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A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska

JAY M. VER HOEF and KATHRYN J. FROST

Alaska Department of Fish and Game, 1300 College Road, Fairbanks, Alaska 99701, U.S.A.
E-mail: ffjmv@uaf.edu

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Bayesian hierarchical models were used to assess trends of harbor seals, *Phoca vitulina richardsi*, in Prince William Sound, Alaska, following the 1989 *Exxon Valdez* oil spill. Data consisted of 4–10 replicate observations per year at 25 sites over 10 years. We had multiple objectives, including estimating the effects of covariates on seal counts, and estimating trend and abundance, both per site and overall. We considered a Bayesian hierarchical model to meet our objectives. The model consists of a Poisson regression model for each site. For each observation the logarithm of the mean of the Poisson distribution was a linear model with the following factors: (1) intercept for each site and year, (2) time of year, (3) time of day, (4) time relative to low tide, and (5) tide height. The intercept for each site was then given a linear trend model for year. As part of the hierarchical model, parameters for each site were given a prior distribution to summarize overall effects. Results showed that at most sites, (1) trend is down; counts decreased yearly, (2) counts decrease throughout August, (3) counts decrease throughout the day, (4) counts are at a maximum very near to low tide, and (5) counts decrease as the height of the low tide increases; however, there was considerable variation among sites. To get overall trend we used a weighted average of the trend at each site, where the weights depended on the overall abundance of a site. Results indicate a 3.3% decrease per year over the time period.

Keywords: trend analysis, abundance estimation, population monitoring, Markov Chain Monte Carlo, Poisson regression, aerial surveys, *Exxon Valdez* oil spill, harbor seal, *Phoca vitulina richardsi*, Prince William Sound

1. Introduction

Monitoring programs to track long-term changes in population size are important for applied ecological studies. Such monitoring programs often have multiple objectives that include monitoring trends, estimating abundance, and estimating the effects of covariates, both for large areas and smaller areas that comprise the larger area. In this paper we develop a Bayesian hierarchical model for analyzing trend, abundance, and the effects of covariates for monitoring programs of multiple sites, and we apply it to counts of harbor seals following the *Exxon/Valdez* oil spill of 1989 in the Prince William Sound, Alaska.

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Harbor seals are one of the most common marine mammal species in Prince William Sound (PWS), Alaska, and adjacent parts of the Gulf of Alaska. PWS has over 4800 km of coastline, consisting of many fiords, bays, islands, and offshore rocks. The exact number of harbor seals inhabiting the region is unknown, but is at least several thousand (T. R. Loughlin, unpublished report, National Marine Mammal Laboratory, NMFS, Seattle, WA.). Between 1984 and 1988 the number of seals counted at haulout sites in eastern and central PWS declined by about 40% (Frost *et al.*, 1994). The harbor seal population was monitored by flying aerial surveys during 1989–1999 subsequent to the *Exxon/Valdez* oil spill as part of damage assessment and restoration programs.

Many studies have demonstrated effects of time of day, date, and tide on the hauling out behavior of harbor seals (Schneider and Payne, 1983; Stewart, 1984; Harvey, 1987; Pauli and Terhune, 1987; Yochem *et al.*, 1987; Thompson and Harwood, 1990; Moss, 1992; Frost, *et al.*, 1999). The data to describe those behavioral patterns has usually come from continuous or repetitive visual observations of seal haulouts, or from telemetry studies. Information derived from those studies has been used in the design of harbor seal surveys, to the extent that survey programs are generally designed to occur on dates and at times when the greatest number of seals is expected to be out of the water and available for counting (Pitcher, 1990; Harvey *et al.*, 1990; Olesiuk *et al.*, 1990; Huber, 1995). However, once a ''survey window'' has been established counts have usually been treated as replicates during analyses, and the possible effects of other factors on annual abundance estimates have been ignored. In fact there are generally two ways to account for the effects of covariates. One is to use a design that ''standardizes'' for all of the effects, such as picking a narrow range of dates, having a particular weather condition, a particular time of day, a particular time in the tide cycle, etc. While desirable, the problem with the standardized design approach, for our study, is that date, weather and tide cycles rarely cooperate to provide standardized conditions year after year. We adopt an alternative where we pick a relatively broad range of dates and count seals when weather allows. We then make adjustments to counts based on data collected on covariates that are known to have an effect on counts. Of course, the estimation of the effects of the covariates themselves is also of interest.

There are often several statistical methods to analyze such data. One of the most fundamental differences among statistical methods occurs when making a choice between Bayesian and classical (frequentist) methods. While there are strong philosophical differences, in practice results can be quite similar, and the choice can be made on practical considerations. In this study, we consider models of trend and abundance that include the effects of covariates for twenty-five sites individually. Then it is natural to give the parameters of all 25 sites a common distribution, thus developing a hierarchical model. The advantage of this approach is that the problems of estimating trend, abundance, and the effects of covariates are given a single unified probability framework. The hierarchical model also helps stabilize estimates in cases where sample sizes for individual components are small.

This paper presents an analysis of aerial survey counts of harbor seals in PWS. The objectives are to develop a Bayesian hierarchical model to (1) estimate trends at individual sites, (2) estimate trends in the study area as a whole, (3) estimate yearly abundance at each site, (4) estimate yearly abundance for all sites combined, and (5) study the effects of covariates: date, time of day, time relative to low tide, and tide height, on seal counts.

While we developed this model for harbor seal data, we believe it has broader application in many other monitoring situations.

2. Methods

2.1 *Aerial surveys*

Harbor seals generally have high fidelity to a haulout site during the molting period. They haul out near low tide, which allows them to be counted on multiple occasions. We conducted aerial surveys along a trend count route that covered 25 harbor seal haulout sites in eastern and central PWS (Fig. 1). The route included 7 sites that were substantially affected by the *Exxon Valdez* oil spill and 18 unoiled sites that were outside of the primary affected area (Frost *et al*., 1994). Surveys were flown during the molting period (August–September) in 1984 and 1988–1999.

Visual counts of seals were conducted from a single-engine fixed-wing aircraft (Cessna 185) at altitudes of 200–300 m, usually with the aid of 7-power binoculars. Counts were usually conducted from two hours before low tide to two hours after low tide. A survey normally included counts at all 25 sites, but occasionally some sites could not be counted because of poor weather or a rapidly rising tide. For each survey the date, time and height of low tide, and time of sunrise and sunset were recorded for each site. Each site was circled until the observer was confident that an accurate count had been made, and the time of the count was recorded. For larger groups of seals (generally those of 40 or more) color photographs were taken using a hand-held 35-mm camera, and seals were counted from images projected on a white surface. Several survey flights, usually 7–10, were made each year. The effects of the oil spill on harbor seal numbers has been extensively described (e.g., Frost *et al*., 1994; Lowry *et al*., 1994; Morris and Loughlin, 1994). In this paper, we only consider data after the 1989 oil spill, from 1990 to 1999. The total number of counts for all sites for the time period was 1739.

