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Simple Capture–Recapture Models Permitting Unequal Catchability and Variable Sampling Effort

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SUMMARY

We consider two capture–recapture models that imply that the logit of the probability of capture is an additive function of an animal catchability parameter and a parameter reflecting the sampling effort. The models are special cases of the Rasch model, and satisfy the property of quasi-symmetry. One model is log-linear and the other is a latent class model. For the log-linear model, point and interval estimates of the population size are easily obtained using standard software, such as GLIM.

1. Introduction

An enormous literature exists on capture–recapture methods for estimating the population size of an animal population. Estimators have been proposed based on a wide variety of approaches, including a nonparametric formulation using a generalized jackknife (Burnham and Overton, 1978), a hierarchical Bayesian model (George and Robert, 1992), martingale estimating equations (Yip, 1991; Lloyd, 1992), a Poisson model that applies when the number of sampling occasions is large and the probability of capture at each is small (Chao, 1989), and log-linear models (Fienberg, 1972; Cormack, 1989). The Burnham–Overton and Chao estimators assume that the probability of capture for a given animal is the same for all samples. They are members of a class of models, denoted by M_h in much of the literature, permitting heterogeneity only among animals. The other estimators assume that the probability of capture at a given sample is the same for all animals. They are members of a class of models, denoted by M_t , permitting time effects only.

This note considers a simple form of a model in the class denoted by M_{th} , allowing time effects and heterogeneity among animals. There is relatively little literature for this case, recent papers by Chao, Lee, and Jeng (1992) on a nonparametric approach and Lloyd and Yip (1991) using martingales being exceptions. The models we consider imply that the logit of the probability of capture is an additive function of an animal catchability parameter and a parameter reflecting the sampling effort at that occasion. Two special cases, a log-linear model and a latent class model, imply quasi-symmetry for a contingency table displaying the data. We consider closed populations, assuming no immigration, births, or deaths during the period of sampling.

2. Quasi-Symmetric Log-linear Modeling

Let p_{ij} denote the probability that animal i is captured in the sample taken at occasion j ($i = 1, \dots, N; j = 1, \dots, t$). The object is to estimate N . The model

$$\text{logit}(p_{ij}) = \alpha_i + \beta_j \quad (1)$$

Key words: Item-response models; Latent class models; Log-linear model; Quasi-symmetry; Rasch model.

assumes a lack of interaction between animal catchability and the sampling occasion. This model form has “subject-specific” probabilities. It is commonly used in item-response modeling, where it is called the Rasch model (Rasch, 1961). In fitting it, one assumes that successive responses are independent, given the parameters. We consider two capture–recapture models that satisfy this structure. This section discusses a log-linear model, and Section 4 discusses a latent class model.

Let $n(i_1, \dots, i_t)$ denote the frequency of outcome i_j on occasion j ($j = 1, \dots, t$), where $i_j = 0$ denotes “not captured” and $i_j = 1$ denotes “captured.” These are cell counts in a 2^t contingency table. We treat these counts as realizations of independent Poisson variates, with expected values $\{m(i_1, \dots, i_t)\}$. Note that N is the sum of the 2^t cell counts, but $n(0, \dots, 0)$ is unobserved. It is easily shown (e.g., Duncan, 1985; Darroch and McCloud, 1986) by averaging over the animal population that model (1) implies that the expected frequencies satisfy

$$\log m(i_1, \dots, i_t) = \mu + \beta_1 I(i_1 = 1) + \dots + \beta_t I(i_t = 1) + \lambda(i_1, \dots, i_t), \quad (2)$$

where $\lambda(i_1, \dots, i_t)$ is invariant to permutations of the argument. It is convenient to use parameter codings for which $\lambda(0, \dots, 0)$ (and any lower-order relatives, in simpler models) equal zero, so that μ simply represents $\log m(0, \dots, 0)$. One can then use the standard error of $\hat{\mu}$ to get a confidence interval for $\log m(0, \dots, 0)$ and hence $m(0, \dots, 0)$ and N . Such coding is the default in GLIM, for instance.

