Limited-Information Modeling of Loggerhead Turtle Population Size

Abstract

We attempt to estimate the size of a population of female loggerhead turtles. In traditional capture-recapture experiments to estimate the size of an animal population, individual animals are tagged and the information about which individuals are captured repeatedly is crucial. For these loggerhead turtle data, information about individual turtles is not available. Rather, we observe only the counts of successful and failed nestings at a location over a series of days (in our case, three). We view the turtles' nesting behavior as an alternating renewal process, model it using parametric distributions, and then derive probability distributions that describe the behavior of the turtles during the three days via a 3-way contingency table. We adopt a Bayesian approach, formulating our model in terms of parameters about which strong prior information is available. We use a Gibbs sampling algorithm to sample from the posterior distribution of our random quantities, the most crucial of which is the number of turtles remaining offshore during the entire sampling period. We illustrate the method using data sets from loggerhead turtle sites along the South Carolina coast. We provide a simulation study which illustrates the quality and robustness of the method and investigates sensitivity to prior parameter specification.

KEY WORDS: Bayesian methods, Capture-recapture, Ecological applications, Environmental applications, Gibbs sampling, Mark-recapture, Renewal process.

1 Introduction

The loggerhead sea turtle (scientific name: *Caretta caretta*) is listed as a threatened species in the United States under the Endangered Species Act (NOAA Office of Protected Resources 2011). In particular, loggerheads in the Atlantic Ocean from Florida to North Carolina have been reported as declining in number (Murphy and Griffin 2005). Thus having statistically sound estimates of loggerhead population size is a critical scientific goal. Reports of a decline in numbers are based in part on long-term surveys of nesting activity/nest abundance. Though these surveys were not originally designed to determine population size, we propose a method for estimating the population size of female loggerhead turtles using survey data designed instead to track nest abundance.

Traditional capture-recapture models have a long history of use in estimating the size of a population (e.g., an animal population) whose members cannot be counted exactly because, practically, many remain hidden to investigators. In such an experiment, a particular site is visited repeatedly (say, T times), and individual animals that are captured at a site visit are tagged and released. Traditional capture-recapture analysis observes animals over a period of D days, recording counts of captures for individual animals $n_{s_1 s_2 \cdots s_D}$, where s_j is the status (Present or Absent) for each day. For example, let $0 =$ Absent and $1 =$ Present. Then (in a three-day study, say) n_{010} would be the counts of animals that were absent on Days 1 and 3 and spotted on Day 2. All such counts would be observed except n_{000}, the count of animals that were unseen on each day of the study. A common classical approach to capture-recapture inference uses a Rasch-type (1961) model

$$\text{logit}[P(Y_{ij} = 1 | u_i)] = u_i + \beta_j$$

to model the log-odds of capture for animal i on day j, where $u_i \sim N(0, \sigma^2)$ is an animal-specific random effect, and β_j represents capturability on day j (Agresti 2002). Otis et al. (1978) presented a comprehensive set of capture-recapture models ranging from a simple model assuming a unique probability of capture across visits and across animals to models allowing for various forms of variation in capture probability. This

work was extended and generalized by Evans, Bonett, and McDonald (1994).

Capture-recapture research makes the distinction between *closed populations* (in which we assume no animals were born, died, or migrated into or out of the habitat during the study period) and *open populations* (which permit the possibility of deaths or new arrivals during the study period). Agresti (2002, Sec. 12.3.6 and Sec. 13.1.3) discusses closed-population capture-recapture models in the context of random-effects models and latent-class models. The random-effects presentation is based on a 2^T contingency table and is related to previous work by Fienberg (1972) and the log-linear modeling approach of Cormack (1989). Pledger et al. (2003) studied heterogeneity in capture and survival probabilities for an open population model using a finite mixture approach.

While our primary goal is to estimate an unknown population size, the data-gathering mechanism we investigate in this paper is quite different than those in previous studies. Data gathered on loggerhead turtle abundance rarely involves tagging. The information we have is therefore far more limited than in a traditional capture-recapture situation. We consider adapting principles of capture-recapture analysis to the problem of estimating (in the absence of tagging) the population of female loggerhead turtles living off a given beach area.

The unique nesting pattern of these turtles plays a fundamental role in the analysis of the detection data. During their nesting season, loggerhead turtles come ashore at night when they are biologically ready to lay eggs, and only during these shore excursions can they be "counted." A turtle may nest successfully during the first night's attempt; on the other hand, the attempt may be unsuccessful, which is known as a "false crawl." False crawls may occur because of disturbances (e.g., from the presence of humans) or because of the turtle's momentary discomfort with an environmental factor such as the beach characteristics or temperature (Dodd 1988; Raymond 1984; Stoneburner and Richardson 1981). In some cases the reason for the false crawl is simply unknown (Dodd 1988). When a false crawl occurs, the turtle will return on successive nights, each night nesting or false-crawling. Once a nest is successfully made, the turtle returns to the ocean. Therefore, on each night, every turtle's status

can be labeled by one of {Offshore, False Crawl, Nest} (abbreviated {O, F, N}).

The data in such studies are typically gathered by researchers and volunteers who search the beach (on foot or via aerial surveys) early in the morning, looking for signs of the previous night's turtle activity. Evidence that indicates a turtle excursion includes crawl tracks in the sand leading from the ocean to the higher beach and the digging of a "body pit" and/or "egg chamber" in the sand (Dodd 1988). A successful nesting is further evidenced by eggs dropped in the chamber and the turtle's filling and concealing the body pit with sand before it returns to the ocean. A false crawl may consist of a brief trail through the sand, or it may include digging the body pit and/or egg chamber. Once the turtle begins to drop eggs, however, it usually completes the nesting process (Margaritoulis 1985).

Experienced researchers are typically good at distinguishing a false crawl from a nest, although these can appear similar to an untrained eye. The researchers count the number of successful nests and the number of false crawls from the previous night, typically gathering these counts on D consecutive mornings during the nesting season. In this paper we assume that counts are available for at least $D = 3$ consecutive nights during the middle of the season. In studies of nesting behavior, the ultimate goal is to estimate the total number of nests over the course of a season based on multiple sets of consecutive-day surveys. Using assumptions based on scientific knowledge of turtle nesting behavior, these surveys of nesting activity can actually be used to construct estimates of population size.

We assume turtles make their first onshore excursion of the season at somewhat evenly distributed times over the early weeks of the season (which will motivate a uniform distribution for the length of time before a nominal start of the season and the first arrival in our simulated data of Section 5). The mean number of excursions per season has been estimated to be around 3 or 4 by Frazer and Richardson (1985) and around 2.5 by Richardson and Richardson (1982). This number is not crucial for us, however, except to confirm the usual length of the season, since we are interested in turtle counts in the middle of the season. Turtles tend to remain in the same general area between nesting excursions (Limpus and Reed 1985); this justifies modeling the

turtle population as closed, an assumption we will make henceforth.

Some key differences exist between the information available in the turtle study and that available in traditional capture-recapture studies. For example, the status for each animal in a traditional study is binary (Detected, Not Detected) whereas the turtles have three possible states (two of which represent a type of detection). Also, in traditional studies, detected animals are individually identified and tagged. The turtles are not seen individually, so we only have the total counts of the two "detection states" for each night.