Prior to further data analysis, the covariates: date, time-of-day, time-relative-to-low-tide, and tide-height were rescaled to prevent computer overflows during estimation. The effect of year was rescaled by setting 1994 as year 0. Specifically, the covariates were adjusted as follows:

$$
\begin{aligned}
j &= \text{Year}-1994,\\
x_{1ijk} &= \frac{(\text{Date with August 1 as day 1}-28)}{100},\\
x_{2ijk} &= \frac{(\text{Time-of-day from midnight [in minutes]}-720)}{1000},\\
x_{3ijk} &= \frac{(\text{Time-relative-to-low-tide [in minutes]})}{100},\\
x_{4ijk} &= \frac{(\text{Tide-height of low tide [in feet]})}{10},
\end{aligned}
$$

for the k-th flight at site i in year j.

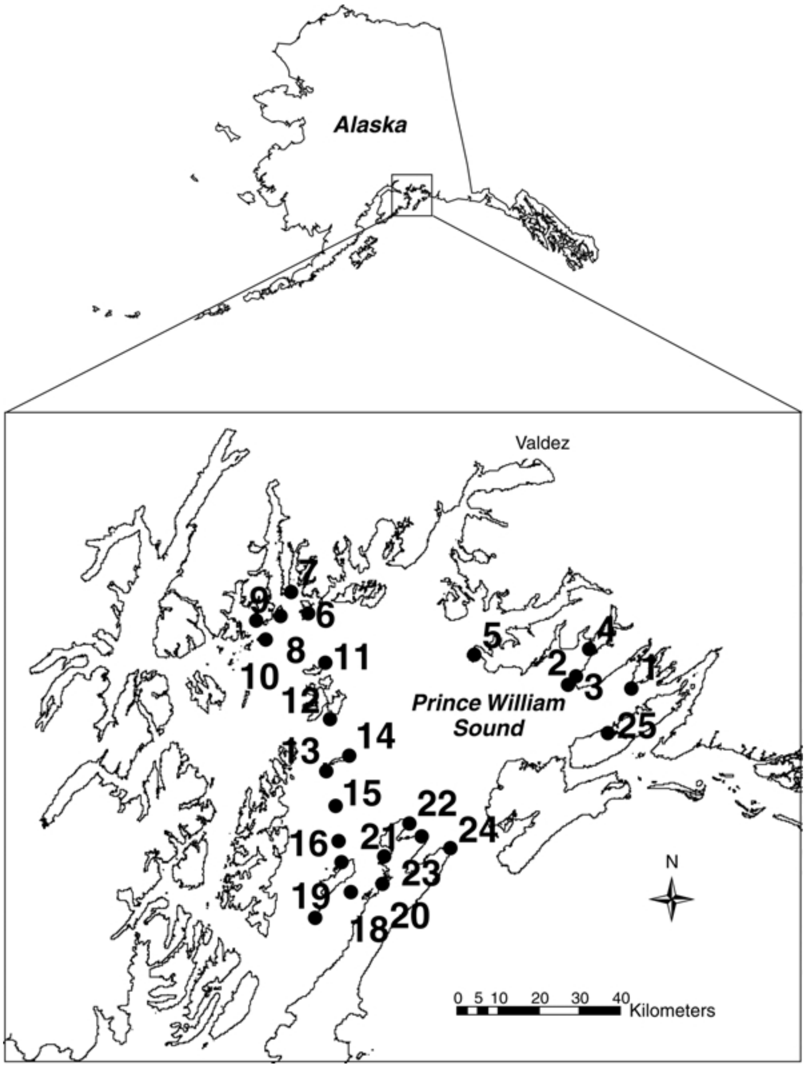

Figure 1. Map showing trend-count sites for aerial surveys of harbor seals in Prince William Sound, Alaska, 1990–1999.

2.2 *Previous methods—Poisson regression for all sites combined*

Frost *et al*. (1999) used a generalized linear model (McCullagh and Nelder, 1989) with a log link function and a Poisson distribution to analyze the factors that may affect the number of seals hauled out and available to be counted during surveys. The model may be written as: $\Pr(Z_{ijk} = z) = \exp(-\lambda_{ijk})\lambda_{ijk}^{z}/z!$ with $\ln(\lambda_{ijk}) = \boldsymbol{\beta}'\boldsymbol{x}_{ijk}$ where $\boldsymbol{\beta}$ is a parameter vector and $\boldsymbol{x}_{ijk}$ is a vector containing information on the state of covariates: site, year, date, time of day, time relative to low tide, and tide height, for the k-th flight at site i in year j. Loglikelihood ratios were used to obtain a parsimonious model. Then the count data were adjusted to a standardized set of covariates. The adjustment amounted to the expected count at each site for each year under optimal conditions. Next, to assess overall trend, linear regression and Poisson regression models were fitted to the adjusted yearly count estimates. The analysis of Frost *et al.* (1999) was complicated because they first adjusted yearly counts for each site to a standardized date, time of day, and time relative to low tide, then summed over sites to get a yearly index, and then used the index in a trend regression analysis. Under these circumstances, it is difficult to take all of the uncertainty associated with adjusting the counts and then using trend analysis on the adjusted counts. Therefore, they used bootstrap methods (Efron and Tibshirani, 1993; Manly, 1997) for the whole procedure.

