from which we drew a sample, and, thus, we impose a hierarchical structure. We chose a normal distribution for the conception dates because we believe the distribution is symmetric, and there is no evidence in the literature to assume otherwise. Because β represents the growth rate, we wanted to restrict it to the positive real line, thus, our choice of the log normal distribution. Finally, lacking any additional knowledge, we used a conjugate prior distribution for σ^2 .

In the next stage, we specify distributions for the hyperparameters of the prior distribution of the conception dates, θ_i ,

$$\pi(\mu|m_\mu, s_\mu^2) \sim N(m_\mu, s_\mu^2) \quad \text{and} \quad \pi(\tau^2|a_\tau, b_\tau) \sim IG(a_\tau, b_\tau),$$

parturition dates, x_{FBL_i} ,

$$\pi(\chi|m_\chi, s_\chi^2) \sim N(m_\chi, s_\chi^2) \quad \text{and} \quad \pi(\omega^2|a_\omega, b_\omega) \sim IG(a_\omega, b_\omega),$$

and fetal birth lengths, FBL_i ,

$$\pi(v|m_v, s_v^2) \sim N(m_v, s_v^2) \quad \text{and} \quad \pi(\kappa^2|a_\kappa, b_\kappa) \sim IG(a_\kappa, b_\kappa).$$

Each of the prior distributions is assumed to be independent of the others with the θ_i, FBL_i , and x_{FBL_i} being independent of one another conditional on the mean and variance of the prior distribution.

The final step in our formulation involves setting values for the hyperparameters ($m_\mu, s_\mu^2, a_\tau, b_\tau, m_\chi, s_\chi^2, a_\omega, b_\omega, m_v, s_v^2, a_\kappa, b_\kappa, \gamma, \lambda, \zeta$, and η). Here, we offer some biological observations to justify our hyperparameter choices displayed in Table 1.

Table 1. Hyperparameter Values for Prior Distributions

Parameter	Hyperparameters		
β	$\gamma = -6.2$	$\lambda = .25$	
σ^2	$\zeta = 102$	$\eta = .0001$	
v	$m_v = 430$	$s_v = 10$	
κ^2	$a_\kappa = 22.0$	$b_\kappa = .0005$	
χ	$m_\chi = 480.0$	$s_\chi = 10.0$	
ω^2	$a_\omega = 22$	$b_\omega = .00005$	
μ	$m_\mu = 75.0$	$s_\mu = 5.0$	
τ^2	$a_\tau = 580.0$	$b_\tau = .00001$	

Nerini et al. (1984) estimated that typical fetal birth lengths fall in the range of 400–450 cm, where 430 cm is the most likely value. On this basis, we chose $m_v = 430$ and $s_v^2 = 100$. These ranges suggest that a standard deviation of fetal birth lengths is approximately 10 cm. Hyperparameter values of $a_\kappa = 22$ and $b_\kappa = 0.005$ are consistent with this belief. The collection of smaller fetuses in April and May, in addition to empirical biological evidence of sexual play in April and May, indicate that conception probably occurs in March (Nerini et al. 1984; Koski et al. 1993). The range of observed copulatory behavior implies that bowhead whales conceive within a 1 month window. On this basis, we chose m_μ , the hypermean of the parameter μ , to be 75 (March 15). By choosing $a_\tau = 580$ and $b_\tau = .00001$, the prior distribution for the variance of the conception dates has a mean of 50. The hyperparameter values listed in Table 1 are consistent with these observations.

Koski et al. (1993) gave approximate quantiles for the time of parturition. Rice (1983) studied growth rates for gray whales and found that values of approximately .0015 were consistent and that the variability was not significant. Thus, we chose hyperparameters (γ and λ) with a mean of .0015 and a standard deviation of .0005. The hyperparameter values for the error variance (ζ and η) were set to allow a mean standard error from the fitted curve of 10 cm. We wanted to allow some variability from this value and, thus, we allowed the variance of this deviation to be 100.

