Bayesian Capture-Recapture Models that Facilitate Recursive Computing

Mevin B. Hooten*† Michael R. Schwob† Devin S. Johnson† and Jacob S. Ivan§

Abstract. Ecologists increasingly rely on Bayesian capture-recapture models to estimate abundance of wildlife populations. Capture-recapture models account for imperfect detectability in individual-level presence data. A variety of approaches have been used to implement such models, including integrated likelihood, parameter-expanded data augmentation, and combinations of those. Recently proposed conditional specifications have improved the stability of algorithms for fitting capture-recapture models. We arrive at similar conditional specifications of capture-recapture models by considering recursive implementation strategies that facilitate fitting models to large data sets. Our approach enjoys the same computational stability but also allows us to fit the desired model in stages and leverage parallel computing resources. Our model specification includes a component for the capture history of detected individuals and another component for the sample size which is random before observed. We demonstrate this approach using three examples including simulation and two data sets resulting from capture-recapture studies of different species.

Keywords: abundance, Bayesian filtering, MCMC, population estimation.

1 Introduction

Bayesian models for capture-recapture (CR) data have become popular for learning about wildlife population demographics (Royle et al., 2013). Despite their increasing popularity in ecological science, fully hierarchical CR models are often challenging to implement using standard Markov chain Monte Carlo (MCMC) methods (Royle and Converse, 2014). As a result, approaches based on integrated likelihoods are often sought (e.g., Efford, 2011; Yackulic et al., 2020). Numerical integration approaches commonly used to fit CR models can be more stable (Bonner and Schofield, 2014; King et al., 2016) but can also be computationally intensive. MCMC algorithms that use numerical integration usually require tuning to result in well-mixed Markov chains. In contrast to previous approaches, we arrive at conditionally specified CR model formulations by explicitly considering recursive implementation strategies for fitting them. These methods allow us to use parallel computing environments and develop unsupervised algorithms for fitting CR models. Also, as discussed in King et al. (2016), conditional specification allows us to generalize CR models in ways that would not be apparent

*mevin.hooten@austin.utexas.edu
†Department of Statistics and Data Sciences, The University of Texas at Austin, Austin, Texas, U.S.A.
‡Pacific Islands Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Honolulu, Hawaii, U.S.A.
§Colorado Parks and Wildlife, Fort Collins, Colorado, U.S.A.
otherwise. In what follows, we present the hierarchical capture-recapture model using parameter-expanded data augmentation and then show how to write it conditionally in a way that can be used in recursive computing.

Conventional CR models utilize data comprising binary detections of a subset of individual animals from a wildlife population when they are individually recognizable (either naturally or by artificial marking). Bayesian CR models are often implemented using a parameter-expanded data augmentation (PX-DA) approach (Royle et al., 2007; Royle and Dorazio, 2012). In this setting, individuals are observed over a set of sampling periods (or “occasions”) \( j = 1, \ldots, J \), and we record binary detection/nondetection measurements \( y_{i,j} \) for a set of \( n \) observed individuals. It is often assumed that \( y_{i,j} \) are conditionally independent across occasions and the population is “closed” with respect to changes in demography and movement. Thus, the count \( y_i = \sum_{j=1}^{J} y_{i,j} \) represents the number of detections of individual \( i \) with conditional (on \( z_i \) and \( p \)) mixture binomial distribution

\[
y_i \sim \begin{cases} \text{Binom}(J,p) & , z_i = 1 \\ \mathbb{1}_{\{y_i=0\}} & , z_i = 0 \end{cases}
\]

(1)

where \( z_i \) is a latent population membership indicator for \( i = 1, \ldots, M \), with \( M \) chosen so that it provides a realistic upper bound for population abundance (usually \( M >> n \), where \( n \) is the number of observed individuals). In this type of PX-DA scenario, the data are augmented with all-zero capture histories such that \( y_i = 0 \) for all \( i = n + 1, \ldots, M \) and the latent indicators are modeled as \( z_i \sim \text{Bern}(\psi) \) (Royle, 2009). After the data are observed, \( z_i = 1 \) for \( i = 1, \ldots, n \) and the remaining \( z_i \) for \( i = n + 1, \ldots, M \) are treated as unknown latent variables.

In the Bayesian setting, priors are specified for the detection probability \( p \) and membership probability \( \psi \) in the homogeneous CR model in (1). The PX-DA procedure induces a binomial process model on the total abundance of animals \( N = \sum_{i=1}^{M} z_i \) such that \( N \sim \text{Binom}(M,\psi) \). When the prior for \( \psi \) is uniform (i.e., \( \psi \sim \text{Beta}(\alpha,\beta) \) with \( \alpha = \beta = 1 \)), it implies a discrete uniform prior for \( N \) with support \( \{0, 1, \ldots, M\} \) when marginalized over \( \psi \) (but see Link (2013) and Villa and Walker (2014) for varying perspectives on this choice of prior).

Abundance models based on CR data have been generalized in a variety of ways, most of which are based on heterogeneity in detection probability such that \( p_i \) is allowed to vary. In some cases, \( p_i \) is expressed as a function of environmental features or endogenous characteristics associated with individual \( i \). As CR models have been extended to accommodate spatially-explicit information, such as distance between the center of an individual’s activity region and the detector, they have also become more challenging to implement.

In what follows, we show how to reformulate Bayesian CR models based on a conditional partitioning of the likelihood that is motivated by a recursive computing procedure. This allows us to use recursive Bayesian computing methods to fit CR models to data. These methods can facilitate implementation by allowing us to perform many of the necessary calculations in parallel between computing stages.
We review recursive Bayes and then show how to apply it to the homogeneous CR model which suggests a way to formulate a broad class of capture-recapture models such that they are amenable to multi-stage computing strategies. We extend the approach to heterogeneous CR models and demonstrate it using data collected as part of a study of salamanders in Great Smoky Mountains National Park and a study of snowshoe hares in central Colorado, USA.

2 Recursive Bayes for Capture-Recapture

We present a recursive Bayesian procedure that involves two or more computational stages to fit the CR model to data. A variety of multistage computing strategies may be used with this framework including sequential Monte Carlo (SMC; Chopin et al. 2013) and the meta-analytic two-stage MCMC procedure described by Lunn et al. (2013) that was generalized by Hooten et al. (2021), where it was referred to as “prior-proposal recursive Bayesian” (PPRB) computation. Recursive approaches to fitting certain classes of Bayesian ecological models have been demonstrated (e.g., Hooten et al., 2016; Gerber et al., 2018; McCaslin et al., 2021; Feuka et al., 2022; Leach et al., 2022), but have been less commonly used in Bayesian population modeling using capture-recapture data.