2.3 *Bayesian hierarchical model*

The Bayesian hierarchical model begins with Poisson regression for each observation. Let Z_{ijk} be a random variable of the number of seals counted for the k-th replicate flight in the j-th year at the i-th site. Write

$$f(z_{ijk}) = \exp(-\lambda_{ijk})\lambda_{ijk}^{z_{ijk}}/z_{ijk}!$$

with

$$\ln(\lambda_{ijk}) = \theta_{ij} + x_{1ijk}\beta_{1i} - x_{1ijk}^2 b_{2i} + x_{2ijk}\beta_{3i} - x_{2ijk}^2 b_{4i} + x_{3ijk}\beta_{5i} - x_{3ijk}^2 b_{6i} + x_{4ijk}\beta_{7i} + \varepsilon_{ijk}, \quad (1)$$

where θ_{ij} is an intercept, ε_{ijk} is an overdispersion parameter, and x_{pijk} is the p-th explanatory variable containing observed values of the covariates: x_{1ijk} = date, x_{2ijk} = time of day, x_{3ijk} = time relative to low tide, and x_{4ijk} = height of tide, for the k-th flight at site i in year j. For the effects of date, time of day, and time relative to low tide, we wanted a model that would be unimodal with a single peak value, so we forced b_{2i}, b_{4i}, and b_{6i} to be positive by reparameterizing; e.g., $b_{2i} = \exp(\beta_{2i})$, where $-\infty \leq \beta_{2i} \leq \infty$. Thus, the two terms $x_{1ijk}\beta_{1i} - x_{1ijk}^2 b_{2i}$ form a Gaussian curve when exponentiated. We assume that conditional on the covariates, all observations are independent, so the joint density is,

$$f(z|\boldsymbol{\theta}, \boldsymbol{\beta}) \equiv \Pi f(z_{ijk}).$$

In the next level of the hierarchy, we develop a separate trend model for each site, $f(\theta_{ij}|\tau_{0i}, \tau_{1i}, \delta^2) = N(\tau_{0i} + \tau_{1i} \times j, \delta^2)$, where $N(m, V)$ is a normal distribution with mean m and variance V, and jointly,

$$f(\boldsymbol{\theta}|\boldsymbol{\tau}, \delta^2) = \prod_{i=1}^{25} \prod_{j=-4}^{5} f(\theta_{ij}|\tau_{0i}, \tau_{1i}, \delta^2).$$

Next, we group the site-specific covariate parameters and give them a distribution; $f(\beta_{pi}|\mu_p, \sigma_p^2) = N(\mu_p, \sigma_p^2)$, where jointly,

$$f(\boldsymbol{\beta}|\boldsymbol{\mu}, \boldsymbol{\sigma}) = \prod_{p=1}^{7} \prod_{i=1}^{25} f(\beta_{pi}|\mu_p, \sigma_p^2).$$

For the trend parameters, we will also group the site-specific covariate parameters and give them a distribution; $f(\tau_{qi}|\eta_q, \gamma_q^2) = N(\eta_q, \gamma_q^2)$, where jointly,

$$f(\boldsymbol{\tau}|\boldsymbol{\eta}, \boldsymbol{\gamma}) = \prod_{q=0}^{1} \prod_{i=1}^{25} f(\tau_{qi}|\eta_q, \gamma_q^2).$$

We also group the overdispersion parameters and give them a distribution; $f(\varepsilon_{ijk}|\mathbf{0}, \xi_i^2) = N(0, \xi_i^2)$, where jointly,

$$f(\boldsymbol{\varepsilon}|\mathbf{0}, \boldsymbol{\xi}) = \prod_{i=1}^{25} \prod_{j=-4}^{5} \prod_{k=1}^{n_{ij}} f(\varepsilon_{ijk}|0, \xi_i^2),$$

and $f(\boldsymbol{\xi}_i|\nu_a, \nu_b) = GAM(\nu_a, \nu_b)$, where $GAM(a, b)$ is a gamma distribution with parameters a and b, where jointly,

$$f(\boldsymbol{\xi}|\nu_a, \nu_b) = \prod_{i=1}^{25} f(\xi_i|\nu_a, \nu_b).$$

In the fourth and final level of the hierarchy, we give diffuse prior distributions, $f(\mu_p)$ and $f(\eta_q)$ are $N(0, 1{,}000{,}000)$; and $f(\delta^2)$, $f(\sigma_p^2)$, $f(\gamma_q^2)$, $f(\nu_a)$ and $f(\nu_b)$ are $GAM(0.001, 0.001)$. Jointly,

$$f(\boldsymbol{\mu}) = \prod_{p=1}^{7} f(\mu_p), f(\eta) = \prod_{q=0}^{1} f(\eta_q), f(\boldsymbol{\sigma}) = \prod_{p=1}^{7} f(\sigma_p^2), \text{ and } f(\boldsymbol{\gamma}) = \prod_{q=0}^{1} f(\gamma_q^2).$$

The hierarchical model is shown diagrammatically in Fig. 2. Using the hierarchical setup, Bayes theorem allows us to write the posterior distribution:

$$f(\boldsymbol{\theta}, \boldsymbol{\beta}, \boldsymbol{\tau}, \boldsymbol{\varepsilon}, \delta^2, \xi, \boldsymbol{\mu}, \boldsymbol{\sigma}, \boldsymbol{\eta}, \boldsymbol{\gamma}, \nu_a, \nu_b|z) \propto$$
$$f(z|\boldsymbol{\beta}, \boldsymbol{\theta})f(\boldsymbol{\theta}|\boldsymbol{\tau}, \delta^2)f(\boldsymbol{\beta}|\boldsymbol{\mu}, \boldsymbol{\sigma})f(\boldsymbol{\varepsilon}|\mathbf{0}, \boldsymbol{\xi})f(\boldsymbol{\tau}|\boldsymbol{\eta}, \boldsymbol{\gamma})f(\delta^2)f(\boldsymbol{\xi}|\nu_a, \nu_b)f(\boldsymbol{\mu})f(\boldsymbol{\sigma})f(\boldsymbol{\eta})f(\boldsymbol{\gamma})f(\nu_a)f(\nu_b). \quad (2)$$

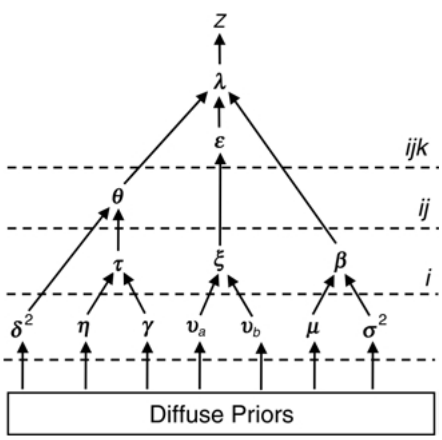

Figure 2. Diagrammatic scheme of hierarchical model.

It is difficult to obtain an analytical solution to the above equation; however the modern techniques of Markov Chain Monte Carlo (MCMC, see, for example, Gilks *et al.*, 1996) allow us to obtain samples from the posterior distribution. From these samples we can compute functions and summaries of the posterior distribution, such as expectation, standard errors, quantiles, etc. The resulting tables use covariates on their standardized scale, but the figures show the effects back on the original scale. Rescaling the covariates helped to stabilize the MCMC methods.

