

1 Likelihood

- S_t : the t -th sample.
- $S_T^{in} = \bigcup_{t=1}^T S_t$: set of sampled individuals up to and including T -th sample.
- S_T^{out} : set of individuals that has not been sampled after T sample draws. ($S_T^{out} \cap S_T^{in} = \emptyset$).
- $\mathcal{P} = S_T^{in} \cup S_T^{out}$: the entire population.
- $d_{i(T)}$: number of samples that contained individual i :

$$d_{i(T)} = \sum_{t=1}^T \mathbb{1}\{i \in S_t\}$$

Assuming that samples are drawn independently:

$$\mathbb{E}[d_{i(T)}] = \sum_{t=1}^T \pi_i = T\pi_i$$

where π_i denotes inclusion probability of i . This suggests estimating π_i by

$$\hat{\pi}_i = \frac{d_{i(T)}}{T} \quad \text{or} \quad \hat{\pi}_i = \frac{1 + d_{i(T)}}{1 + T} \quad (1)$$

where the latter comes from enforcing the probabilities to be non-zero. Note that in this case $\hat{\pi}_i = \frac{1}{1+T} \forall i \in S_T^{out}$.

Consider the problem from the Bayesian perspective. Assume Beta prior for inclusion probabilities:

$$\pi_i \sim Be(\alpha, \beta)$$

Then

$$\mathbb{E}\left[\sum_{i \in \mathcal{P}} \pi_i\right] = \sum_{i \in \mathcal{P}} \frac{\alpha}{\alpha + \beta} = |\mathcal{P}| \frac{\alpha}{\alpha + \beta} = (|S_T^{out}| + |S_T^{in}|) \frac{\alpha}{\alpha + \beta}$$

Let $n_t := |S_t|$ be the sample size. While we assume independent replications of the same sampling scheme, depending on the chosen scheme, it is possible for n_t to be random. However, for simplicity, assume here that $n_t = n$ is fixed.

$$\mathbb{E}\left[\sum_{i \in \mathcal{P}} \pi_i\right] = \mathbb{E}[n_t] \Leftrightarrow (|S_T^{out}| + |S_T^{in}|) \frac{\alpha}{\alpha + \beta} = n \quad (2)$$

(in case of random n_t , we can estimate $\mathbb{E}[n_t]$ by $T^{-1} \sum_{t=1}^T n_t$).

Condition (2) will be the constraint for our model.

The likelihood would be

$$d_{i(T)} | \pi_i \sim Bin(T, \pi)$$

Then the posterior distribution is

$$\begin{aligned} f(\pi_i | d_{i(T)} = k) &= \frac{\mathbb{P}(d_{i(T)} = k | \pi_i) f(\pi_i)}{\mathbb{P}(d_{i(T)} = k)} \\ &\propto \pi_i^k (1 - \pi_i)^{T-k} \pi_i^{\alpha-1} (1 - \pi_i)^{\beta-1} \\ &= \pi_i^{\alpha+k-1} (1 - \pi_i)^{\beta+T-k-1} \\ &\Rightarrow \pi_i | d_{i(T)} = k \sim Be(\alpha + k, \beta + T - k) \\ &\Rightarrow \mathbb{E}[\pi_i | d_{i(T)} = k] = \frac{\alpha + k}{\alpha + \beta + T} \end{aligned}$$

The marginal likelihood is:

$$\begin{aligned}\mathbb{P}(d_{i(T)} = k) &= \int_0^1 f(\pi_i, d_{i(T)}) d\pi_i = \int_0^1 \mathbb{P}(d_{i(T)} = k | \pi_i) f(\pi_i) d\pi_i \\ &= \binom{T}{k} \frac{B(\alpha + k, \beta + T - k)}{B(\alpha, \beta)}\end{aligned}$$

Note that we never observe $d_{i(T)} = 0$. The observed frequencies $d_{i(T)} > 0$ for $i \in S_T^{in}$ follow a truncated distribution:

$$\begin{aligned}\mathbb{P}(d_{i(T)} = k | d_{i(T)} > 0) &= \begin{cases} \frac{\mathbb{P}(d_{i(T)}=k)}{1-\mathbb{P}(d_{i(T)}=0)}, & \text{if } k > 0 \\ 0, & \text{otherwise} \end{cases} \\ &= \begin{cases} \binom{T}{k} \frac{B(\alpha+k, \beta+T-k)}{B(\alpha, \beta) - B(\alpha, \beta+T)}, & \text{if } k > 0 \\ 0, & \text{otherwise} \end{cases}\end{aligned}$$