Our approach to recursive Bayes relies on the ability to partition the data into two or more components and then write the posterior distribution as a product of conditional posterior distributions for each data partition given all those that were assimilated before it. In the context of PX-DA and the conventional CR model with homogeneous detection probability that we presented in the previous section, the full posterior distribution can be written as

\[
[p, \psi, z_{(n+1):M} | y_{1:M}] \propto \left( \prod_{i=1}^{M} [y_i | p, z_i] [z_i | \psi] \right) [p | \psi],
\]

(2)

where \(z_i = 1\) for \(i = 1, \ldots, n\) and \(z_{(n+1):M} = (z_{n+1}, \ldots, z_M)\) are unknown binary membership variables. In this specification, we express the conditional data model as

\[
[y_i | p, z_i] = [y_i | p] z_i 1^{1-z_i}_{([y_i]=0)},
\]

(3)

where \([y_i | p]\) is a binomial probability mass function with \(J\) trials and probability \(p\). The product of data and process models can be marginalized over \(z_i\) to yield the full likelihood component for individual \(i\)

\[
[y_i | p, \psi] = \psi [y_i | p] + (1 - \psi) 1_{(y_i=0)},
\]

(4)

which implies a mixture that is equivalent to a zero-inflated binomial model.

Following King et al. (2016), we partition the data into those that were observed \(y_{1:n}\) and those that were augmented \(y_{(n+1):M}\) (as zeros). This allows us to express the posterior distribution from (2) as proportional to (with respect to \(p\) and \(\psi\)) the product of two terms

\[
[p, \psi | y_{1:n}, y_{(n+1):M}, n] \propto [y_{(n+1):M} | p, \psi, y_{1:n}, n] [p | y_{1:n}, n],
\]

(5)
where we have used the likelihood in (4) to reduce notation with respect to the latent variables \( z_i \). Critically, our partitioning scheme depends on \( n \) (the number of observed individuals). Conditioning on \( n \) implies that we know which of the \( M \) possible individuals in the superpopulation were observed. Thus, the second term on the right-hand side of (5) can be written as

\[
[p, \psi | y_{1:n}, n] \propto \left( \prod_{i=1}^{n} [y_i | p, \psi] \mathbb{1}_{\{y_i > 0\}} \right) [n | p, \psi] [p | \psi],
\]

(6)

where the conditional data model in (6) is a zero-truncated binomial with PMF

\[
[y_i | p, \psi] \mathbb{1}_{\{y_i > 0\}} \propto \frac{[y_i | p]}{1 - (1 - p)^J},
\]

(7)

such that \([y_i | p, \psi]\) arises from (4) and does not depend on \( \psi \) when \( y_i > 0 \).

The number of observed individuals is the sum of individual-level indicator variables that express which individuals were detected/undetected as \( n = \sum_{i=1}^{M} \mathbb{1}_{\{y_i > 0\}} \). Conditional on \( p \) and \( \psi \), the probability of detecting an individual from the superpopulation is

\[
\Pr(\mathbb{1}_{\{y_i > 0\}} = 1 | p, \psi) = \psi(1 - (1 - p)^J),
\]

(8)

and \( \mathbb{1}_{\{y_i > 0\}} \) are conditionally independent Bernoulli trials before \( y_{1:n} \) are observed. Thus, the number of observed individuals is distributed conditionally as \( n \sim [n | p, \psi] = \text{Binom}(M, \psi(1 - (1 - p)^J)) \) under this model.

In most other recursive implementations, we would need to evaluate the conditional data distribution \([y_{(n+1):M} | p, \psi, y_{1:n}, n]\) in the first term on the right-hand side of (5). However, in this PX-DA situation where \( y_{(n+1):M} = 0 \) are augmented data, the conditional data distribution is proportional to \( \prod_{i=n+1}^{M} \mathbb{1}_{\{y_i = 0\}} = 1 \). Thus, we do not need to consider the augmented data \( y_{(n+1):M} \) in this framework, only the observed data \( y_{1:n} \) and the sample size \( n \). The data augmentation merely suggests that we can reformulate the homogeneous CR model as in (6).

King et al. (2016) noted that a similar posterior distribution as in (6) suggests an alternative specification for a more general class of CR models. We show that these have associated recursive Bayesian computing strategies. In our case, the alternative specification involves a model for the observed data conditioned on \( n \) and the model parameters (e.g., \( p \) and \( \psi \)) and also a model for \( n \) conditioned on the parameters. Similar CR model specifications were discussed by Borchers and Efford (2008) and differ from capture-recapture model specifications that are based on \( N \), the total abundance, directly (e.g., King et al., 2016). Neither Borchers and Efford (2008) nor King et al. (2016) leveraged the formulation to facilitate recursive Bayesian computing.

In the case of the homogeneous CR model we described, we can fit it recursively in the following way. For the first stage, we fit a Bayesian model using a stochastic sampling procedure (e.g., importance sampling, MCMC, Hamiltonian Monte Carlo) based on the
conditional data model and priors for \( p \) and \( \psi \) in (6) comprising a temporary posterior distribution proportional to

\[
\left( \prod_{i=1}^{n} [y_i | p, \psi] \mathbb{1}_{\{y_i > 0\}} \right) [p] [\psi].
\] (9)

Then, in the second stage of the procedure, we use a randomly selected first-stage sample \( (p^{(\ast)}, \psi^{(\ast)}) \) as a proposal in either an importance (e.g., Chopin, 2002) or Metropolis-Hastings ratio depending on whether SMC or MCMC is preferred for the second stage. For MCMC, the second-stage Metropolis-Hastings ratio can be written as

\[
| \begin{bmatrix} n \mid p^{(k-1)}, \psi^{(k-1)} \end{bmatrix} | / | \begin{bmatrix} n \mid p^{(k)}, \psi^{(k)} \end{bmatrix} | ,
\] (10)

for MCMC iteration \( k \) and we let \( p^{(k)} = p^{(\ast)} \) and \( \psi^{(k)} = \psi^{(\ast)} \) with probability \( \min(r, 1) \); we retain \( p^{(k)} = p^{(k-1)} \) and \( \psi^{(k)} = \psi^{(k-1)} \) otherwise (Supporting Information, Appendix A; Hooten et al. 2021). The second stage does not involve tuning parameters and is unsupervised.

