Estimating Natality Rate of Steller Sea Lions at Chiswell Island Rookery, Alaska

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Summary. Maniscalco et al. (2009) analyzed natality of individually marked Steller sea lion females on the Chiswell Island rookery in the Gulf or Alaska. Their data consisted of females identified via unique markings such as scares and fungal patches. From this process MHP estimated average annual natality to be between 0.54 – 0.64. Using a hierarchical model to fully account for survival, detection, and individual heterogeneity on the observed natality process we estimate a population average natality to be 0.54 (95% CI: 0.46 – 0.63). Moreover, the model illustrates that there seems to be a mixture of "quality" in individual natality. Our estimates differ due to the fact that we allow for heterogeneous natality rates among individual females as well as accounting for survival and detection probability.

1. Introduction

Maniscalco et al. (2009) (hereafter MHP) estimated natality rates for individually marked Steller sea lions at Chiswell Island rookery in the Gulf of Alaska. Individuals were identified via natural markings such as scars and fungal patches. MHP then attempted to identify known individuals every breeding season (and opportunistically in between seasons) and record evidence of natality.

used a rather *ad hoc* method of estimating natality while accounting for detectability of individuals over time. Thus, their estimates do not adequately represent the full picture of the natural natality process.

2. A Hierarchical Model for Estimating Natality Rate

2.1. *General hierarchical models*

A basic hierarchical model is composed of two main parts: (1) process model and (2) the data model. The desired level of inference usually concerns the process model. This is usually

a mathematical description of a process (P) occurring in nature. The data model is added to account for the types of data (D) that can be collected to measure the process. Usually the data cannot directly measure P, so a hierarchy is build by conditioning the data model on the unknown "true" state of the process to obtain the joint model $[D, P] = [D|P] \times [P]$, where "$[x|y]$" represents a probability model for x conditioned on y.

2.2. *A process model for natality*

The process of interest here is the natality rate of an individual female, say θ_{it}, where i indexes an individual and t indexes year. For this basic analysis we assume that $\theta_{it} = \theta_i$ (i.e., natality is constant through time for an individual). The first process model fitted was an individual Gaussian random effects model

$$\theta_i = \frac{1}{1 + \exp\{-\mu_\theta - \gamma_{\theta,i}\}}, \qquad i = 1, \ldots, n,$$

where μ is the average individual effect, $\gamma_{\theta,i}$ has a $N(0, \sigma_\theta^2)$ distribution, and n is the number of observed females.

In addition to heterogeneity in natality, it is also presumed that there will exist some level of heterogeneity in annual survival, say ϕ_i, of individuals. Accounting for survival in this analysis is crucial due to the fact that a female which is not seen after a certain time period still has some probability of being alive. She may just not be visiting the rookery before the end of the study. Therefore, we postulate a survival process similar to the natality process,

$$\phi_i = \frac{1}{1 + \exp\{-\mu_\phi - \gamma_{\phi,i}\}}, \qquad i = 1, \ldots, n,$$

where ϕ_i is the annual survival rate of female $i = 1, \ldots, n$, μ_ϕ is the average individual effect, and $\gamma_{\phi,i}$ has a $N(0, \sigma_\phi^2)$ distribution.

It is assumed that the survival process is independent of the natality process. Note, that this does not imply that for an individual female that realizations of these processes are independent. This assumption simply implies that an individual will have a high (or low) natality *rate* independent of its *rate* of survival. Thus we have the joint natality and survival model

$$[\theta, \phi|\mu_\theta, \mu_\phi, \sigma_\theta, \sigma_\phi] = [\theta|\mu_\theta, \sigma_\theta][\phi|\mu_\phi, \sigma_\phi].$$

This is the joint model of the natural processes underlying the data we will obtain.

2.3. *The data model*

Next, we will model the data obtained by MHP at Chiswell Is. MHP performed 2 analyses, the first using all data for a female, beginning with the first year she was identified, the second

beginning after the first observed birth. In the present analysis, we started the record for a female the year following her first identification on Chiswell Is. during the breeding season. Let f_i be the first year a female is seen on Chiswell. My analysis uses data from year $f_i + 1$ till the end of the study.

