Online Supplementary Material for

"Estimation of population size when capture probability depends on individual states"

A State-Dependent Population Size

We implement a forward-backward-type algorithm to estimate the state-dependent abundance on each occasion. Here we describe the process for model M_h^R, the method can be applied to other models with appropriate changes to the parameters used.

To implement a forward-backward-type algorithm to find the conditional state probabilities (from which we can then obtain state abundance) we need to calculate the forward and backward probabilities for each observed individual $i = 1, \ldots, n$, along with the forward and backward probabilities of an all-zero capture history to account for those individuals that were missed (n_m) so that we can estimate state abundance for the whole population $N = n + n_m$.

Let X_{it} represent the random variable associated with the observation of individual i on occasion t and S_{it} the random variable associated with the state individual i is in on occasion t. For a set of discrete observable states $\mathcal{R}$, which for convenience we label $r = 1, \ldots, R$, $X_{it} \in \{0, 1, \ldots, R\}$ and $S_{it} \in \{1, \ldots, R\}$ for $i = 1, \ldots, n$ and $t = 1, \ldots, T$ (where T is the total number of capture occasions). Let $\boldsymbol{f} = \{f_{it}(r) : i = 1, \ldots, n,\ t = 1, \ldots, T,\ r = 1, \ldots, R\}$ denote the forward probabilities for all observed individuals. These forward probabilities are the joint probabilities

$$f_{it}(r) = \mathbb{P}(X_{i1} = x_{i1}, X_{i2} = x_{i2}, \ldots, X_{it} = x_{it},\ S_{it} = r)$$

where $\boldsymbol{x}_i = \{x_{it} : t = 1, \ldots, T\}$ is the capture history of individual $i = 1, \ldots, n$. Recalling the parameters of the model associated with moving between states (initial discrete state probabilities $\boldsymbol{\alpha} = \{\alpha(r) : r = 1, \ldots, R\}$ and transition probabilities $\boldsymbol{\psi} = \{\psi(s, r) : s =$

$1,\dots,R,\ r=1,\dots,R\}$) we initialise the forward probabilities on occasion 1,

$$f_{i1}(r) = \alpha(r)\mathbb{P}(X_{i1} = x_{i1} \mid S_{i1} = r).$$

For the remaining occasions $t = 2,\dots,T$ we calculate the forward probabilities recursively,

$$f_{it}(r) = \sum_{s\in\mathcal{R}} f_{it-1}(s)\psi(s,r)\mathbb{P}(X_{it} = x_{it} \mid S_{it} = r).$$

The conditional probability $\mathbb{P}(X_{it} \mid S_{it})$ is the probability of observing the outcome x_{it} given the individual is in state r (e.g. $\mathbb{P}(X_{it} = 1 \mid S_{it} = 1) = p(1)$, $\mathbb{P}(X_{it} = 1 \mid S_{it} = 2) = 0$).

Let $\boldsymbol{b} = \{b_{it}(r) : i = 1,\dots,n,\ t = 1,\dots,T,\ r = 1,\dots,R\}$ denote the backward probabilities for all observed individuals. These backward probabilities are the conditional probabilities

$$b_{it}(r) = \mathbb{P}(X_{it+1} = x_{it+1}, X_{it+2} = x_{it+2},\dots,X_{iT} = x_{iT} \mid S_{it} = j).$$

The backward probabilities are initialised for the final occasion T,

$$b_{iT}(r) = 1,$$

for the preceding occasions $t = 1,\dots,T-1$ the backward probabilities are calculated recursively,

$$b_{it}(r) = \sum_{s\in\mathcal{R}} \psi(r,s)\mathbb{P}(X_{it+1} = x_{it+1} \mid S_{it+1} = s)b_{it+1}(s).$$

It can then be shown that

$$f_{it}(r) \times b_{it}(r) = \mathbb{P}(X_{i1} = x_{i1}, X_{i2} = x_{i2},\dots,X_{iT} = x_{iT},\ S_{it} = r)$$

for $t = 1,\dots,T$ and $r = 1,\dots,R$.