4. RESULTS

Given the hyperparameters, determination of the posterior distributions is still complicated because not all the prior distributions are conjugate priors. The exact joint posterior distribution cannot be found in closed form. However, an MCMC algorithm can be used. The details of our implementation can be found in the Appendix. We used time series plots of the generated observations to assess mixing, and each plot showed similar patterns of sufficient mixing. Given the joint posterior distribution, the marginal distribution and any other characteristic of the joint posterior distribution can be calculated. In Table 2, we show the posterior means of the parameters.

As noted in Section 2, the data consist of both fetuses and neonates. Figure 1 suggests that there may be different rates of growth for the neonates and fetuses. To address this issue, we present results for analyses based on two sets of observations, one including neonates and one with fetuses only.

The predictive distribution of the conception dates [Figure 3(a)] indicates a mean time of conception (the same

Table 2. Bayesian Parameter Estimates for Bowhead Whale Data

Parameter	Estimate	Standard deviation
Neonates excluded		
FBL_i	range 416–427	range 10.2–11.1
x_{FBL_i}	range 462–526	range 9.2–19.5
β	1.99×10^{-3}	1.45×10^{-4}
θ_i	range 75–100	range 10.3–14.7
Neonates included		
FBL_i	range 417–427	range 10.1–11.0
x_{FBL_i}	range 460–521	range 8.4–19.4
β	2.05×10^{-3}	1.20×10^{-4}
θ_i	range 75–99	range 10.4–14.2

for both sets of observations) of around March 24. The 90% predictive interval is March 2 to April 14 with neonates included and March 3 to April 13 without neonates. The predictive distribution of parturition dates is shown in Figure 3(b). By using an estimated conception date (posterior mean) for each fetus and integrating over the fetal birth length distribution, we plotted the fetal length as a function of the estimated fetal age, that is, y_i versus $x_i - \hat{\theta}_i$, in Figure 4. Superimposing our growth curve on this plot shows that our model fits the data well (including or excluding neonates).

Figure 5 contains the predictive distribution of length of gestation integrated over the hierarchical prior distribution for fetal birth lengths for the cases in which the neonates were included in the analysis and when the neonates were excluded.

The predictive distribution for length of gestation (excluding neonates) has a mean of 425 days, or 14.0 months, with a 90% prediction interval of (394, 462) days, or 13.0–15.2 months. Although this interval is narrower than many intervals recorded in the literature, we ran the analysis again with less informative prior distributions and obtained similar results. The results with neonates yielded a mean gestation time of 423 days, or 13.9 months, with a 90% prediction interval of (389, 457) days, or 12.8–15.0 months.

We applied Laws’s (1959) linear regression approach to our data, which indicated a total gestation period of 13.8 months. Laws’s work did not include interval estimation, but by using an approach similar to that of Carroll, Spiegelman, and Sacks (1988), we computed a confidence interval of (364, 567) Julian days, or 12.0–18.7 months.

In addition to other problems, Laws’s approach treats x_i , the Julian date, as the fetal age. If unique conception dates are assumed, then the x_i are measured with error. Making the moment adjustment for bias due to measurement error in simple linear regression (Fuller 1987), 13.2 months is an estimate of the length of gestation with an interval of 11.0 to 17.8 months. In comparison, likelihood-based estimation of (3) (see Table 3 for parameter estimates) produces estimates of time of gestation (for a fetal birth length of 430 cm) of 418 days, or 13.8 months.