Model (2) is the log-linear model of *quasi-symmetry*. Tjur (1982) showed that maximum likelihood (ML) estimates of $\{\beta_j\}$ in (2) are conditional ML estimates of $\{\beta_j\}$ in (1), given values of sufficient statistics for $\{\alpha_j\}$. Thus, when assumptions underlying model (1) hold, log-linear models for capture–recapture satisfy the property of quasi-symmetry. In particular, that property implies that the binary response (not captured, captured) has the same association for each pair of occasions. Log-linear models for capture–recapture have been used that permit associations and/or higher-order interactions among captures at various occasions (e.g., Cormack, 1989). The quasi-symmetric form of log-linear model does not seem to have been explicitly considered for this application, though Cormack (1993) used a special case of (2) with identical two-factor terms.

Unfortunately, we cannot use the fit of the full model (2) to estimate $m(0, \dots, 0)$ and hence N . This is because there is a separate likelihood equation

$$\hat{m}(0, \dots, 0) = n(0, \dots, 0) \quad (3)$$

for that cell, so *any* count for it can be consistent with the model. However, one can test the adequacy of the quasi-symmetry model fitted to the $2^t - 1$ observed cell counts. If it fits well, one can then consider simpler, special cases of it that do not require (3). For instance, one can fit models without the highest-order interaction term, thus being “unsaturated on the main diagonal.” When a reduced model fits well, one can estimate the unobserved count by the fitted value $\hat{m}(0, \dots, 0)$ for it.

3. Rabbits Redux

Cormack (1985, 1989) reported a capture–recapture study having $t = 6$ consecutive trapping days for a population of snowshoe hares. Table 1 displays the data. Table 2 lists several models and summarizes their fits and population size estimates. The quasi-symmetry model (2) fits the 63 observed cell counts well. The likelihood-ratio goodness-of-fit statistic equals $G^2 = 47.1$, based on 52 degrees of freedom (df). The data are sparse, but cellwise inspection reveals no seriously large residuals. We fitted the special case of (2) having identical two-factor associations, but no higher-order interactions. This model has form

$$\log m(i_1, \dots, i_6) = \mu + \beta_1 I(i_1 = 1) + \dots + \beta_6 I(i_6 = 1) + \binom{\sum i_j}{2} \lambda, \quad (4)$$

where we use coding such that the association term λ for each pair of occasions enters when the indices for both occasions are at the second level (i.e., $i_j = 1$), and where $\binom{a}{b} = 0$ when $a < b$. This model also fits well, having $G^2 = 50.7$ with $\text{df} = 55$. The model has only one more parameter (λ) than the mutual independence model, which fits more poorly ($G^2 = 58.3$, $\text{df} = 56$). The latter model corresponds to $\alpha_1 = \dots = \alpha_N$ in (1), or animal homogeneity. More complex log-linear models do not provide significantly better fits.

The simple two-factor quasi-symmetry model (4) has $\hat{m}(0, \dots, 0) = 22.5$. Its logarithm has an estimated standard error of .474, which leads to a 95% confidence interval for $m(0, \dots, 0)$ of (8.9, 56.9). Since the total of the observed counts is 68, we have $\hat{N} = 90.5$, and a confidence interval for