Following empirical Bayes approach, maximise the marginal likelihood to obtain hyper-parameters α and β .

$$\begin{aligned}L(\alpha, \beta) &:= L(\alpha, \beta; T, d_{i(T)} = k_i \forall i \in S_T^{in}) \\ &\stackrel{\text{indep}}{=} \prod_{i \in S_T^{in}} \binom{T}{k_i} \frac{\Gamma(\alpha + k_i) \Gamma(\beta + T - k_i)}{\Gamma(\alpha + \beta + T)} \cdot \frac{1}{\frac{\Gamma(\alpha) \Gamma(\beta)}{\Gamma(\alpha + \beta)} - \frac{\Gamma(\alpha) \Gamma(\beta + T)}{\Gamma(\alpha + \beta + T)}} \\ &= \prod_{i \in S_T^{in}} \binom{T}{k_i} \frac{\Gamma(\alpha + k_i) \Gamma(\beta + T - k_i) \Gamma(\alpha + \beta)}{\Gamma(\alpha) \Gamma(\beta) \Gamma(\alpha + \beta + T) - \Gamma(\alpha) \Gamma(\beta + T) \Gamma(\alpha + \beta)}\end{aligned} \tag{3}$$

Using the recursive formula of gamma function $\Gamma(x) = (x-1)\Gamma(x-1)$ and the fact that $T, k_i \in \mathbb{N}_0 := \mathbb{N} \cup \{0\}$ allows us to rewrite the marginal likelihood as:

$$\begin{aligned}L(\alpha, \beta) &\propto \prod_{i \in S_T^{in}} \frac{\Gamma(\alpha) \Gamma(\beta) \Gamma(\alpha + \beta)}{\Gamma(\alpha) \Gamma(\beta) \Gamma(\alpha + \beta)} \\ &\times \frac{\prod_{j=1}^{k_i} (\alpha + k_i - j) \prod_{j=1}^{T-k_i} (\beta + T - k_i - j)}{\prod_{j=1}^T (\alpha + \beta + T - j) - \prod_{j=1}^T (\beta + T - j)} \\ &= \prod_{i \in S_T^{in}} \frac{\prod_{j=1}^{k_i} (\alpha + k_i - j) \prod_{j=1}^{T-k_i} (\beta + T - k_i - j)}{\prod_{j=1}^T (\alpha + \beta + T - j) - \prod_{j=1}^T (\beta + T - j)}\end{aligned}$$

The parameters α and β must satisfy (2), so equation (3) is to be maximised subject to the constraint. The optimisation problem can be simplified by solving the constraint for β and plugging into the objective function:

$$\begin{aligned}\max_{\alpha, \beta} L(\alpha, \beta) \quad \text{s.t.} \quad & |\mathcal{P}| \frac{\alpha}{\alpha + \beta} = n \\ \Leftrightarrow & \beta = \left(\frac{|\mathcal{P}|}{n} - 1 \right) \alpha := q\alpha \\ \Rightarrow & \max_{\alpha, q} L(\alpha, q)\end{aligned}$$

More explicitly,

$$\begin{aligned}
\max_{\alpha, \beta} L(\alpha, \beta) \quad \text{s.t.} \quad & (|S_T^{in}| + |S_T^{out}|) \frac{\alpha}{\alpha + \beta} = n \\
\Leftrightarrow & \beta = n^{-1} \alpha |S_T^{in}| + n^{-1} \alpha |S_T^{out}| - \alpha \\
\Rightarrow & \max_{\alpha, |S_T^{out}|} L(\alpha, |S_T^{out}|)
\end{aligned}$$