Rice (1983) found that gestation for the gray whale was approximately 418 days (13.7 months). Nerini et al. (1984) stated that the length of gestation for the bowhead whale is between 13 and 14 months, using an approach similar to that of Laws (1959), but gave no interval estimate. Koski et al. (1993) indicated that the length of gestation for bowhead

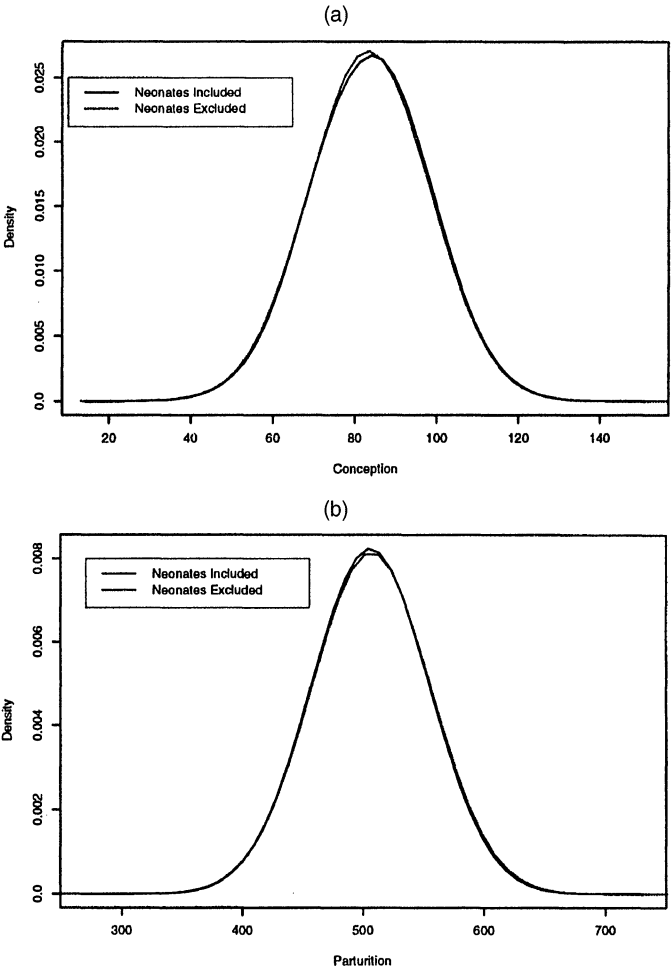


Figure 3. (a) Conception Date Posterior Distributions. [90% predictive interval of (63,104) with neonates included and (62,103) without neonates.] This indicates that a likely time of conception is March 3 to April 13. (b) Parturition date posterior distributions. [90% predictive interval of (447,513) with neonates included and (450,515) without neonates.]

whales is 12 to 16 months, based on a nonlinear fit of a model with an S-shaped curve. Our formulation indicates that gestation length is higher than that reported by Nerini et al. (1984) and in the middle of the range reported in Koski et al.

Also of biological interest are the locations of the whales at conception and parturition. Based on a comprehensive examination of the BCBS stock, Moore and Reeves (1993) suggested that most BCBS bowhead whales are in the Bering Sea and the southern Chukchi Sea (Figure 6) in mid to late March. Our conception date suggests that most successful breeding occurs in the Bering Sea, possibly within the St. Lawrence Island and Sirenikovskaya polynyas. On the basis of this observation and the length of gestation predictive distribution, it appears parturition is likely to occur in mid May to mid June at a time when most bowhead whales are between the Bering Strait and Point Barrow. This is consistent with observations from the region, which include the following: (a) many neonates are seen during the whale census in late May, whereas relatively few term females (4 out of 37 mature females since 1980) have been taken at Barrow