From the posterior distribution, several parameters have particular interest. The parameter τ_{1i} is the slope parameter for the i-th site, and η_1 is the mean of all 25 sites, which is an overall indication of trend among all sites. However, η_1 is not entirely satisfactory because it weights all sites equally (actually, it depends on their sample sizes—in this study, they are all relatively equal). In order to give sites with greater abundance more weight, we can consider the following:

$$\alpha_1 = \frac{\sum_{i=1}^{25} \exp(\tau_{0i})\tau_{1i}}{\sum_{i=1}^{25} \exp(\tau_{0i})}, \tag{3}$$

as an indicator of overall trend. Other weighting schemes are possible, such as weighting by the last year, or the average of all years. The hierarchical Bayes method using MCMC makes it easy to obtain inference on α_1—we simply use the samples from the posterior distributions of $\tau_{0\mathrm{i}}$ and τ_{1i} to compute the posterior distribution of α_1. Another function of the parameters that has particular interest is an indication of overall abundance for each year, which we compute as,

$$\phi_j = \sum_{i=1}^{25} \exp(\theta_{ij} + x_{1s}\beta_{1i} - x_{1s}^2 b_{2i} + x_{2s}\beta_{3i} - x_{2s}^2 b_{4i} + x_{3s}\beta_{5i} - x_{3s}^2 b_{6i} + x_{4s}\beta_{7i}). \tag{4}$$

where $x_{ks}; k = 1, \ldots, 4$, are specified values for the covariates.

We performed some model diagnostics. A common measure for the fit of the model is to compute a Chi square discrepancy (see, for example, Gelman *et al.*, page 172). In general, it is defined as, $[y - E(Y)]^2/\mathrm{var}(Y)$. For our application, we computed the posterior distribution of the Chi square discrepancy for each site,

$$R_i = \frac{1}{N_i} \sum_{j=-4}^{5} \sum_{k=1}^{n_{ij}} \frac{(Z_{ijk} - \lambda_{ijk})^2}{\lambda_{ijk}},$$

where N_i is the total number of observations over all replicates and years for the ith site. If the model is fitting well, we expect R_i to be near one for each site. We compute R_i by site to highlight whether lack of fit occurs locally or globally.

The statistical package *WinBUGS* was used for the Bayesian hierarchical model. For the MCMC, we let the chain ''burn in'' for 4000 samples, and then computed the means, standard errors, and percentiles based on the next 10,000 simulations. We started the chain from several different points and obtained very similar results, and examination of the trace of the chain did not reveal any irregularities. Typically the autocorrelation in the chain for each parameter dropped to near zero well before 30 iterations.

3. Results

3.1 *Covariates*

Four primary factors were considered that might affect the counts of seals during aerial surveys. Figs 3 to 6 show the effects of date, time of day, time relative to low tide, and tide height for each site. There graphs were developed by first transforming the covariates as described in Section 2, call them $x_{ks}; k = 1, \ldots, 4$. Then each panel is a graph of

$$\exp\left(x_{ks}\hat{\beta}_{pi} - x_{ks}^2\hat{b}_{qi}\right), \quad (5)$$

for the i-th site, where $\hat{\beta}_{pi}$ is the mean of the MCMC sample from the posterior distribution for that β associated with x_{ks}, and $\hat{b}_{qi}$ is the mean of the MCMC sample from the posterior distribution for $b_{qi} = \exp(\beta_{qi})$. Notice that Fig. 6 only contains the term $x_{ks}\hat{\beta}_{pi}$. Also notice that another estimate that easily allows credibility intervals can be obtained for the graphs by using,

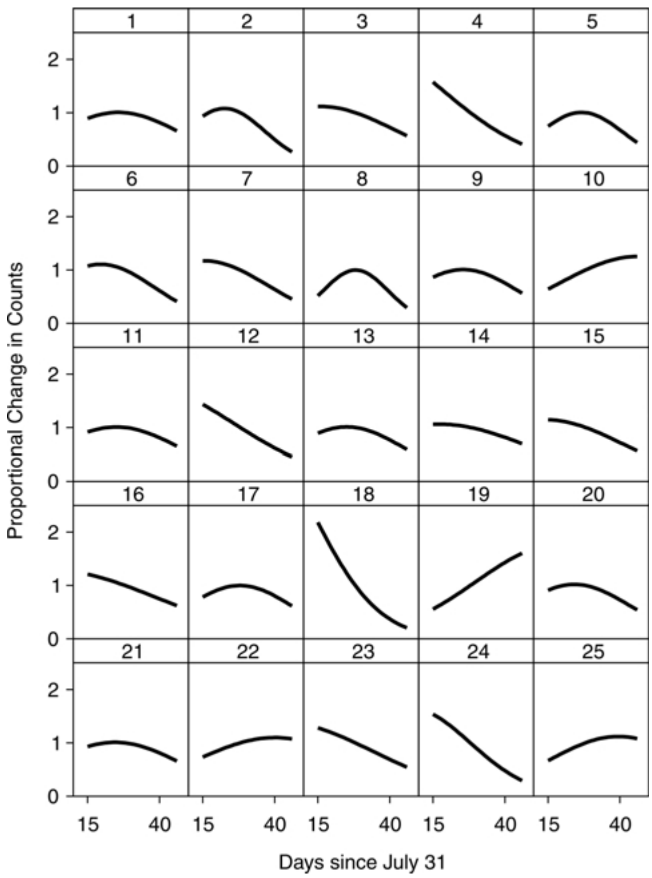

Figure 3. Effect of date on counts of harbor seals for each of the 25 haul-out locations in Prince William Sound, Alaska.