1.1 Variant 1

$$L(\alpha, q) \propto \prod_{i \in S_T^{in}} \frac{\prod_{j=1}^{k_i} (\alpha + k_i - j) \prod_{j=1}^{T-k_i} (q\alpha + T - k_i - j)}{\prod_{j=1}^T (\alpha + q\alpha + T - j) - \prod_{j=1}^T (q\alpha + T - j)}$$

$$\begin{aligned}
l(\alpha, q) &:= \log L(\alpha, q) \\
&= \text{const} - |S_T^{in}| \log \left[\prod_{j=1}^T (\alpha + q\alpha + T - j) - \prod_{j=1}^T (q\alpha + T - j) \right] \\
&\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} \log(\alpha + k_i - j) + \sum_{j=1}^{T-k_i} \log(q\alpha + T - k_i - j)
\end{aligned} \tag{4}$$

Derivatives:

$$\begin{aligned}
\frac{\partial l(\alpha, q)}{\partial \alpha} &= -|S_T^{in}| \frac{\sum_{j=1}^T (1+q) \prod_{1 \leq m \neq j \leq T} (\alpha + q\alpha + T - m) - \sum_{j=1}^T q \prod_{1 \leq m \neq j \leq T} (q\alpha + T - m)}{\prod_{j=1}^T (\alpha + q\alpha + T - j) - \prod_{j=1}^T (q\alpha + T - j)} \\
&\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} (\alpha + k_i - j)^{-1} + q \sum_{j=1}^{T-k_i} (q\alpha + T - k_i - j)^{-1} \\
&= - (1+q) |S_T^{in}| \frac{\prod_{j=1}^T (\alpha + q\alpha + T - j) \sum_{j=1}^T (\alpha + q\alpha + T - j)^{-1}}{\prod_{j=1}^T (\alpha + q\alpha + T - j) - \prod_{j=1}^T (q\alpha + T - j)} \\
&\quad + q |S_T^{in}| \frac{\prod_{j=1}^T (q\alpha + T - j) \sum_{j=1}^T (q\alpha + T - j)^{-1}}{\prod_{j=1}^T (\alpha + q\alpha + T - j) - \prod_{j=1}^T (q\alpha + T - j)} \\
&\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} (\alpha + k_i - j)^{-1} + q \sum_{j=1}^{T-k_i} (q\alpha + T - k_i - j)^{-1} \\
&= - (1+q) |S_T^{in}| \frac{A_p(\alpha, q) A_s(\alpha, q)}{A_p(\alpha, q) - B_p(\alpha, q)} + q |S_T^{in}| \frac{B_p(\alpha, q) B_s(\alpha, q)}{A_p(\alpha, q) - B_p(\alpha, q)} \\
&\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} (\alpha + k_i - j)^{-1} + q \sum_{j=1}^{T-k_i} (q\alpha + T - k_i - j)^{-1}
\end{aligned} \tag{5}$$

$$\begin{aligned}
\frac{\partial l(\alpha, q)}{\partial q} &= -|S_T^{in}| \frac{\sum_{j=1}^T \alpha \prod_{1 \leq m \neq j \leq T} (\alpha + q\alpha + T - m) - \sum_{j=1}^T \alpha \prod_{1 \leq m \neq j \leq T} (q\alpha + T - m)}{\prod_{j=1}^T (\alpha + q\alpha + T - j) - \prod_{j=1}^T (q\alpha + T - j)} \\
&\quad + \sum_{i \in S_T^{in}} \alpha \sum_{j=1}^{T-k_i} (q\alpha + T - k_i - j)^{-1} \\
&= -\alpha |S_T^{in}| \frac{\prod_{j=1}^T (\alpha + q\alpha + T - j) \sum_{j=1}^T (\alpha + q\alpha + T - j)^{-1}}{\prod_{j=1}^T (\alpha + q\alpha + T - j) - \prod_{j=1}^T (q\alpha + T - j)} \\
&\quad + \alpha |S_T^{in}| \frac{\prod_{j=1}^T (q\alpha + T - j) \sum_{j=1}^T (q\alpha + T - j)^{-1}}{\prod_{j=1}^T (\alpha + q\alpha + T - j) - \prod_{j=1}^T (q\alpha + T - j)} \\
&\quad + \alpha \sum_{i \in S_T^{in}} \sum_{j=1}^{T-k_i} (q\alpha + T - k_i - j)^{-1} \\
&= -\alpha |S_T^{in}| \frac{A_p(\alpha, q) A_s(\alpha, q) - B_p(\alpha, q) B_s(\alpha, q)}{A_p(\alpha, q) - B_p(\alpha, q)} + \alpha \sum_{i \in S_T^{in}} \sum_{j=1}^{T-k_i} (q\alpha + T - k_i - j)^{-1}
\end{aligned} \tag{6}$$