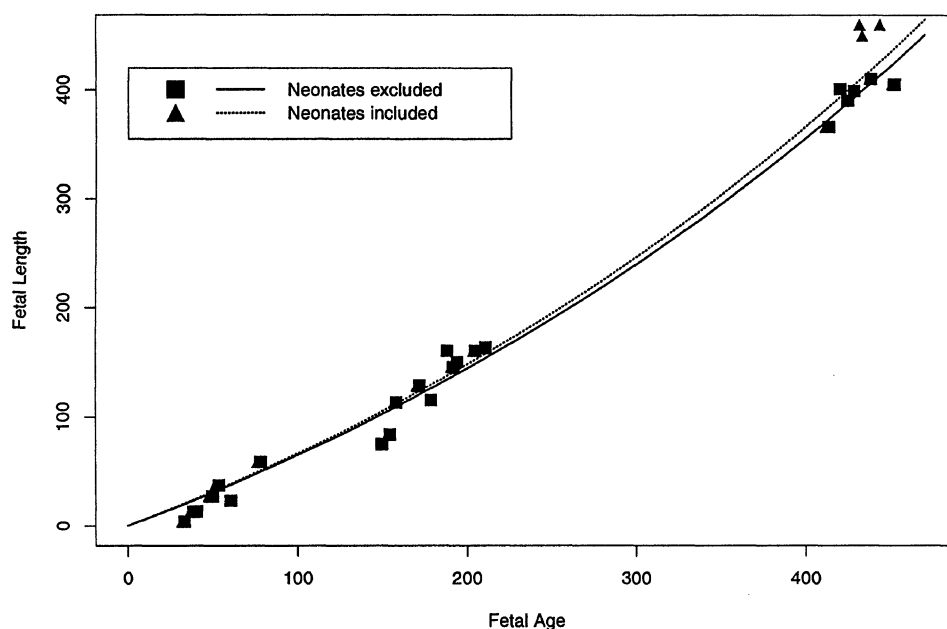


Figure 4. Fitted Growth Models for Bowhead Whale Data With and Without Neonates Included in Analysis.

(George et al. 1995); (b) St. Lawrence Island whale hunters report relatively few neonate-cow pairs; (c) the females examined with term pregnancies appeared close to parturition (evident lactation and dilation); and (d) most of the herd is believed to have migrated past Barrow by late May, with the exception of some large mature animals, which tend to migrate later than smaller size classes (Withrow and Angliss 1992; Zeh et al. 1993; George et al. 1995; C. Oozeva, personal communication, May 1998). Reports of a few neonates seen in April near Gambell and in the Canadian Beaufort Sea in August suggest that not all embryos are conceived in mid to late March,

however (Koski et al. 1993; C. Oozeva, personal communication, May 1998).

5. BAYES FACTORS AND SENSITIVITY ANALYSIS

In Section 3, we argued for the choice of the Schnute class of growth models over other models because of its mathematical behavior and biological interpretability. We can use Bayes factors (Kass and Raftery 1995) to compare the model of unique conception date, θ_i , and unique parturition date, x_{FBL_i} , for each fetus with the simpler model of only a mean conception date, θ , and mean parturition date, x_{FBL} . The two