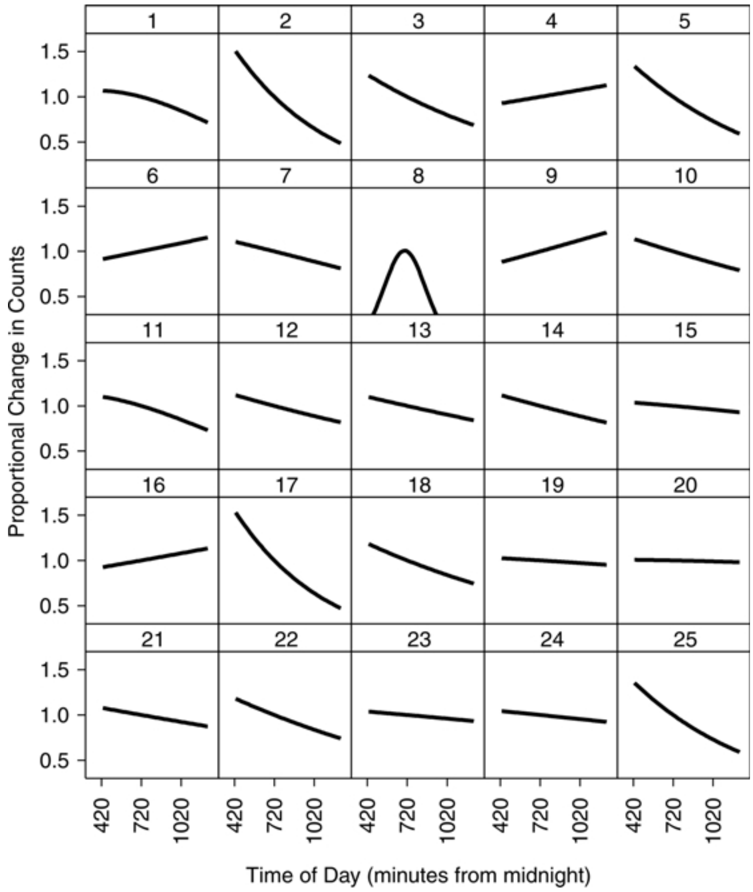

Figure 4. Effect of time of day on counts of harbor seals for each of the 25 haul-out locations in Prince William Sound, Alaska.

$$\frac{1}{N}\sum_{L=1}^{N}\exp(x_{ks}\beta_{pi}^{(L)} - x_{ks}^2\beta_{qi}^{(L)}),$$

rather than (5), where L indexes the MCMC iteration. However, all iterations must be stored for various x values, so it requires more storage.

Note that $\hat{b}_{qi}$ is enforced to be positive, which forces all curves in Figs 3 to 5 to be Gaussian with a single maximum (which may be off the range of the abscissa). We chose to do this because, from a biological viewpoint, we expect seals to spend most of their time hauled out during the molting period, which is around mid to late August. Thus, there should be a well-defined maximum during these molting dates for Fig. 3. Likewise, we expect a peak time of day for haulout, and a peak time relative to low tide. However, we expect only a linear trend (on the log scale) for tide height.

Finally, note that for standardized states of the covariates, Equation (1) can be written as

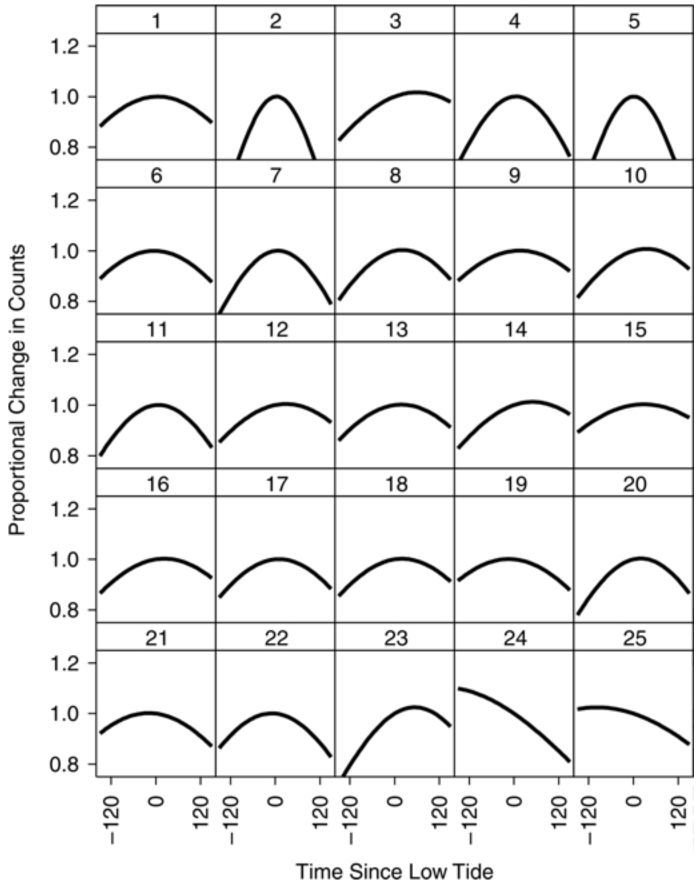

Figure 5. Effect of time relative to low tide on counts of harbor seals for each of the 25 haul-out locations in Prince William Sound, Alaska.

$$\lambda_{ij} = \exp(\theta_{ij}) \exp(x_{1s}\beta_{1i} - x_{1s}^2 b_{2i}) \exp(x_{2s}\beta_{3i} - x_{2s}^2 b_{4i}) \exp(x_{3s}\beta_{5i} - x_{3s}^2 b_{6i}) \exp(x_{4s}\beta_{7i}), \tag{6}$$

so (5) can be seen as a multiplicative factor for each effect that controls the proportional change in the expected counts for the i-th site in the j-th year.

The overall effects of covariates are given in Fig. 7. The model predicted that, overall, maximum counts occur near the 15th of August, after which counts decrease. Counts are about 10% lower on the 21st of August compared to the 15th, and about 20% lower by the beginning of September (Fig. 7(a)). The model predicted that overall counts would decrease throughout the day, with counts 10% lower at noon than at 7:00 am, and another 10% lower at 5:00 pm than at noon (Fig. 7(b)). Relative to low tide, the model predicted the highest counts near low tide, with lower counts (about 10% lower) at $\pm$ 2 hrs from low tide (Fig. 7(c)). There is a small effect due to the height of the low tide (Fig. 7(d)), with slightly higher counts at lower tides.

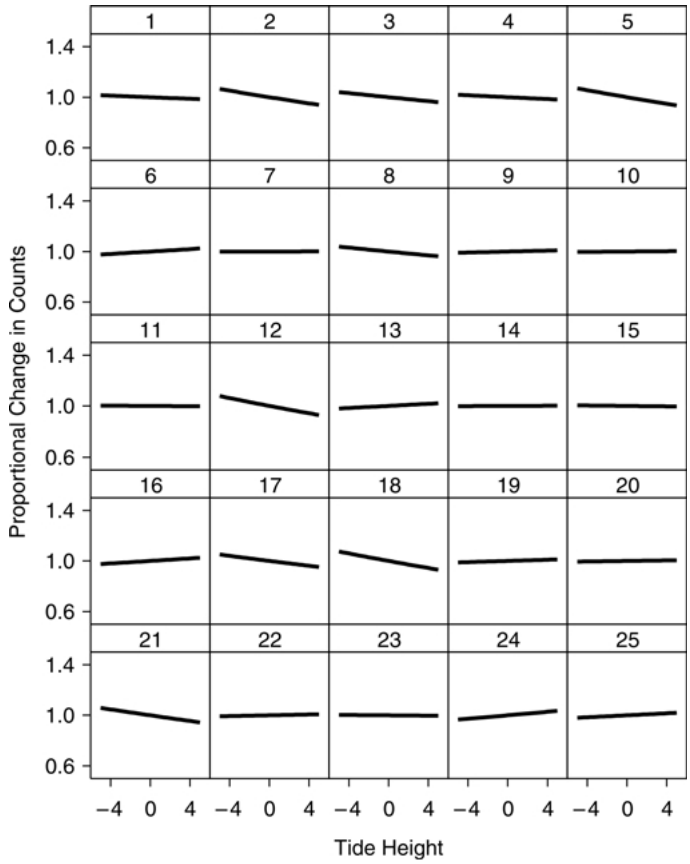

Figure 6. Effect of the height of the low tide on counts of harbor seals for each of the 25 haul-out locations in Prince William Sound, Alaska.