where

$$\begin{aligned}
A_p(\alpha, q) &:= \prod_{j=1}^T (\alpha + q\alpha + T - j), \quad A_s(\alpha, q) := \sum_{j=1}^T (\alpha + q\alpha + T - j)^{-1} \\
B_p(\alpha, q) &:= \prod_{j=1}^T (q\alpha + T - j), \quad B_s(\alpha, q) := \sum_{j=1}^T (q\alpha + T - j)^{-1}
\end{aligned}$$

The product terms $A_p(\alpha, q)$ and $B_p(\alpha, q)$ are computationally expensive to calculate, as even small values of T will lead yield extremely large quantities. For practical purposes, one can factor out $q\alpha + T$ from both expressions. Then the log-likelihood and the derivatives can be re-written as

$$\begin{aligned}
l(\alpha, q) &= \text{const} - T|S_T^{in}| \log(q\alpha + T) - |S_T^{in}| \log \left[\widetilde{A}_p(\alpha, q) - \widetilde{B}_p(\alpha, q) \right] \\
&\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} \log(\alpha + k_i - j) + \sum_{j=1}^{T-k_i} \log(q\alpha + T - k_i - j)
\end{aligned}$$

$$\begin{aligned}
\frac{\partial l(\alpha, q)}{\partial \alpha} &= -(1+q)|S_T^{in}| \frac{\widetilde{A}_p(\alpha, q) A_s(\alpha, q)}{\widetilde{A}_p(\alpha, q) - \widetilde{B}_p(\alpha, q)} + q|S_T^{in}| \frac{\widetilde{B}_p(\alpha, q) B_s(\alpha, q)}{\widetilde{A}_p(\alpha, q) - \widetilde{B}_p(\alpha, q)} \\
&\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} (\alpha + k_i - j)^{-1} + q \sum_{j=1}^{T-k_i} (q\alpha + T - k_i - j)^{-1}
\end{aligned}$$

$$\frac{\partial l(\alpha, q)}{\partial q} = -\alpha |S_T^{in}| \frac{\widetilde{A}_p(\alpha, q) A_s(\alpha, q) - \widetilde{B}_p(\alpha, q) B_s(\alpha, q)}{\widetilde{A}_p(\alpha, q) - \widetilde{B}_p(\alpha, q)} + \alpha \sum_{i \in S_T^{in}} \sum_{j=1}^{T-k_i} (q\alpha + T - k_i - j)^{-1}$$

where

$$\widetilde{A}_p(\alpha, q) := \prod_{j=1}^T \left(1 - \frac{j - \alpha}{q\alpha + T}\right), \quad \widetilde{B}_p(\alpha, q) := \prod_{j=1}^T \left(1 - \frac{j}{q\alpha + T}\right)$$

1.2 Variant 2

$$L(\alpha, |S_T^{out}|) \propto \prod_{i \in S_T^{in}} \frac{\prod_{j=1}^{k_i} (\alpha + k_i - j) \prod_{j=1}^{T-k_i} (n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| - \alpha + T - k_i - j)}{\prod_{j=1}^T (n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| + T - j) - \prod_{j=1}^T (n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| - \alpha + T - j)}$$

$$\begin{aligned} l(\alpha, |S_T^{out}|) &:= \log L(\alpha, |S_T^{out}|) \\ &= \text{const} - |S_T^{in}| \log [A_p(\alpha, |S_T^{out}|) - B_p(\alpha, |S_T^{out}|)] \\ &\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} \log(\alpha + k_i - j) + \sum_{j=1}^{T-k_i} \log(n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| - \alpha + T - k_i - j) \\ &= \text{const} - T |S_T^{in}| \log(n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| + T) - |S_T^{in}| \log [\widetilde{A}_p(\alpha, |S_T^{out}|) - \widetilde{B}_p(\alpha, |S_T^{out}|)] \\ &\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} \log(\alpha + k_i - j) + \sum_{j=1}^{T-k_i} \log(n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| - \alpha + T - k_i - j) \end{aligned} \tag{7}$$