In the PX-DA framework based on the hierarchical CR model, \( N = \sum_{i=1}^{M} z_i \) is treated as a derived quantity. In a recursive framework, we can obtain an MCMC sample for \( N \) in a third computing stage where \( N_0 \) is sampled from its full-conditional distribution as \( N_0^{(k)} \sim \text{Binom}(M - n, \psi^{(k)}(1 - p^{(k)})^J / (\psi^{(k)}(1 - p^{(k)})^J + 1 - \psi^{(k)})) \) and then \( N^{(k)} = n + N_0^{(k)} \) for MCMC iteration \( k = 1, \ldots, K \). The quantity \( N_0 \) represents the undetected individuals from the superpopulation that were part of our study population. Critically, our model fit does not depend on this third stage, but the inference we obtain about abundance \( N \) as a derived quantity is fully Bayesian. This is in contrast to the “empirical Bayes” estimator proposed by Dorazio (2013) which depends on a point estimate of \( N_0 \) that is based on maximum likelihood estimators of the parameters.

We demonstrate the application of recursive Bayes by fitting the hierarchical CR model to simulated data in the Supporting Information, Appendix B. We compared inference from both the conventional single-stage MCMC algorithm and the PPRB procedure and illustrated their equivalence.

3 Generalizations and Alternative Models for \( n \)

An important aspect of expressing the posterior distribution as in (6) is that it admits other specifications of the model for the number of observed individuals \( n \). In the previous section, we derived a conditional binomial distribution for \( n \) that is consistent with the assumptions of the original PX-DA implementation of the homogeneous CR model. Alternatively, we could assume a conditional Poisson model for \( n \) instead. Similar Poisson models for \( n \) (and \( N \)) have been suggested previously (e.g., Borchers and Efford, 2008; Johnson et al., 2010; Dorazio, 2013; Schofield and Barker, 2014; King et al., 2016), and we could justify it in a variety of ways for our model. For example, if we assume \( M \to \infty \) (a common assumption in PX-DA implementations of CR models)
and \( \psi \to 0 \) such that \( \lambda = \psi M \) is constant, then the binomial converges in distribution to the Poisson such that \( n \sim \text{Pois}(\lambda(1 - (1 - p)^J)) \).

For large \( M \), which is a user choice, the Poisson and binomial approaches yield the same posterior distribution (6). For smaller values of \( M \), especially those that constrain the upper tail of the distribution of \( n \), the Poisson and binomial models will result in slightly different inference. However, the use of a Poisson model for \( n \) may facilitate the implementation of more general CR models, as we show in the examples that follow.

Consider the hierarchical CR model with heterogeneous detection probability that varies by individual and is implemented using PX-DA such that \( y_{1:n} \) are observed counts of detections for a set of \( n \) individuals and \( y_{(n+1):M} = 0 \) represent the augmented individuals (Royle and Dorazio, 2008; Schofield and Barker, 2014). The conventional hierarchical specification for this heterogeneous CR model is \( y_i \sim \psi[y_i|p_i] + (1 - \psi)1\{y_i = 0\} \) with the individual-specific detection probabilities modeled as \( \text{logit}(p_i) \sim N(\mu, \sigma^2) \) for \( i = 1, \ldots, M \). This model treats the detection probabilities as random effects and thus requires priors \( [\mu, \sigma^2] \). Also, the heterogeneous CR model is a good candidate for recursive computing strategies because it can be challenging to implement (King et al., 2016; White and Cooch, 2017).

The heterogeneous CR model can be reformulated as described in the previous section based on a recursive implementation where we condition on \( n \) in the first computing stage which yields the zero-truncated binomial data model for positive counts \( y_i \sim [y_i|p_i]/(1 - (1 - p_i)^J) \) for \( i = 1, \ldots, n \) (Borchers and Efford, 2008). We write the associated posterior distribution for this model as

\[
\begin{align*}
\text{logit}(p_{1:n}), \mu, \sigma^2, \psi | y_{1:n}, n & \propto \left( \prod_{i=1}^n \frac{[y_i|p_i]}{1 - (1 - p_i)^J} \right) [n|p_{1:n}, \mu, \sigma^2, \psi] \text{logit}(p_{1:n})|\mu, \sigma^2][\mu][\sigma^2][\psi], \\
\end{align*}
\]

(11)

where \( p_{1:n} = (p_1, \ldots, p_n)^\prime \) and \( \text{logit}(p_{1:n})|\mu, \sigma^2] = \prod_{i=1}^n \text{logit}(p_i)|\mu, \sigma^2] \). The partially integrated conditional distribution for \( n \) in the joint distribution on the right hand side of (11) can be calculated as an \((M - n)\)-dimensional integral

\[
[n|p_{1:n}, \mu, \sigma^2, \psi] = \int [n|p_{1:n}, p_{(n+1):M}, \psi] \text{logit}(p_{(n+1):M})|\mu, \sigma^2] d\text{logit}(p_{(n+1):M}),
\]

(12)

where \( \text{logit}(p_{(n+1):M})|\mu, \sigma^2] = \prod_{i=n+1}^M \text{logit}(p_i)|\mu, \sigma^2] \) and the conditional distribution \([n|p_{1:n}, p_{(n+1):M}, \psi]\) is Poisson-binomial with \( M \) trials and probabilities \( \psi(1 - (1 - p_i)^J) \) for \( i = 1, \ldots, M \) (Fernández and Williams, 2010), as implied by the conventional heterogeneous CR model. However, the Poisson-binomial PMF is numerically inefficient to calculate, often requiring a Fourier transform approach. Alternatively, using similar limiting arguments as we did for the homogeneous CR model, we could assume that each detection indicator is Poisson distributed with intensity \( \psi(1 - (1 - p_i)^J) \). Then, if we assume large \( M \) and the detections are conditionally independent, the sum \( n = \sum_{i=1}^M 1_{\{y_i > 0\}} \) can be modeled as \( n \sim \text{Pois}(\psi \sum_{i=1}^M (1 - (1 - p_i)^J)) \). The Poisson PMF is much more numerically tractable and leads to a faster algorithm for approximating the integral in (12).
To fit the model with posterior distribution in (11) using the PPRB approach, we first obtain a sample from the posterior distribution associated with the observed data $y_{1:n}$ and then assimilate the number of observed individuals $n$ in a second stage. However, there are several important implementation details that arise for this heterogeneous CR model. In a first computing stage, we use a standard algorithm to obtain a MCMC sample based on the posterior

$$\text{logit}(p_{1:n}) \propto \prod_{i=1}^{n} \left[ \frac{y_i}{1 - (1 - p_i)^J} \right] \text{logit}(p_{1:n}) \mid \mu, \sigma^2, \psi,$$

(13)

which requires Metropolis-Hastings updates for $\text{logit}(p_{1:n})$, but facilitates Gibbs updates for $\mu$ and $\sigma^2$. We draw an independent Monte Carlo sample for $\psi$ from its prior because it does not appear in the zero-truncated binomial likelihood.