3.2 *Trend and abundance*

In the model (Equation (1)), the intercept term θ_{ij} contains information on the expected counts. The value $\exp(\theta_{ij})$ can be interpreted as the abundance for the i-th site in the j-th year, for some standardized values of the covariates where $x_{ks} = 0$ for each $k, k = 1, \ldots, 4$. This can be seen in Equation (1), which was given in multiplicative form in Equation (6). The mean value of $\exp(\theta_{ij})$ from the posterior distribution, for all years $j = 1, 2, \ldots, 10$, for each of the sites $i = 1, 2, \ldots, 25$, is given in Fig. 8. The actual counts are also given in Fig. 8. Notice that the value of $\exp(\theta_{ij})$ from the posterior distribution may be quite far from the actual counts because $\exp(\theta_{ij})$ is standardized for certain values of the covariates, while the actual counts may have occurred under a different set of values for the covariates.

The estimated trend is also given in Fig. 8, which is the posterior distribution of $\exp(\tau_{0i} + \tau_{1i} \times j)$ for $j = -4, -3, \ldots, 5$ where $j = -4$ is the re-indexed value for year

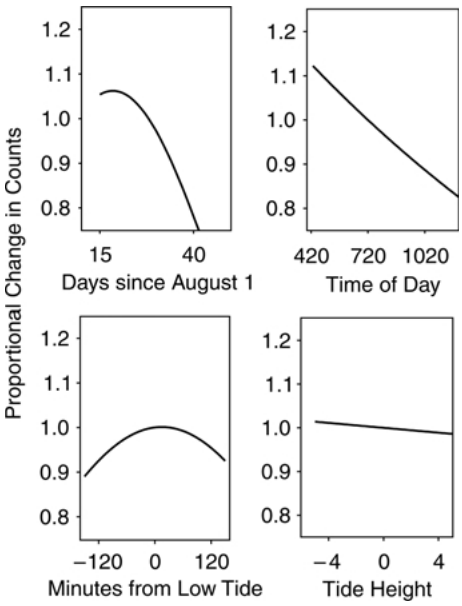

Figure 7. Overall effects of date, time of day, time relative to low tide, and height of low tide, on counts of harbor seals for all of the 25 haul-out locations in Prince William Sound, Alaska.

1990. Fig. 8 shows that most sites have a decreasing trend. The credibility intervals, which are not shown, often do not contain zero.

An example of the full range of inference on trend and abundance for a specific site is given in Fig. 9 for site 4. Notice that we give estimates of abundance for each year, along with the 2.5% and 97.5% credibility limits of the parameter estimates from the posterior distribution. The estimated trend curve is also given, along with 2.5% and 97.5% bounds for the curve from the posterior distribution. Notice that the actual counts show a slight increase over the years but the estimated abundance and trend is downward. This is explained by the fact that counts in earlier years were generally obtained later in the season (often in September). The effect of decreasing counts with date for site 4 can be seen in Fig. 3. Because of scaling to the standardized date (August 28), the abundance estimates show a pattern different than the observed data.

Using a sample from the posterior distribution (2), Fig. 10 shows the posterior distribution of both the mean trend parameter estimate η_1 and the weighted trend estimate α_1, given by Equation (3). The mean of the posterior distribution of η_1 is − 18.5% change per year with a standard deviation of 6.08% and a 95% credibility interval of − 30.6% to − 6.5%; the mean of the posterior distribution of α_1 is − 2.5% change per year with a standard deviation of 1.36% and a 95% credibility interval of − 5.21% to 0.14%. The contrast in the results is interesting, and due to the fact that several small sites dropped to zero, creating several steep negative trends that had a large effect on η_1 but having little effect on α_1. Nevertheless, both results indicate that over the 10 years from 1990 to 1999, there has been a significant overall declining trend in harbor seal numbers. Frost *et al.* (1999) estimated a 4.6% yearly decline from the period 1990 to 1997.

The overall abundance estimates for each year, given by Equation (4), were also determined using a sample from the posterior distribution (2). The results for two different

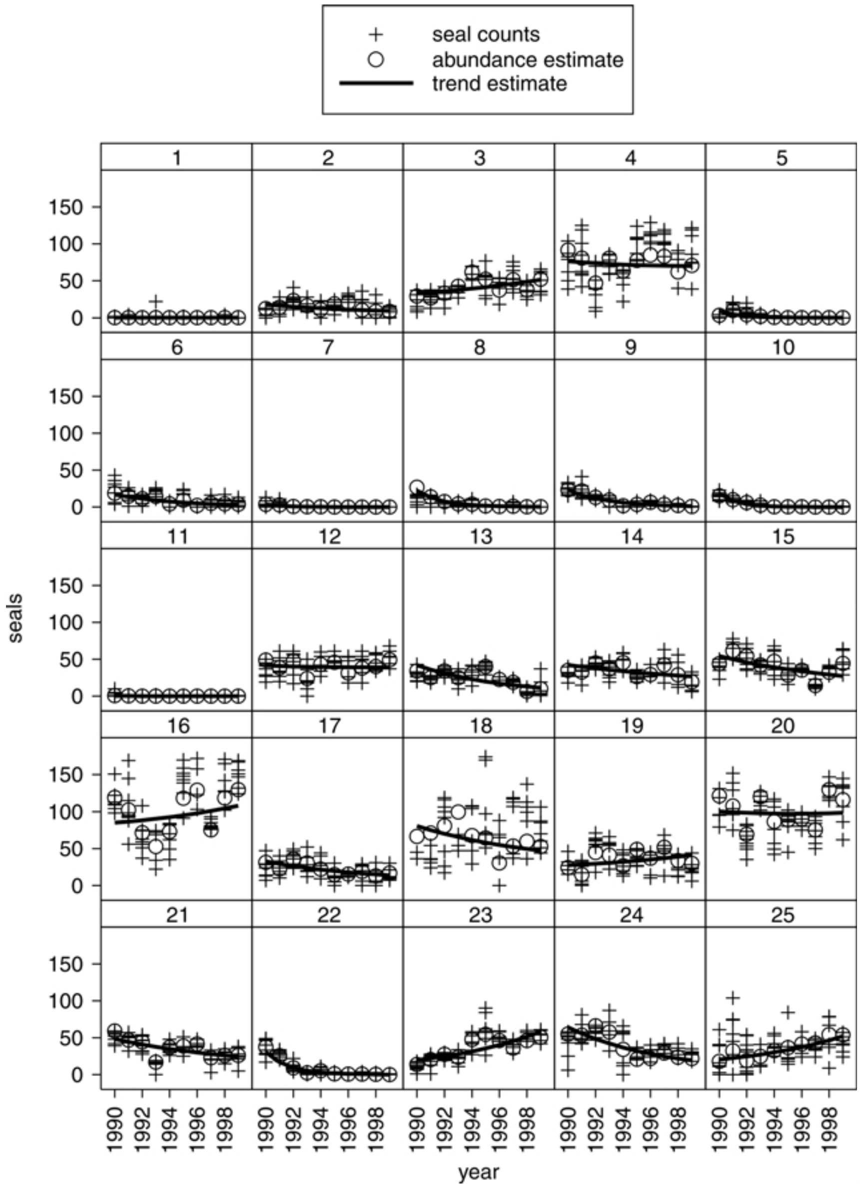

Figure 8. Trend and abundance for each of the 25 haul-out locations in Prince William Sound, Alaska.

sets of covariate values are shown in Fig. 11. In Fig. 11, the results of Frost *et al*. (1999) are also shown, where the abundance estimates were standardized to optimum conditions under their model. Although absolute estimates of abundance vary (due mostly to differing covariate adjustments), the temporal patterns are very similar.

Fig. 12 shows the model assessment, using Chi squared discrepancy, R_i, for each site. We initially tried a model without the overdispersion parameter. As Fig. 12 shows, most

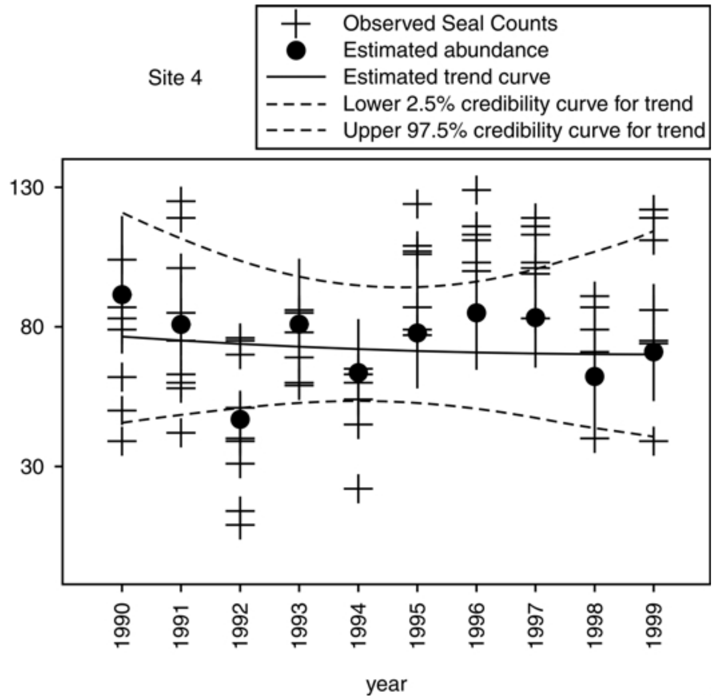

Figure 9. Trend and abundance for site 4 in Prince William Sound, Alaska.

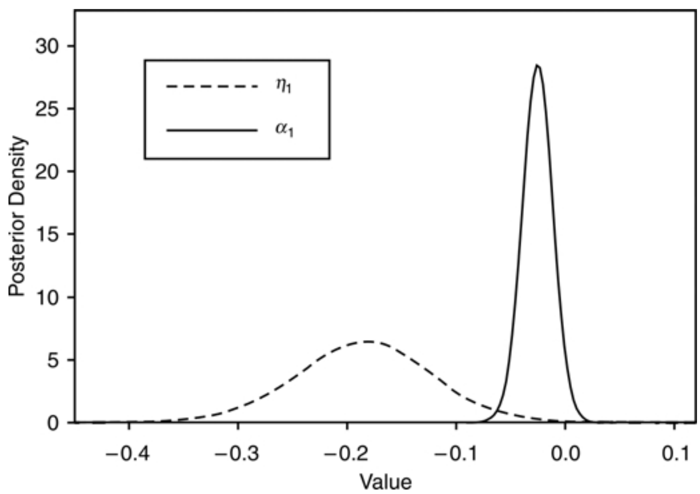

Figure 10. Posterior distribution for η_1 and α_1.

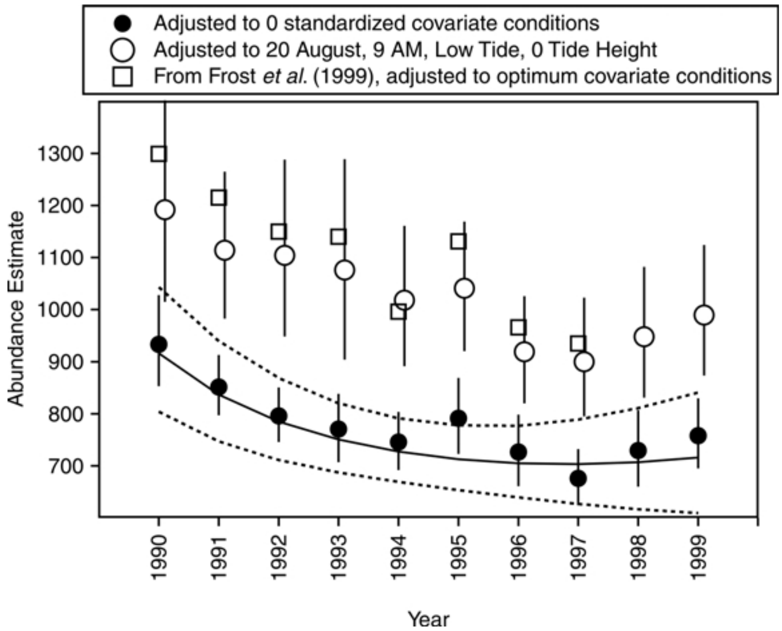

Figure 11. Overall abundance for all 25 sites in Prince William Sound, Alaska.

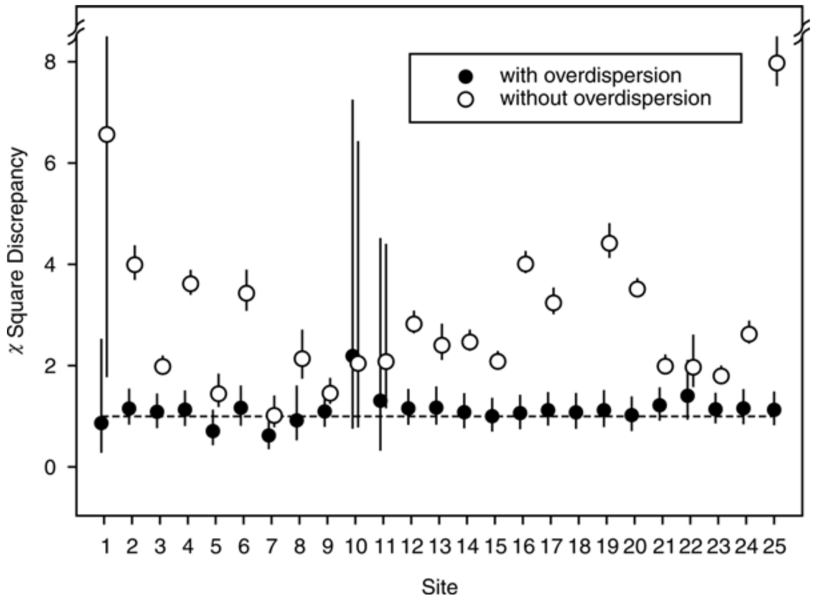

Figure 12. Chi squared discrepancy for all 25 sites in Prince William Sound, Alaska. The vertical bars indicate the 95% credibility interval from the posterior distribution.

sites had more variability than explained with only covariates in (1). The addition of the overdispersion parameter ε_{ijk} in (1) gives a good model fit for these data.

Other parameters from the posterior distribution have less interest and are not given.

4. Discussion

The goals for monitoring ecological populations, even within a single study, are varied. We may often be interested in population estimates at a given time and/or trend estimates for each location or a collection of sites. We may also be interested in functions of population estimates, trends, or their combination. Finally, we may have information on covariates, and we may be interested in the effect of covariates on population trends and abundance. In this paper, we considered a general setup where we have repeated samples within years, at several sites, across several years. In this setup, there are four sources of variability due to: (1) effect of covariates on observations, (2) sampling to estimate the population at some site at some time, (3) the error of the true population at some time about the hypothetical trend curve for that site, and (4) differences in trend among sites. For this setup, we considered the Bayesian treatment of hierarchical models to be the ideal method of statistical inference for several reasons: (1) the 4 sources of variability described earlier could be put into one unified probability framework, (2) estimates of populations or trend ‘‘borrowed strength’’ from the unified probability framework, (3) using MCMC methods, it was relatively easy to make a wide range of inferences on functions of population estimates and trends for collections of locations, and (4) we could make inferences on the effect of covariates.

There is some need to discuss the modeling of trend with a simple linear model for each site. True populations are fluctuating according to a model that we have no hope of ever knowing completely. A linear trend component for the model is useful because a single parameter, the slope, captures the essence of how we visualize ‘‘trend.’’ We realize that the linear model is smoothing over true population fluctuations. Our view is that this is desirable; for our application, and many others, we want to smooth over the small variations in time and look at trend over longer time frames. Also, we could add quadratic and higher terms in the model. This might be desirable in order to assess whether a population has ‘‘bottomed out.’’ Bayes factors (see, for example, Gelman *et al.*, 1995, page. 175) could be used to make decisions on competing models. It was not our goal to make such a decision, but rather to model trend, so our linear model is appropriate.

Other enhancements to the model could be considered. For example, it is possible that the date for peak haulout has been trending through time, getting either later or earlier in the season. In that case, (6), which is equal to (1), can be reparameterized so that it contains $\exp((x_{1s} - \beta_{1ij})^2/b_{2i})$, and then β_{1ij} can be given a linear trend per site (call it a date trend). The date trend parameters can be given a distribution, just as the abundance trend parameters. Once again, Bayes factors could be used to decide if this model provided an improvement.

The Bayesian hierarchical model was used to assess trends of harbor seals, *Phoca vitulina richardsi*, in Prince William Sound, Alaska, following the 1989 *Exxon Valdez* oil spill. With respect to covariates, results showed that overall, (1) counts decreased with date, (2) counts decreased throughout the day, (3) counts were at a maximum near low tide, and (4) there was very little effect of tide height; however, there was considerable variation among sites. To get the overall trend we used a weighted average of the trend at each site, where the weights depended on the overall abundance of a site. The overall trend indicated a continued significant decrease in the harbor seal population. To get overall abundance for each year, we summed the abundance estimates for each site. We used MCMC methods to obtain a sample from the posterior distribution of the parameters, which also yields a sample from the posterior distribution of the overall trend and abundance. Other studies have shown site-specific trends and patterns of behavior in harbor seals (Thompson *et al.*, 1997). Other researchers have also used Bayesian hierarchical models to assess trends in wildlife populations (e.g., Craig *et al.*, 1997), although the models vary depending on the wildlife species and sampling method. Here, the use of a Bayesian hierarchical model allowed assessment of trend, abundance, and effects of covariates both at specific sites and overall.

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Biographical sketches

Jay M. Ver Hoef obtained a B.S. in Botany from Colorado State University in 1979, an M.S. in Botany from the University of Alaska, Fairbanks in 1985, and a co-major Ph.D. in both Statistics and EEB (Ecology and Evolutionary Biology) from Iowa State University in 1991. Since then he has been a biometrician with the Alaska Department of Fish and Game in Fairbanks. He is also an adjunct professor with the Department of Mathematical Sciences at the University of Alaska, Fairbanks. He acts as a consulting statistician on a variety of wildlife research and management projects. His research interests are in spatial statistics and Bayesian methods, and he applies them to ecological, environmental, and wildlife data.

Kathryn J. Frost obtained a B.S. in Biology from Tulane University in 1970 and an M.S. in Marine Sciences from University of California Santa Cruz in 1977. She was employed by the Alaska Department of Fish and Game from 1975–2000 as a Marine Mammals Research Biologist. She retired from the ADF&G in 2000, and is currently an Affiliate Associate Professor of Marine Science at the University of Alaska Fairbanks. She is a fellow of the Arctic Institute of North America and a Charter Member of the Society for Marine Mammalogy. Her research interests include the natural history, population biology and ecology of ice associated pinnipeds, beluga whales and harbor seals.