

# Recursive Estimation in Capture-Recapture Methods

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## التقدير الشرطي المتكرر لمجموعة حيوانية

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خلاصة : هذا المقال يعالج مسألة مهمة في الإحصاء البيئي وهي مسألة حساب تعداد الحيوان . الطريقة المستعملة تفسر كالتالي : تؤخذ عينة عشوائية من المجموعة الحيوانية وتميز بإشارة خاصة ثم يطلق سراحها لتتضمن لبقية القطيع . وبعد فترة تؤخذ عينة عشوائية من القطيع ككل ويحصى منها الأفراد المميزين بالإشارة الخاصة ومن هذه المعلومات تستعمل طرق تغيير القياس لتقدير التوزيع الشرطي المتكرر لهذه المجموعة الحيوانية .

ABSTRACT: An important problem in statistical ecology is how to determine the size of an animal population. The best known technique is the capture-recapture technique. A random sample of individuals is captured, tagged in some way and released back into the population. After allowing time for the marked and unmarked individuals to mix sufficiently, a second random sample is taken and the marked ones are observed. Using measure change techniques, we estimate recursively conditional distributions of various quantities.

**Key Words:** Capture Recapture, measure change, unnormalized conditional distributions, parameter estimation, Gaussian noise.

Hidden Markov Models (Elliott *et al*, 1995) have been used extensively in such areas as Engineering, Computer Science, Communications, Medical Imaging etc. In this paper we are using measure change techniques to estimate the hidden number of individuals in an animal population using partial information provided by the so-called capture-recapture technique.

A random sample of individuals are captured, tagged or marked in some way, and then released back into the population. After allowing time for the marked and unmarked individuals to mix sufficiently, a second simple random sample is taken and the marked ones are observed.

At epoch  $l$  write  $N_l$  for the population size,  $m_l$  for the number of marked and released individuals,  $\bar{n}_k = \sum_{l=1}^k m_l$  for the total number of captured and marked individuals up to time  $k$ ,  $M_l$  for the sample size,  $n_l$  for the number of available marked individuals for sampling and  $y_l$  for the number of captured (or recaptured) marked individuals.

Recursive estimation and Maximum Posterior estimators are discussed.

The model proposed in Section 2 (see autoregressive equation 1 below) leads to recursions for the unnormalized conditional probability distribution of the hidden number of individual which involves integrations. However the model proposed in Section 3 (a finite state Markov chain) leads to finite dimensional filters involving only finite summations. Finally the case where tags could be lost between samples is discussed and a Martingale 'noise' present in Markov chains is replaced by a Gaussian noise as suggested by (Krichagina *et al*, 1985).

### A First Model

All random variables are defined initially on a probability space  $(\Omega, F, P)$ . All the filtrations defined here will be assumed to be complete.

Write  $G_k = \sigma(N_l, n_l, y_l, M_l, l \leq k)$ , and  $y_k = \sigma(y_l, l \leq k)$ . We assume here that

1. The population size  $N$  follow the dynamics:

$$N_k = N_{k-1} + s(N_{k-1})v_k \quad (1)$$

$N_0$  has distribution  $\pi_0$  and  $v_k$  is a sequence of independent random variables with densities  $\phi_k$ .

2. The  $n_k$  are random variables with conditional binomial distributions with parameters

$p_k = p(\tilde{n}_k, y_1, \dots, y_k, \theta)$  and  $\tilde{n}_k$ . For example

$$\begin{aligned} p_1 &= \frac{\theta m_1}{m_1} = \theta \\ p_2 &= \frac{\theta m_2 + \theta^2 m_1}{m_1 + m_2} = \frac{\theta m_2 + \theta^2 m_1}{\tilde{n}_2}, \dots \\ p_k &= \frac{\sum_{i=1}^k m_i \theta^{k-i+1}}{\tilde{n}_k} = \frac{\tilde{n}_{k-1}}{\tilde{n}_k} \theta p_{k-1} + \theta \frac{m_k}{\tilde{n}_k}. \end{aligned} \quad (2)$$

$0 < \theta \leq 1$  is a parameter assumed to be known or it is to be estimated. The powers of  $\theta$  express our belief that as time goes by early marked individuals are becoming less and less available for recapture due to various causes including deaths, emigration, etc.

If the number of captured and marked individuals  $\tilde{n}_k$  is kept constant (2) takes the form:

$$p_k(\theta) = \frac{k-1}{k} p_{k-1} + \frac{\theta^k}{k}.$$

3. The observed random variable  $y_k$  is assumed to have a conditional binomial distribution:

$$p(y_k = m | G_{k-1}, N_k, M_k) = \binom{M_k}{m} \left( \frac{n_k}{N_k} \right)^m \left( 1 - \frac{n_k}{N_k} \right)^{M_k - m}$$

Define  $\lambda_0 = 1$ . For  $l \geq 1$  and for suitable density functions  $\psi_l$  write:

$$\lambda_l = \frac{s(N_{l-1})\Psi_l(N_l)}{\phi_l(v_l)} \frac{1}{2^{M_l \cdot \tilde{n}_l}} p_l^{-n_l} (1-p_l)^{-\tilde{n}_l \cdot n_l} \left( \frac{n_l}{N_l} \right)^{y_l} \left( 1 - \frac{n_l}{N_l} \right)^{y_l - M_l}$$

and  $\Lambda_k = \prod_{l=0}^k \lambda_l$

LEMMA 2.1: The process  $\Lambda_k$  is a G-martingale

PROOF:  $E[\Lambda_k | G_{k-1}] = \Lambda_{k-1} E[\lambda_k | G_{k-1}]$ , so we must show that  $E[\lambda_k | G_{k-1}] = 1$ .