In the second computing stage, we use a random draw from the first stage MCMC sample as the proposal $\{p^{(\ast)}_{1:n}, \mu^{(\ast)}, \sigma^2^{(\ast)}, \psi^{(\ast)}\}$ and update using the Metropolis-Hastings ratio

$$r = \frac{[n|p^{(\ast)}_{1:n}, \mu^{(\ast)}, \sigma^2^{(\ast)}, \psi^{(\ast)}]}{[n|p^{(k-1)}_{1:n}, \mu^{(k-1)}, \sigma^2^{(k-1)}, \psi^{(k-1)}]} ,$$

(14)

where we can approximate the partially integrated PMF for $n$ using Monte Carlo integration based on (12), or other numerical approach (see King et al. 2016 for a quadrature method).

As eluded to previously, in our experience, the second stage of the recursive procedure can be computationally limiting because we need to approximate the PMFs in (14) on each iteration. However, in addition to using a conditional Poisson distribution for $n$, a major advantage of the recursive procedure using either SMC or MCMC is that we can perform the necessary approximation to evaluate the partially integrated PMFs for $n$ in parallel. Additionally, we know the proposed parameter values before the second computing stage and this further reduces the necessary calculations. As described by Hooten et al. (2021), this parallel computing procedure is similar to pre-fetching (Brockwell, 2006).

In a third computing stage, we sample the population abundance parameter using the MCMC output from the second stage and an approach similar to what we described for the homogeneous model. Thus, to obtain a MCMC sample for $N$ based on the heterogeneous model, we draw $N_0^{(k)}$ from its full-conditional distribution and let $N^{(k)} = n + N_0^{(k)}$.

For example, if we specified our conditional model $[n|p_{1:n}, p_{(n+1):M}, \psi]$ as Pois($\psi \sum_{i=1}^{M} (1 - (1 - p_i)^J)$), then we obtain a MCMC sample for $N$ by drawing

$$N_0^{(k)} \sim \text{Pois}(\bar{\psi}^{(k)}(M - n)) ,$$

(15)

where the term $\bar{\psi}^{(k)}$ is the full-conditional probability of population membership for an augmented individual averaged over the conditional distribution of $\text{logit}(p)$ and is
homogeneous for all \( i = n + 1, \ldots, M \). We calculate \( \bar{\psi}^{(k)} \) as
\[
\bar{\psi}^{(k)} = \int \left( \frac{\psi^{(k)}(1-p)^J}{\psi^{(k)}(1-p)^J + 1 - \psi^{(k)}} \right) \logit(p)|\mu^{(k)}, \sigma^2^{(k)}| d\logit(p),
\]
for \( k = 1, \ldots, K \) second-stage MCMC iterations.

Wildlife biologists are often interested in assessing their sampling strategy and study design. In such cases, it is common to infer the “power to detect,” which is the probability of detecting a randomly selected individual from the population in \( J \) sampling occasions (e.g., Dupont et al., 2021). In simple closed-population models with homogeneous detection probability \( p \), the conditional power to detect is calculated as
\[
Pr(\tilde{y} > 0 | \tilde{z} = 1, p) = 1 - (1 - p)^J.
\]
This quantity can be readily extended to Bayesian CR models with heterogeneous detectability by considering the posterior power to detect
\[
Pr(\tilde{y} > 0 | \tilde{z} = 1, y) = \int \int \int \int 1_{\{\tilde{y} > 0\}} \tilde{y} | \mu, \sigma^2 | \logit(p) d\mu d\sigma^2 d\tilde{y},
\]
which is a derived posterior predictive quantity. We can use composition sampling to obtain a MCMC sample \( \tilde{y}^{(k)} \) for \( k = 1, \ldots, K \) and then Monte Carlo integration to approximate the posterior power to detect as
\[
Pr(\tilde{y} > 0 | \tilde{z} = 1, y) = \sum_{k=1}^K 1_{\{\tilde{y}^{(k)} > 0\}} / K.
\]

### 3.1 Application: Salamander abundance

We demonstrate the PPRB approach to implementing the heterogeneous CR model using a data set comprised of encounter histories based on \( J = 4 \) sampling occasions for red-cheeked salamander (\textit{Plethodon jordani}). These data were collected in Great Smoky Mountains National Park in a 15 m \( \times \) 15 m fenced plot to ensure closure of the population under study (Bailey et al., 2004; Hooten and Hefley, 2019). The measurement process resulted in \( n = 93 \) observed individuals with 78, 11, and 4 detected on 1, 2, and 3 sampling occasions, respectively. This species is known to have low detectability, thus we augmented the data with \( M - n = 1407 \) all-zero encounter histories, which implies \( M = 1500 \) total individuals in our superpopulation.

A variety of factors can result in heterogeneous capture probabilities for red-cheeked salamanders (Bailey et al., 2004). To account for individually varying detectability, we fit heterogeneous CR models to these data using the two-stage PPRB procedure. For comparison, we fit two heterogeneous CR models; one based on the conditional Poisson-binomial assumption for \( n \) and the other based on the conditional Poisson assumption for \( n \). We specified priors for both models as: \( \mu \sim N(-1,1) \), \( \sigma^2 \sim IG(0.01,0.01) \), and \( \psi \sim \text{Beta}(1,1) \). We fit the models using \( K = 100000 \) MCMC iterations which required approximately 7.9 hours for the Poisson-binomial version and only 12.2 minutes for the Poisson version.

The posterior results are summarized in Figure 1. Fitting the two heterogeneous CR models results in remarkably similar posterior distributions for the parameters \( \mu, \sigma^2 \), and...
ψ (Figure 1a-c). However, there were slight differences in the posterior distributions for abundance N (Figure 1d). In particular, the conventional heterogeneous CR model with Poisson-binomial distribution for n had a smaller posterior mean abundance \( E(N|y) = 261.3 \) than the model with Poisson distribution for n \( E(N|y) = 263.6 \) and narrower 95% credible interval [195, 356] versus [180, 407]. Although, when considered in the range of values between \( n = 92 \) and \( M = 1500 \), the two marginal posterior distributions for N are quite similar. Similarly, for both models, the posterior power to detect was approximately \( \Pr(\tilde{y} > 0|\tilde{z} = 1, y) = 0.36 \) for this species, based on \( J = 4 \) sampling occasions. This result implies that we have a 36% chance of detecting a randomly selected individual in the population.