Derivatives:

$$\begin{aligned} \frac{\partial l(\alpha, |S_T^{out}|)}{\partial \alpha} &= - |S_T^{in}| (n^{-1} |S_T^{in}| + n^{-1} |S_T^{out}|) \frac{A_p(\alpha, |S_T^{out}|) A_s(\alpha, |S_T^{out}|)}{A_p(\alpha, |S_T^{out}|) - B_p(\alpha, |S_T^{out}|)} \\ &\quad + |S_T^{in}| (n^{-1} |S_T^{in}| + n^{-1} |S_T^{out}| - 1) \frac{B_p(\alpha, |S_T^{out}|) B_s(\alpha, |S_T^{out}|)}{A_p(\alpha, |S_T^{out}|) - B_p(\alpha, |S_T^{out}|)} \\ &\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} (\alpha + k_i - j)^{-1} + \left(\frac{|S_T^{in}|}{n} + \frac{|S_T^{out}|}{n} - 1 \right) \sum_{j=1}^{T-k_i} \left(\alpha \frac{|S_T^{in}|}{n} + \alpha \frac{|S_T^{out}|}{n} - \alpha + T - k_i - j \right)^{-1} \\ &= - |S_T^{in}| (n^{-1} |S_T^{in}| + n^{-1} |S_T^{out}|) \frac{\widetilde{A}_p(\alpha, |S_T^{out}|) A_s(\alpha, |S_T^{out}|)}{\widetilde{A}_p(\alpha, |S_T^{out}|) - \widetilde{B}_p(\alpha, |S_T^{out}|)} \\ &\quad + |S_T^{in}| (n^{-1} |S_T^{in}| + n^{-1} |S_T^{out}| - 1) \frac{\widetilde{B}_p(\alpha, |S_T^{out}|) B_s(\alpha, |S_T^{out}|)}{\widetilde{A}_p(\alpha, |S_T^{out}|) - \widetilde{B}_p(\alpha, |S_T^{out}|)} \\ &\quad + \sum_{i \in S_T^{in}} \sum_{j=1}^{k_i} (\alpha + k_i - j)^{-1} + \left(\frac{|S_T^{in}|}{n} + \frac{|S_T^{out}|}{n} - 1 \right) \sum_{j=1}^{T-k_i} \left(\alpha \frac{|S_T^{in}|}{n} + \alpha \frac{|S_T^{out}|}{n} - \alpha + T - k_i - j \right)^{-1} \end{aligned} \tag{8}$$

$$\begin{aligned}
\frac{\partial l(\alpha, |S_T^{out}|)}{\partial |S_T^{out}|} &= -n^{-1}\alpha |S_T^{in}| \frac{A_p(\alpha, |S_T^{out}|)A_s(\alpha, |S_T^{out}|) - B_p(\alpha, |S_T^{out}|)B_s(\alpha, |S_T^{out}|)}{A_p(\alpha, |S_T^{out}|) - B_p(\alpha, |S_T^{out}|)} \\
&\quad + n^{-1}\alpha \sum_{i \in S_T^{in}} \sum_{j=1}^{T-k_i} \left(\alpha \frac{|S_T^{in}|}{n} + \alpha \frac{|S_T^{out}|}{n} + T - k_i - j \right)^{-1} \\
&= -n^{-1}\alpha |S_T^{in}| \frac{\widetilde{A}_p(\alpha, |S_T^{out}|)A_s(\alpha, |S_T^{out}|) - \widetilde{B}_p(\alpha, |S_T^{out}|)B_s(\alpha, |S_T^{out}|)}{\widetilde{A}_p(\alpha, |S_T^{out}|) - \widetilde{B}_p(\alpha, |S_T^{out}|)} \\
&\quad + n^{-1}\alpha \sum_{i \in S_T^{in}} \sum_{j=1}^{T-k_i} \left(\alpha \frac{|S_T^{in}|}{n} + \alpha \frac{|S_T^{out}|}{n} + T - k_i - j \right)^{-1}
\end{aligned} \tag{9}$$