$$\begin{aligned} E[\lambda_k | G_{k-1}] &= E \left[ \frac{s(N_{k-1})\Psi_k(N_k)}{\phi_k(v_k)} \frac{1}{2^{M_k \cdot \tilde{n}_k}} \left( \frac{n_k}{N_k} \right)^{y_k} \left( 1 - \frac{n_k}{N_k} \right)^{y_k - M_k} p_k^{-n_k} (1-p_k)^{-\tilde{n}_k \cdot n_k} | G_{k-1} \right] \\ &= \frac{1}{2^{M_k \cdot \tilde{n}_k}} E \left[ \frac{s(N_{k-1})\Psi_k(N_k)}{\phi_k(v_k)} p_k^{-n_k} (1-p_k)^{-\tilde{n}_k \cdot n_k} E \left[ \left( \frac{n_k}{N_k} \right)^{y_k} \left( 1 - \frac{n_k}{N_k} \right)^{y_k - M_k} | G_{k-1}, N_k, n_k, M_k \right] | G_{k-1} \right] \\ &= \frac{1}{2^{M_k \cdot \tilde{n}_k}} E \left[ \frac{s(N_{k-1})\Psi_k(N_k)}{\phi_k(v_k)} p_k^{-n_k} (1-p_k)^{-\tilde{n}_k \cdot n_k} \sum_{m=0}^{M_k} \binom{M_k}{m} | G_{k-1} \right] \\ &= \frac{1}{2^{\tilde{n}_k}} E \left[ \frac{s(N_{k-1})\Psi_k(N_k)}{\phi_k(v_k)} p_k^{n_k} (1-p_k)^{-\tilde{n}_k \cdot n_k} E \left[ \left( \frac{n_k}{N_k} \right)^{y_k} \left( 1 - \frac{n_k}{N_k} \right)^{y_k - M_k} | G_{k-1} \right] \right] \\ &= E \left[ \frac{s(N_{k-1})\Psi_k(N_{k-1} + s(N_{k-1})v_k)}{\phi_k(v_k)} | G_{k-1} \right] \\ &= \int \frac{s(N_{k-1})\Psi_k(N_{k-1} + s(N_{k-1})v)}{\phi_k(v)} \phi_k(v) dv = \int \Psi_k(u) du = 1 \end{aligned}$$

A new probability measure  $Q$  can be defined by setting  $dQ/dP|_{G_k} = \Lambda_k$ . The point here is that:

LEMMA 2.2: Under the new probability measure  $Q$ ,  $N_k$ ,  $n_k$  and  $y_k$  are three sequences of independent random variables which are independent of each other. Further,  $N_k$  has density  $\psi_k$ ,  $n_k$  has distribution bin  $(\tilde{n}_k, \frac{1}{2})$  and  $y_k$  has distribution bin  $(M_k, \frac{1}{2})$ .

PROOF: For any integrable real-valued functions  $f$ ,  $g$  and  $h$  and using a version of Bayes' theorem (see Elliott *et al*, 1995) we can write:

$$\begin{aligned}
 E_Q[f(N_k)g(n_k)h(y_k)|G_{k-1}] &= \frac{E[f(N_k)g(n_k)h(y_k)\Lambda_k|G_{k-1}]}{E[\Lambda_k|G_{k-1}]} \\
 &= E[f(N_k)g(n_k)h(y_k)\lambda_k|G_{k-1}] \\
 &= E[f(N_k)g(n_k)h(y_k) \frac{s(N_{k-1})\psi_k(N_k)}{\phi_k(v_k)} \frac{1}{2^{\tilde{n}_k}} p_k^{-n_k} (1-p_k)^{-\tilde{n}_k-n_k} \\
 &\quad \left. E\left[h(y_k) \frac{1}{2^{M_k}} \binom{n_k}{N_k}^{-y_k} \left(1 - \frac{n_k}{N_k}\right)^{y_k-M_k} | G_{k-1}, N_k, n_k, M_k\right] | G_{k-1} \right] \\
 &= E[f(N_k)g(n_k)h(y_k) \frac{s(N_{k-1})\psi_k(N_k)}{\phi_k(v_k)} \frac{1}{2^{\tilde{n}_k}} p_k^{-n_k} (1-p_k)^{-\tilde{n}_k-n_k} \\
 &\quad \left[ \sum_{m=0}^{M_k} h(m) \binom{n_k}{N_k}^m \left(1 - \frac{n_k}{N_k}\right)^{-m-M_k} \binom{M_k}{m} \frac{1}{2^{M_k}} \binom{n_k}{N_k}^{-m} \left(1 - \frac{n_k}{N_k}\right)^{m-M_k} \right] \\
 &= E\left[f(N_k)g(n_k)h(y_k) \frac{s(N_{k-1})\psi_k(N_k)}{\phi_k(v_k)} \frac{1}{2^{\tilde{n}_k}} p_k^{-n_k} (1-p_k)^{-\tilde{n}_k-n_k} \right. \\
 &\quad \left. \left[ \sum_{m=0}^{M_k} h(m) \binom{M_k}{m} \frac{1}{2^{M_k}} \right] | G_{k-1} \right] \\
 &= E_Q[h(y_k)] E\left[f(N_k)g(n_k) \frac{s(N_{k-1})\psi_k(N_k)}{\phi_k(v_k)} \frac{1}{2^{\tilde{n}_k}} (1-p_k)^{-\tilde{n}_k-n_k} | G_{k-1} \right] \\
 &= E_Q[h(y_k)] E_Q[g(n_k)] E\left[f(N_{k-1}+v_k) \frac{s(N_{k-1})\psi_k(N_{k-1}+s(N_{k-1})v_k)}{\phi_k(v_k)} | G_{k-1} \right] \\
 &= E_Q[h(y_k)] E_Q[g(n_k)] \int f(N_{k-1}+s(N_{k-1})v) s(N_{k-1})\psi_k(N_{k-1}+s(N_{k-1})v) dv \\
 &= E_Q[h(y_k)] E_Q[g(n_k)] \int f(u)\psi_k(u) du \\
 &= E_Q[h(y_k)] E_Q[g(n_k)] E_Q[f(N_k)]
 \end{aligned}$$

That is, under  $Q$  the three processes are independent sequences of random variables with the desired distributions.