Table 1
Results of capture–recapture of snowshoe hares

Capture 6	Capture 5	Capture 4	Capture 3, Capture 2, Capture 1							
			0 0 0	0 0 1	0 1 0	0 1 1	1 0 0	1 0 1	1 1 0	1 1 1
0	0	0	— (22.5) ^a (9.1) ^b	3 (2.3) (2.1)	6 (5.4) (4.8)	0 (.9) (1.1)	5 (3.2) (2.8)	1 (.5) (.6)	0 (1.2) (1.5)	0 (.3) (.3)
0	0	1	3 (4.8) (4.2)	2 (.8) (1.0)	3 (1.8) (2.2)	0 (.5) (.5)	0 (1.1) (1.3)	1 (.3) (.3)	0 (.6) (.7)	0 (.2) (.2)
0	1	0	4 (3.9) (3.5)	2 (.6) (.8)	3 (1.5) (1.8)	1 (.4) (.4)	0 (.9) (1.1)	1 (.2) (.2)	0 (.5) (.6)	0 (.2) (.1)
0	1	1	1 (1.3) (1.6)	0 (.3) (.4)	0 (.8) (.8)	0 (.3) (.2)	0 (.5) (.5)	0 (.2) (.1)	0 (.4) (.3)	0 (.3) (.1)
1	0	0	4 (6.8) (6.0)	1 (1.1) (1.3)	1 (2.6) (3.1)	1 (.6) (.7)	2 (1.5) (1.9)	0 (.4) (.4)	2 (.9) (1.0)	0 (.3) (.2)
1	0	1	4 (2.3) (2.8)	0 (.6) (.6)	3 (1.3) (1.5)	0 (.5) (.3)	1 (.8) (.9)	0 (.3) (.2)	2 (.7) (.5)	0 (.4) (.2)
1	1	0	2 (1.9) (2.3)	0 (.5) (.5)	1 (1.1) (1.2)	0 (.4) (.3)	1 (.6) (.7)	0 (.3) (.2)	1 (.6) (.4)	0 (.4) (.1)
1	1	1	1 (1.0) (1.1)	1 (.4) (.2)	1 (.9) (.6)	0 (.5) (.2)	0 (.5) (.3)	0 (.3) (.1)	1 (.7) (.3)	2 (.7) (2.0)

^a Simple quasi-symmetric log-linear model.
^b Quasi-symmetric latent class model.

Table 2
Likelihood-ratio goodness-of-fit statistics for models fitted to Table 1

Model	Structure of capture prob.	Likelihood-ratio statistic	df	Estimate of <i>N</i>	95% CI
Log-linear					
a. Symmetry	M_h	58.0	57	—	—
b. Mutual independence	M_t	58.3	56	75.1	(70.0, 80.4)
c. Two-factor quasi-symmetric	M_{th}	50.7	55	90.5	(76.9, 124.9)
d. Quasi-symmetry	M_{th}	47.1	52	—	—
e. No three-factor interaction	M_t	32.4	41	104.8	(81.3, 169.6)
Latent class					
f. Quasi-symmetric ($L = 2$)	M_{th}	47.7	54	77.3	(73.1, 84.9)
g1. Ordinary ($L = 2$)	M_{th}	41.2	49	85.2	(76.2, 104.0)
g2. Ordinary ($L = 3$)	M_{th}	33.1	42	81.3	(72.0, 103.6)

N of (76.9, 124.9). This is similar to the interval (74.8, 125.1) obtained for this model using a profile likelihood approach (Cormack, 1992), which is based on the values of $n(0, \dots, 0)$ for which the likelihood-ratio statistic for the model applied to the complete table increases by 3.84, the 95th percentile of a chi-squared distribution with 1 degree of freedom. Table 1 displays the fit of model (4). Likelihood equations for this and other log-linear models containing heterogeneous single-factor terms imply that the fitted totals of ‘‘captured’’ at the various occasions are identical to the observed counts.

For such sparse data, quite different models can appear to fit adequately yet can provide highly diverse point and interval estimates of *N*. For instance, the mutual independence model gives $\hat{m}(0, \dots, 0) = 7.1$, $\hat{N} = 75.1$, and a confidence interval of (70.0, 80.4), whereas the no-three-factor interaction model gives $\hat{m}(0, \dots, 0) = 36.8$, $\hat{N} = 104.8$, and a confidence interval of (81.3, 169.6).