First we consider the "state" of the animal (i.e., alive or dead in the population of interest), because, for obvious reasons, this will affect the probability that a female will give birth. For female i, denote the state of the animal at time t by S_{it} which equals 1 if the animal is known to be alive in breeding season t and 0 if the female is dead. Of course the 0s are unobservable. So, at some point the female may not be observed for the remainder of the study. From this time on, S_{it} = "NA" (i.e., missing). Let $\mathbf{S}_i = \{S_{it}\}_{t=1}^{k}$, where k is the maximum year resights were conducted, be the recorded state of female i. An example is

$$\mathbf{S}_i = [0\ 1\ 1\ 1\ \text{NA}\ \text{NA}].$$

In this example the female was first identified on $t = 2$, last seen on $t = 4$, its state is unknown after this point. The corresponding capture-history (detection) of this female would be

$$\mathbf{D}_i = [0\ 1\ 1\ 1\ 0\ 0].$$

In addition to the capture-history, $\mathbf{D}_i$ (which gives $\mathbf{S}_i$). MHP also noted whether or not the female in question gave birth in year t. This gives another vector of measurements $\mathbf{B}_i$. For the example female, say,

$$\mathbf{B}_i = [0\ 1\ 1\ 1\ \text{NA}\ \text{NA}].$$

Note, that it is possible to measure birth without detecting the female at Chiswell during the breeding season. A female may be detected just after the breeding season without a pup.

A model for these data conditioned on the individual natality rates and survival rates was constricted in a hierarchical fashion as well. First we condition on the state of the animal. An animal must be alive to give birth, therefore, we considered the Bernoulli model

$$[B_{it}|S_{it}] \sim (\theta_i S_{it})^{B_{it}}(1 - \theta_i S_{it})^{1-B_{it}} \qquad i = 1, \ldots, n;\ t = f_i + 1, \ldots, k.$$

If $S_{it} = 0$, then natality rate = 0. The capture-history data was conditioned on S_{it} and B_{it} because a female has to be alive to be seen and has a higher chance of being seen if she is giving birth (more likely to be at Chiswell, hence detected). So, we consider the detection model

$$[D_{it}|S_{it}, B_{it}] \sim (\delta_{it} S_{it})^{D_{it}}(1 - \delta_{it} S_{it})^{1-D_{it}} \qquad i = 1, \ldots, n;\ t = f_i + 1, \ldots, k,$$

where $\delta_{it} = \delta_0$ if $B_{it} = 0$, else, $\delta_{it} = \delta_1$. Finally, we get to the last piece, a model for the state, S_{it}. The female must be alive at time $t - 1$ to survive to time t, therefore, we consider

the Bernoulli model

$$[S_{it}|S_{i,t-1}] \sim (\phi_i S_{i,t-1})^{S_{it}}(1-\theta_i S_{i,t-1})^{1-S_{it}} \qquad i = 1,\ldots,n;\ t = f_i+1,\ldots,k,$$

where $S_{i,f_i} = 1$ by definition. Putting the three parts together we obtain the data model

$$[D_{it}, B_{it}, S_{it}] \sim [D_{it}|B_{it}, S_{it}, \delta_{it}]\ [B_{it}|S_{it}, \theta_i]\ [S_{it}|S_{i,t-1}, \phi_i] \qquad t = f_i+1,\ldots,k,$$

for each female $i = 1,\ldots,n$.

3. Parameter Estimation

First, an examination of the population of inference. In the analysis performed by MHP, they concluded that their results could be applied to a large area (if not the whole) Gulf of Alaska population f Steller sea lions. I do not believe that these data can be extended beyond those females that had some probability of breeding at Chiswell Island over the course of study. This model depends on the fact that there is positive probability of a female returning to breed on Chiswell Island. If she "dies" (actually dies or emigrates) the effect has to be the same on natality. She contributes no new pups to the Chiswell population. There is no information for estimating these quantities for animals that do not breed at sometime at Chiswell Island.

For a complex hierarchical model such as this estimation can be tricky and there are many potential parameters and derived parameters (functions of parameters) that could be of interest. The most straightforward method to handle both of these issues is Bayesian inference via MCMC (Markov chain Monte Carlo). For this data I used JAGS (v. 1.0.3) to accomplish the sampling. I refrain from giving a description of MCMC here as it is a relatively ubiquitous method. The MCMC algorithm provides a sample from the posterior distribution of the parameters given the data. Essentially, the MCMC inverts the hierarchical model so we can examine the distribution of the parameters given the data we actually observed. This is often termed "Bayesian learning."

3.1. *Prior distributions*

In order to use Bayes methods prior distributions must be specified for the parameters to obtain a complete probability model. Table 1 gives the priors were used for this analysis.

Table 1

Prior distributions used in Bayesian analysis of Chiswell Is. natality data.