Using this fact we derive a recursive equation for the unnormalized conditional distribution of  $N_k$  given  $y_k$ . For any measurable test function  $f$  consider:

$$E[f(N_k)|Y_k] = \frac{E_Q[f(N_k)\Lambda_k^{-1}|Y_k]}{E_Q[\Lambda_k^{-1}|y_k]} \quad (3)$$

The denominator of (3) being a normalizing factor we focus only on the expectation under  $Q$  in the numerator. Write

$$E_Q[f(N_k)\Lambda_k^{-1}|Y_k] = \int f(z)q_k(z)dz. \quad (4)$$

In view of Lemma 2.2 the left hand side of (4) is:

$$\begin{aligned}
 &= E_{\mathcal{Q}}[f(N_k)\Lambda_{k-1}^{-1}\lambda_k^{-1}|Y_k] \\
 &= 2^{\tilde{n}_k} E_{\mathcal{Q}} \left[ \sum_{i=0}^{\tilde{n}_k} \int f(z) \left(\frac{i}{z}\right)^{\gamma_k} \left(1-\frac{i}{z}\right)^{M_k-\gamma_k} \frac{\Phi_k\left(\frac{z-N_{k-1}}{s(N_{k-1})}\right)}{s(N_{k-1})\Psi_k(z)} \psi_k(z) \right. \\
 &\quad \left. p_k^i (1-p_k)^{\tilde{n}_k-i} dz \frac{1}{2^{\tilde{n}_k}} \binom{\tilde{n}_k}{i} \Lambda_{k-1}^{-1} |Y_k \right] \\
 &= 2^{M_k} \sum_{i=0}^{\tilde{n}_k} \int \int f(z) \left(\frac{i}{z}\right)^{\gamma_k} \left(1-\frac{i}{z}\right)^{M_k-\gamma_k} \frac{\Phi_k\left(\frac{z-u}{s(u)}\right)}{s(u)} \\
 &\quad p_k^i (1-p_k)^{\tilde{n}_k-i} \binom{\tilde{n}_k}{i} q_{k-1}(u) dz du.
 \end{aligned}$$

Comparing this last expression with the right hand side of (4) we have:

**THEOREM 2.3:** The unnormalized conditional probability density function of the hidden Markov model given by (1) follows the recursions:

$$\begin{aligned}
 q_k(z) &= 2^{M_k} \sum_{i=0}^{\tilde{n}_k} \left(\frac{i}{z}\right)^{\gamma_k} \left(1-\frac{i}{z}\right)^{M_k-\gamma_k} \binom{\tilde{n}_k}{i} \\
 &\quad \cdot p_k^i (1-p_k)^{\tilde{n}_k-i} \int \frac{\Phi_k\left(\frac{z-u}{s(u)}\right)}{s(u)} q_{k-1}(u) du \quad (5)
 \end{aligned}$$

(Note: we take  $0^0 = 1$ ).

**REMARK 2.4:** The normalized conditional density of  $N_k$  is given by  $\frac{q_k(z)}{\int q_k(u) du}$ . The initial

(normalized) probability density of  $N_0$ , prior to sampling, is  $\pi_0(\cdot)$ , so:

$$q_0(z) = \pi_0(z)$$

$$\begin{aligned}
 q_1(z) &= 2^{M_1} \sum_{i=0}^{\tilde{n}_1} \left(\frac{i}{z}\right)^{\gamma_1} \left(1-\frac{i}{z}\right)^{M_1-\gamma_1} \binom{\tilde{n}_1}{i} p_1^i (1-p_1)^{\tilde{n}_1-i} \\
 &\quad \int \frac{\Phi_1\left(\frac{z-u}{s(u)}\right)}{s(u)} \pi_0(u) du \quad (6)
 \end{aligned}$$

and further estimates follow from (8).

If the distribution of  $N_0$  is a delta function concentrated at some number  $A$ , (9) becomes:

$$q_1(z) = 2^{M_1} \sum_{i=0}^{\tilde{n}_1} \left(\frac{i}{z}\right)^{\gamma_1} \left(1-\frac{i}{z}\right)^{M_1-\gamma_1} \binom{\tilde{n}_1}{i} p_1^i (1-p_1)^{\tilde{n}_1-i} \frac{\Phi_1\left(\frac{z-A}{s(A)}\right)}{s(A)} \quad (7)$$

**PARAMETRIC ESTIMATION:** Our model is function of the parameter  $p_k$ , the proportion of the accessible marked individuals at epoch  $k$ . Suppose  $p_k$  has dynamics given by (2). We also assume that  $\theta$  will take values in some measurable space  $(\Theta, \beta, \gamma)$ . We now derive a recursive joint conditional unnormalized distribution for  $N_k$  and  $\theta$ . We keep working under the probability measure  $\mathcal{Q}$ .

**THEOREM 2.5:** Write

$q_k(z, \theta) dz d\theta = E_{\mathcal{Q}}[f(N_k \in dz, \theta \in d\theta) \Lambda_k^{-1} | Y_k]$ . Then:

$$\begin{aligned}
 q_k(z, \theta) &= 2^{M_k} \sum_{i=0}^{\tilde{n}_k} \left(\frac{i}{z}\right)^{\gamma_k} \left(1-\frac{i}{z}\right)^{M_k-\gamma_k} p_k^i(\theta) (1-p_k(\theta))^{\tilde{n}_k-i} \binom{\tilde{n}_k}{i} \\
 &\quad \cdot \int \frac{\Phi_k\left(\frac{z-u}{s(u)}\right)}{s(u)} q_{k-1}(u, \theta) du \quad (8)
 \end{aligned}$$

**PROOF:** Let  $f, g$  be integrable test functions.

$$E_{\mathcal{Q}}[f(N_k)g(\theta)\Lambda_k^{-1}|y_k] = \int \int f(z)g(v)q_k(z, v) dz d\gamma(v). \quad (9)$$