When different models appear to fit well, knowledge of the biological context may provide some guidance in choosing a model and estimate of N . As with other types of log-linear modeling, simpler models have advantages and disadvantages compared to more complex models. Unless the sample size is large, the smoothing that a well-fitting simple model provides can result in a better estimator, in terms of a criterion such as mean squared error. This is true even if the simple model does not truly hold, as we expect in practice. Simpler models also have smaller standard errors associated with parameter estimates. Simpler models have the potential for greater bias, however, and the smaller standard errors and the related narrower confidence intervals are deceiving. Particularly with small sample sizes, a model selection procedure may suggest a model that is much simpler than one that truly represents reality well, leading to confidence intervals for N that tend to be too narrow. Unless one has biological grounds for a choice of model, intervals based on the same data used for model selection tend to be overly optimistic (Regal and Hook, 1991). For Table 1, since quasi-symmetry model (4) fits better than the mutual independence model, we have little faith in the narrow confidence interval for N generated from the latter model.

Table 3 shows how easy it is to fit the quasi-symmetry models using the GLIM package for generalized linear models. The default parameterization results in the estimate $\hat{\mu} = \log \hat{m}(0, \dots, 0)$, thus giving immediate standard errors for this by displaying the estimates. The factor called “sym” takes different values for each (i_1, \dots, i_t) having a different sum and hence a different set of permutations. Including this in the model gives the term $\lambda(i_1, \dots, i_t)$ for the full quasi-symmetry model. The special case of (2) with $\beta_1 = \dots = \beta_t$ is the complete symmetry model. It corresponds to homogeneous occasion effects in (1). Comparison of the fits of the symmetry ($G^2 = 58.0$) and quasi-symmetry ($G^2 = 47.1$) models gives a statistic (based on $df = t - 1 = 5$) for testing the hypothesis of homogeneous occasion effects in (1), or marginal homogeneity in (2). Comparison of the fits of the mutual independence ($G^2 = 58.3$) and quasi-symmetry models gives a statistic (based on $df = t - 2 = 4$) for testing the hypothesis of homogeneous animal catchability in (1).

Table 3

GLIM code for fitting simple quasi-symmetric and other log-linear models to Table 1

```

$units 64
$data count $read      !      Data from Table 1
0 3 6 0 5 1 0 0      3 2 3 0 0 1 0 0
4 2 3 1 0 1 0 0      1 0 0 0 0 0 0 0
4 1 1 1 2 0 2 0      4 0 3 0 1 0 2 0
2 0 1 0 1 0 1 0      1 1 1 0 0 0 1 2
$calc a = %gl(2,1): b = %gl(2,2): c = gl(2,4) d = %gl(2,8): e = %gl(2,16): f = %gl(2,32) $
      ! generates levels for 6 capture occasions
$calc wt = 1: sym = a + b + c + d + e + f - 5 $
$ edit 1 wt 0 $ ! zero weight for unobserved cell
$calc ab=(a-1)*(b-1): ac=(a-1)*(c-1): ad=(a-1)*(d-1): ae=(a-1)*(e-1): af=(a-1)*(f-1):
bc=(b-1)*(c-1): bd=(b-1)*(d-1): be=(b-1)*(e-1): bf=(b-1)*(f-1): cd=(c-1)*(d-1): ce=(c-1)*(e-1):
cf=(c-1)*(f-1): de=(d-1)*(e-1): df=(d-1)*(f-1): ef=(e-1)*(f-1) $ ! association terms
$calc asso = ab+ac+ad+ae+af+bc+bd+be+bf+cd+ce+cf+de+df+ef $ ! common two-factor assoc.
$wei wt
$fac  a 2 b 2 c 2 d 2 e 2 f 2 sym 7
$yvar count $err pois
$fit sym: +a + b + c + d + e + f $ ! Fits symmetry and quasi symmetry
$fit - sym $ ! Fits mutual independence model
$fit + asso $ ! Fits simple quasi-symmetry model
$dis e r $ ! Displays estimates and fitted values with residuals
$fit +ab+ac+ad+ae+af+bc+bd+be+bf+cd+ce+cf+de+df+ef $ ! No-3-factor interaction
$end