We used a standard MCMC algorithm for stages one and two to fit both models but performed the numerical approximations (e.g., Bonner and Schofield, 2014) of the partially integrated conditional distribution in (12) in parallel, utilizing 20 3GHz cores to calculate the elements of the Metropolis-Hastings ratios in (14) a priori. The algorithm we used to fit the heterogeneous CR model with Poisson distribution for n yielded results two orders of magnitude faster than for the conventional model with Poisson-binomial distribution for n. This highlights an advantage in having the flexibility to generalize the model specification easily by modifying the conditional distribution for n.
4 Recursive Bayes for Spatial Capture-Recapture

We can apply the recursive procedure described in previous sections to fit spatial CR (SCR; Royle and Young 2008) models. In the spatially explicit setting, individuals may be detected at an array of “traps” (i.e., detectors) located at positions $x_l$ for $l = 1, \ldots, L$. Thus, we retain the CR data model from before

$$y_{i,l} \sim \begin{cases} \text{Binom}(J, p_{i,l}) & z_i = 1 \\ \mathds{1}_{\{y_{i,l} = 0\}} & z_i = 0 \end{cases},$$

for $i = 1, \ldots, n, n + 1, \ldots, M$ and where $z_i \sim \text{Bern}($ψ$)$ are binary variables indicating population membership as before. Using PX-DA, the observed data are augmented with all-zero capture histories such that $y_{i,l} = 0$ for $i = n + 1, \ldots, M$ and $l = 1, \ldots, L$. In SCR, heterogeneity in detection/capture probability is often characterized as a function of the distance between (unknown) individual-based activity centers $s_i$ and the (known) trap locations $x_l$. For example, we can use a logit link function such that

$$\text{logit}(p_{i,l}) = \beta_0 + \beta_1 ||s_i - x_l||^2_2,$$ (20)

where we treat $s_i$ as random effects with distribution $s_i \sim [s_i]$. We note that alternative link functions (e.g., ‘cloglog’) are also popular in SCR models (e.g., Hooten and Hefley, 2019, ch. 27). In many cases, the distribution $[s_i]$ serves as a prior and is specified as a bivariate uniform distribution, which implies a complete spatial random point process for $s_i$ before the data are observed. Various approaches have been proposed to generalize the conditional model for $s_i$ such as allowing it to be a heterogeneous spatial point process (e.g., Sutherland et al., 2015).

Following the procedure we described in the previous section, we can express the posterior distribution associated with the SCR model as

$$[S_{1:n}, \beta, \psi|Y_{1:n}, n] \propto \left( \prod_{i=1}^{n} \left( \prod_{l=1}^{L} \frac{[y_{i,l} p_{i,l}]}{1 - (1 - p_{i,l})^J} \right) [s_i] \right) [n|S_{1:n}, \beta, \psi][\beta][\psi],$$ (21)

where $S_{1:n} \equiv (s_1, \ldots, s_n)$ and the conditional distribution of $n$ is

$$[n|S_{1:n}, \beta, \psi] = \int [n|S_{1:n}, S_{(n+1):M}, \psi][S_{(n+1):M}]dS_{(n+1):M},$$ (22)

where the joint prior for the activity centers is $[S_{(n+1):M}] = \prod_{i=n+1}^{M} [s_i]$ and $[n|S_{1:n}, S_{(n+1):M}, \psi]$ is either Poisson-binomial under the conventional PX-DA model specification or, as we demonstrate in the example that follows, can be approximated by a Poisson PMF with intensity $\sum_{i=1}^{M} (1 - \prod_{l=1}^{L} (\psi(1 - p_{i,l})^J + 1 - \psi))$ such that $p_{i,l} = \text{logit}^{-1}(\beta_0 + \beta_1 ||s_i - x_l||^2_2)$. This Poisson intensity is derived as before by considering the number of observed individuals as a sum of detection indicators. In the context of our SCR model, $n = \sum_{i=1}^{M} \mathds{1}_{\{\sum_{l=1}^{L} y_{i,l} > 0\}}$, where each $\mathds{1}_{\{\sum_{l=1}^{L} y_{i,l} > 0\}}$ is a binary random variable with success probability

$$P(\mathds{1}_{\{\sum_{l=1}^{L} y_{i,l} > 0\}} = 1|p_i, \psi) = 1 - P(\mathds{1}_{\{\sum_{l=1}^{L} y_{i,l} > 0\}} = 0|p_i, \psi),$$ (23)
\[ 1 - \prod_{l=1}^{L} P(y_{i,l} = 0 | p_{i,l}, \psi) , \tag{24} \]

\[ 1 - \prod_{l=1}^{L} (\psi(1 - p_{i,l}))^{J} + 1 - \psi . \tag{25} \]

Thus, assuming large \( M \) and conditional independence, we treat each probability in (25) as an intensity and sum across \( M \) individuals in the superpopulation to obtain the total Poisson intensity for \( n \).

To fit this version of the SCR model using recursive Bayes, we can use the same sequence of computing stages described in the previous section. In stage 1, we use MCMC to fit the model with posterior

\[ [S_{1:n}, \beta, \psi | Y_{1:n}] \propto \left( \prod_{i=1}^{n} \left( \prod_{l=1}^{L} \frac{[y_{i,l} | p_{i,l}]}{1 - (1 - p_{i,l})^{J}} \right) [s_{i}] [\beta][\psi] , \tag{26} \]

which involves Metropolis-Hastings updates for \( s_{i} \) and \( \beta \), but direct Monte Carlo sampling for \( \psi \) from its prior because it does not appear in the conditional data model. After we acquire the stage 1 MCMC sample, we evaluate the conditional PMF \([n | S_{1:n}, \beta, \psi]\) for all realizations of \( S_{1:n}, \beta, \) and \( \psi \) from the first stage. This step requires numerical integration (e.g., Bonner and Schofield, 2014) to approximate (22).

In stage 2, we use PPRB to update the latent activity centers and model parameters using joint random draws from the first stage MCMC sample as proposals \( \{S_{1:n}^{(s)}, \beta^{(s)}, \psi^{(s)}\} \) and the Metropolis-Hastings ratio

\[ r = \frac{[n | S_{1:n}^{(s)}, \beta^{(s)}, \psi^{(s)}]}{[n | S_{1:n}^{(k)}, \beta^{(k)}, \psi^{(k)}]} . \tag{27} \]

This second stage can be performed quickly using a look-up table for the pre-computed conditional PMFs for \( n \) resulting from the first stage.