2 Model and Notation

A key benefit of the method we will present is that our model is formulated in terms of parameters about which strong prior information (based on previous subject-matter studies and expert opinions) exists, i.e., the parameters that govern the turtles' biological nesting traits. Our approach permits us to take full advantage of this well-founded knowledge.

2.1 Justification of Prior Distributions and Beliefs

We make a few distributional assumptions about the data, which reasonably reflect expert opinion about the turtles' nesting behavior. We assume that the interarrival spacings (the numbers of days between a turtle's nesting and the next time she comes ashore to nest again) follow a normal distribution (technically an integer normal). While the mean μ and standard deviation σ of this distribution are unknown, biologists strongly believe μ to be near 13 days (Dodd 1988; Talbert et al. 1980). We therefore choose a $N(\mu_\mu, \sigma_\mu^2)$ prior distribution for μ, with $\mu_\mu = 13$ and $\sigma_\mu^2 = 0.65^2$. Gallagher et al. (1972) suggest 12-14 days as the typical set of values this interarrival time takes; using the rule of thumb (McClave and Sincich 2006) of approximating the standard deviation as $Range/4$, we may assume σ is near 0.75. We place an inverse gamma (IG) prior on σ with parameters $\alpha_\sigma = 9$ and $\beta_\sigma = 6$ for a prior expected value $E(\sigma) = 6/(9 - 1) = 0.75$.

We also assume the number of false crawls before a successful nesting is modeled as a geometric random variable, with nesting probability p and false crawl probability $q = 1 - p$. The geometric model assumes that the probability of false crawling is constant across nights, which are assumed independent. This independence assumption appears justified (Griffin, Personal communication, 2009), at least for several consecutive nights. Note that the probability of a large series of false crawl nights in a row (after which point p might change) is fairly negligible. (The issue of whether p is constant or random across turtles is addressed in Section 5.2.) We may obtain a prior expectation for p based on scientific literature. Dodd (1980) gives estimates from a variety of sources of the proportion of onshore excursions that are false crawls. Talbert et al. (1980) gave such a value as 40.5%, using South Carolina coastal data. Stoneburner (1981) gave figures of 30.8%, 41.2%, and 50.4% for three locations along the southeastern Atlantic coast. Raymond (1984) and Crouse (1984) report roughly half of excursions resulted in false crawls. All in all, this prior information indicates the proportion of excursions that are false crawls is near 0.4. Hence our prior on p is a beta$(6, 4)$, which implies $E(p) = 0.6$ and $P[0.35 < p < 0.85] \approx 0.9$ *a priori.*

In Section 4, we will develop a prior distribution for the number of turtles offshore all three sampled nights.

2.2   Marginal, Conditional, and Joint Probabilities

Since the "nesting state" lasts one night, we can write marginal probabilities of each of the three states O, F, N. These expressions, which represent the proportion of time a turtle can be expected to be in each state, are justified by treating the process as a 3-state alternating renewal process (see Ross 1996). These proportions are the expected lengths of time in each state, divided by the sums of the three expected lengths. Note that the expected time offshore is the normal mean μ; the expected number of nights of false crawls is the geometric mean q/p; and the expected number of nights nesting is the constant 1:

$$p_O = \frac{\mu}{\mu + 1 + q/p} \qquad p_N = \frac{1}{\mu + 1 + q/p} \qquad p_F = \frac{q/p}{\mu + 1 + q/p}$$

The above representation of the marginal probabilities of each state technically holds for nonlattice random variables, while the "number of days" is a lattice random variable. Still, this marginal probability distribution provides a reasonable and coherent probability model for our process. We point out that this model works best for data gathered within the interior of the nesting season: The initial time to nesting may follow a different distribution than do the interarrival times after a turtle has nested and has eased into its "equilibrium pattern" for that season; i.e., the process for the *entire* season is actually a delayed renewal process (Ross 1996). We note that the counts of turtle activity are typically gathered during the middle of the nesting season.

In addition, specific biological properties of the nesting process yield conditional probabilities for the states, given below (where $p_{B|A}$ denotes the probability of being in state B on day j given the turtle was in state A on day $j-1$):

$$p_{O|O} = \omega \qquad\qquad p_{N|O} = p(1-\omega) \qquad\qquad p_{F|O} = q(1-\omega)$$

$$p_{O|N} = 1 \qquad\qquad p_{N|N} = 0 \qquad\qquad p_{F|N} = 0$$

$$p_{O|F} = 0 \qquad\qquad p_{N|F} = p \qquad\qquad p_{F|F} = q$$

The parameter ω, the probability that an offshore turtle remains offshore, plays an important role in our model. Given a pair (μ, σ), we can calculate ω, as we show in Section 2.3, and thus our solid prior knowledge of (μ, σ) yields a trustworthy prior expectation for ω.

Using these marginal and conditional probabilities, we can construct joint probabilities for the possible successive three-day outcomes ABC, where $A \in \{O, F, N\}, B \in \{O, F, N\}, C \in \{O, F, N\}$ (see Table 1). In deriving these joint probabilities we assume a kind of Markov property, assuming that $p_{C|(A,B)} = p_{C|B}$, so that $p_{ABC} = p_A p_{B|A} p_{C|B}$. (We assume one practical exception to this property, setting $p_{O|(N,O)} = 1$ rather than $p_{O|(N,O)} = p_{O|O} = \omega$, since a turtle who nested on the first observed day will virtually certainly remain offshore on the following two days.)

[[Table 1 goes around here]]

2.3 Calculation of Probability of Remaining Offshore

For given μ and σ, calculating $\omega = p_{O|O}$ is possible. This expression depends on the number of days since the last nesting episode (denoted k in the following equation), so it may be expressed as a weighted average of discrete normal hazards:

$$\omega \approx 1 - \sum_{k=1}^{\infty} \frac{\Phi\left(\frac{k+0.5-\mu}{\sigma}\right) - \Phi\left(\frac{k-0.5-\mu}{\sigma}\right)}{1 - \Phi\left(\frac{k+0.5-\mu}{\sigma}\right)} g\left(\frac{k - 0.5 - \mu}{\sigma}\right), \tag{1}$$

where the 0.5 values are continuity corrections, since the data are recorded in days (a discrete variable). The density $g(\cdot)$ is a "waiting density." Note that for any given offshore turtle, we do not know how long it has been since the last nesting episode. The mean waiting time (say U) until the next onshore excursion could vary randomly from 0 days (if the turtle last nested long ago and is ready to nest again) to μ days (if the turtle just finished nesting). Specifically, if

$$U \sim U(0, \mu), \; X|U \sim \max\{0, N(U, \sigma^2)\},$$

then $g(\cdot)$ results from integrating U out of the joint density of (X, U).

Given our prior expectations that $\mu = 13$, $\sigma = 0.75$, we evaluate (1) – in practice truncating the infinite sum at a reasonable cutoff – and obtain the prior expected value for $\omega \approx 0.923$ in our case. This implies a prior expectation that just over 90% of turtles offshore one night will remain offshore the following night. Plugging prior expectations for μ, p, and ω into the expression in the top left cell of Table 1 yields the prior expected $p_{OOO} = 0.755$. Previous years' data (or expert guesses) about total population size can be combined with this value to develop a prior for the number of turtles offshore all three sampled nights, as we will do in Section 4.