where

$$\begin{aligned}
A_p(\alpha, |S_T^{out}|) &:= \prod_{j=1}^T (n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| + T - j) \\
A_s(\alpha, |S_T^{out}|) &:= \sum_{j=1}^T (n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| + T - j)^{-1} \\
B_p(\alpha, |S_T^{out}|) &:= \prod_{j=1}^T (n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| - \alpha + T - j) \\
B_s(\alpha, |S_T^{out}|) &:= \sum_{j=1}^T (n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| - \alpha + T - j)^{-1}
\end{aligned}$$

and

$$\begin{aligned}
\widetilde{A}_p(\alpha, |S_T^{out}|) &:= \prod_{j=1}^T \left(1 - \frac{j}{n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| + T} \right) \\
\widetilde{B}_p(\alpha, |S_T^{out}|) &:= \prod_{j=1}^T \left(1 - \frac{j + \alpha}{n^{-1}\alpha |S_T^{in}| + n^{-1}\alpha |S_T^{out}| + T} \right)
\end{aligned}$$

2 Simulation results

We simulate capture-recapture procedure to produce $d_{i(T)}$ as follows:

1. Set the true population size to N , sample size at each capture to n and number of captures to T .
2. Set the true parameters α and β .
3. Draw N values from $\pi \sim \text{Beta}(\alpha, \beta)$.
4. Normalise π_i by dividing by the sum $\sum_{i=1}^N \pi_i$.
5. At each replication $t = 1, \dots, T$:

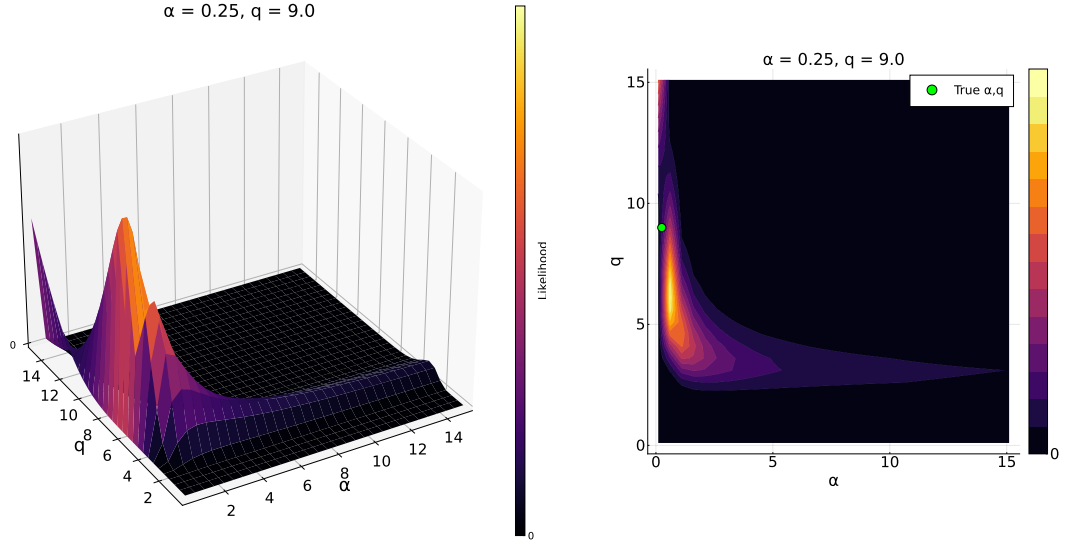


Figure 1: Likelihood function for data simulated by $\pi \sim \text{Beta}(1, 4)$, $N = 100$, $n = 25$, $T = 2$