We follow the procedure described in the previous section to obtain a MCMC sample for population abundance \( N \) in a third computing stage. Under the SCR model based on a conditional Poisson assumption for \( n \), we sample \( N_{0}^{(k)} \) as

\[ N_{0}^{(k)} \sim \text{Pois}(\bar{\psi}^{(k)}(M - n)) , \tag{28} \]

and then let \( N^{(k)} = n + N_{0}^{(k)} \) for \( k = 1, \ldots, K \) second-stage MCMC iterations. This form of full-conditional updating is possible because, after we condition on \( n \), we know that the additional undetected individuals (\( N_{0} \)) from our population are indistinguishable and independent with full-conditional membership probability

\[ \bar{\psi}^{(k)} = \int \left( \frac{\psi^{(k)} \prod_{l=1}^{L} (1 - p_{l}^{(k)})^{J}}{\psi^{(k)} \prod_{l=1}^{L} (1 - p_{l}^{(k)})^{J} + 1 - \psi^{(k)}} \right) [s] ds , \tag{29} \]
where \( \hat{p}_1^{(k)} = \logit^{-1}(\beta_0^{(k)} + \beta_1^{(k)} ||s - x||^2) \) for \( k = 1, \ldots, K \) second-stage MCMC iterations. Furthermore, the sampling of \( N_0 \) can be performed in parallel post hoc because all quantities in the full-conditional distribution (28) have already been obtained in the second computing stage.

We can calculate the posterior power to detect for the SCR model using a similar approach as described in the previous section. However, because we have collected CR data across an entire trap array, the probability of detecting a random individual in \( J \) sampling occasions is

\[
\Pr \left( \sum_{l=1}^{L} \tilde{y}_l > 0 \mid \bar{z} = 1, Y \right) = \int \mathbb{1}_{\{\sum_{l=1}^{L} \tilde{y}_l > 0\}} [\tilde{y} | \tilde{z} = 1, Y] d\tilde{y},
\]

which involves a multidimensional integral, but can still be approximated using composition sampling to obtain a posterior predictive MCMC sample for \( \tilde{y}_l^{(k)} \) for \( l = 1, \ldots, L \) and \( k = 1, \ldots, K \). Monte Carlo integration can then be used to calculate the posterior power to detect as

\[
\Pr \left( \sum_{l=1}^{L} \tilde{y}_l > 0 \mid \tilde{z} = 1, Y \right) = \frac{\sum_{k=1}^{K} \mathbb{1}_{\{\sum_{l=1}^{L} \tilde{y}_l^{(k)} > 0\}}}{K}.
\]

### 4.1 Application: Snowshoe hare abundance

We demonstrate the PPRB approach to implementing the SCR model using a data set comprised of encounter histories of \( n = 13 \) snowshoe hares (\textit{Lepus americanus}) based on \( J = 5 \) sampling occasions at an array of \( L = 84 \) traps in central Colorado, USA (Ivan et al., 2014) during winter 2007. The snowshoe hare SCR data are shown in Figure 2 on a regular grid of trap locations spaced 50m apart at which individuals were captured with live traps and marked using passive integrated transponder tags that identified individuals on recapture (data in Appendix C).

We fit the SCR model with both the Poisson-binomial and Poisson conditional distributions for \( n \) to the data shown in Figure 2. For priors, we specified \( \beta \sim N(0, 1000 \cdot I) \), \( \psi \sim \text{Beta}(1, 1) \), and \( s_i \sim \text{Unif}(A) \), where \( A \) is a rectangular region extending 100 m beyond the trap array in each direction (dashed region in Figure 2; 37.5ha area). We assumed a total of \( M = 50 \) in the superpopulation, which implies \( M - n = 37 \) augmented individuals with all-zero encounter histories. However, similar to our implementation of the heterogeneous model in the previous section, we do not actually augment the data set to fit this SCR model. Instead, \( M \) is involved in computing the components (22) of the second stage Metropolis-Hastings ratios (27).

We fit the models using \( K = 100000 \) MCMC iterations, which required 69.9 minutes total for stages one and two (and the intermediate parallel stage to evaluate the partially integrated full-conditional distributions for \( n \) in the Poisson-binomial case and 20.3 minutes total for the Poisson case. After fitting the models, we obtained a posterior sample for abundance \( N \) as described previously, by computing \( \tilde{\psi}^{(k)} \) and sampling \( N_0^{(k)} \) in parallel, which required 10.4 minutes using 20 3Ghz cores for the Poisson-binomial case and 10.3 minutes for the Poisson case.

The posterior results from fitting the SCR model with conditional Poisson-binomial and Poisson assumptions for \( n \) to the snowshoe hare data are summarized in Figure 3.
Figure 2: SCR data for $n = 13$ snowshoe hare individuals over a $7 \times 12$ array of $L = 84$ traps spaced 50m apart. Positions of numbers represent trap locations in array and values correspond to the number of detections for each individual at each trap (cases with $y_{k,l} > 0$ shown in red). Support for activity centers $s$ is shown as a dashed box; expanded 100 m in each direction from the extent of the trap array.
Our results indicate that the capture probabilities of snowshoe hares are small in general.

Figure 3: Marginal posterior distributions for a) $\beta_0$, b) $\beta_1$, c) $\psi$, and d) $N$. Distributions shown are a result of the recursive Bayes algorithm used to fit the SCR model with conditional Poisson-binomial (orange) and Poisson (blue) assumption for $n$. Subfigure d shows marginal posterior probability mass functions for $N$. (i.e., $E(p|Y) \approx 0.07$ for a trap placed at the individual activity center using either model specification) and they decrease away from the activity centers as we expect given the space use mechanism associated with the SCR model (e.g., $E(p|Y) \approx 0.027$ for a trap 100m away from the individual activity center using either model specification). In fact, Figure 4 shows the estimated detection function associated with our SCR models over a range of distances spanning half the maximum distance in the study trap array. These results indicate very low probability of detecting an individual with a trap farther than 200 m from the individual’s activity center.

In terms of abundance, our Poisson-binomial model fit estimated posterior mean abundance as $E(N|Y) = 14.2$ with a 95% posterior credible interval of (13, 17). For the Poisson model fit, $E(N|Y) = 14.3$ with a 95% posterior credible interval of (13, 18). Thus, despite the low detection probability, with $J = 5$ sampling occasions, most of the individuals in the population were observed ($n = 13$) with only a few individuals possibly going undetected in our study area. In fact, the posterior power to detect for both models was approximately $Pr \left( \sum_{i=1}^{J} \tilde{y}_i > 0 | \tilde{z} = 1, Y \right) = 0.81$ based on $J = 5$ sampling occasions for a random individual from our population in the study area (dashed region in Figure 2).
Figure 4: Pointwise 95% credible intervals (shaded) and posterior means (solid) for the detection function $p$ based on fitting the SCR model with Poisson-binomial (P-b; orange) and Poisson (Pois; blue) assumption for the conditional distribution of $n$. 
5 Discussion

A variety of approaches to formulating and implementing CR models have been developed since early work in this area in the mid-20th century (Schofield and Barker, 2016). Many modern implementations of CR models are Bayesian, and a substantial portion of those rely on some form of data augmentation strategy (Durban and Elston, 2005; Royle and Dorazio, 2012). The data augmentation perspective is intuitive and facilitates model generalizations that can account for real-world complexities such as the effect of animal space use patterns on the detection function associated with an array of traps. However, as these data sets grow in size and variety, conventional algorithms to fit complicated CR models to augmented data sets may not be computationally efficient (Yackulic et al., 2020).