3 Estimation Method

Recall that our situation differs from classical capture-recapture, in part, because we do not have the observed counts in the 3-way data table that corresponds to the table of joint 3-day cell probabilities. Rather, we observe the 6-element vector

$\mathbf{y} = (N_1, N_2, N_3, F_1, F_2, F_3)'$, where N_i, $i = 1, 2, 3$ is the total count of Nestings for day i, and F_i, $i = 1, 2, 3$ is the total count of False Crawls for day i. One approach is to treat this observed vector $\mathbf{y}$ as a set of fixed marginals, and apply the profile likelihood approach for the Rasch-type model to the interior cells of the 3-way table to estimate a total count by using the relationships among the cell probabilities in Table 1 to estimate the unknown parameters (p, μ, ω) in Table 1. Such classical likelihood approaches produce stable estimates of the parameter p, the parameter product $\mu(1 - \omega)$ and the interior cell counts in Table 1. However, estimates of parameters μ and ω and hence N_{tot} are not stable, primarily due to identifiability issues involving μ and ω. Intuitively, the product $\mu(1 - \omega)$ represents the rate at which turtles arrive onshore, and the rate, which can remain constant as μ and ω are manipulated, is the only information about μ and $1 - \omega$ we can retrieve from the marginal cell counts.

Furthermore, $\mathbf{y}$ is not a genuine multinomial observation since a given turtle could contribute to more than one cell of $\mathbf{y}$. For example, a turtle could false crawl on days 1 and 2 and nest on day 3, contributing to each of the F_1, F_2, and N_3 counts.

3.1 Development of Model for Number of Days Onshore

Given the problems with the classical likelihood approach, the natural limitations inherent in our observed data, and the strong prior information available about the turtles' biological processes, we adopt a Bayesian analysis. Bayesian methods for traditional capture-recapture analyses have been proposed (Gazey and Staley 1986; George and Robert 1992; Dupuis 1995; Brooks et al. 2000); see also Cummings (2011) for related references. The nontraditional structure of the turtle data necessitates a somewhat different approach than those.

Recall $\mathbf{y} = (N_1, N_2, N_3, F_1, F_2, F_3)'$ is the observed data vector. Let

$$\mathbf{p} = (p_{OOO}, p_{OOF}, p_{OON}, p_{OFF}, p_{OFN}, p_{ONO}, p_{FFF}, p_{FFN}, p_{FNO}, p_{NOO})'$$

be the vector for the cell probabilities in Table 1, i.e., for a 10-category (unobserved) multinomial random variable. Then define $C \in \{0, 1, 2, 3\}$ to be the number of cells in

$\mathbf{y}$ to which a particular turtle contributes. That is, C_i = the number of days *onshore* (out of three) for turtle i. Each cell in Table 1 can be assigned to one value of C, yielding the unconditional distribution of C, which is multinomial with probabilities:

$$P(C = 0) = p_{OOO}$$
$$P(C = 1) = p_{NOO} + p_{ONO} + p_{OON} + p_{OOF}$$
$$P(C = 2) = p_{FNO} + p_{OFN} + p_{OFF}$$
$$P(C = 3) = p_{FFN} + p_{FFF}$$

Define the vector $\mathbf{m} = (m_1, m_2, m_3)'$ to contain counts of the number of unique turtles for which $C = i$, for $i = 1, 2, 3$. (Note m_0, the number of turtles for which $C = 0$, is simply N_{OOO}.) The individual counts in $\mathbf{m}$ are unknown; however, we know the total number of unique observed turtles is $N_{obs} = \sum_{i=1}^{3} m_i = N_1 + N_2 + N_3 + F_3$, which is determined from the observed $\mathbf{y}$.

3.2   Gibbs Sampling Approach

Using a Bayesian approach, we consider the collection of unknown quantities in our problem to be $(N_{OOO}, \mathbf{m}, \mu, \sigma, p)$. We will use a Gibbs sampling approach to approximate the joint posterior $f(N_{OOO}, \mathbf{m}, \mu, \sigma, p|\mathbf{y})$ by sampling iteratively from the respective full conditional distributions. Note that the nature of our data vector $\mathbf{y}$ makes it infeasible to write the likelihood using a standard model, essentially because the fact that each observed turtle can contribute to 1, 2, or 3 cells of $\mathbf{y}$, precluding a multinomial model. Although $\mathbf{y}$ follows a multivariate discrete probability distribution, the likelihood cannot be written in a closed-form way. However, we propose that the conditional distribution of each parameter singly (given the others and $\mathbf{y}$) can be sampled from.

By Bayes' theorem, $f(N_{OOO}|\mathbf{m}, \mu, \sigma, p, \mathbf{y}) \propto L(N_{OOO}|\mathbf{m}, \mu, \sigma, p, \mathbf{y})f(N_{OOO})$ where $L(\cdot|\cdot)$ denotes a likelihood and $f(N_{OOO})$ is the prior for N_{OOO}. Considering turtles to be "successes" or "failures" according to whether they came onshore at all or not, respectively, we treat N_{OOO} as a count of "failures" at the point of $N_{obs} =$

$\sum_{i=1}^{3} m_i$ successes. Thus we model $N_{OOO}|\mathbf{m}, \mu, \sigma, p, \mathbf{y}$ as negative binomial with "size" parameter $r = N_{obs}$ and success probability $1 - p_{OOO}$ (note p_{OOO} is a function of μ, σ, and p). To incorporate prior knowledge about N_{OOO}, we use a negative binomial; the prior parameters for our specific data set are justified in Section 4. So the full conditional of N_{OOO} is

$$f(N_{OOO}|\mathbf{m}, \mu, \sigma, p, \mathbf{y}) \propto NB(N_{OOO}, N_{obs}, 1 - p_{OOO}) \times NB(N_{OOO}, r_{\mathrm{pri}}, p_{\mathrm{pri}}),$$

where $NB(\cdot, r, \mathrm{prob})$ denotes a negative binomial density and r_{pri} and p_{pri} are prior parameters. This full conditional is not a standard distribution, but one can sample from it via an Accept-Reject algorithm.

We take our prior on $\mathbf{m}$ to be a noninformative yet proper prior by choosing it to be a 3-dimensional discrete uniform (constant) prior over an extremely diffuse set. Given $N_{OOO}, \mu, \sigma, p, \mathbf{y}$, determining $\mathbf{m}$ is tantamount to allocating the N_{obs} turtles into three classes with probabilities proportional to $(P(C=1), P(C=2), P(C=3))$. So the full conditional of $\mathbf{m}$ becomes a three-category multinomial:

$$\begin{aligned}
f(\mathbf{m}|N_{OOO}, \mu, \sigma, p, \mathbf{y}) &\propto L(\mathbf{m}|N_{OOO}, \mu, \sigma, p, \mathbf{y})f(\mathbf{m}) \\
&\propto L(\mathbf{m}|N_{OOO}, \mu, \sigma, p, \mathbf{y}) \\
&\sim MN\Big(N_{obs}; P(C=1)/K, P(C=2)/K, P(C=3)/K\Big),
\end{aligned}$$

where $K = \sum_{i=1}^{3} P(C=i)$ and the values of $\mathbf{m}$ are constrained to be in the set defined in the prior, which is diffuse enough to include any reasonable value for $\mathbf{m}$.