Using the independence assumption under  $\mathcal{Q}$  the left hand side of (12) is:

$$\begin{aligned}
 &= E_{\mathcal{Q}}[f(N_k)g(\theta)\Lambda_{k-1}^{-1}\lambda_k^{-1}|Y_k] \\
 &= 2^{M_k} E_{\mathcal{Q}} \left[ \sum_{i=0}^{\tilde{n}_k} \int \int f(z)g(v) \left(\frac{i}{z}\right)^{\gamma_k} \left(1-\frac{i}{z}\right)^{M_k-\gamma_k} \frac{\Phi_k\left(\frac{z-N_{k-1}}{s(N_{k-1})}\right)}{s(N_{k-1})\Psi_k(z)} \psi_k(z) \right. \\
 &\quad \left. \cdot p_k^i(v) (1-p_k(v))^{\tilde{n}_k-i} dz d\gamma(v) \binom{\tilde{n}_k}{i} \Lambda_{k-1}^{-1} |Y_k \right] \\
 &= 2^{M_k} \left[ \sum_{i=0}^{\tilde{n}_k} \int \int \int f(z)g(v) \left(\frac{i}{z}\right)^{\gamma_k} \left(1-\frac{i}{z}\right)^{M_k-\gamma_k} \frac{\Phi_k\left(\frac{z-u}{s(u)}\right)}{s(u)} \right. \\
 &\quad \left. \cdot p_k^i(v) (1-p_k(v))^{\tilde{n}_k-i} \binom{\tilde{n}_k}{i} q_{k-1}(u, v) dz dud\gamma(v) \right]
 \end{aligned}$$

Comparing this last expression with the right hand side of (9) gives (8). If at time 0,  $\theta$  has density  $h(\theta)$  then:

$$q_1(z, \theta) = 2^{M_1} \sum_{i=0}^{\tilde{n}_1} \left(\frac{i}{z}\right)^{y_1} \left(1 - \frac{i}{z}\right)^{M_1 - y_1} p_1(\theta)^i \left(1 - p_1(\theta)\right)^{\tilde{n}_1 - i} \binom{\tilde{n}_1 - i}{i} h(\theta) \int \frac{\phi_k\left(\frac{z-u}{s(u)}\right)}{s(u)} \pi_0(u) du$$

and further updates are given by Theorem 2.5

If no dynamics enter the population size and  $N_k$  has density  $\phi_k(\cdot)$  independently of  $N_l$ ,  $l < k$ , the recursion in Theorem 2.5 simplifies to:

$$q_k(z, \theta) = \phi_k(z) q_{k-1}(z, \theta) 2^{M_k} \sum_{i=0}^{\tilde{n}_k} \left(\frac{i}{z}\right)^{y_k} \left(1 - \frac{i}{z}\right)^{M_k - y_k} p_k(\theta)^i \left(1 - p_k(\theta)\right)^{\tilde{n}_k - i} \binom{\tilde{n}_k}{i} \quad (10)$$

**MAXIMUM POSTERIOR ESTIMATORS:** Quantity (6) (or 7) is a function of the unknown population size and could be maximized with respect to  $z$  yielding a critical value  $\hat{N}_1$  which is the Maximum Posterior estimate of  $N$  at epoch 1 given  $y_1$ . Similar maximizations at later times will provide Maximum posterior Estimators (MAP) for the population size at these times.

**PATHWISE ESTIMATION:** We now derive a recursive equation, which does not involve any integration, for the unnormalized density of the whole path up to epoch  $k$ . Write

$$q_k(z_0, \dots, z_k) dz_0 \dots dz_k := E_Q [I(z_0 \in dz_0) \dots I(z_k \in dz_k) \Lambda_k^{-1} | Y_k].$$

**THEOREM 2.6:**

$$q_k(z_0, \dots, z_k) = 2^{M_k} \sum_{i=0}^{\tilde{n}_k} \left(\frac{i}{z}\right)^{y_k} \left(1 - \frac{i}{z}\right)^{M_k - y_k} \binom{\tilde{n}_k}{i} p_k^i \left(1 - p_k\right)^{\tilde{n}_k - i} \frac{\phi_k\left(\frac{z_k - z_{k-1}}{s(z_{k-1})}\right)}{s(z_{k-1})} q_{k-1}(z_0, \dots, z_{k-1}) \quad (11)$$

Again we have:

$$q_0(z) = \pi_0(z)$$

$$q_1(z_0, z_1) = 2^{M_1} \sum_{i=0}^{\tilde{n}_1} \left(\frac{i}{z}\right)^{M_1 - y_1} \binom{\tilde{n}_1}{i} p_1^i \left(1 - p_1\right)^{\tilde{n}_1 - i} \frac{\phi_1\left(\frac{z_1 - z_0}{s(z_0)}\right)}{s(z_0)} \pi_0(z_0)$$

and further estimates follow from (11).

However no integration is needed in subsequent recursions.

**MAXIMUM POSTERIOR ESTIMATORS:** Expression (11) is a function of the path  $(z_0, \dots, z_k)$  and could be maximized yielding a critical path  $(\hat{N}_0, \dots, \hat{N}_k)$ . Since no integration is involved here one could substitute, at a time  $k$  say, the sequence of critical values  $\hat{N}_0, \dots, \hat{N}_{k-1}$  and then maximize  $q_k(\hat{N}_0, \dots, \hat{N}_{k-1}, z_k)$  with respect to the variable  $z_k$  to obtain an estimate for  $N_k$ .

## A Second Model

Suppose that on a probability space  $(\Omega, \mathcal{F}, \mathcal{Q})$  are given three sequences of independent random variables  $N_k$ ,  $n_k$  and  $y_k$ . For  $k \in \mathbb{N}$ ,  $N_k$  is uniformly distributed over some finite set  $S = \{s_1, \dots, s_l\} \subset \mathbb{N} - \{0\}$ ,  $n_k$  has a binomial distribution with parameters  $\left(\tilde{n}_k, \frac{1}{2}\right)$  and  $y_k$  has a binomial distribution with parameters  $\left(M_k, \frac{1}{2}\right)$  where  $M_k \in \mathbb{N} - \{0\}$  is given.