Following King et al. (2016), we showed how to reformulate a large class of CR models in a way that is based on the intuitive PX-DA framework. We then showed how to fit them using recursive computing strategies. The natural partitioning of observed versus augmented data illuminates an explicit conditioning on the number of observed individuals $n$, which, in turn, has its own conditional model that depends on parameters and is implied by the PX-DA scheme. Similar model specifications have been derived from alternative perspectives (e.g., Borchers and Efford, 2008; King et al., 2016) but have not been leveraged to facilitate recursive Bayesian computing strategies.

Conditional perspectives are not new in the analysis of CR data (e.g., Sanathanan, 1972; Huggins, 1989, 1991; Worthington et al., 2015; King et al., 2016). However, writing CR models as a product of a conditional distribution for the detections and a distribution for sample size allows for new model formulations.

Using a recursive implementation, we showed how to fit these respecified CR models in two stages. The first computing stage fits a zero-truncated CR model to the observed data (of dimension $n$ only). We then resample the first-stage output based on a secondary algorithm that assimilates the sample size information $n$. For MCMC specifically, calculating the necessary ratios in the second stage can be a computing bottleneck because it requires numerical integration. However, we can accelerate the second computing stage substantially by evaluating the components in parallel between stages. Thus, the first-stage only involves $n$ observations, the intermediate parallel computing scales with the number of available cores, and the second stage only requires a look-up table to compute the necessary ratios. Inference for abundance $N$ can be obtained after model fitting, where the undetected number of individuals $N_0$ is sampled from its full-conditional distribution. This final step can also be parallelized to reduce computation time.

Our application of recursive computing techniques to fit CR models aligns well with other recent developments in CR research, including multiple imputation and the explicit consideration of ancillarity in these types of models (Worthington et al., 2015; Schofield and Barker, 2016). In fact, a promising area of future research should seek to formally connect the ancillarity concepts with recursive computing strategies. Our approach reduces the dimension associated with the state-space in hierarchical CR models by performing computation sequentially where the first stage is conditioned on observed
data only and the second stage marginalizes over the augmented individuals in the superpopulation. Our approach also aligns well with other calls for Rao-Blackwellization (i.e., marginalization) in the Bayesian implementation of CR models (e.g., Yackulic et al., 2020). One additional benefit of the multi-stage computing approach to implementing these models is that the first computing stage can be performed using automatic Bayesian software that may incorporate adaptive tuning techniques and alleviate the need for supervised MCMC algorithms altogether.

For completeness, it is important to note that a variety of other approaches exist for implementing CR models, including those using numerical integration approaches (Coull and Agresti, 1999; Borchers and Efford, 2008) and transdimensional methods like reversible-jump MCMC (King and Brooks, 2008; McLaughlin, 2019). In fact, King et al. (2016) noted that working with the integrated likelihood based on the PX-DA model formulation may be sufficient for fitting certain classes of CR models. Thus, recursive computing strategies may not always be necessary. However, our focus herein is to illuminate alternative ways to specify CR models that may not have been apparent otherwise. The resulting models themselves could be implemented using a variety of computing strategies depending on the goals and constraints of the study.

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Appendices for “Bayesian Capture-Recapture Models to Facilitate Recursive Computing”

Appendix A

To fit the homogeneous CR model using a single-stage MCMC algorithm, we consider the joint posterior distribution for \( p \) and \( \psi \). Under the PX-DA framework, this posterior distribution can be written as

\[
[p, \psi|y_{1:n}, y_{(n+1):M}, n] \propto [y_{(n+1):M}|p, \psi, y_{1:n}, n][p, \psi|y_{1:n}, n] ,
\]

\[
\propto [y_{(n+1):M}|p, \psi, y_{1:n}, n][y_{1:n}|n|p, \psi][\psi] ,
\]

\[
\propto [y_{1:n}|p, n][n|p, \psi][\psi] ,
\]

where the full-conditional distribution of \( y_{(n+1):M} \) is proportional to one when conditioned on \( n \) (and hence drops out of the right hand side) and the conditional distribution of \( y_{1:n} \) is proportional to the product of zero-truncated binomials

\[
[y_{1:n}|p, n] \propto \prod_{i=1}^{n} [y_i|p] \frac{p^n}{(1 - (1 - p)^n)} .
\]

For a given joint proposal distribution \( [p, \psi]^* \), the associated Metropolis-Hastings ratio to update \( p \) and \( \psi \) jointly is

\[
r = \frac{[y_{1:n}|p^*(s), n][n|p^*(s), \psi^*(s)][\psi^*(s)][p^{(k-1)}, \psi^{(k-1)}]^*}{[y_{1:n}|p^{(k-1)}, n][n|p^{(k-1)}, \psi^{(k-1)}][\psi^{(k-1)}][p^*(s), \psi^*(s)]^*} .
\]

To implement the model using PPRB following Hooten et al. (2021), we obtain an initial MCMC sample for \( p \) and \( \psi \) by fitting the CR model to the observed data while conditioning on fixed and known \( n \). The posterior distribution for the first stage is proportional to

\[
[y_{1:n}|p, n][p][\psi] ,
\]

with respect to \( p \) and \( \psi \), and the associated first-stage Metropolis-Hastings ratio is

\[
r = \frac{[y_{1:n}|p^*(s), n][n|p^*(s), \psi^*(s)][\psi^*(s)][p^{(k-1)}, \psi^{(k-1)}]^*}{[y_{1:n}|p^{(k-1)}, n][n|p^{(k-1)}, \psi^{(k-1)}][\psi^{(k-1)}][p^*(s), \psi^*(s)]^*} .
\]

At this first stage, we use a temporary proposal distribution \( [p, \psi]^* \) that is convenient.

For the second stage of the PPRB implementation, we assume that the proposal distribution is

\[
[p, \psi]^* \propto [y_{1:n}|p, n][p][\psi] ,
\]

which is equivalent to the first-stage posterior, and randomly sample (with replacement) joint first-stage MCMC realizations to use as proposals in the second stage Metropolis-Hastings updates. The resulting second-stage Metropolis-Hastings ratio becomes

\[
r = \frac{[y_{1:n}|p^*(s), n][n|p^*(s), \psi^*(s)][\psi^*(s)][p^{(k-1)}, \psi^{(k-1)}]^*}{[y_{1:n}|p^{(k-1)}, n][n|p^{(k-1)}, \psi^{(k-1)}][\psi^{(k-1)}][p^*(s), \psi^*(s)]^*} ,
\]
\[ \frac{[n|p^{(s)}, \psi^{(s)}]}{[n|p^{(k-1)}, \psi^{(k-1)}]}, \quad (40) \]

because the proposal cancels with the data model and priors. Thus, the second-stage Metropolis-Hastings ratio is merely a quotient involving the conditional model for \( n \) and can be evaluated easily using the first-stage MCMC sample.