Our interarrival mean μ is assumed independent of σ, so that $f(\mu|N_{OOO}, \mathbf{m}, p, \sigma, \mathbf{y}) = f(\mu|N_{OOO}, \mathbf{m}, p, \mathbf{y})$. Our expression for the full conditional for μ is motivated by the fact that — as argued in the Appendix — the information about μ in $(N_{OOO}, \mathbf{m}, \mathbf{y})$ is contained in the relative sizes of N_{obs} and N_{OOO}, or specifically in the ratio $N_{obs}/(N_{OOO} + N_{obs})$, so that:

$$\begin{aligned}
f(\mu|N_{OOO}, \mathbf{m}, p, \mathbf{y}) &\propto f(N_{OOO}, \mathbf{m}, p, \mathbf{y}|\mu)f(\mu) \\
&\propto f(N_{obs}/(N_{OOO} + N_{obs})|p, \mu)f(p|\mu)f(\mu) \\
&\propto f(N_{obs}/(N_{OOO} + N_{obs})|p, \mu)f(\mu)
\end{aligned}$$

since the distribution $f(p|\mu)$ is actually free of μ. The details of the derivation of the full conditional are given in the Appendix. In summary, the full conditional for μ is normal and incorporates information from the normal prior on μ and from the data and N_{OOO} (via the ratio $N_{obs}/(N_{OOO} + N_{obs})$):

$$f(\mu|N_{OOO}, \mathbf{m}, \sigma, p, \mathbf{y}) \sim N\left(\frac{\frac{\mu_\mu}{\sigma_\mu^2} + \frac{M}{V}}{\frac{1}{\sigma_\mu^2} + \frac{1}{V}}, \frac{\sigma_\mu^2 V}{\sigma_\mu^2 + V}\right) \tag{2}$$

where $M = (3 + q/p)(N_{OOO} + N_{obs})/N_{obs} - (1 + q/p)$ and $V = [(3 + q/p)^2(N_{OOO} + N_{obs})N_{OOO}]/N_{obs}^3$.

We assume σ is independent of μ and p so that the full conditional for σ is

$$f(\sigma|N_{OOO}, \mathbf{m}, \mu, p, \mathbf{y}) \propto f(N_{OOO}, \mathbf{m}, \mathbf{y}|\sigma)f(\sigma)$$

Similarly as argued for μ above, the information about σ in $(N_{OOO}, \mathbf{m}, \mathbf{y})$ is in the proportion $N_{OOO}/(N_{OOO} + N_{obs})$. Modeling that proportion with a normal distribution and choosing $f(\sigma)$ to be inverse gamma, the full conditional for σ is:

$$f(\sigma|N_{OOO}, \mathbf{m}, \mu, p, \mathbf{y}) \propto Z(z(\sigma)) \times IG(\sigma, \alpha_\sigma, \beta_\sigma),$$

where $Z(\cdot)$ denotes a standard normal density, $IG(\cdot, \alpha, \beta)$ denotes an inverse gamma density and

$$z(\sigma) = \frac{N_{OOO}/(N_{OOO} + N_{obs}) - p_{OOO}}{\sqrt{p_{OOO}(1 - p_{OOO})/(N_{OOO} + N_{obs})}}$$

is a standardized version of the proportion of turtles that came onshore. (Recall that p_{OOO} depends on σ through ω.) This full conditional is not a standard distribution, but again one can sample from it via Accept-Reject.

The nesting probability p is assumed independent of σ, so we have

$$
\begin{aligned}
f(p|N_{OOO}, \mathbf{m}, \mu, \sigma, \mathbf{y}) &= f(p|N_{OOO}, \mathbf{m}, \mu, \mathbf{y}) \\
&\propto f(N_{OOO}, \mathbf{m}, \mu, \mathbf{y}|p)f(p) \\
&= f(N_{OOO}, \mathbf{m}, \mu|p)f(\mathbf{y}|N_{OOO}, \mathbf{m}, \mu, p)f(p) \tag{3}
\end{aligned}
$$

The information in $(N_{OOO}, \mathbf{m})$ about p is contained in the ratio $N_{obs}/(N_{OOO} + N_{obs})$, so the first piece of (3) is the same as the full conditional for μ, but with p as the

random variable rather than μ. Based on the observed vector $\mathbf{y}$, the totals of nests and false crawls for the three days, $N_1 + N_2 + N_3$ and $F_1 + F_2 + F_3$ are sufficient statistics for the nesting probability p. Treating excursions as Bernoulli trials (independent by our geometric model assumption), we model the nest count $N_1 + N_2 + N_3$ as binomial with success probability p. So the second piece of (3) is proportional to

$$p^{N_1+N_2+N_3}(1-p)^{F_1+F_2+F_3}.$$

Augmented with the beta prior for p, we see the full conditional for p is proportional to the density from (2)(treated as a function of p) times a beta($N_1 + N_2 + N_3 + \alpha_p$, $F_1 + F_2 + F_3 + \beta_p$) density. We can again sample from this using Accept-Reject.

Given these full conditional expressions, we provide initial values for $(N_{OOO}, \mu, \sigma, p)$ and cycle through, sampling from each full conditional in turn. The main subchain of interest is the one for N_{OOO}, since our parameter of interest is $N_{tot} = N_{OOO} + N_{obs}$ (recall N_{obs} is known). Thus from the sampled N_{OOO} values, we can make inference about N_{tot}. We now show how our method can be applied to a real data set.

4   Application to Real Three-Day Nesting Data

The loggerhead turtle nesting season runs from roughly May to August (Dodd 1988). While turtle excursions may be haphazard at the beginning of the season, during the middle of the season, the patterns will have progressed into a kind of equilibrium state that should be well approximated by our model. Table 5 lists a typical observed data set. It gives raw counts of false crawls and nests observed over three consecutive days by South Carolina Department of Natural Resources researchers for June 16-18, 2000 on a particular set of South Carolina beaches.

Recall that our priors for μ, σ, and p were given in Section 2.1. Note that our prior expectations for μ, σ, and p imply a prior expected $p_{OOO} = 0.755$. The South Carolina Department of Natural Resources (SCDNR) provides — based on standardized ground surveys — seasonal counts (starting in 1982) of nests on selected "index beaches" (`http://www.dnr.sc.gov/seaturtle/ibs.htm`). These index beaches are only a subset of the set of all South Carolina beaches that we are considering; SCDNR

estimates that the index count is roughly 41% of nesting activity. For the five years previous to 2000, an annual average of around 1400 nests were counted on the index beaches. Thus a prior expected number of nests on the larger set of beaches is $1400/0.41 \approx 3415$. Turtles nest multiple times per season; expert guesses of the average number of nests per female range from 2.5 to around 4 (Frazer and Richardson 1985; Richardson and Richardson 1982). A best prior guess for the total number of females in the nesting area could be, say, $3415/3.25 \approx 1051$. A reasonable interval for this guess would be $(3415/4, 3415/2.5) \approx (854, 1366)$. Thus we set the prior expectation for N_{OOO} be $0.755 \times 1051 \approx 794$ and assume *a priori* that N_{OOO} is likely within $(0.755 \times 854, 0.755 \times 1366) \approx (645, 1031)$. We choose a negative binomial prior for N_{OOO} having mean 794 and size $r = 80$, which satisfies our conditions nicely.