We wish to define a new probability measure  $P$  such that  $y_k$  has a binomial distribution with parameters  $\left(M_k, \frac{n_k}{N_k}\right)$ ,  $N_k$  is a Markov chain with state space  $S$  and stochastic matrix  $C = \{c_{ij}\} = P[N_{k+1} = s_j | N_k = s_i]$ ,  $n_k$  are random variables with conditional distributions with parameters  $(p_k, \tilde{n}_k)$ .

Define the G-predictable sequences

$$\alpha'_i = \sum_{j=1}^l I(N_{i-1} = s_j) c_{ij}$$

for  $i = 1, \dots, L$ . In vector notation this is

$$\alpha'_i(N_{i-1}) = C^T I(N_{i-1})$$

where  $I(N_{i-1}) = (I(N_{i-1} = s_1), \dots, I(N_{i-1} = s_l))$

Now write  $\lambda_0 = 1$ ,

$$\hat{\lambda}_i = 2^{M_i - \tilde{n}_i} p_i^{n_i} (1 - p_i)^{\tilde{n}_i - n_i} \left(\frac{n_i}{N_i}\right)^{y_i} \left(1 - \frac{n_i}{N_i}\right)^{M_i - y_i} \prod_{j=1}^i (L A_j)^{I(N_j = s_j)}$$

$$\text{and} \quad \Lambda_k = \prod_{l=0}^k \hat{\lambda}_l$$

The process  $\Lambda_k$  is a G-martingale and a new probability measure  $P$  can be defined by setting  $\frac{dp}{dQ}|_{G_k} = \lambda_k$ .

LEMMA 3.1: Under the probability measure  $P$  the above processes obey the desired dynamics, i.e.  $N_k$  is a Markov chain with state space  $S$  and stochastic matrix  $C$ ,  $y_k$  and  $n_k$  are random variables with conditional binomial distributions with parameters  $(M_k, \frac{n_k}{N_k})$  and  $(p_k, \tilde{n}_k)$  respectively.

PROOF: We give proof only for the first statement regarding  $N_k$ .

$$\begin{aligned}
 P[N_k=s|G_{k-1}] &= E[I(N_k=s)|G_{k-1}] \\
 &= \frac{E_Q[I(N_k=s)\Lambda_k|G_{k-1}]}{E_Q[\Lambda_k|G_{k-1}]} \\
 &= E_Q[I(N_k=s)\lambda_k|G_{k-1}] \\
 &= E_Q[I(N_k=s)2^{M_k \cdot n_k} p_k^{n_k} (1-p_k)^{\tilde{n}_k - n_k} \left(\frac{n_k}{s_j}\right)^{M_k \cdot y_k} L\alpha'_k |G_{k-1}] \\
 &= L\alpha'_k 2^{M_k \cdot n_k} E_Q[I(N_k=s) p_k^{n_k} (1-p_k)^{\tilde{n}_k - n_k} \left(\frac{n_k}{s_j}\right)^{y_k} \left(1 - \frac{n_k}{s_j}\right)^{M_k \cdot y_k} |G_{k-1}] \\
 &= \alpha'_k L 2^{M_k \cdot n_k} \frac{1}{L} \sum_{n=0}^{\tilde{n}_k} \sum_{m=0}^{M_k} \binom{M_k}{m} \left(\frac{n}{s_j}\right)^m \left(1 - \frac{n}{s_j}\right)^{m \cdot m} \frac{1}{2^{M_k}} \\
 &\quad \left(\frac{\tilde{n}_k}{n}\right) p_k^n (1-p_k)^{\tilde{n}_k - n} \frac{1}{2^{M_k}} \\
 &= \alpha'_k = P[N_k=s|N_{k-1}].
 \end{aligned}$$

Working under the probability measure  $Q$ , we derive recursive equations for the unnormalized conditional probability distribution of  $N_k$ . Write

$$\begin{aligned}
 P[N_k=s_j|Y_k] &= E[I(N_k=s_j)|Y_k] \\
 &= \frac{E_Q[I(N_k=s_j)\Lambda_k|Y_k]}{E_Q[\Lambda_k|Y_k]}
 \end{aligned}$$

and  $q_k^{s_j} = E_Q[I(N_k=s_j)\Lambda_k|Y_k]$ .

THEOREM 3.2:

$$\begin{aligned}
 q_k^{s_j} &= 2^{M_k} \sum_{n=0}^{\tilde{n}_k} \binom{n}{s_j}^{y_k} \left(1 - \frac{n}{s_j}\right)^{M_k \cdot y_k} \left(\frac{\tilde{n}_k}{n}\right) p_k^n (1-p_k)^{\tilde{n}_k - n} \\
 &\quad \cdot \sum_{j=1}^L c_{y_j} q_{k-1}^{s_j} \quad (12)
 \end{aligned}$$

If at time 0,  $q_0 = \pi = (\pi_1, \dots, \pi_L)$

$$q_1^{s_j} = 2^{M_1} \sum_{n=0}^{\tilde{n}_1} \binom{n}{s_j}^{y_1} \left(1 - \frac{n}{s_j}\right)^{M_1 \cdot y_1} \left(\frac{\tilde{n}_1}{n}\right) p_1^n (1-p_1)^{\tilde{n}_1 - n} \sum_{j=1}^L c_{y_j} \pi_j \quad (13)$$

If  $N_0 = s_a$  with probability one:

$$q_1^{s_j} = 2^{M_1} \sum_{n=0}^{\tilde{n}_1} \binom{n}{s_j}^{y_1} \left(1 - \frac{n}{s_j}\right)^{M_1 \cdot y_1} \left(\frac{\tilde{n}_1}{n}\right) p_1^n (1-p_1)^{\tilde{n}_1 - n} c_{j,a} \quad (14)$$

and further updates are given by (12).