**Appendix B**

To demonstrate the PPRB implementation of the hierarchical CR model, we fit the model to simulated data using the single-stage and two-stage approaches. To simulate CR data for this example, we set \( M = 100 \) individuals in the superpopulation, membership probability \( \psi = 0.4 \), and detection probability \( p = 0.25 \). Then we used the hierarchical model in Section 2 as a generative process to simulate data based on \( J = 3 \) occasions which resulted in \( N = 39 \) individuals in our population, with \( n = 19 \) individuals observed by our measurement process. The simulated observed data \( y_i \), for \( i = 1, \ldots, n \), can be summarized by the values \( y = (1, 1, 1, 1, 1, 1, 2, 2, 1, 1, 1, 1, 2, 1, 1, 2, 1, 1)'. \)

In the PX-DA implementation, we assumed \( M - n = 81 \) augmented individuals with all-zero capture histories. Thus, we assumed the same \( M \) as in our data simulation and this allows us to infer the true \( \psi \). We note that the estimation of \( N \) is not constrained by \( M \) empirically in this example, therefore we could use larger values of \( M \) with negligible influence on the inference for parameter \( p \).

We fit the hierarchical CR from Section 2 to our simulated data using two approaches: 1) a standard single-stage MCMC algorithm based on the full hierarchical model and 2) a two-stage PPRB algorithm based on the point process formulation of the same model, as described in the main text.

We fit the hierarchical CR model to the simulated data using both approaches and \( K = 200000 \) MCMC iterations. The results of our analyses are summarized in Figure 5. The posterior comparison shown in Figure 5 indicates that the two-stage PPRB approach yields the same inference as the conventional single-stage MCMC algorithm. Both approaches fit exactly the same model, but the recursive framework suggests that other specifications for the conditional model for \( n \) (e.g., Poisson) are trivial to implement. Furthermore, in more complicated models, we can benefit from parallel evaluation of the PMF for \( n \) which can improve stability and facilitate computation for large data sets.
Figure 5: Marginal posterior distributions for a) $p$, b) $\psi$, c) $N$. Distributions shown are a result of the single-stage MCMC algorithm (black), first-stage of the two-stage MCMC algorithm (red), and second-stage of the two-stage MCMC algorithm (green). Subfigure c shows marginal posterior probability mass functions; black line shown for single-stage for comparison.
Appendix C

The snowshoe hare SCR data used to fit the model in Section 4 are presented below. The first column is the trap ID (i.e., [1.] indicates trap 1), the second two columns correspond to the $L = 84$ trap locations $X$ in meters, and the remaining 13 columns contain values that correspond to the sum of detections associated with each individual at each trap.

| Trap ID | X1 (m) | X2 (m) | Detection Sum |
|--------|--------|--------|---------------|
| 1      | 0      | 0      | 0             |
| 2      | 50     | 0      | 0             |
| 3      | 100    | 0      | 0             |
| 4      | 150    | 0      | 0             |
| 5      | 200    | 0      | 0             |
| 6      | 300    | 0      | 0             |
| 7      | 350    | 0      | 0             |
| 8      | 400    | 0      | 0             |
| 9      | 450    | 0      | 0             |
| 10     | 500    | 0      | 0             |
| 11     | 0      | -50    | 0             |
| 12     | 50     | -50    | 1             |
| 13     | 100    | -50    | 0             |
| 14     | 150    | -50    | 0             |
| 15     | 200    | -50    | 0             |
| 16     | 250    | -50    | 0             |
| 17     | 300    | -50    | 0             |
| 18     | 350    | -50    | 0             |
| 19     | 400    | -50    | 0             |
| 20     | 450    | -50    | 1             |
| 21     | 500    | -50    | 2             |
| 22     | 0      | -100   | 0             |
| 23     | 50     | -100   | 1             |
| 24     | 100    | -100   | 0             |
| 25     | 150    | -100   | 0             |
| 26     | 200    | -100   | 0             |
| 27     | 250    | -100   | 0             |
| 28     | 300    | -100   | 0             |
| 29     | 350    | -100   | 0             |
| 30     | 400    | -100   | 0             |
| 31     | 450    | -100   | 0             |
| 32     | 500    | -100   | 0             |
| 33     | 0      | -150   | 0             |
| 34     | 50     | -150   | 0             |
| 35     | 100    | -150   | 0             |
| 36     | 150    | -150   | 0             |
| 37     | 200    | -150   | 0             |
| 38     | 250    | -150   | 0             |
| 39     | 300    | -150   | 0             |
| 40     | 350    | -150   | 0             |
| 41     | 400    | -150   | 0             |
| 42     | 450    | -150   | 0             |
| 43     | 500    | -150   | 0             |
| 44     | 0      | -200   | 0             |
| 45     | 50     | -200   | 0             |
| 46     | 100    | -200   | 0             |
| 47     | 150    | -200   | 0             |
| 48     | 200    | -200   | 0             |
| 49     | 250    | -200   | 0             |
| 50     | 300    | -200   | 0             |
| 51     | 350    | -200   | 0             |
| 52     | 400    | -200   | 0             |
| 53     | 450    | -200   | 0             |
| 54     | 500    | -200   | 0             |
| 55     | 0      | -250   | 0             |
| 56     | 50     | -250   | 0             |
| 57     | 100    | -250   | 0             |
| 58     | 150    | -250   | 0             |
| 59     | 200    | -250   | 0             |
| 60     | 250    | -250   | 0             |
| 61     | 300    | -250   | 0             |
| 62     | 350    | -250   | 0             |
| 63     | 400    | -250   | 0             |
| 64     | 450    | -250   | 0             |
| 65     | 500    | -250   | 0             |
| 66     | 0      | -300   | 0             |
| 67     | 50     | -300   | 0             |
| 68     | 100    | -300   | 0             |
| 69     | 150    | -300   | 0             |
| 70     | 200    | -300   | 0             |
| 71     | 250    | -300   | 0             |
| 72     | 300    | -300   | 0             |
| 73     | 350    | -300   | 0             |
| 74     | 400    | -300   | 0             |
| 75     | 450    | -300   | 0             |
| 76     | 500    | -300   | 0             |
|   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 79 | 300 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 80 | 350 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 81 | 400 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 82 | 450 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 83 | 500 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 84 | 550 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |