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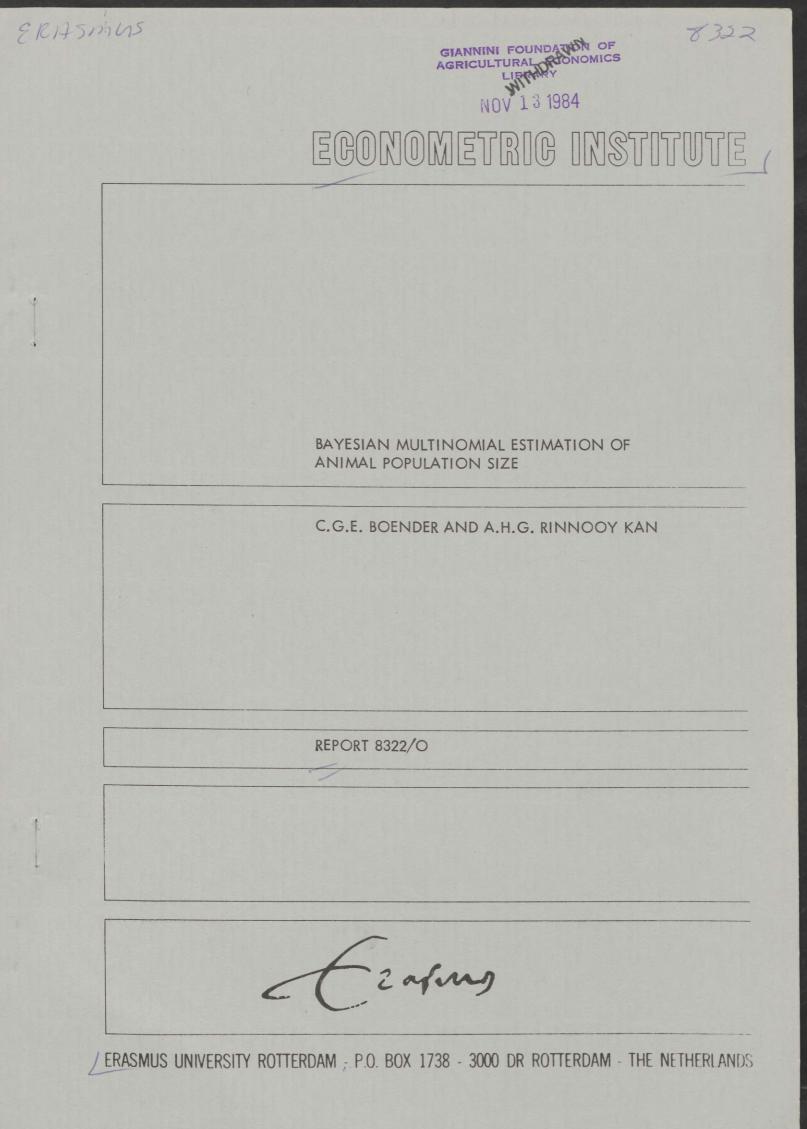
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BAYESIAN MULTINOMIAL ESTIMATION OF ANIMAL POPULATION SIZE

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Summary

This paper deals with the problem of estimating the size k of a closed animal population from data obtained by sampling one animal at a time, which is marked and then immediately returned to the population. It is assumed that conditional on a capture, each animal i (i=1,...,k) has a fixed probability θ_i of being the victim $(\theta_1 + \ldots + \theta_k = 1)$, which need not be equal for all animals. Since a trapped animal is immediately put back, the above assumption implies that the result of a sequence of captures follows a multinomial distribution with an unknown number of cells which is equal to the population size k, and unknown cell probabilities which correspond to the catch probabilities $\theta_1, \ldots, \theta_k$ of the animals in the population. This observation is used to derive a Bayesian method to estimate the population method is tested on a fictive population of k = 500 animals with equal catch probabilities $\theta_i = 1/500$ (i=1,...,k), as well as on a sample from a population of butterflies.

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Keywords: Closed population; Population size estimation; Bayesian inference; Multinomial distribution with unknown number of cells.

1. Introduction

We consider the problem of estimating the size of a population from capturerecapture data. For a review on the available methods in this field and an extensive bibliography, see the recent book by Seber [1982].

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Our approach differs from the existing ones by assuming that, given a capture, each animal of the population of size k has a probability θ_i (i=1,...,k) of being the sampled one, where $\theta_1 + \ldots + \theta_k = 1$. These catch probabilities are further assumed to remain fixed in the course of the experiment. Obviously these assumptions require that the animals are taken one at a time, and, after being marked, are immediately returned to the population. Note that we do not make further assumptions about the catch probabilities such as, for example, $\theta_i = \theta_j$ (i,j=1,...,k) which is required by most other estimation methods in this area.

The above assumptions imply that the result of a number of captures follows a multinomial distribution with an unknown number of cells which is equal to the population size, and with unknown cell probabilities which are equal to the catch probabilities of the animals.

In [Zielinski 1981; Boender & Zielinski 1982; Boender & Rinnooy Kan 1983] Bayesian estimates of the parameters of a multinomial distribution with an unknown number of cells are derived under the a priori assumption that each number of cells in the interval $[1,\infty)$ is equiprobable, and that, given a population size k, the cell probabilities θ_i (i=1,...,k) are uniformly distributed on the unit simplex $\theta_1 + \ldots + \theta_k = 1$. In this paper the results obtained in these papers are applied to the estimation of population size. However, the Bayesian estimate of the population size is derived here under the assumption of an arbitrary discrete prior distribution for the population size and a Dirichlet distribution with equal parameters $\alpha > 0$ for the catch probabilities. If we choose $\alpha = 1$ then the Dirichlet is equal to the uniform distribution on the unit simplex. For $\alpha > 1$ the Dirichlet is increasingly concentrated in the neighbourhood of $\theta_i = 1/k$ (i=1,...,k). Finally if $0 < \alpha < 1$, then more probability mass is located in the corners of the simplex $\theta_1 + \dots + \theta_k = 1$. Section 5, which contains a numerical example, will show that especially the introduction of the hyperparameter α which has to be chosen by the user, has in important effect on the quality of the estimates. In Section 2 the multinomial distribution with an unknown number of cells is examined. The prior distribution is described in Section 3, and the posterior results are derived in Section 4. Section 5 concludes the paper with some numerical examples.

2. The multinomial model

We consider the problem of estimating the size of a closed animal population, given that the animals are captured, marked, and then immediately returned to the population. In Section 1, we observed that, given a number of captures, the result obtained is a sample of a multinomial distribution whose cells correspond to the animals of the population: the number of cells of the distribution is equal to the population size, and the cell probabilities are equal to the catch probabilities of the animals. Hence, if

- k = the population size,
- θ_i = the catch probability of animal i (i=1,...,k),
- n = the number of captures,
- \underline{N}_{i} = the random variable defined as the number of times animal i is sampled in n captures (i=1,...,k),

then

$$Pr_{\left(\theta_{1},\ldots,\theta_{k}\right)}\left\{\left(\underline{N}_{1},\ldots,\underline{N}_{k}\right)=\left(n_{1},\ldots,n_{k}\right)\right\}=\frac{n!}{\prod_{i=1}^{k}n_{i}!}\prod_{i=1}^{k}\theta_{i}^{n_{i}}.$$
(2.1)

Since we do not know to which probability θ_i (i=1,...,k) a caught animal corresponds, it is impossible to use (2.1) directly to obtain statistical estimates about the population size. If, for example, in three captures one animal has been observed once, and another twice, it is impossible to distinguish the individual events $(n_1,n_2) = (1,2)$, $(n_1,n_2) = (2,1)$, $(n_1,n_2,n_3) = (1,0,2)$, $(n_1,n_2,n_3,n_4,n_5) = (0,1,0,2,0)$ etc. A possible solution to this problem is to define <u>aggregates</u> of the individual events, so that for each sample outcome we do know exactly to which aggregate it belongs.

To arrive at such aggregates, let

 \underline{W}_n = the number of different observed animals in n captures, $\overline{\underline{N}_i}$ = the number of times an observed animal is sampled in n captures

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$$(i=1,\ldots,\underline{W}_n, \sum_{i=1}^{\underline{W}_n} \overline{\underline{N}}_i = n).$$

The outcome of the n captures now corresponds to the set $\{\overline{N}_1, \ldots, \overline{N}_W, M_n\}$. To calculate the probability that this outcome is equal to $\{\overline{n}_1, \ldots, \overline{n}_W\}$ $(\overline{n}_i > 0, \Sigma_{i=1}^W \overline{n}_i = n)$, let

 h_j = the number of \overline{n}_i 's that are equal to j (j=1,...,n), $S_k[w]$ = the set of all permutations of w different elements from {1,...,k}.

The required probability is then given by

$$Pr_{\left(\theta_{1},\ldots,\theta_{k}\right)}\left\{\left\{\underline{\overline{N}}_{1},\ldots,\underline{\overline{N}}_{\underline{W}}\right\}\right\} = \left\{\overline{n}_{1},\ldots,\overline{n}_{w}\right\}\right\} =$$

$$= \frac{1}{\prod_{j=1}^{n} h_{j}!} \frac{n!}{\prod_{i=1}^{w} \overline{n}_{i}!} \sum_{\left(g_{1},\ldots,g_{w}\right) \in S_{k}\left[w\right]} \prod_{i=1}^{w} \theta_{g_{i}}^{n_{i}},$$

$$(2.2)$$

which, considered as a function of $k, \theta_1, \ldots, \theta_k$, is our likelihood function.

It is easily seen from (2.2) that the maximum likelihood estimate for the population size k is equal to ∞ for all possible outcomes $\{\overline{n}_1, \ldots, \overline{n}_w\}$. We therefore adopt a Bayesian procedure in which the unknown population size k, and the catch probabilities $\theta_1, \ldots, \theta_k$ are assumed to be themselves random variables $\underline{K}, \underline{\theta}_1, \ldots, \underline{\theta}_K$, for which a prior distribution can be specified. Given the outcome of a number of captures, we then use Bayes theorem to compute the posterior distribution of the unknowns, which obviously incorporates both the prior beliefs about $k, \theta_1, \ldots, \theta_k$, and the sample information $\{\overline{n}_1, \ldots, \overline{n}_w\}$. Next an optimal estimate of the population size is computed from the posterior distribution estimate.

3. Prior distribution

For the population size \underline{K} we will assume an arbitrary discrete prior distribution, i.e.

$$\Pr\{\underline{K}=k\} = \psi_{l} \quad \text{for } k \in [l, u] \cap \mathbb{N}^{\dagger}, \tag{3.1}$$

where the hyperparameters $\ell, u, \psi_{\ell}, \dots, \psi_{u}$ have to be chosen by the user. The posterior distribution will also be given for the special case of (3.1) where each integer population size in the interval $[\ell, u] = [1, \infty)$ is equiprobable. (This choice, of course, amounts to an improper prior distribution).

Given <u>K</u> = k, the catch probabilities $\underline{\Theta}_1, \dots, \underline{\Theta}_K$ are a priori assumed to follow a k-dimensional Dirichlet distribution with parameters $\alpha_i = \alpha > 0$ (i=1,...,k):

$$\Pr\{(\underline{\Theta}_{1},\ldots,\underline{\Theta}_{k}) = (\theta_{1},\ldots,\theta_{k}) | \underline{K}=k\} = \frac{(\alpha k-1)!}{[(\alpha-1)!]^{k}} \prod_{i=1}^{k} \theta_{i}^{\alpha-1}, \sum_{i=1}^{k} \theta_{i}^{a}=1. \quad (3.2)$$

To gain some intuition about (3.2), note that for $\alpha_i = \alpha = 1$ it corresponds to the uniform distribution on the (k-1)-dimensional unit simplex $\theta_1 + \ldots + \theta_k = 1$. For $\alpha \neq 1$ the Dirichlet distribution is symmetric around the centre of gravity $\theta_i = 1/k$ (i=1,...,k) of the simplex. For $\alpha > 1$ the distribution attains a unique maximum at this centre, whose relative size increases if α gets larger. For $0 < \alpha < 1$ the distribution attains a unique minimum in the centre, and is infinitely large in the k vertices of the simplex. If α gets smaller, then the minimum decreases and more probability mass is concentrated in the corners of the simplex. Note that the fact that for $0 < \alpha < 1$ the probability mass is equally concentrated in all the corners of the simplex is in accordance with our assumption that, for any sampled animal, we do not know to which of the probabilities θ_i (i=1,...,k) it corresponds. This assumption does force us to restrict ourselves to a Dirichlet prior distribution with equal parameters.

The expected value E, and standard deviation σ of the $\underline{\Theta}_i$'s are given by [Wilks 1962]

$$E\{\underline{\Theta}_{\underline{i}} | \underline{K}=k\} = \frac{1}{k} \quad (\underline{i}=1,\ldots,k), \qquad (3.3)$$

$$\sigma\{\underline{\Theta}_{i} | \underline{K}=k\} = \sqrt{\frac{k-1}{\alpha k+1}} \cdot \frac{1}{k} \quad (i=1,\ldots,k)$$

$$\approx \frac{1}{\sqrt{\alpha \cdot k}} \quad (\text{for } \alpha \text{ large})$$

$$\approx \frac{1}{\sqrt{k}} \quad (\text{for } \alpha \text{ small})$$
(3.4)

The user is asked to choose a positive value for α . If he or she thinks that the catch probabilities are approximately equal, then α should be chosen larger than or equal to 1. If the user has an a priori belief that, given a population size k, the catch probabilities differ substantially from 1/k and are located in the corner of the simplex, then α should be chosen in the interval (0,1). In view of (3.3) and (3.4) the user has the freedom, by choosing $\alpha \neq 1$, to specify a smaller or larger standard deviation from the expected equal catch probabilities than the one corresponding to the uniform distribution on the simplex $\theta_1 + \ldots + \theta_k = 1$.

Since

$$\Pr\{(\underline{\Theta}_1, \dots, \underline{\Theta}_{\underline{K}}) = (\theta_1, \dots, \theta_k)\} = \Pr\{(\underline{\Theta}_1, \dots, \underline{\Theta}_k) = (\theta_1, \dots, \theta_k) | \underline{K} = k\} \Pr\{\underline{K} = k\}$$
(3.5)

our (joint) prior distribution now follows by multiplication of (3.1) and (3.2).

4. Posterior results

Theorem 1. Posterior distribution of the population size K:

$$\Pr\{\underline{K}=k \mid \{\underline{\overline{N}}_{1}, \dots, \underline{\overline{N}}_{W}\} = \{\overline{n}_{1}, \dots, \overline{n}_{W}\} = \frac{\psi_{k} \frac{(\alpha k-1)!}{(n+\alpha k-1)!} \frac{k!}{(k-w)!}}{\sum_{m=\max\{w, k\}}^{u} \psi_{m} \frac{(\alpha m-1)!}{(n+\alpha m-1)!} \frac{m!}{(m-w)!}}, \quad (4.1)$$

 $k \in [max{w,l}, u].$

<u>Proof</u> Application of Bayes' theorem to the likelihood function (2.2) and the prior distribution (3.5) yields

$$\Pr\{\underline{K}=k \mid \{\underline{\overline{N}}_{1}, \dots, \underline{\overline{N}}_{\underline{W}_{n}}\} = \{\overline{n}_{1}, \dots, \overline{n}_{W}\}\}$$

$$= \frac{\psi_{k} \cdot \frac{(\alpha k-1)!}{[(\alpha-1)!]^{k}} \sum_{(g_{1}, \dots, g_{W}) \in S_{k}[w]} \int \dots \int_{I_{k-1}} \pi_{i=1}^{w} \theta_{g_{i}}^{\overline{n}_{i}} \pi_{i=1}^{k} \theta_{i}^{\alpha-1}}{\sum_{m=max\{w, k\}}^{u} \psi_{m} \frac{(\alpha m-1)!}{[(\alpha-1)!]^{m}} \sum_{(g_{1}, \dots, w) \in S_{m}[w]} \int \dots \int_{I_{m-1}} \pi_{i=1}^{w} \omega_{g_{i}}^{n_{i}} \pi_{i=1}^{m} \theta_{i}^{\alpha-1} \pi_{i=1}^{m} d\omega_{i}}$$

$$(4.2)$$

where \boldsymbol{I}_{i} denotes the i-dimensional unit simplex. We observe that

$$\frac{(n+\alpha m-1)!}{\prod_{i=1}^{W}(n_{i}+\alpha-1)![(\alpha-1)!]^{m-w}} \prod_{i=1}^{W} \theta_{g_{i}}^{m_{i}} \prod_{i=1}^{m} \theta_{i}^{\alpha-1}$$
(4.3)

is an m-dimensional Dirichlet distribution with parameters $\overline{n}_1 + \alpha, \dots, \overline{n}_w + \alpha, \alpha, \dots, \alpha$, so that (4.2) simplifies to

$$\frac{\psi_{k} \frac{(\alpha k-1)!}{[(\alpha-1)!]^{k}} \sum_{(g_{1},\dots,g_{w})\in S_{k}[w]} \frac{\prod_{i=1}^{w} (\overline{n}_{i}+\alpha-1)! [(\alpha-1)!]^{k-w}}{(n+\alpha k-1)!}}{\sum_{m=\max\{w, k\}}^{u} \psi_{m} \frac{(\alpha m-1)!}{[(\alpha-1)!]^{m}} \sum_{(g_{1},\dots,g_{w})\in S_{m}[w]} \frac{\prod_{i=1}^{w} (\overline{n}_{i}+\alpha-1)! [(\alpha-1)!]^{m-w}}{(n+\alpha m-1)!}}{(n+\alpha m-1)!}}$$

$$(4.4)$$

$$= \frac{\psi_{k}(\alpha k-1)! \sum_{(g_{1},\ldots,g_{w}) \in S_{k}[w]} \frac{1}{(n+\alpha k-1)!}}{\sum_{m=\max\{w,\ell\}}^{u} \psi_{m}(\alpha m-1)! \sum_{(g_{1},\ldots,g_{w}) \in S_{m}[w]} \frac{1}{(n+\alpha m-1)!}}$$

$$=\frac{\psi_{k} \frac{(\alpha k-1)!}{(n+\alpha k-1)!} \frac{k!}{(k-w)!}}{\sum_{m=\max\{w,k\}}^{u} \psi_{m} \frac{(\alpha m-1)!}{(n+\alpha m-1)!} \frac{m!}{(m-w)!}}$$

From Theorem 1 we easily obtain the posterior expectation of the population size, which is well known to be the optimal Bayesian estimator under a

quadratic loss function:

$$\mathbb{E}\{\underline{K} \mid \{\underline{\overline{N}}_{1}, \dots, \underline{\overline{N}}_{\underline{W}_{n}}\} = \{\overline{n}_{1}, \dots, \overline{n}_{w}\} = \frac{\sum_{k=\max\{w, \ell\}}^{u} k \cdot \psi_{k} \cdot \frac{(\alpha k-1)!}{(n+\alpha k-1)!} \cdot \frac{k!}{(k-w)!}}{\sum_{m=\max\{w, \ell\}}^{u} \psi_{m} \frac{(\alpha m-1)!}{(n+\alpha m-1)!} \frac{m!}{(m-w)!}}$$
(4.5)

and its standard deviation

$$\sigma\{\underline{K}|\underline{\overline{N}}_{1},\ldots,\underline{\overline{N}}_{W}\} = \{\overline{n}_{1},\ldots,\overline{n}_{W}\} =$$
(4.6)

$$\begin{bmatrix} \sum_{k=\max\{w,\ell\}}^{u} k^{2}\psi_{k} \frac{(\alpha k-1)!}{(n+\alpha k-1)!} \frac{k!}{(k-w)!} \\ \sum_{m=\max\{w,\ell\}}^{u} \psi_{m} \frac{(\alpha m-1)!}{(n+\alpha m-1)!} \frac{m!}{(m-w)!} \end{bmatrix} - \begin{pmatrix} \sum_{k=\max\{w,\ell\}}^{u} k\psi_{k} \frac{(\alpha k-1)!}{(n+\alpha k-1)!} \frac{k!}{(k-w)!} \\ \sum_{m=\max\{w,\ell\}}^{u} \psi_{m} \frac{(\alpha m-1)!}{(n+\alpha m-1)!} \frac{m!}{(m-w)!} \end{pmatrix} \end{bmatrix}$$