MAP estimators of  $N_1, \dots, N_k$  are provided by:

$$\begin{aligned}
 \hat{N}_1 &= \arg \max \{q_1^{s_1}, q_1^{s_2}, \dots, q_1^{s_L}\}, \dots, \\
 \hat{N}_k &= \arg \max \{q_k^{s_1}, q_k^{s_2}, \dots, q_k^{s_L}\}.
 \end{aligned}$$

RECURSIVE PARAMETER ESTIMATION: The previous model is a function of the parameters  $p_k$  and  $C = c_{ij}$ . Let  $R = p_k(\theta_1)$  and  $C = C(\theta_2) = c_{ij}(\theta_2)$  and  $\theta = (\theta_1, \theta_2)$ . Suppose  $\theta$  belongs to some measurable space  $(\Theta, \beta, \gamma)$ .

Working again under the probability measure  $Q$  write

$$q_k^{s_j}(\theta) d\theta = E_Q[I(N_k=s_j)I(\theta \in d\theta)\Lambda_k | Y_k]$$

THEOREM 3.3:

$$\begin{aligned}
 q_k^{s_j}(\theta) &= 2^{M_k} \sum_{n=0}^{\tilde{n}_k} \binom{n}{s_j}^{y_k} \left(1 - \frac{n}{s_j}\right)^{M_k \cdot y_k} \left(\frac{\tilde{n}_k}{n}\right) p_k^n(\theta) \\
 &\quad \cdot (1-p_k(\theta))^{\tilde{n}_k - n} \sum_{j=1}^L c_{y_j}(\theta) q_{k-1}^{s_j}(\theta)
 \end{aligned}$$

If  $\theta_1$  has density  $h(\cdot)$  and  $\theta_2$  has density  $g(\cdot)$ :

$$\begin{aligned}
 q_1^{s_j}(\theta) &= 2^{M_1} \sum_{n=0}^{\tilde{n}_1} \binom{n}{s_j}^{y_1} \left(1 - \frac{n}{s_j}\right)^{M_1 \cdot y_1} \left(\frac{\tilde{n}_1}{n}\right) p_1^n(\theta_1) \\
 &\quad \cdot (1-p_1(\theta_1))^{\tilde{n}_1 - n} h(\theta_1) g(\theta_2) \sum_{j=1}^L c_{y_j}(\theta_2) \pi_j
 \end{aligned}$$

**A Tags Loss Model**

In this section we propose a model where the marks or tags are not permanent. In this situation the marking is done using double tagging where each individual is marked with two tags. For simplicity we assume that the two tags on each individual are nondistinguishable and that individuals can retain or lose their tags independently.

We start again with a probability space  $(\Omega, F, Q)$  on which are given two sequences of independent random variables  $N_k$  and  $y_k$ . For  $k \in \mathbb{N}$ ,  $N_k$  is uniformly distributed over some finite set  $S = \{s_1, \dots, s_L\} \subset \mathbb{N} - \{0\}$ , and  $y_k$  has a trinomial distribution with parameters  $\left(M_k, \frac{1}{3}\right)$  where  $M_k \in \mathbb{N} - \{0\}$  is given.

At any epoch  $l$  each individual in the population is in any of three states, namely unmarked, marked with only one tag, or marked with two tags which states we shall call 0, 1, 2 respectively. We suppose that each individual behaves like an independent time homogenous Markov chain with transition matrix  $\{p_{ij}\}$ .

At each time  $l$  the population size  $N_l$  is distributed or partitioned into three groups  $N_l(2)$ ,  $N_l(1)$ , and  $N_l(0) = N_l - N_l(2) - N_l(1)$  among the three states and we would like to define the set of all such partitions as the states of a three dimensional Markov chain  $(N_l(0), N_l(1), N_l(2))$ . Recall that at each epoch  $l$ ,  $0 \leq N_l(2), N_l(1) \leq \tilde{n}_l$ .

$$P_{(i_0, i_1, i_2), (j_0, j_1, j_2)} = P[(N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2) | (N_{k-1}(0), N_{k-1}(1), N_{k-1}(2)) = (j_0, j_1, j_2)]$$

Write and for any real numbers  $x_0, x_1, x_2$  define the function

$$F(x_0, x_1, x_2, j_0, j_1, j_2) = \left(\sum_{l=0}^2 p_{l0} x_l\right)^{j_0} \left(\sum_{l=0}^2 p_{l1} x_l\right)^{j_1} \left(\sum_{l=0}^2 p_{l2} x_l\right)^{j_2}$$

Then  $p(j_0, j_1, j_2, i_0, i_1, i_2)$  is the coefficient of  $x_0^{i_0} x_1^{i_1} x_2^{i_2}$  in  $F(x_0, x_1, x_2, j_0, j_1, j_2)$ .

We wish to define a new probability measure  $P$  such that  $y_k$  has a conditional trinomial distribution with parameters  $\left(M_k, \frac{N_k(0)}{N_k}, \frac{N_k(1)}{N_k}, \frac{N_k(2)}{N_k}\right)$ ,  $N_k$  is a Markov chain

with state space  $S$  and stochastic matrix  $C = \{c_{ij}\}$ . The Markov chain  $(N_l(0), N_l(1), N_l(2))$  is the same under both probability measures.

$$\alpha_l^j = \sum_{j'=1}^L I(N_{l-1}=s_{j'}) c_{j'j}, j=1, \dots, L.$$

Define again the G-predictable sequences. Now write  $\lambda_0 = 1$ ,

$$\lambda_l = 3^{M_l} \left(\frac{N_l(0)}{N_l}\right)^{y_l(0)} \left(\frac{N_l(1)}{N_l}\right)^{y_l(1)} \left(\frac{N_l(2)}{N_l}\right)^{y_l(2)} \prod_{i=1}^L (L \alpha_i)^{I(N_l=s_i)}$$

and 
$$\Lambda_k = \prod_{l=0}^k \lambda_l$$

The process  $\Lambda_k$  is a G-martingale and a new probability measure  $P$  can be defined by setting  $\frac{dP}{dQ}|_{G_k} = \Lambda_k$ . It can be checked that under  $P$  the above processes have the desired distributions. Working under the probability measure  $Q$ , we derive recursive equations for the unnormalized conditional joint probability distribution of  $N_k$  and  $(N_k(0), N_k(1), N_k(2))$ . Write

$$\begin{aligned} P[N_k = s_r, (N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2) | Y_k] &= E[I(N_k = s_r) I((N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2)) | Y_k] \\ &= \frac{E_Q[I(N_k = s_r) I((N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2)) \Lambda_k | Y_k]}{E_Q[\Lambda_k | Y_k]} \end{aligned}$$

and

$$q_k(s_r, i_1, i_2) = E_Q[I(N_k = s_r, N_k(2) = i_2, N_k(1) = i_1, N_k(0) = s_r - i_1 - i_2) \Lambda_k | Y_k].$$

It can be shown that  $q_k(S_l, i_1, i_2)$  is given by the following recursions:

**THEOREM 4.1:**

$$\begin{aligned} q_k(s_r, i_1, i_2) &= 3^{M_k} \left(\frac{s_r - i_1 - i_2}{s_r}\right)^{y_k(0)} \left(\frac{i_1}{s_r}\right)^{y_k(1)} \left(\frac{i_2}{s_r}\right)^{y_k(2)} \sum_{j=1}^L c_{ij} \\ &\cdot \sum_{j_1, j_2=0}^{\tilde{n}_{k-1}} P_{(s_r - i_1 - i_2, j_1, j_2), (s_r, j_1, j_2)} q_{k-1}(s_r, j_1, j_2) \end{aligned}$$

The expected value of  $N_k$  given the observations  $Y$  is given by:

$$E[N_k|Y_k] = \frac{\sum_{i=1}^L s_i \sum_{i_1+i_2=0}^{\tilde{n}_k} q_k(s_i, i_1, i_2)}{\sum_{i=1}^L \sum_{i_1+i_2=0}^{\tilde{n}_k} q_k(s_i, i_1, i_2)}$$

Another way of looking at the problem is by considering only the subpopulation of tagged individuals in the definition of the Markov chain  $(N_k(0), N_k(1), N_k(2))$ . In this case the state space is the set of all the partitions of the totality of tagged individuals into three groups: the one with two tags, the ones with one tag and the ones who lost both tags. Hence we write the total number of tagged individuals as  $\tilde{n}_k = \tilde{n} = N_k(2) + N_k(1) + N_k(0)$ . Note that, when sampling, we cannot observe directly members belonging to the group of individuals who lost their two tags as they become undistinguishable from the unmarked ones in the sample.

Now we assume that under  $Q$  the observation process is multinomial with parameters  $(M_k, \frac{1}{4})$

and under  $P$  it is (conditional) multinomial with

$$\text{parameters } \left( M_k, \frac{N_k(0)}{N_k}, \frac{N_k(1)}{N_k}, \frac{N_k(2)}{N_k}, \frac{N_k(u)}{N_k} \right).$$

Here  $N_k(u)$  is the number of unmarked individuals in the population. Again note that  $N_k(u)$  is not  $N_k(0)$ . Given  $y_k(1), y_k(2)$ , the unobserved component  $y(0)$ , under the probability measure  $Q$ , is binomial with parameters

$$(M_k - y_k(1) - y_k(2), \frac{1}{2}).$$

Write

$$\begin{aligned} P[N_k = s_i, (N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2) | Y_k] \\ = E[I(N_k = s_i) I((N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2)) | Y_k] \\ = \frac{E_Q[I(N_k = s_i) I((N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2)) \Lambda_k | Y_k]}{E_Q[\Lambda_k | Y_k]} \end{aligned}$$

and

$$\begin{aligned} q_k(s_i, i_0, i_1, i_2) &= E_Q[I(N_k = s_i) I((N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2)) \Lambda_k | Y_k] \\ &= E_Q[I(N_k = s_i) I((N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2)) 4^{M_k} \left(\frac{i_0}{s_i}\right)^{y_k(0)} \\ &\quad \cdot \left(\frac{i_1}{s_i}\right)^{y_k(1)} \left(\frac{i_2}{s_i}\right)^{y_k(2)} \left(\frac{i_2}{s_i}\right)^{y_k(u)} L \sum_{j=1}^L I(N_{k-1} = s_j) c_j \Lambda_{k-1} | Y_k] \\ &= 4^{M_k} \left(\frac{i_1}{s_i}\right)^{y_k(1)} \left(\frac{i_2}{s_i}\right)^{y_k(2)} \\ &\quad \cdot E_Q \left[ \left(\frac{i_0}{s_i}\right)^{y_k(0)} \left(\frac{s_i - i_2 - i_1 - i_0}{s_i}\right)^{M_k - y_k(2) - y_k(1) - y_k(0)} \right. \\ &\quad \cdot \sum_{j=1}^L I(N_{k-1} = s_j) c_j I((N_k(0), N_k(1), N_k(2)) = (i_0, i_1, i_2)) \\ &\quad \cdot \left. \sum_{j_0, j_1, j_2 = \tilde{n}} I((N_{k-1}, N_{k-1}(1), N_{k-1}(2)) = (j_0, j_1, j_2)) \Lambda_{k-1} | Y_k \right] \\ &= 4^{M_k} \left(\frac{i_1}{s_i}\right)^{y_k(1)} \left(\frac{i_2}{s_i}\right)^{y_k(2)} \\ &\quad \cdot E_Q \left[ \sum_{m=0}^{M_k - y_k(2) - y_k(1)} \left(\frac{i_0}{s_i}\right)^m \left(\frac{s_i - i_2 - i_1 - i_0}{s_i}\right)^{M_k - y_k(2) - y_k(1) - m} \right. \\ &\quad \cdot \binom{M_k - y_k(2) - y_k(1)}{m} \left(\frac{1}{2}\right)^{M_k - y_k(2) - y_k(1)} \sum_{j=1}^L I(N_{k-1} = s_j) c_j \\ &\quad \cdot \left. P_{(i_0, i_1, i_2)(j_0, j_1, j_2)} \Lambda_{k-1} | Y_k \right] \end{aligned}$$