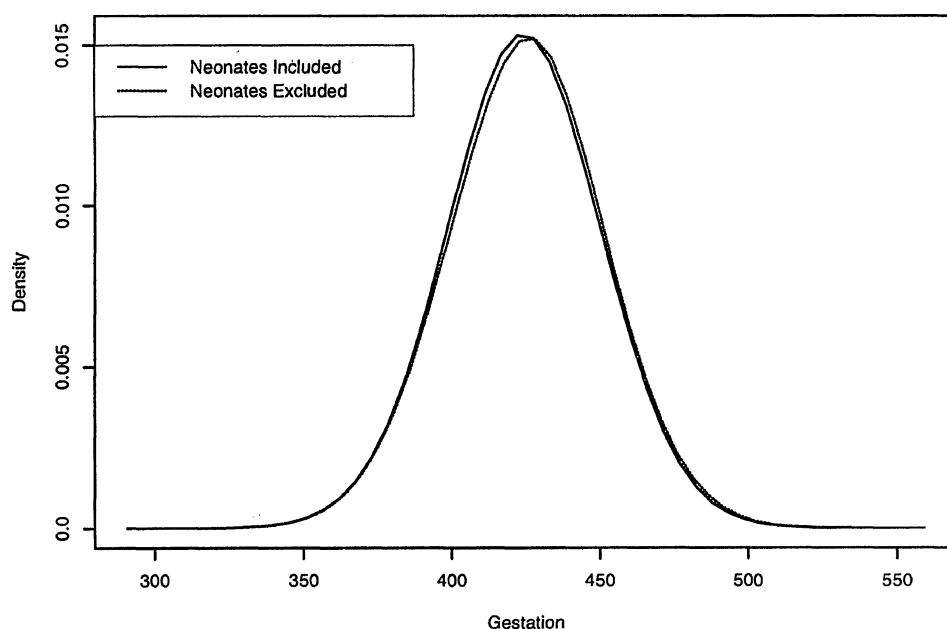


Figure 5. Gestational Period Posterior Distribution Integrated Over the Distribution of Fetal Birth Lengths. [90% predictive interval of (389,457) with neonates included and (394,462) without neonates.]

Table 3. Likelihood Based Parameter Estimates for Bowhead Whale Data

Parameter	Estimate	Standard error
x_{FBL}	536.886	7.88
β	1.11×10^{-3}	5.477×10^{-4}
θ	104.316	12.26

models p_1 (model with θ_i) and p_2 (model with θ) are compared by computing

$$B_{12} = \frac{\int p_1(y|\Omega_1)\pi_1(\Omega_1)d\Omega_1}{\int p_2(y|\Omega_2)\pi_2(\Omega_2)d\Omega_2}, \quad (6)$$

where Ω_1, Ω_2 are the parameters and π_1, π_2 are the prior distributions for models p_1 and p_2 , respectively. By applying a volume-corrected modification of the Laplace approximation (DiCiccio et al. 1997) to the numerator and to the denominator, we find $\log B_{12} \approx 3.84$, so that the data favor the model with unique conception dates and unique parturition dates, albeit weakly. The Bayes factor for comparing models with unique conception dates but nonunique parturition dates (model 3) versus a model with only a mean conception and mean parturition date $\log B_{13} \approx 2.71$. Allowing unique parturition dates but nonunique conception dates (model 4) produces a Bayes factor of $\log B_{14} \approx 2.89$. It is not surprising that the evidence in the data are weak, given the small sample size. Thus, given the biological plausibility of unique conception dates and parturition dates, we believe that the model that includes both unique conception dates and unique parturition dates is the more appropriate one.

To examine the sensitivity to our prior structure, we constructed a 2^{16-10} fractional factorial design of resolution IV (Wu and Hamada 2000). A 2^{16-10} fractional factorial design of resolution IV is one for which only $\frac{1}{1,024}$ of the required 2^{16}

Table 4. Sensitivity Analysis Hyperparameter Values

Hyperparameter	Low	High
γ	-12.5	-3.0
λ	.03	.12
ζ	82.0	122.0
η	5.0×10^{-5}	2.0×10^{-4}
m_v	400.0	460.0
s_v	5.0	20.0
a_κ	11.0	44.0
b_κ	2.5×10^{-4}	1.0×10^{-3}
m_χ	400.0	560.0
s_χ	5.0	20.0
a_ω	11.0	44.0
b_ω	2.5×10^{-5}	1.0×10^{-4}
m_μ	60.0	90.0
s_μ	2.5	10.0
a_τ	290.0	1160.0
b_τ	5.0×10^{-6}	2.0×10^{-5}

runs are performed, and no main effect is confounded with any other main effect or two-way interaction, but could be confounded with three-way and higher interactions. The high and low values for our hyperparameters are presented in Table 4. Using the current hyperparameters as the center points, the high and low values were chosen by increasing and decreasing, respectively, the current value by a factor of two. In some cases, the resulting hyperparameter values were too unrealistic and, thus, a reasonable adjustment was made while maintaining the current hyperparameter value as the center point.