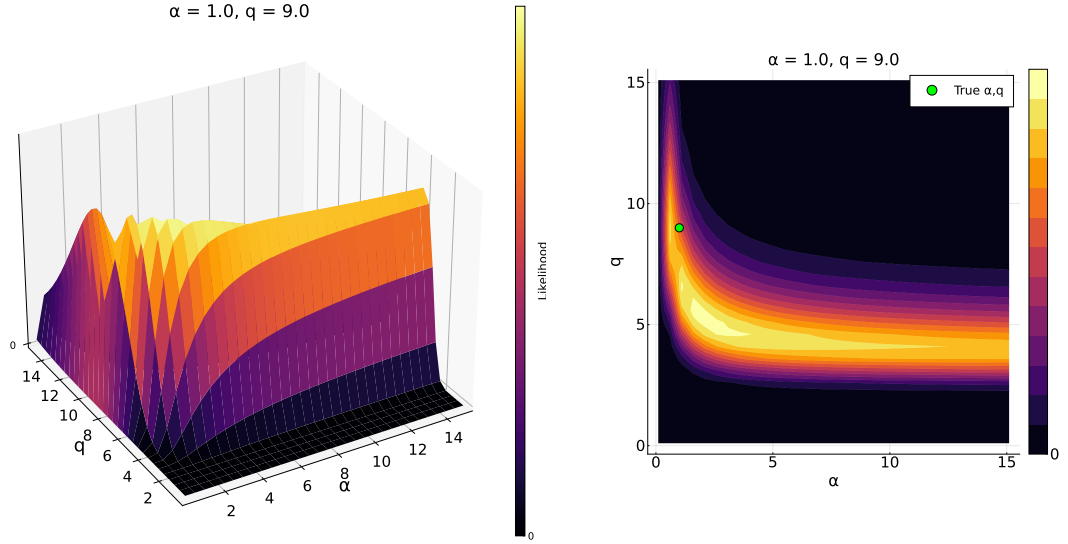


Figure 2: Likelihood function for data simulated by $\pi \sim \text{Beta}(1, 1)$, $N = 100$, $n = 25$, $T = 2$

- Draw a sample of n numbers from $\{1, \dots, N\}$. Denote with s_t .
- For each $i \in s_t$, increment $d_{i(T)}$ by 1. If $d_{i(T)}$ was never recorded before set $d_{i(T)} = 1$.

Once we acquire $d_{i(T)}$, it is possible to calculate the exact likelihood using (3) multiplied by the product of binomial coefficients $\binom{T}{k_i}$. Figures 1-3 show surface and contour plots of the likelihood function for data simulated using different true α, β at parameter values $\{0.1, 0.6, \dots, 15.1\}$. The population size was set to 100, two samples of size 25 were drawn.

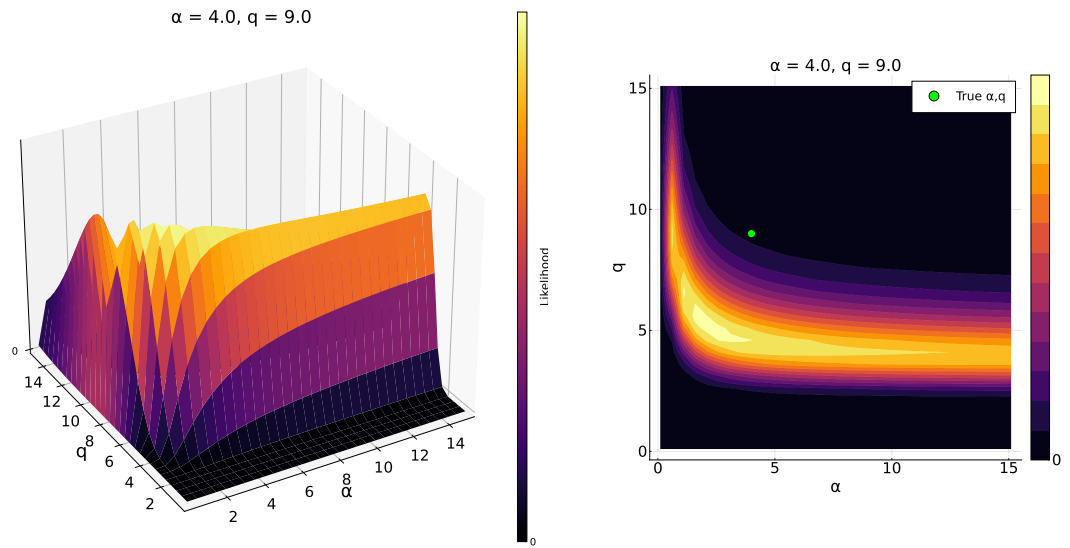


Figure 3: Likelihood function for data simulated by $\pi \sim \text{Beta}(4, 1)$, $N = 100$, $n = 25$, $T = 2$