Using the definition of  $q$  we have:

THEOREM 4.2:

$$q_k(s_i, i_0, i_1, i_2) = 2^{M_k \cdot y_k(1) + y_k(2)} \left(\frac{i_1}{s_i}\right)^{y_k(1)} \left(\frac{i_2}{s_i}\right)^{y_k(2)} \sum_{m=0}^{M_k - y_k(2) - y_k(1)} \left(\frac{i_0}{s_i}\right)^m \cdot \left(\frac{s_i - i_2 - i_1 - i_0}{s_i}\right)^{M_k - y_k(2) - y_k(1) - m} \binom{M_k - y_k(2) - y_k(1)}{m} \cdot \sum_{j=1}^l c_{ij} \sum_{j_0, j_1, j_2 = \bar{n}} P_{(i_0, i_1, i_2)(j_0, j_1, j_2)} q_{k-1}(s_j, j_0, j_1, j_2)$$

**Gaussian Noise Approximation**

An approximate but simpler form of the recursion in Theorem 4.2 is to use a suggestion proposed by [2] where the martingale increment “noise” present in the representation of a Markov chain is replaced by Gaussian noise. To this effect, let’s identify, as it is explained in [1], the three states 0, 1, 2 with the standard unit (column) vectors  $e_1, e_2, e_3$  of  $\mathbb{R}^3$ . Write  $X_k^n \in \{e_1, e_2, e_3\}$  for the state of the  $n$ -th individual at time,  $k, 1 \leq n \leq \bar{n}$ . Then each individual behaves like a Markov chain on  $(\Omega, F, P)$  with transition matrix  $P$ .

Define  $X_k = \frac{1}{\bar{n}} \sum_{n=1}^{\bar{n}} X_k^n$ . Then

$$X_k = P X_{k-1} + M_k \tag{15}$$

where  $M_k$  is a martingale increment. The suggestion made in [2] is to replace the martingale increment  $M_k$  in (15) by an independent Gaussian random variable  $G_k$  of mean 0 and covariance matrix  $E[M_k M_k^T]$  whose density is denoted by  $\phi_k$ .

That is, the signal process  $x_k$ , taking values in  $\mathbb{R}^3$ , has dynamics

$$x_k = P x_{k-1} + v_k \tag{16}$$

We assume that under  $Q$  the observation process is multinomial with parameters  $\left(M_k, \frac{1}{4}\right)$ ,  $x_k$  has density  $\phi_k$  and  $N_k$  uniformly distributed over the set  $(s_1, \dots, s_L)$ . Under the ‘real world’ probability measure  $P$ ,  $N_k$  is a Markov chain with transition matrix  $C$ ,  $x_k$  has dynamics (16) and  $y_k$  has conditional probability distribution given

$$P[y_k = y_k(2) + y_k(1) + y_k(0) + y_k(u) | M_k, N_k = s_i, x_k = (x_0, x_1, x_2), N_k(u) = s_i - x_2 - x_1 - x_0] = \binom{M_k}{y_k(2), y_k(1), y_k(0), y_k(u)} \left(\frac{x_0}{s_i}\right)^{y_k(1)} \cdot \left(\frac{x_2}{s_i}\right)^{y_k(2)} \left(\frac{x_1}{s_i}\right)^{y_k(1)} \left(\frac{s_i - x_2 - x_1 - x_0}{s_i}\right)^{M_k - y_k(2) - y_k(1) - y_k(0)}$$

$P$  is defined in terms of  $Q$  using the G-martingale

$$\Lambda_k = \prod_{l=0}^k 4^{M_l} \binom{x_l(0)}{N_l}^{y_l(0)} \binom{x_l(1)}{N_l}^{y_l(1)} \binom{x_l(2)}{N_l}^{y_l(2)} \cdot \left(\frac{x_2}{s_l}\right)^{y_l(2)} \left(\frac{x_1}{s_l}\right)^{y_l(1)} \left(\frac{s_l - x_2 - x_1 - x_0}{s_l}\right)^{M_k - y_k(2) - y_k(1) - y_k(0)}$$

Nest theorem is the analog of Theorem 4.2

THEOREM 5.1: The unnormalized joint conditional probability distribution of  $N_k$  and  $x_k$ ,  $E_Q[I(N_k = s_i) I(x_k \in dx) \Lambda_k | y_k] =: q_k^{s_i}(x) dx$ , is given recursively as follows:

$$q_k^{s_i}(x) = 2^{M_k \cdot y_k(2) + y_k(1)} \left(\frac{x_1}{s_i}\right)^{y_k(1)} \left(\frac{x_2}{s_i}\right)^{y_k(2)} \sum_{m=0}^{M_k - y_k(2) - y_k(1)} \left(\frac{x_0}{s_i}\right)^m \cdot \left(\frac{s_i - x_2 - x_1 - x_0}{s_i}\right)^{M_k - y_k(2) - y_k(1) - m} \binom{M_k - y_k(2) - y_k(1)}{m} \cdot \sum_{j=0}^l L c_{ij} \int \phi_k(x - P u) q_{k-1}^{s_j}(u) du$$

**Acknowledgements**

R.J. Elliott wishes to acknowledge support of the Natural Sciences and Engineering Research Council of Canada, grant A7964.

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Received 13 October 1997  
 Accepted 15 June 1998