An analysis of variance with the posterior mean of the gestation time as the response variable is included in Table 5. The sensitivity analysis indicates a strong sensitivity to the specification of γ , the prior mean of β , the growth rate. The growth rate is a major contributor to the overall shape of the growth curve. The results also indicate sensitivity to the specification of m_χ , the mean hyperparameter for parturition dates, and m_μ and s_μ^2 , the hyperparameters for conception dates. These parameters are biologically interpretable parameters; thus, they are known with more certainty than the prior for the growth rate. Nonetheless, sensitivity to these hyperparameters indi-

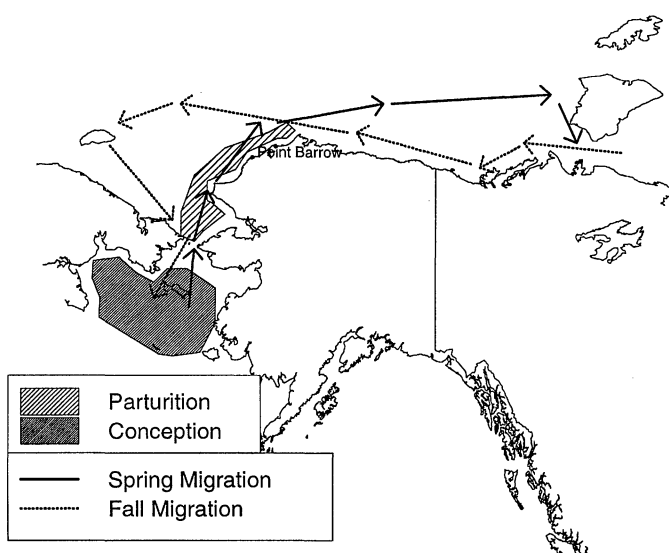


Figure 6. Map of Alaska. Point Barrow is where most of the data are collected. The arrows indicate the approximate route of migration for the Bowhead whale.

Table 5. Sensitivity Analysis of Variance Results

Source	DF	SS	MS	F	Pr(F)
γ	1	372113.1	372113.1	126.28	.00
λ	1	4724.0	4724.0	1.60	.22
ζ	1	39.1	39.1	.01	.91
η	1	238.7	238.7	.08	.78
m_v	1	7127.9	7127.9	2.41	.13
s_v	1	2339.1	2339.1	.79	.39
a_κ	1	45.1	45.1	.03	.90
b_κ	1	192.1	192.1	.41	.80
m_χ	1	26285.9	26285.9	8.92	.01
s_χ	1	4210.7	4210.7	1.42	.25
a_ω	1	107.1	107.1	.03	.85
b_ω	1	1223.1	1223.1	.41	.53
m_μ	1	22604.3	22604.3	7.67	.01
s_μ	1	32449.6	32449.6	11.01	.00
a_τ	1	2486.0	2486.0	.84	.37
b_τ	1	1732.9	1732.9	.58	.46
Residuals	47	144623.7	3077.1		

cates that extreme care should be taken when specifying these priors.

To assess the source of the hyperparameter sensitivity, we temporarily added additional observations to gaps in the data and, thus, examined ways to reduce sensitivity to hyperparameter specification. Observations added to the very early phases of growth yielded a dramatic reduction in the sensitivity of hyperparameter specification for m_χ , m_μ , and s_μ^2 . The additions of these observations made these effects nonsignificant in the subsequent analysis of variance. Additionally, the magnitude of the sensitivity to specification for γ was reduced as well, although it was still significantly sensitive.

6. DISCUSSION

Two separate analyses were performed, one with neonates included and another with the neonates extracted from the data. Figures 4 and 5 particularly emphasize the difference in results with the neonates included and excluded. Because fetal growth rates are likely to be different than growth rates for newly born whales (as they are with humans), we suggest more emphasis be placed on the analysis that excludes the neonates.

We developed a nonlinear model for fetal growth in the bowhead whale to estimate the length of gestation. Such information is useful for understanding bowhead reproductive biology and for building population dynamics models to be used in herd management. Our approach indicates an average length of gestation of 13.9 months, with a predictive distribution of 12.8 to 15.0 months. The sensitivity analysis indicated that this result is somewhat sensitive to the hyperparameter specification. Well-designed supplemental data collection should help eliminate this problem, and we are holding discussions with the North Slope Borough about data collection for this purpose.