These joint probabilities can now be used to find the probability of being in each state on each occasion taking into account the whole observed capture history. We use the result,

$$\mathbb{P}(S_{it} = r \mid X_{i1} = x_{i1}, X_{i2} = x_{i2},\dots,X_{iT} = x_{iT}) = \frac{\mathbb{P}(X_{i1} = x_{i1}, X_{i2} = x_{i2},\dots,X_{iT} = x_{iT},\ S_{it} = r)}{\mathbb{P}(X_{i1} = x_{i1}, X_{i2} = x_{i2},\dots,X_{iT} = x_{iT})}$$

where division by

$$\mathbb{P}(X_{i1} = x_{i1}, X_{i2} = x_{i2},\dots,X_{iT} = x_{iT}) = f_{it}(\cdot)b_{it}(\cdot)^T$$

($f_{it}(\cdot) = \{f_{it}(r) : r = 1, \dots, R\}$, $b_{it}(\cdot) = \{b_{it}(r) : r = 1, \dots, R\}$ and $b_{it}(\cdot)^T$ denotes the transpose) ensures that on each occasion the sum over the conditional state probabilities over all states is 1.

In this situation of capture-recapture data where the state is also observed as a discrete covariate, on occasions when an individual is captured the state is known with certainty ($x_{it} = S_{it} = r$) and so $\mathbb{P}(S_{it} = r \mid X_{i1} = x_{i1}, \dots, X_{it} = x_{it}(= r), \dots, X_{iT} = x_{iT}) = 1$. On occasions when an individual is not captured the state is not known ($x_{it} = 0$) and the conditional state probabilities give the probability for each state taking into account the whole of the capture history. Typically when applied to HMMs, the forward-backward algorithm identifies the most probable *hidden* state, i.e. the states are never observed. In the application considered here the states are not hidden but partially observed (only unknown when an individual is not captured) and so we call this a forward-backward-type algorithm.

The above process calculates the conditional state probabilities for all observed individuals, the same approach can be applied to find the conditional state probabilities for an all-zero capture history, $\mathbb{P}(S_t = r \mid X_1 = 0, X_2 = 0, \dots, X_n = 0)$, dropping the i notation for simplicity.

If we were to take the approach of using these conditional state probabilities to find the most probable state on each occasion (by assigning the state with highest probability) we could 'locally decode' the whole state sequence as is typical in the HMM framework. However, to do so would result in all individuals with identical capture histories being assigned the same state sequence. We believe this to be unrealistic in practice and instead have implemented a probabilistic argument. We do not assign the most probable state (and sum over these most probable states to get state abundance), we instead sum the conditional state probabilities for each state over all N individuals. The conditional state probabilities already account for occasions when the state is known, the uncertainly arises on occasions when the individual is not captured.

The estimators for time- and state-dependent abundance $N_t(r)$ for $t = 1, \dots, T$ and

$r = 1, \ldots, R$ are then given by,

$$N_t(r) = \left(\sum_{i=1}^{n} \mathbb{P}(S_{it} = r \mid X_{i1} = x_{i1}, X_{i2} = x_{i2}, \ldots, X_{it} = x_{it}) \right) + \left(n^m \times \mathbb{P}(S_t = r \mid X_1 = 0, X_2 = 0, \ldots, X_t = 0) \right).$$

For a given state and occasion, the first term sums the conditional state probabilities for all observed individuals $i = 1, \ldots, n$, the second term accounts for the conditional state probabilities for the estimated number of individuals with an all zero capture history.

B Simulation Study Bias Plots for State-dependent Population Size

Boxplots of the bias of the estimated population size for each state and each occasion for the cases considered in the simulation study. Figures 1 and 2 give the bias in the case of two and three states respectively.