[[Table 5 goes around here]]

The observed number of unique turtles N_{obs} for this sample was $N_1 + N_2 + N_3 + F_3 = 77 + 76 + 71 + 72 = 296$, so 296 was added to each value in the subchain of N_{OOO} values to create a sample of N_{tot} values. We ran the Gibbs sampler for 10500 iterations and removed the first 500 values as burn-in. To reduce some very modest autocorrelation, we then thinned the sample by taking every second value of N_{tot}. The resulting autocorrelation plot, shown in Figure 1 (bottom), indicated no serious autocorrelation among sampled values. A time series plot is given in Figure 1 (top), showing apparently fast convergence and mixing for the chain. The test of Geweke (1992) for convergence of the chain showed no apparent problems with convergence ($z = -0.16$).

[[Figure 1 goes around here]]

A histogram of the remaining 5000 N_{tot} values is shown in Figure 2. The posterior sample is unimodal, mound-shaped, and symmetric. Our point estimate of N_{tot} is the median of the N_{tot} values, which is 1125 in this case. A 90% credible interval for N_{tot} is (1031, 1223), constructed from the 0.05 and 0.95 quantiles of the N_{tot} values.

[[Figure 2 goes around here]]

As an informal judgment about whether our estimate is reasonable, we note from the literature two estimates of nesting activity during the 2000 season. Murphy

and Griffin (2005) give a rough estimate (based on aerial surveys) of around 3400 total nests throughout the 2000 season. In addition, the South Carolina Department of Natural Resources provides — based on standardized ground surveys — a count for the 2000 season of around 1150 nests for a group of selected "index beaches" (`http://www.dnr.sc.gov/seaturtle/ibs.htm`). Our three-day data includes counts from these index beaches, plus numerous other South Carolina beaches. In our data set, 36.2% of the nests (81 out of $N_1 + N_2 + N_3 = 224$ total nests) came from those index beaches. Dividing the seasonal index-beach nest count of 1150 by 0.362 gives a rough estimate of around 3180 total nests on our (larger) set of beaches.

With an approximate total nest count of either 3400 or 3180, our interval estimate of between 1031 and 1223 female turtles implies roughly 2.5 to 3.5 nesting episodes per season per turtle, on average, which lines up well with previous estimates (Frazer and Richardson 1985; Richardson and Richardson 1982). In short, our estimate of the population size is, at the very least, reasonable.

While population size was our primary parameter of interest, we also note the posterior median and 90% credible intervals for μ (13.04, [12.06, 13.99]) and p (0.510, [0.471, 0.548]). Both posterior samples showed symmetric, bell-shaped distributions.

In a similar way, we examined data from July 9-11, 2002, for which $\mathbf{y} = (N_1, N_2, N_3, F_1, F_2, F_3)$ = $(51, 45, 41, 58, 47, 56)$, i.e., comparatively smaller counts than the June 2000 data. We used the same priors except that our prior on N_{OOO} (derived similarly based on the previous five years of index-beach counts) had mean 708 and size 100. We obtained posterior medians and 90% credible intervals for N_{tot} (785, [715, 863]), μ (13.46, [12.47, 14.45]) and p (0.464, [0.418, 0.511]). Compared to June 2000, this shows a smaller nesting population of females, basically similar estimated mean interarrival time, and an apparently lower nesting probability than in 2000.

5 Simulation Study

In this section we describe a simulation study designed to gauge our method's performance on simulated data sets following our model (and data having some depar-

tures from our model). The twin purposes of these simulations are to investigate (1) the sensitivity of our procedure to prior specifications and (2) the robustness of the method to a violation of our geometric model assumption. We simulated full-season data records for a population of $N_{tot} = 1000$ turtles in the following way. For the ith turtle, $(i = 1, \ldots, N_{tot})$, we generated a sequence of states, where each state value was one of $\{O, F, N\}$ (representing Offshore, False Crawl, Nest). For any particular turtle, the sequence was obtained by

1. Generate a string of O's of length $\lceil U \rceil$, where $U \sim U(0, 30)$. (This implies a turtle's first onshore arrival of the season occurred randomly between day 1 and day 30.)

2. Follow this with a string of F's whose length follows a geometric(p) distribution.

3. Follow this with a single N.

4. Follow this with a string of O's of length $\lceil W \rceil$, where $W \sim N(\mu, \sigma^2)$.

5. Repeat steps (2)-(4) until 100 "days" have been generated for each turtle.

For these simulated data, we set the true values of our parameters to be $\mu = 13$, $\sigma = 0.75$, and $p = 0.6$. Once the entire season of records was generated, a sequence of three consecutive days (the starting day was selected at random from day 50 through day 98 so that the selected days would be well into the "season") was chosen. (We are only interested in generating data that match reality for the middle of the season, not for the end of the season when turtle activity would tail off.) The counts of F's and N's were taken across all the turtle records for each of the three days, resulting in a simulated data set whose structure resembled that of Table 5.

Each of 200 such simulated data sets was analyzed using the approach outlined in Section 3. For each data set, a point estimate (posterior median) for N_{tot} and a 90% credible interval for N_{tot} were obtained based on 10000 Gibbs iterations (10500 iterations were done overall, with the first 500 discarded as burn-in). To reduce modest autocorrelation (noted in our real data analysis) we thinned the sample by taking every other value of N_{tot}.

Knowing the true population size (1000), we calculated (1) the empirical coverage probability; (2) the average (across the 200 simulated sets) width of the interval; and (3) the average bias of the posterior median.

To examine the effect of various factors on the method's performance, the simulations were run for a variety of settings:

- We varied the values of the prior mean for μ, allowing prior means for μ that were alternately lower and higher than the true value of μ. Simultaneously we varied the prior variance for μ, allowing the prior for μ to be alternately more or less informative.

- We varied the values of the prior mean for N_{OOO}, allowing prior means for N_{OOO} that were alternately lower and higher than the true value. Simultaneously we varied the size parameter for the prior on N_{OOO}, allowing the prior for N_{OOO} to be alternately more or less informative.

- We generated data in which the nesting probability p was different for each turtle. Rather than fixing $p = 0.6$ in the population, we generated distinct p_i values from (various) beta distributions having mean 0.6, $i = 1, \ldots, N_{tot}$.

5.1 Gauging the Sensitivity to the Priors for μ and N_{OOO}

[[Table 2 goes around here]]

When the prior expected value for μ matches 13, the true μ of the simulated data, the empirical coverage probability is very good, slightly higher than the nominal level of 0.90. The point estimator appears essentially unbiased in this case. The average width of the credible intervals depends primarily on the value of σ_μ, which measures the spread of the prior distribution. Naturally, a more informative prior (having lower σ_μ) yields a narrower credible interval on average, while a more diffuse prior (having higher σ_μ) yields wider credible intervals. When the prior is "mis-centered" so that $\mu_\mu \neq 13$, the coverage probability suffers slightly and the posterior median reveals a bias in the direction of the (misspecified) prior expected value. These problems are

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mitigated when the prior is made more diffuse (e.g., the bottom row of Table 2), in which case the method is remarkably robust to a misspecified μ_μ. It is quite natural that a tighter prior leads to prior information dominating and a more diffuse prior places more weight on data information. We recommend that an analyst having little confidence in the choice of prior expectation μ_μ simply choose a fairly large σ_μ to decrease the effect of the prior. For our turtle data in Section 4, we believe $\mu_\mu = 13$ and $\sigma_\mu = 0.65$ are justified.

