

Individual Heterogeneity in Models of Population Size Under Closure

A Conceptual Overview

Individual heterogeneity is the bane of population size estimation. This brief document attempts to state the problem and outline several conceptual solutions that are now available in program MARK.

The Problem

Clearly animals of a given species vary in their capturability; some are easily caught while others are caught only rarely. These differences are caused by or associated with a host of factors, including differing movements due to the age or sex of the animal, whether the female has young, distance from the animal to the nearest trap, etc. Heterogeneity is omnipresent in animal populations.

Virtually all estimators of population size (N) have a canonical form:

$$\hat{N} = \frac{n}{p},$$

where n is a count (related to the number caught in some group at some point in time) and p is the probability of capture related to the count. If one were to take a strict *random* sample (i.e., avoiding any heterogeneity), one would *expect* the estimator to perform well. In the case of heterogeneity, animals caught tend to be the most catchable, thus the estimate of p is "too high" (overestimated). Thus, the estimates of population size (N) are too low because \hat{p} is in the denominator. This is a general result: if one uses a model that *assumes* equal capturability, the estimates of population size will be too low (underestimated) if, in fact, there is heterogeneity in capture probabilities. This bias is often substantial. Deriving models to allow for heterogeneity has been very difficult.

Note that estimators of survival probabilities are little affected by heterogeneity. Define survival (S) and its estimator,

$$\hat{S} = \frac{\hat{N}_{t+1}}{\hat{N}_t}.$$

Notice if the estimates of population size have approximately the same bias (say, about 20%), then because this bias occurs in both the numerator and denominator, they *tend* to cancel out. This is not to imply that the bias exactly cancels, only that they tend to cancel and thus, the bias in \hat{S} is substantially less than the bias in \hat{N} . Models to estimate survival probabilities can often be based on the homogeneity assumption (i.e., $p_i = p$) and the MLE \hat{S} is quite robust to heterogeneity.

Several attempts have been made to deal effectively with heterogeneity to produce estimators of population size that perform well. The original thrust of this work was to model the heterogeneity in p_i (where i denotes animal i) as a beta distribution. Here, rather than deal with all the individual p_i (there are N of these), one merely estimates α and β , the parameters in the beta distribution. Several people followed this path independently after Ken Burnham looked at this in the late 1960s. The result of this neat approach was that the likelihood function for N was essentially flat and this provided estimates that had very poor properties. Other approaches had to be developed. Three of these approaches are outlined in the material below.

Burnham's Jackknife

Burnham realized that the capture frequencies (f_j) were minimal sufficient statistics regardless of the form of the distribution of capture probabilities. Thus, why not derive an estimator of N that is a function of the capture frequencies? [The capture frequencies are the number of animals that were captured exactly j times.] John Tukey's jackknife was popular at the time and this simple, but general, method provides a way to lessen the bias in an estimator. Thus, one could start with the naive estimator

$$\hat{N} = M_{t+1}$$

and employ the jackknife method to correct for the bias (or at least some of it). It turns out that there are a family of estimators, each one attempting to correct for more of the bias. As one might expect, there is a bias vs. variance trade-off here and one must decide which *order* of the jackknife to use for the analysis of a particular data set. As an example, the first-order jackknife is

$$\hat{N} = M_{t+1} + \left(\frac{t-1}{t}\right) \cdot f_1,$$

where t is the number of trapping occasions. Note, the final term attempts to correct the bias in M_{t+1} by adding some value to it. Other estimators in this family are given in Otis et al. (1978:109). This clever framework works very well and still performs in the same league as newer approaches. Its main drawback is that it is outside the likelihood framework, thus many such advantages (e.g., model selection and model averaging) are unavailable.

Huggins' Conditional Likelihood

Richard Huggins (1991) provided an interesting approach whereby he tried to account for the heterogeneity by observable covariates such as age, sex, weight, trapping history, rainfall, etc. Clearly, not all heterogeneity could be accounted for as some important variables cannot be measured. However, the notion here is that the effect of heterogeneity could be substantially lessened. Thus, instead of looking at the distribution of the p_i to get an estimator of N , he proposed *modeling* the capture probabilities as

$$\text{logit}(p_{ik}) = \beta_o + \sum \beta_j x_{jk},$$

where x_j are the measured covariates for individual k . This general approach is interesting, but what is to be done with the animals that were not captured (and, therefore, no covariates are available)? This cul-de-sac was avoided by the use of conditional likelihood theory. Here, you condition on only the animals captured, but this eliminates the parameter N from the likelihood! Opps. Huggins uses a form of the Horvitz-Thompson estimator, but where the capture probabilities are estimated,

$$\hat{N} = \sum_{k=1}^{M_{t+1}} \frac{1}{\hat{p}_k^*}, \text{ where } \hat{p}_k^* = 1 - (1 - \hat{p}_{1k})(1 - \hat{p}_{2k}) \dots (1 - \hat{p}_{tk}).$$

Note that \hat{p}^* is just the estimated probability that an animal is captured 1 or more times, i.e., 1 minus the probability it was never captured. This approach has been shown to be generally useful, given the relevant covariates are measured. In addition, it provides insights into *why* animals are captured and this is often of interest to biologists. The main drawback in this method is that it makes assumptions that captured and uncaptured animals are the same; however, if capture probabilities are high (the goal of *all* C-R studies) then this assumption is of less importance.

Pledger's Mixed Models

Shirley Pledger (2000) has built on the work of Agresti (1994) and Norris and Pollock (1955, 1996a) dealing with mixture models. This work on mixtures is very important in that all 8 of the basic models in Otis et al. (1978) are placed in a likelihood framework, while allowing for heterogeneity. The mathematics here can get overwhelming, but the concept is somewhat intuitive if you work at it. Start with the notion that it is the variance in the distribution of the p_i that is important (not necessarily the shape of the distribution). This interesting result has been known since the mid-1980s.

Now, consider the notion that animals are in only 2 groups; some proportion (π) of the total number of animals have low capture probabilities (p_L) and the rest ($1-\pi$) have high capture probabilities (p_H). Capture probability is then a *mixture* of the 2 groups. Then, under Model M_o for example, model the usual capture probability parameter (p) as

$$p = \pi p_L + (1 - \pi) p_H.$$

Thus, in the likelihood for Model M_o , one replaces p with $\pi p_L + (1 - \pi) p_H$. Now the likelihood has $K = 4$ parameters: $\mathcal{L}(N, p_L, p_H, \pi)$, so one gets the MLEs for p_L , p_H , π and \hat{N} .

This scheme can be extended to the other models in Otis et al. (1978) and to more than two groups (often 2 groups is all that the data can support). Pledger's models are all in a likelihood framework, thus allowing AIC model selection, model averaging, profile likelihoods, etc., etc. Very clever and illustrates the advantages of likelihood theory.

Literature Cited

- Agresti, A. 1994. Simple capture-recapture models permitting unequal catchability and variable sampling effort. *Biometrics* 50:494-500.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725-732.
- Norris, J. L., and K. H. Pollock. 1996. Nonparametric MLE under two closed capture-recapture models with heterogeneity. *Biometrics* 52:639-649.
- Otis, D. L., K. P. Burnham, White, G. C., and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 61:1-135.
- Pledger, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics* 56:434-442.