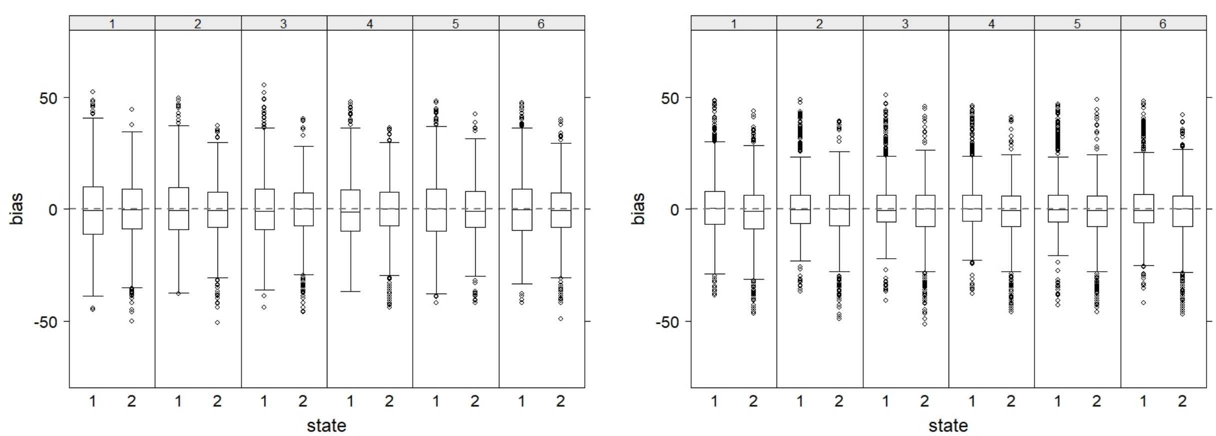

Figure 1: Boxplots of the bias of state-dependent population size for the true model M_h^2 for the simulated cases of low mobility (left) and high mobility (right). Parameter values used are given in the main text.

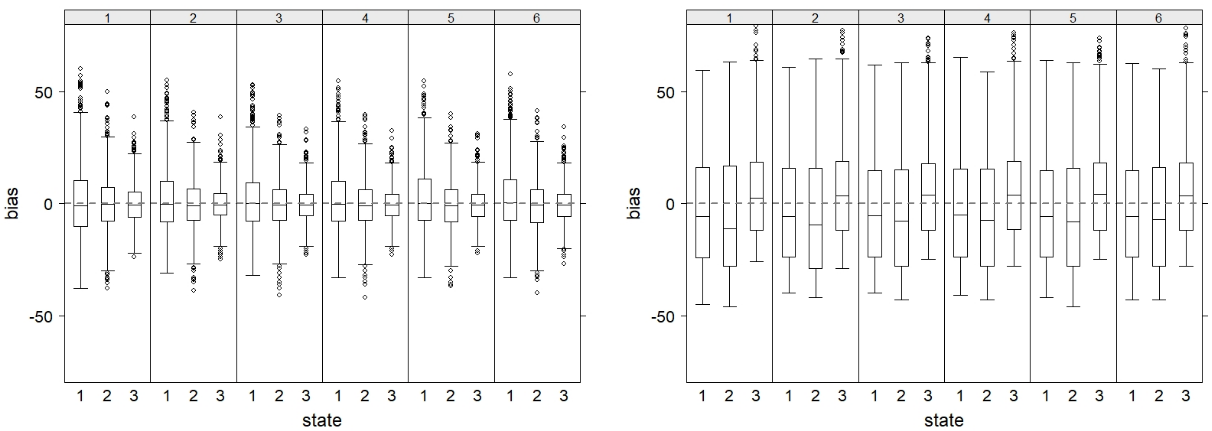

Figure 2: Boxplots of the bias of state-dependent population size for the true model M_h^3 for the simulated cases of low mobility (left) and high mobility (right). Parameter values used are given in the main text.