Note that the posterior distribution of <u>K</u>, and a fortiori its expected value and standard deviation, do not depend on the values $\overline{n_1}, \dots, \overline{n_w}$, but only on the realization of <u>W</u>_n. Thus, with respect to the populaiton size, all the sample information is incorporated in the number of different animals observed .

Although the formulae (4.1), (4.5) and (4.6) do not look easy, they can very efficiently be computed by considering the relations between successive terms. Conditional on any observed result (n,w), the posterior expected population size, for example, requires $(4\alpha+3)(u-\max\{w,\ell\})$ multiplications. Thus, even if α is chosen very large, say equal to 100, then $(4\alpha+3)(u-\max\{w,\ell\}) \approx 400,000$ multiplications suffice. Further, if the upperbound u is chosen to be very large with respect to the real population size, then for all formulae (4.1), (4.5) and (4.6) the terms will ultimately get negligibly small. Since the tail of the posterior distribution of <u>K</u> is monotonic, the computations can be stopped as soon as this point is reached.

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For the special case that l=1, $u=\infty$, $\psi_i=\psi_j(i, j=1, 2, ...)$, $\alpha=1$ (i.e., the case that for the population size k each positive integer value is a priori assumed equiprobable, and that, given <u>K</u>=k, the catch probabilities follow a uniform distribution on the unit simplex), (4.5) and (4.6) are especially simple to evaluate. Then we have [Boender & Rinnooy Kan 1983]

$$\Pr\{\underline{K}=k \mid \{\underline{\overline{N}}_{1}, \dots, \underline{\overline{N}}_{W}_{n}\} = \{\overline{n}_{1}, \dots, \overline{n}_{W}\} = \frac{(k-1)!k!(n-1)!(n-2)!}{w!(w-1)!(n-w-2)!(n+k-1)!(k-w)!} (n \ge w+2)$$

(4.7)

$$\mathbb{E}\{\underline{K} \mid \{\underline{\overline{N}}_{1}, \dots, \underline{\overline{N}}_{W}_{M}\} = \{\overline{n}_{1}, \dots, \overline{n}_{W}\} = W \frac{n-1}{n-W-2} \quad (n \ge W+3), \qquad (4.8)$$

$$\sigma\{\underline{K} \mid \{\underline{\overline{N}}_{1}, \dots, \underline{\overline{N}}_{\underline{W}}\} = \{\overline{n}_{1}, \dots, \overline{n}_{w}\}\} = \left(\frac{w(w+1)(n-1)(n-2)}{(n-w-2)^{2}(n-w-3)}\right)^{\frac{1}{2}} \quad (n \ge w+4). \quad (4.9)$$

As a result of the improperness of the prior distribution of the population size, the above posterior results can only be evaluated if at least 2 different animals have been sampled.

5. Numerical example

In this Section we will first consider a fictive population of k = 500 animals with equal catch probabilities $\theta_i = 1/500$ (i=1,...,k). Table 1 for a number of captures n shows the expected number of different animals which will be sampled in the course of these n trials if the animals are taken one at a time from the above population and then immediately put back. Next, given a prior distribution on the assumed unknown parameters of the population, Table 2 shows the posterior the expectation E, the standard deviation σ and a 95% posterior credible interval C₉₅ of the unknown population size.

Table 1

Sampling results on a population with k = 500 animals with equal catch probabilities $\theta_i = 1/500$ (i=1,...,k).

