Emily Dennis, Byron Morgan and Martin Ridout

The N-mixture model

Data

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Multivariate Poisson model

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## N-mixture models

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## Stats Lab, Cambridge, 1973



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## What the N-mixture model does

- N-mixture models can estimate animal abundance from a set of counts with both spatial and temporal replication whilst accounting for imperfect detection.
- A benefit of the N-mixture model is the reasonably low cost and effort required for data collection compared to alternative sampling methods.
  - Applies for many citizen-science based monitoring programs.
  - Highly cited paper: Royle(2004, *Biometrics*).
- Many extensions exist, including
  - The use of covariates to examine spatial patterns in abundance and detection.
  - The creation of maps of spatial abundance.

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## Basic Data

## Point count data for American redstart

	Sample									
Site	1	2	3	4	5	6	7	8	9	10
1	0	0	0	1	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	1	0	0	0	0	0	0	0	0	0
4	0	1	1	3	1	2	2	1	0	1
5	2	0	1	1	0	0	1	0	0	0

Results in an estimated expected number of 2.81, when 50 sites are sampled.

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## Forming the likelihood

A set of counts is made during t = 1, ..., T sampling occasions at i = 1, ..., R sites of a closed population.

- Each individual has the same detection probability, p.
- The counts *n<sub>it</sub>* at site *i* and time *t* are

$$n_{it} \sim \operatorname{Bin}(N_i, p),$$

where  $N_i$  is the unknown population size at site *i*.

• Assuming  $N_i$  to be independent random variables with probability function  $f(N; \theta)$ , such as Poisson or negative binomial, the likelihood is

$$L(p,\theta; \{n_{it}\}) = \prod_{i=1}^{R} \left\{ \sum_{N=\max_{t}n_{it}}^{\infty} \left( \prod_{t=1}^{T} \operatorname{Bin}(n_{it}; N, p) \right) f(N; \theta) \right\}$$

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## To infinity and beyond

A set of counts is made during t = 1, ..., T sampling occasions at i = 1, ..., R sites of a closed population.

- Each individual has the same detection probability, p.
- The counts *n<sub>it</sub>* at site *i* and time *t* are

$$n_{it} \sim \operatorname{Bin}(N_i, p),$$

where  $N_i$  is the unknown population size at site *i*.

 Assuming N<sub>i</sub> to be independent random variables with probability function f(N; θ), such as Poisson or negative binomial, the likelihood is

$$L(p,\theta;\{n_{it}\}) = \prod_{i=1}^{R} \left\{ \sum_{N=\max_{t}n_{it}}^{K} \left( \prod_{t=1}^{T} \operatorname{Bin}(n_{it};N,p) \right) f(N;\theta) \right\}$$

## • Requires selection of a value, K, for $\infty$ .

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## Computer packages

- PRESENCE
- unmarked

Both of these have a default value for K. As we shall see, this can be dangerous. It would be nice to avoid having to choose K, and we now show how this can be done.

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## Equivalence with the multivariate Poisson model

- The N-mixture model is equivalent to the multivariate Poisson with a particular covariance structure.
- The equivalence can be illustrated via comparison of probability generating functions.
- Here we illustrate the bivariate Poisson model (T = 2).

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## The bivariate Poisson

• Consider *T* = 2 and counts *n*<sub>1</sub> and *n*<sub>2</sub> for a particular site written as

$$n_1 = X_1 + X_{12}$$
 and  $n_2 = X_2 + X_{12}$ 

- $X_1, X_2 \sim \text{Pois}(\theta_1)$ , where  $\theta_1 = \lambda p(1-p)$ , and  $X_{12} \sim \text{Pois}(\theta_0)$ , where  $\theta_0 = \lambda p^2$ .
- All values are independent.
- Note relationship with capture-recapture: Cormack (1989)
- Then  $(n_1, n_2)$  follow a bivariate Poisson distribution, with  $corr(n_1, n_2) = p$ , and the likelihood is

$$L(p,\lambda;\{n_{it}\}) = e^{-(2\theta_1+\theta_0)} \prod_{i=1}^{R} \left\{ \frac{\theta_1^{n_{i1}+n_{i2}}}{n_{i1}!n_{i2}!} \sum_{m=0}^{\min(n_{i1},n_{i2})} {n_{i1} \choose m} {n_{i2} \choose m} m! \left(\frac{\theta_0}{\theta_1^2}\right)^m \right\}$$



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## Performance of the bivariate Poisson model

- Investigate model performance via simulation.
  - 1000 simulations for λ = 5, p = 0.25 and R = 20.
- In some cases estimates for  $\lambda$  were very large.
  - Associated with small or negative values of the product moment sample correlation.



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# A covariance diagnostic for T = 2

 Negative values of an estimate of the covariance diagnose high estimates of λ.

$$\mathsf{ov}^*(n_1, n_2) = \mathsf{mean}(n_1 * n_2) - \{\mathsf{mean}(n_1 + n_2)\}$$



- Hence in these instances λ̂ is actually infinite (and p̂ = 0) and high estimates are obtained as an artefact of the optimisation routine stopping prematurely when the likelihood is flat.
- Simulations suggest that the diagnostic extends for T > 2.

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# The effect of the choice of K on fitting the N-mixture model

- The infinite values of \$\hat{\lambda}\$ for the bivariate Poisson are limited by the value of K in the N-mixture model.
- unmarked  $K = \max(\text{count}) + 100$ (dotted)
- PRESENCE K = 200 (dashed)
- The model should always be fitted for multiple values of *K*.



covariance diagnostic  $\leq 0$ 

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# Application to Hermann's tortoise data

- Analyse data from a study of the threatened Hermann's tortoise *Testudo hermanni* in southeastern France.
- R=118 sites were each surveyed T=3 times.
- Sample covariance diagnostic suggests stable estimates from the N-mixture model (1.052).
- From the N-mixture model with Poisson mixing distribution  $\hat{\lambda} = 4.70$  and  $\hat{p} = 0.28$ , and were stable for  $K \ge 30$ .
- But the negative binomial model is better, and estimates using the negative binomial distribution do not stabilise for increasing values of *K*.
  - Hence results presented for the negative binomial will vary with *K*.

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## Hermann's tortoise



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## Discussion

- The N-mixture model can produce infinite estimates of abundance.
  - Particularly when the number of sampling occasions and/or sites is limited and detection probability low.
- The equivalence with the multivariate Poisson was used to understand and diagnose this behaviour.
  - Avoids the requirement to select an upper bound K.
- Is there a suitable diagnostic for the Negative Binomial distribution?
- Use R package.
- Note the use of N-mixture for fitting Multivariate Poisson (EM and composite likelihood currently used).

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## Recent work

- Peter Jupp, proving results regarding the diagnostic criterion.
- Takis Besbeas, using Hidden Markov Models to fit N-mixture models, including the Open case. These are fast, but still require specification of K, and multiple such values in the open case.
- Linda Haines, writing the likelihood in terms of a hypergeometric function, and then using recent work on the numerical evaluation of such functions. Speed is comparable to fixing K and using the binomial mixture, but does not require a value for K. A concentrated likelihood allows analytical advance, and investigation of the test criterion.
- Relationship with parameter redundancy.

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