[[Table 3 goes around here]]

When the prior expected value for N_{OOO} is correctly specified at 755 ($= 0.755 \times 1000$), the empirical coverage probability is slightly higher than the nominal level. Even when the prior mean for N_{OOO} is misspecified, the coverage probability remains high, especially when the prior is chosen to be fairly diffuse (note that a smaller "size" parameter implies a more diffuse prior distribution). Point estimation may be somewhat biased with a misspecified prior mean. Again, if the researcher is uncertain about the prior mean of N_{OOO}, a wide prior (having small "size") should be chosen; this yields wider credible intervals with at least nominal coverage.

5.2   Gauging the Effect of Allowing p to Vary Across Turtles

Fixing the prior on μ as $N(13, 0.75^2)$ and the prior on N_{OOO} to have mean 755 and size 80, and generating data such that $\mu = 13$ and $\sigma = 0.75$, we allowed p to vary across turtles, $p_i \sim \text{beta}(a, b), i = 1, \ldots, N_{tot}$, such that $E(p_i) = 0.6$. The results are given in Table 4.

[[Table 4 goes around here]]

Our estimation method is based on a constant p. When p varies across turtles, the results are similar to the case when p is constant. Thus if in reality the nesting probability varies across turtles, using our method should not be detrimental.

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5.3 Comparison with a Simple Point Estimator

We note that our method requires a variety of modeling specifications that must be made by the user. A simpler approach to estimating N_{tot} is to specify a prior expectation p^*_{OOO} for p_{OOO} (e.g., as we do in Section 2.3) and define the point estimate $\widehat{N}_{tot} = N_{obs}/(1 - p^*_{OOO})$. Does this simple estimator perform as well as our more complicated Bayesian estimator? We compare these point estimators based on the absolute value of their average bias across 200 simulations, for five different choices of prior mean for μ. As Figure 3 shows, our estimator has an average bias uniformly closer to zero than the simple estimator. While using the simpler estimator would save time, it would increase the magnitude of the average bias by at least 60% compared to our estimator for all settings examined. An intuitive reason why the Bayesian estimator outperforms the simple estimator is that the simple estimator (by using only N_{obs}) ignores the information in F_1 and F_2, while the Bayesian estimator incorporates this information, most notably in the full conditional for p.

[[Figure 3 goes around here]]

6 Discussion

The length D of the series of days for which counts are available merits further discussion. We have assumed that counts of nestings and false crawls are available for at least three consecutive days. We could have obtained (or chosen to use) only two consecutive days of counts; we could then construct a 3×3 two-way table of joint probabilities similar to Table 1. The counts in the two-day table, however, do not incorporate as much information on false crawl behavior as the counts in the three-day table. Specifically, if the probability of a nesting is $p \approx 0.6$, then the additional information on p gained from a third day of observation is substantive under the assumption of a geometric distribution for false crawl/nesting behavior.

On the other hand, counts could conceivably be gathered for $D \geq 4$ consecutive days. We did not explore this scenario in this article for reasons both practical and mathematical. First of all, the turtle survey is limited by logistical considerations.

The consecutive-day survey takes place only during spring tides, which occur during the full moon and new moon (Hopkins-Murphy et al. 2001). Spring tides produce extreme high and low tides, and researchers favor days when the extreme low tides occur in the morning, thus exposing more of the beach, and hence providing better conditions for detecting turtle activity. This specific set of conditions lasts for only a few days.

Secondly, the crucial table of joint probabilities would have 3^D cells — 81 for a four-day study, for example. While many of these cells would be structural zeroes, clearly the analysis becomes somewhat more unwieldy for four or more days. And we can appeal to the behavior of a geometric random variable once again to note that little additional information about false crawl behavior would be gained by including a fourth day in the study for the values of p assumed in this study.

While our approach assumes a constant nesting probability p across turtles, it is conceivable that certain environmental conditions (such as geographic location or weather) could cause the nesting probability to vary. To some degree, our results in Section 5.2 that our inferences are robust under a random p lend confidence in our method in this scenario. Some interesting future research might allow the nesting probability to depend on observable covariates (perhaps via a logistic regression model) such as beach type (as a factor) or simply beach (as a random effect); admittedly, this would complicate our approach substantially. Another direction for future research is allowing the possibility of misdetection of nests and false crawls in the model. While we view misdetection as negligible in our data set, analyses of other data might directly model this possibility.

In the most recent decade or two, statisticians have often sought effective methods of analysis (e.g., data mining) of massive data sets. The problem presented here is quite the opposite scenario: We want to demonstrate a useful analysis on a rather tiny data set (six data values, in the case of the three-day series we analyze). In doing so, to augment the limited information in the data, we must assume a rather informative model for the turtles' nesting behavior. Fortunately, knowledge of the biological nesting process is trustworthy, and we maintain that this scientific knowledge should

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be heavily relied upon in the estimation process. Our Bayesian approach is ideal for marrying the information in the data with the knowledge of the nesting process.

The subject-matter knowledge we have incorporated in our priors is specific to turtle behavior off the coast of the Southeastern United States (and around the time our data set was gathered), but the parameters of our priors could be altered to reflect characteristics of turtles in other locations and years. More generally, our analysis — though specifically a case study of a loggerhead population — provides insight into incorporating subject matter knowledge in a statistical analysis. In numerous observational studies, individuals are possibly repeatedly sampled but not identifiable or trackable. As an example, ecologists tracking waterfowl populations in winter conduct flyover surveys to estimate population size. The researchers are unable to tag the waterfowl — and thus cannot estimate joint probabilities for the repeated survey occasions — but may know that they are moving in a somewhat predictable pattern (e.g., following food sources or warmer weather). The Breeding Bird Survey (Sauer et al. 2012) records songbird activity at almost 3000 25-mile routes in North America and analyzes temporal and spatial trends in relative abundance for breeding birds. From year to year, individual birds are not identifiable or trackable, but assumptions of site fidelity and mortality could be used to refine models of relative abundance.

Our approach (priors reflecting expert judgment, handling data having a non-standard distribution when standard methods are inapplicable) provides trustworthy estimation of the abundance of the threatened loggerhead species and could potentially inform estimation of abundance of other species for which traditional capture-recapture is impossible.

Appendix

We now justify our expression for the full conditional for μ from Section 3.2. First, our assertion that $N_{obs}/(N_{OOO} + N_{obs})$ carries the same information about μ as $(N_{OOO}, \mathbf{m}, \mathbf{y})$ is argued as follows. First note that the relative sizes of the *individual elements* of $\mathbf{m}$ (and of $\mathbf{y}$) are unrelated to μ since they relate strictly to onshore

behavior of the turtles rather than offshore behavior. In addition, $N_{obs} = \sum_{i=1}^{3} m_i$ is also noninformative in isolation. However, consider the bivariate transformation from (N_{OOO}, N_{obs}) to $(N_{obs}/(N_{OOO} + N_{obs}), N_{OOO} + N_{obs})$. By itself, the statistic $N_{tot} = N_{OOO} + N_{obs}$ can be viewed as ancillary for μ since μ is a biological characteristic of individual turtles, independent of the overall size N_{tot} of the turtle population under study.

We thus wish to approximate the distribution of $N_{obs}/(N_{OOO} + N_{obs})$. We argue that the probability of a random turtle being offshore all three days is approximately

$$\frac{\mu - 2}{\mu + 1 + q/p},$$

the denominator being the expected length of the entire offshore-false crawl-nest cycle. (Intuitively, note that if a turtle stays offshore for μ days, it will fall in the OOO category if the survey begins on one of the first $\mu - 2$ of its offshore days.) Therefore, it is sensible to equate $\hat{\xi} = N_{obs}/(N_{OOO} + N_{obs})$ to

$$\xi = 1 - \frac{\mu - 2}{\mu + 1 + q/p} = \frac{3 + q/p}{\mu + 1 + q/p}$$

Since $\hat{\xi} = N_{obs}/(N_{OOO} + N_{obs})$ is a sample proportion, when the denominator is large we can assume that

$$\hat{\xi} \sim N\left(\xi, \frac{\frac{3+q/p}{\mu+1+q/p}\left(1 - \frac{3+q/p}{\mu+1+q/p}\right)}{N_{OOO} + N_{obs}}\right),$$

By the delta method, where

$$g(\xi) = \mu = \frac{1}{\xi}(3 + q/p) - (1 + q/p)$$

we have that

$$g(\hat{\xi}) = \frac{(N_{OOO} + N_{obs})}{N_{obs}}(3 + q/p) - (1 + q/p) \sim N\left(g(\xi), [g'(\xi)]^2 V(\hat{\xi})\right) \qquad (4)$$

and $[g'(\xi)]^2 = (3 + q/p)^2/\xi^4 = (\mu + 1 + q/p)^4/(3 + q/p)^2$. Therefore after estimating the $\xi = \frac{3+q/p}{\mu+1+q/p}$ in the variance expression in (4) with $\hat{\xi} = \frac{N_{obs}}{(N_{OOO}+N_{obs})}$, we have

$$\frac{(N_{OOO} + N_{obs})}{N_{obs}}(3+q/p)-(1+q/p) \sim N\left(\mu, \frac{(3+q/p)^2(N_{OOO}+N_{obs})^4}{N_{obs}^4}\frac{\frac{N_{obs}}{N_{OOO}+N_{obs}}\frac{N_{OOO}}{N_{OOO}+N_{obs}}}{N_{OOO}+N_{obs}}\right)$$

and simplifying yields

$$\frac{(N_{OOO} + N_{obs})}{N_{obs}}(3 + q/p) - (1 + q/p) \stackrel{.}{\sim} N\left(\mu, \frac{(3 + q/p)^2(N_{OOO} + N_{obs})N_{OOO}}{N_{obs}^3}\right).$$

Therefore

$$f(\mu|\mathbf{m}, N_{OOO}) \propto f\big(g(\hat{\xi})|\mu\big)f(\mu)$$

$$\propto \exp\left\{-\frac{1}{2V}(\mu - M)^2\right\}\exp\left\{-\frac{1}{2\sigma_\mu^2}(\mu - \mu_\mu)^2\right\}$$

where $M = (3 + q/p)(N_{OOO} + N_{obs})/N_{obs} - (1 + q/p)$ and $V = [(3 + q/p)^2(N_{OOO} + N_{obs})N_{OOO}]/N_{obs}^3$.

Standard calculations for Bayesian normal-normal models show this reduces to a distribution that is

$$N\left(\frac{\frac{\mu_\mu}{\sigma_\mu^2} + \frac{M}{V}}{\frac{1}{\sigma_\mu^2} + \frac{1}{V}}, \frac{\sigma_\mu^2 V}{\sigma_\mu^2 + V}\right).$$

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		Day 3		
Day 1	Day 2	O	F	N
O	O	$\frac{\mu\omega^2}{\mu+1+q/p}$	$\frac{\mu\omega q(1-\omega)}{\mu+1+q/p}$	$\frac{\mu\omega p(1-\omega)}{\mu+1+q/p}$
O	F	0	$\frac{\mu q^2(1-\omega)}{\mu+1+q/p}$	$\frac{\mu q(1-\omega)p}{\mu+1+q/p}$
O	N	$\frac{\mu p(1-\omega)}{\mu+1+q/p}$	0	0
F	O	0	0	0
F	F	0	$\frac{q^3/p}{\mu+1+q/p}$	$\frac{q^2}{\mu+1+q/p}$
F	N	$\frac{q}{\mu+1+q/p}$	0	0
N	O	$\frac{1}{\mu+1+q/p}$	0	0
N	F	0	0	0
N	N	0	0	0

Table 1: Table of joint probabilities for successive three-day outcomes ABC, where A is the turtle's state on Day 1, B is the turtle's state on Day 2, and C is the turtle's state on Day 3.

	$\mu_\mu = 12$	$\mu_\mu = 13$	$\mu_\mu = 14$
$\sigma_\mu = 0.5$	0.68	0.90	0.85
	(0.033)	(0.021)	(0.025)
	149.44	155.86	161.48
	(0.32)	(0.33)	(0.30)
	-58.98	-7.62	32.33
	(2.97)	(3.28)	(2.96)
$\sigma_\mu = 0.75$	0.805	0.955	0.91
	(0.028)	(0.015)	(0.020)
	163.60	169.17	173.19
	(0.35)	(0.35)	(0.39)
	-47.29	1.38	28.55
	(2.80)	(2.99)	(3.37)
$\sigma_\mu = 1$	0.895	0.985	0.94
	(0.022)	(0.009)	(0.017)
	177.27	181.66	185.02
	(0.35)	(0.35)	(0.38)
	-39.91	-1.50	25.55
	(2.56)	(2.58)	(2.86)

Table 2: Effect of specification of prior on μ. Quality measures [Top of cell: Coverage probability. Middle of Cell: Average Width. Bottom of Cell: Bias.] for 90% Credible Intervals and Point Estimates, averaged across 200 simulated data sets per setting. (Monte Carlo standard errors for the measures are given in parentheses.)

	mean= 700	mean= 755	mean= 800
size= 200	0.815	0.955	0.935
	(0.028)	(0.015)	(0.017)
	132.43	138.33	142.97
	(0.19)	(0.21)	(0.18)
	-40.34	-5.89	19.48
	(2.22)	(2.44)	(2.31)
size= 80	0.89	0.955	0.96
	(0.022)	(0.015)	(0.014)
	163.19	169.17	172.71
	(0.32)	(0.35)	(0.35)
	-35.10	1.38	14.08
	(2.66)	(2.99)	(3.00)
size= 40	0.915	0.94	0.95
	(0.020)	(0.017)	(0.015)
	184.15	187.53	189.63
	(0.44)	(0.47)	(0.50)
	-23.91	-9.54	-2.82
	(3.13)	(3.38)	(3.46)

Table 3: Effect of specification of prior on N_{OOO}. Quality measures [Top of cell: Coverage probability. Middle of Cell: Average Width. Bottom of Cell: Bias.] for 90% Credible Intervals and Point Estimates, averaged across 200 simulated data sets per setting. (Monte Carlo standard errors for the measures are given in parentheses.)