```

4. Latent Class Models

An alternative approach to estimating population size assumes that animals cluster into L latent classes, such that animals in the same class have the same catchability. For instance, for $L = 2$, we might treat the animal population as a mixture of two types, one that shows an aversion to trapping and one that shows an attraction. Within latent classes, one assumes that the t responses by a given animal are independent. Latent class models correspond to the log-linear model for the joint classification of the occasions with the latent variable, such that responses are conditionally

independent given the latent class (Goodman, 1974). As with the approach in Section 2, heterogeneity among animals results in $\{m(i_1, \dots, i_t)\}$ displaying associations. One can use a well-fitting latent class model to obtain an estimate of $m(0, \dots, 0)$ and hence N .

The Rasch model (1) is an example of a latent class model having potentially as many latent classes as there are animals. One could instead consider a special case of that model in which there are only L distinct values of α_i , with animals in the same latent class sharing the same catchability parameter. Lindsay, Clogg, and Grego (1991) discussed Rasch mixture models of this sort. Such models are a special case of ordinary latent class models that have identical associations between the latent variable and the capture status at each occasion j . Having structure (1), they are in class M_{th} and also satisfy quasi-symmetry.

Agresti and Lang (1993) discussed quasi-symmetric latent class models. The EM algorithm they described can also be used to fit those models and ordinary latent class models when certain cell counts are missing or unobservable. Model parameter estimates determine a fitted value $\hat{m}(0, \dots, 0)$ satisfying the model, and hence lead to an alternative quasi-symmetric estimate of N . One can regard latent class models as Poisson log-linear models in which only certain marginal totals are observable; that is, the counts within latent classes are unobservable, but the marginal totals obtained by summing over those classes are observable. In the capture-recapture application, one of those marginal counts is also unobservable. Lang (1992) provided a formula for obtaining asymptotic standard errors of parameter estimates in Poisson log-linear models for which only certain marginal totals are observable. When one uses latent class models to fit capture-recapture data, one can use his formula together with the delta method to get a standard error estimate for the estimated unobservable cell count $n(0, \dots, 0)$. One can use that standard error, or profile likelihood methods, to construct a confidence interval for N .

For Table 1, the ordinary latent class model with two classes fits quite well, having $G^2 = 41.2$ based on $df = 49$. This model yields $\hat{m}(0, \dots, 0) = 17.2$. Using Lang's (1992) approach, we obtain an estimated standard error of .378 for its logarithm. This leads to $\hat{N} = 85.2$, and a 95% confidence interval for N of (76.2, 104.0). The simpler quasi-symmetric latent class model also fits relatively well, having $G^2 = 47.7$ based on $df = 54$. Table 1 also displays this fit. This model yields $\hat{m}(0, \dots, 0) = 9.3$, $\hat{N} = 77.3$, and a confidence interval of (73.1, 84.9). This model shows potentially a strong association between the latent variable and capture status, with the common estimated log odds ratio equaling 3.8. However, the estimated standard error of that estimate equals 2.0, indicating that this fit may not be appreciably different from the mutual independence fit. This also suggests why the confidence interval is not very different from that obtained with the mutual independence model, both intervals being optimistically narrow.

Profile likelihood-based confidence intervals for N tended to be slightly wider. For instance, the interval for the ordinary latent class model was (74.0, 106.4). Latent class models with $L = 3$ do not appear to give substantively better fits. The quasi-symmetric latent class model then has two additional parameters, one for the latent main effects and one for the common association between the latent variable and each capture status, and has the same df as the full quasi-symmetry model; this model and related ones having $L \geq 3$ are equivalent to the full model, and do not provide estimates of population size [see Lindsay et al. (1991) for related remarks].