Number of	captures n	Expected number of dif	ferent
		animals observed w	
50		47	
75		69	
100		90	
150		129	
250		197	
500		316	
1,000		433	

Table 2

Baysesian estimation results for a population of k = 500 animals with equal catch probabilities $\theta_i = 1/500$ (i=1,...,500)

Table 2A

Prior distribution : $\alpha = 100$; $\ell = 100$; u = 1000; $\psi_i = \frac{1}{901}$ (i=100,...,1000)

n	W	E	σ	°C ₉₅
50	47	544	217	[205,963]
75	69	552	184	[250,929]
100	90	548	157	[283,879]
150	129	530	111	[337,758]
250	197	522	63	[406,649]
500	316	506	27	[455,561]
1000	433	503	11	[483,527]

Table 2B

Prior distribut	ion : $\alpha =$	100; $\& = 1, u =$	2500; $\psi_{i} = \frac{1}{2500}$	(i=1,,2500)
n	W	E	σ	C ₉₅
50	47	796	503	[150,1913]
75	69	640	319	[211,1290]
100	9 0	574	204	[266,976]
150	129	531	114	[336,761]
250	197	522	63	[406,649]
500	316	506	27	[455,561]
1000	433	503	11	[483,527]

Table 2C

		l = 1; u = 2500;		
n	W	Е	σ	C ₉₅
50	47	1198	550	[2// 2205]
75	69	1149	459	[344,2305]
100	90	1093	371	[492, 1870]
150	129	1011	237	[603,1489]
250	197	961	136	[712,1235]
500	316	866	64	[744,995]
1000	433	765	32	[703,830]
			2	

т	a	b	1	e	2	2	D

P

rior distributio?	$\alpha = 1;$	$\ell = 1; u = \infty; \psi_i$	$= \psi_j$ (i, j=)	1,2,)
n	W	E	σ	с ₉₅
50	47	2203		[220,6455]
75	69	1276	737	[375,2629]
100	90	1113	421	[481,1939]
150	129	1011	238	[603,1490]
250	197	961	136	[712,1235]
500	316	866	64	[744,995]
1000	433	765	32	[703,830]

The table shows that the prior distributions for which $\alpha = 100$, that is, whose probability mass is heavily concentrated in the neighbourhood of the true parameters of the populaiton, yield precise estimates if at least 10 different animals have been sampled. Also, for $\alpha = 100$, the posterior 95% credible interval always contains the true value of the population size. The table further shows that the quality of the estimation results is far more sensitive to a proper specification of α than to the choice of the a priori range [ℓ ,u] for the size of the population. If $\alpha = 1$, i.e. high a priori probability is given to vectors of unequal catch probabilities, then, since the true catch probabilities of the animals in the population actually are equal, the method (as expected) seriously overestimates the true value of the population size. Of course, if we would have tested the method on a population of animals with unequal catch probabilities, the situation would have been reversed: prior distributions with large values for α would lead to underestimation, and priors with a small value for α would yield more precise estimates.

We conclude with a practical example. [Craig 1953] studied a population of butterflies (Colias eurytheme) by sampling the butterflies one at a time, and observed w = 341 different ones in n = 435 captures.

Assuming that

 (i) all animals have the same probability p_n of being caught in the n-th trial, and

(ii) for any individual the events of being caught in the i-th trial

(i=l,...,n) are independent,

then (see also [Seger 1982]) the maximum likelihood estimate M is the solution of

 $(1 - \frac{W}{M}) = (1 - \frac{1}{M})^n$.

For the population of butterflies, this yields a maximum likelihood of M = 854 butterflies. Under the a priori assumption $[\pounds, u] = [1, 2500], \ \psi_1 = \frac{1}{2500}$ (1=1,...,2500), and $\alpha = 100$ our Bayesian method yields a posterior expectation for the population size E = 876 (σ =78; C₉₅=[730,1033]) which, of course, is very close to the maximum likelihood estimate assuming equal catch probabilities p_n . However, if we assume a priori that $[\pounds, u] = [1, 2500], \alpha = 1$, i.e. each subset of the simplex $\theta_1 + \ldots + \theta_k = 1$ with equal volume is thought to contain the true vector of catch probabilities ($\theta_1, \ldots, \theta_k$) with equal probability, then our estimate is E = 1626 (σ =168; C₉₅=[1292,1946]). So, how many butterflies were there?

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