An important component in our formulation was the unique conception date for each whale, θ_i , and unique parturition date for each whale, x_{FBL_i} . The hierarchical specification of our formulation provided a distribution of conception and parturition dates. The predictive distribution indicated that conception likely occurs in early March to early April, and parturition likely occurs in May or June. Estimates of gestation length are useful for placing a lower bound on the interbirth interval and, hence, estimating birth rates.

Our approach presented a separate assessment of the location of both conception and parturition. The locations were shown to be consistent with empirical observations made in the region. Such information may be useful to state and federal agencies in determining development within the critical habitat of the bowhead whales.

APPENDIX: MCMC Details

Our approach requires the computation of the joint posterior distribution of the parameters given data, $[x_{FBL_1}, \dots, x_{FBL_n}, FBL_1, \dots, FBL_n, \beta, \mu, \tau^2, \sigma^2, \theta_1, \dots, \theta_n | Y_1, \dots, Y_n]$, which is not available in closed form. It can be computed, however, by using an MCMC (Gelfand and Smith 1990) approach based on the distribution of each parameter conditional on the other parameters and the data (called complete conditional distributions). The complete conditional

distributions for our problem are

$$\begin{aligned} [\mu|\cdot] &\sim N\left(\frac{s_\mu^2 \sum_{i=1}^n \theta_i + \tau^2 m_\mu}{ns_\mu^2 + \tau^2}, \frac{s_\mu^2 \tau^2}{ns_\mu^2 + \tau^2}\right), \\ [\tau^2|\cdot] &\sim IG\left[.5n + a_\tau, \left\{.5 \sum_{i=1}^n (\theta_i - \mu)^2 + b_\tau^{-1}\right\}^{-1}\right], \\ [\chi|\cdot] &\sim N\left(\frac{s_\chi^2 \sum_{i=1}^n x_{FBL_i} + \omega^2 m_\chi}{n s_\chi^2 + \omega^2}, \frac{s_\chi^2 \omega^2}{n s_\chi^2 + \omega^2}\right), \\ [\omega^2|\cdot] &\sim IG\left[.5n + a_\omega, \left\{.5 \sum_{i=1}^n (x_{FBL_i} - \chi)^2 + b_\omega^{-1}\right\}^{-1}\right], \\ [v|\cdot] &\sim N\left(\frac{s_v^2 \sum_{i=1}^n FBL_i + \kappa^2 m_v}{n s_v^2 + \kappa^2}, \frac{s_v^2 \kappa^2}{n s_v^2 + \kappa^2}\right), \\ [\kappa^2|\cdot] &\sim IG\left[.5n + a_\kappa, \left\{.5 \sum_{i=1}^n (FBL_i - v)^2 + b_\kappa^{-1}\right\}^{-1}\right], \\ [\sigma^2|\cdot] &\sim IG\left[.5n + \zeta, \left\{.5 \sum_{i=1}^n (Y_i - m_i)^2 + \eta^{-1}\right\}^{-1}\right], \\ [FBL_i|\cdot] &\sim N(c_1, c_2), \\ [\theta_i|\cdot] &\propto \exp\left\{-\frac{(Y_i - m_i)^2}{2\sigma^2} - \frac{(\theta_i - \mu)^2}{2\tau^2}\right\}, \end{aligned}$$

and

$$\begin{aligned} [x_{FBL_i}|\cdot] &\propto \exp\left\{-\frac{(Y_i - m_i)^2}{2\sigma^2} - \frac{(x_{FBL_i} - \xi)^2}{2\omega^2}\right\} \\ [\beta|\cdot] &\propto \frac{1}{\beta} \exp\left\{-\frac{\sum_{i=1}^n (Y_i - m_i)^2}{2\sigma^2} - \frac{(\log \beta - \gamma)^2}{2\lambda^2}\right\}, \end{aligned}$$