There are some hierarchical relationships among the models listed in Table 2. The mutual independence model (b) is the special case of the quasi-symmetric log-linear model (c) and the no-three-factor-interaction model (e) having null values for all higher-order associations, and it is the special case of the quasi-symmetric latent class model (f) having only one latent class. These simple quasi-symmetric models (c) and (f) are themselves special cases of the full quasi-symmetry model (d), as is the symmetry model (a). Finally, the quasi-symmetric latent class model (f) is a special case of the ordinary latent class model (g).

An alternative latent variable approach would assume a continuous distribution for animal catchability. For instance, in model (1), one could treat the animal term as a random effect, and assume for it a normal distribution with mean zero and unknown standard deviation. One could then estimate the model parameters by maximizing a marginal likelihood resulting from integrating over the random effects distribution. One would estimate the probability that a randomly selected animal is not observed at all t sampling occasions by calculating an estimate of that probability for a given α , and then integrating with respect to the estimated distribution of α . This approach is more complex than the others we have presented, and we do not pursue it further. It is worth noting, though, that Tjur (1982) showed that a nonparametric random effects approach leads again to the quasi-symmetric form of model.

5. Comments

Model (1) is a simple, appealing model that has found considerable favor for other sorts of applications, such as item-response modeling of binary test items (Rasch, 1961) and motivation for McNemar's test for comparing matched proportions (Cox, 1958). We have used it to motivate two relatively simple estimates of population size. Since this paper was accepted for publication, an article has appeared (Darroch et al., 1993) using quasi-symmetric log-linear models for an application of capture–recapture modeling to U.S. census population data. When additional covariate information is available for each animal, one can formulate logit models for capture probabilities that incorporate that information, rather than using animal-specific parameters (e.g., Alho, 1990; Huggins, 1989, 1991). Another version of an M_{th} model discussed recently assumes that p_{ij} , rather than the odds, has form $a_i b_j$ (Chao et al., 1992; Lloyd and Yip, 1991).

Limitations of the specialized Rasch models result from their simplicity. The models we discussed will fit poorly if there is substantial animal-by-occasion interaction in catchability. Or, they may fit poorly if there is residual dependence between occasions, given the animal parameters. Either of these departures could be reflected, for instance, by associations between capture statuses that are greater for occasions closer together in time. The models assume an interchangeability of occasions in the association structure, which is unrealistic in many biological applications. This assumption is probably more likely to be realistic for settings in which the entire sampling process occurs over a short period of time, such as in the snowshoe hare example.

Duncan (1985) suggested a way to weaken the strong requirement in the Rasch model of independence of responses, given the subject parameters. This uses a generalization of the model that adds to the subjects' joint distribution a common association term for occasions that are adjacent in time. A corresponding log-linear model is a generalization of the quasi-symmetry models (2) and (4) that adds a parameter having as coefficient the number of pairs of adjacent indices (i_j, i_{j+1}) that equal 1. For capture–recapture applications, one could use the version of this model that has a common association for all adjacent occasions, and another common association for all other pairs of occasions.

In summary, the scope of these specialized Rasch models is limited by their fairly simple structure. The ubiquity of useful applications of Rasch models, however, makes them worthy of note in the capture–recapture literature.

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RÉSUMÉ

Nous considérons deux modèles de capture–recapture dans lesquels la fonction logit de la probabilité de capture est une fonction additive d'un paramètre de risque de capture et d'un paramètre reflétant l'intensité d'échantillonnage. Les modèles sont des cas particuliers du modèle Rasch et satisfont la propriété de quasi-symétrie. L'un des deux modèles est log-linéaire, l'autre appartient à la classe des modèles à variables sous-jacentes. Des estimations ponctuelles et par intervalle de la taille de la population sont aisées à obtenir pour le modèle log-linéaire en utilisant un logiciel standard tel que GLIM.

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