	Measure Of Inferential Quality		
Distribution for p	Empirical Coverage Probability	Average Width	Bias (of posterior median)
0.6 (constant)	0.955	169.17	1.38
	(0.015)	(0.35)	(2.99)
beta(6,4)	0.965	168.37	-10.33
	(0.013)	(0.33)	(2.83)
beta(9,6)	0.975	168.24	-9.09
	(0.011)	(0.32)	(2.64)
beta(12,8)	0.92	168.23	-2.92
	(0.018)	(0.39)	(3.41)

Table 4: Robustness to non-constant nesting probability. Quality measures for 90% Credible Intervals and Point Estimates, averaged across 200 simulated data sets per setting. (Monte Carlo standard errors for the measures are given in parentheses.)

	Day		
	1	2	3
Nests	77	76	71
False Crawls	58	87	72

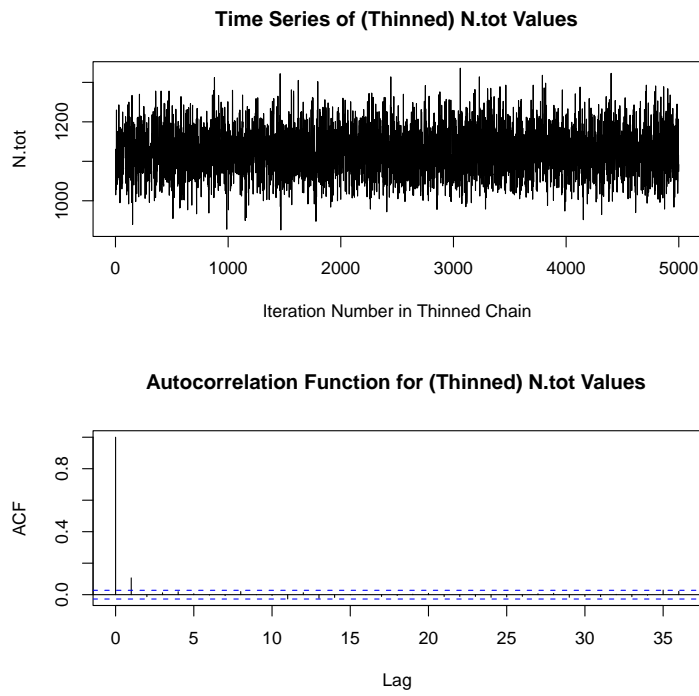Table 5: Table of counts of nests and false crawls: June 16-18, 2000.

Figure 1: Time series plot (top) and autocorrelation function (bottom) of (thinned) posterior sample of N_{tot} values: June 16-18, 2000.
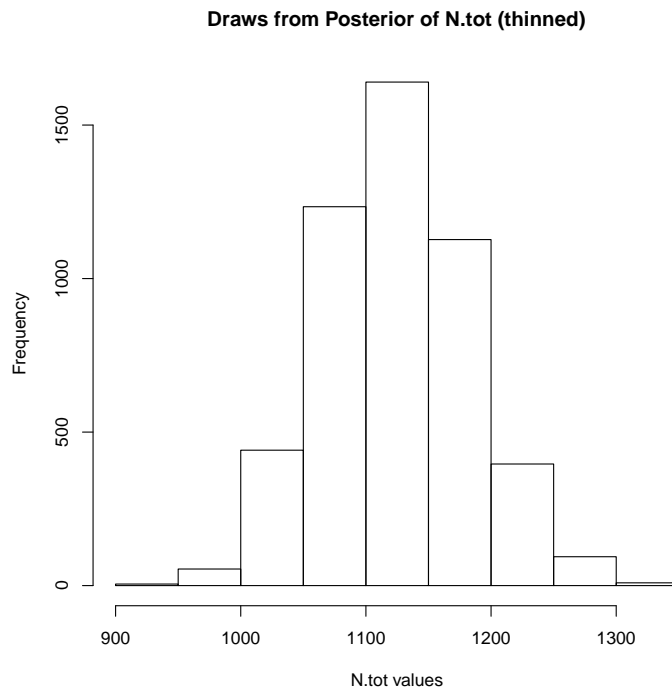
Draws from Posterior of N.tot (thinned)

Figure 2: Histogram of (thinned) posterior sample of N_{tot} values: June 16-18, 2000.
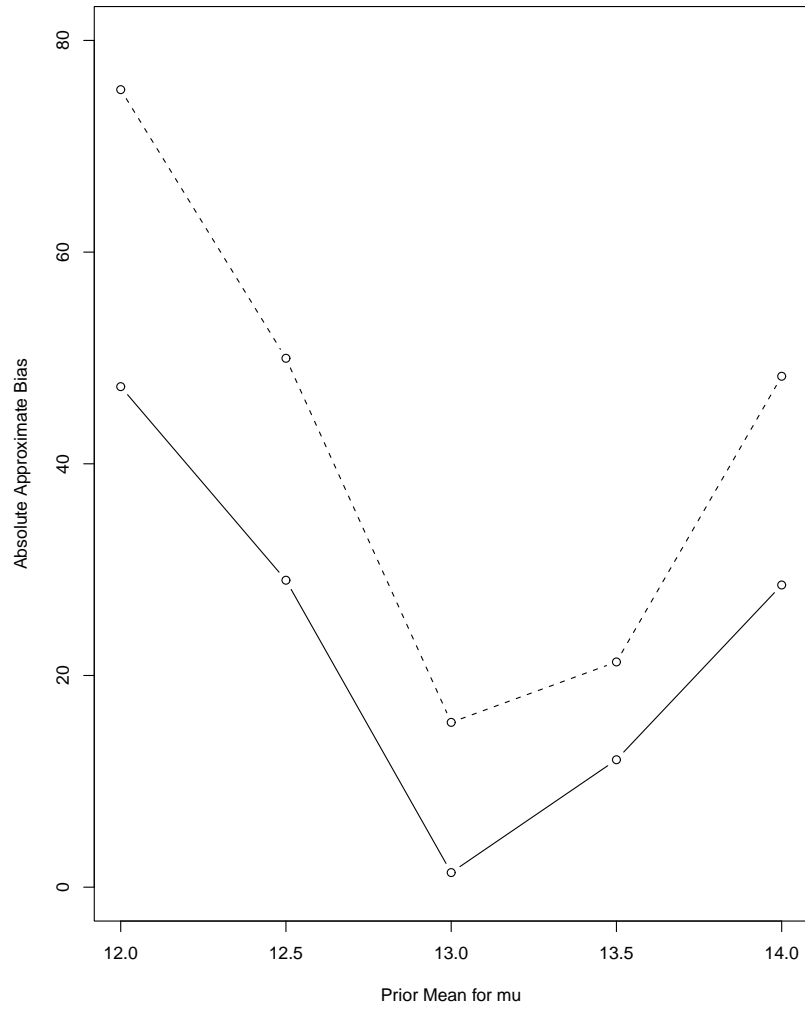
Figure 3: Absolute value of average bias for proposed Bayesian point estimator (solid) and for simple estimator (dashed).