Parameter	Prior Distribution
μ_θ	$N(0, 1.58^2)$
μ_ϕ	$N(0, 1.58^2)$
σ_θ	half $t_{df=5}$
σ_ϕ	half $t_{df=5}$
δ_0	Uniform(0,1)
δ_1	Uniform(0,1)

3.2. *Derived parameters*

In addition to the parameters given in Table 1, there are other parameters which might be of interest. Two of these which we consider are the population average natality rate $\bar{\theta} = E[\theta_i]$. For the hierarchical model proposed,

$$\bar{\theta} = \int \frac{(2\pi)^{-1/2} \exp\{u^2\}}{1 + \exp\{-\mu_\theta - \sigma_\theta u\}} du.$$

This is the average natality rate of all females from the Chiswell breeding population. Also, the median natality rate, $\tilde{\theta} = 1/(1 + \exp\{-\mu_\theta\})$ might be of interest. We can similarly calculate $\bar{\phi}$ and $\tilde{\phi}$. Although, our primary interest is natality, survival is more of a nuisance parameter. The derived parameters can be calculated for every iteration in the MCMC routine which provided a sample from the posterior distribution of the derived parameters.

4. Results and Further Modeling

4.1. *Results of proposed model*

Table 2 gives the posterior mean, standard deviation, and 95% credible intervals for the parameters and derived parameters of interest.

Table 2

Bayesian inference for parameters and derived parameters of interest.

Parameter	Mean	SD	95% CI
$\bar{\theta}$	0.53	0.07	(0.44, 0.61)
$\tilde{\phi}$	0.87	0.03	(0.81, 0.93)
σ_θ	1.91	0.41	(1.16, 2.75)
σ_ϕ	0.65	0.46	(0.00, 1.50)
δ_0	0.20	0.04	(0.12, 0.28)
δ_1	0.96	0.02	(0.93, 0.99)

4.2. *Further investigation*

A rather interesting outcome results when the distribution of the estimated individual natality, $\tilde{\theta}_i$, is examined (Figure 2). Upon examination, one can see that there seems to be a bi-modal distribution on natality rates. There are some reliable producers and some poor producers.

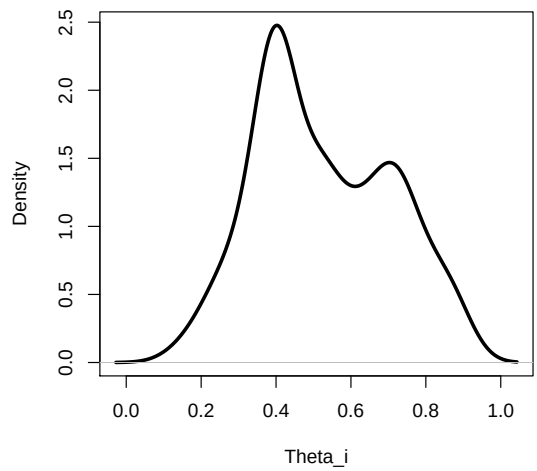

Figure 1 Histogram of estimated individual natality, θ_i, for each of the observed females.

To further investigate I consider the following model for a mixture of natality rates $\theta_i = \theta_1$ with probablity p_Q and θ_0 with probability $1 - p_Q$. Using the mixture model for individual natality gives the following estimates.

Table 3

Bayesian inference for some parameters and derived parameters from the mixture model.

Parameter	Mean	SD	95% CI
$\bar{\theta}$	0.54	0.04	(0.46, 0.63)
θ_0	0.23	0.08	(0.08, 0.40)
θ_1	0.80	0.05	(0.69, 0.90)
$\tilde{\phi}$	0.86	0.03	(0.81, 0.93)
p_Q	0.55	0.10	(0.35, 0.75)
δ_0	0.21	0.04	(0.14, 0.30)
δ_1	0.96	0.02	(0.93, 0.99)

The mean natality $\bar{\theta}$ is nearly identical, but this model gives some extra information. About 55% of the females could be considered quality producers at a rate of 0.8, while the other 45% are poor producers at a rate of about 0.23. There is considerable uncertainty,however, in the mixture (95% CI: 0.35 – 0.75). The question arises as to which model is better. The Gaussian random effects model has an average posterior log-likelihood of -433 and the mixture model has an average likelihood of -450. Therefore, on fit alone, the random effects model is better. If one penalizes based on model complexity, however, the tables are reversed. The estimated "effective" number of parameters in the random effects model is $p_D = 1191$ while $p_D = 1116$ for the mixture model. The DIC (similar to AIC; Akaike's Information Criterion) values for the random effects and mixture models respectively are 2058 and 2017. So, after model complexity corrections, the mixture model is judged to be the most parsimonious.

References

Maniscolco, J. M., Hennen, D., and Parker, P. (2009) Evidence for high natality rates among Steller sea lions in the Gulf of Alaska. Alaska Sea Life Center Technical Report ASLC-0901.