where

$$\begin{aligned} m_i &= \frac{FBL_i [\exp\{\beta(X_i - \theta_i)\} - 1]}{[\exp\{\beta(x_{FBL_i} - \theta_i)\} - 1]}, \\ c_1 &= \frac{(v\sigma)^2 + \frac{Y_i [\exp\{\beta(X_i - \theta_i)\} - 1]}{[\exp\{\beta(x_{FBL_i} - \theta_i)\} - 1]} \kappa^2}{\sigma^2 + \left(\kappa \left(\frac{[\exp\{\beta(X_i - \theta_i)\} - 1]}{[\exp\{\beta(x_{FBL_i} - \theta_i)\} - 1]}\right)\right)^2}, \\ c_2 &= \frac{(\kappa\sigma)^2}{\sigma^2 + \left(\kappa \left(\frac{[\exp\{\beta(X_i - \theta_i)\} - 1]}{[\exp\{\beta(x_{FBL_i} - \theta_i)\} - 1]}\right)\right)^2}, \end{aligned}$$

and $[\mu|\cdot]$ represents the distribution of μ conditional on the rest of the parameters and the data.

Given an initial guess for each of the parameters, $\{x_{FBL_{10}}, \dots, \theta_{n_0}\}$ generating observations from $[x_{FBL_1}, \dots, x_{FBL_n}, FBL_1, \dots, FBL_n, \beta, \mu, \tau^2, \sigma^2, \theta_1, \dots, \theta_n | Y_1, \dots, Y_n]$ is carried out as follows:

1. Generate an observation from $[\mu | x_{FBL_{10}}, \dots, \theta_{n_0}]$ and call the generated observation μ_1 .
2. Generate an observation from $[x_{FBL_1} | \mu_1, \beta_0, \dots, \theta_{n_0}]$ and call the generated observation x_{FBL_1} .
3. Continue to generate from each of the complete conditional distributions given each previously generated observation.
4. Repeat steps 1–3 t times.

As $t \rightarrow \infty$, the distribution of the generated observations, $\{x_{FBL_1}, \dots, \theta_{n_t}\}$ tends to the joint posterior distribution. By using technique described by Raftery and Lewis (1996), we determined that a burn-in of 5,000 and 20,000 realizations was more than sufficient to estimate the posterior distribution.

We were able to obtain observations directly from the complete conditional distributions of μ , τ^2 , χ , ω^2 , v , κ^2 , FBL_1, \dots, FBL_n , and σ^2 . Because the constant of integration for $\theta_1, \dots, \theta_n$,

$x_{FBL_1}, \dots, x_{FBL_n}$, and β was unavailable, we could not sample from these distributions directly. Therefore, we used a Metropolis-Hastings (Hastings 1970) step to generate observations from the complete conditional distributions for θ_i, x_{FBL_i} , and β . Convergence and mixing diagnostics revealed that the chains converged and were mixing well.

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Comment

Naomi S. ALTMAN

I thank the authors for a stimulating article on Bayesian growth curve modeling with only one data point per curve.

Naomi S. Altman is Associate Professor, Department of Biometrics, Cornell University, Ithaca, NY. This work was partially supported by Office of Naval Research grant N0014-96-1-0981. The author thanks the following for assistance with aspects of this discussion; Shane Reese for sharing the fetal size data and the code for the MCMC analysis; Michael Lavine for an enlightening discussion of transformation of multivariate priors; and Kurt Fristrup for reading the portion of the paper discussing visual and acoustic census methods and for assisting with the references. The author thanks Chris W. Clark, who sponsored her 1996–1997 sabbatical at the Bioacoustics Laboratory at Cornell, and Kurt Fristrup and Kathy Dunsmore for stimulating interest in locating and tracking whales by using vocalizations.

This article fits squarely into a growing literature of statistical methods developed for use in managing populations of whales and other large marine mammals.

My own involvement in whale research began in 1996, when I took a sabbatical at the Bioacoustics Laboratory at Cornell to assist with various projects involving the annual census of blue and finback whales off the coast of California and other whale studies.

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