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A Proposal for a Goodness-of-Fit Test to the Arnason-Schwarz Multisite Capture-Recapture Model

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Summary. In an analysis of capture-recapture data, the identification of a model that fits is a critical step. For the multisite (also called multistate) models used to analyze data gathered at several sites, no reliable test for assessing fit is currently available. We propose a test for the JMV model, a simple generalization of the Arnason-Schwarz (AS) model, in the form of interpretable contingency tables. For the AS model, we suggest complementing the test for the JMV model with a likelihood ratio test of AS vs. JMV. The examination of an example leads us to propose further a partitioning that emphasizes the role of the memory model of Brownie et al. (1993 *Biometrics* **49,** 1173–1187) as a biologically more plausible alternative to the AS model.

Key words: Canada goose; Cormack-Jolly-Seber; Memory model; Mixture of multinomials; Multistate models; Peeling-pooling; Test3G; TestM; TestWBWA; Unisite models.

1. Introduction

One of the best sources of information on the dynamics of natural populations is provided by the repeated observations of animals that had been individually marked on their first encounter (Seber, 1982; Lebreton, Pradel, and Clobert, 1993). The analysis of such data must take into account the sampling process, and rests on either hypergeometric or multinomial sampling models (Robson, 1969; Robson and Youngs, 1971; Pollock, 1975).

Essentially due to their computational ease, models of the second type are more widely used. The monograph by Lebreton et al. (1992) expounds a general procedure of analysis; the authors advocate as the first step the identification of a model sufficiently general to adequately describe the data. Since then, the recent emphasis on information-theoretic approaches to model selection (Burnham and Anderson, 1998) has relieved the need for a global model, but the identification of at least one model that fits the data remains critical. However, reliable goodness-of-fit tests are not available for all models, which is one of the major difficulties in conducting a capture-recapture analysis.

Theoretically, an omnibus goodness-of-fit test could be constructed by comparing expected and observed numbers of animals for each possible capture history. However, the number of cells in such a comparison increases much more rapidly with an increase in the number of sampling occasions k than with an increase in the number of available animals. The scarceness of data will rapidly (with k) make the implementation of this test problematic (though a parametric bootstrap procedure could possibly be considered). Now, it is usually reasonable to assume that animals with different capture histories have some characteristics in common such as, for instance, a common probability of surviving a given time interval. It may then become possible to partition the data into a smaller number of alternatives. A model for which a goodness-of-fit test can be built in this way is the reference model for a population inhabiting only one site (Cormack, 1964; Jolly, 1965; Seber, 1965)—specifically, the model which assumes common survival over any time interval, and common capture probability during each sampling occasion for every animal, as well as independence of the fates of individuals. The goodness-of-fit test for this reference model dates back to Robson and Youngs (1971), Seber (1970), and Pollock, Hines, and Nichols (1985), depending on the component considered. This test is divided up into components for which there is a biological interpretation—thus providing good insight into the data (Pradel, 1993; Pradel et al., 1997). Burnham (1991) derives the goodness-of-fit test to the Cormack-Jolly-Seber (CJS) model in an elegant manner which he calls "peeling and pooling."

In this article, we examine whether the peeling and pooling method of Burnham (previously used by Robson, 1969) can be extended to the AS model (Arnason, 1973), which is the direct generalization of the CJS model to the multisite case. We first expound the ideas behind the peeling and pooling method in the unisite case, and then attempt the generalization. Finally, an example is provided for illustration.

2. Definitions

We define a release batch, or simply *batch,* as the set of animals released simultaneously. Because a given animal can be captured more than once, it can belong to more than one batch (we prefer the more neutral term "batch" to "cohort," which has been used in the methodological literature (Burnham et al., 1987), but has a different meaning in the

biological literature). Within each batch, we distinguish *subbatches* of animals with the same previous capture history.

There are three main kinds of statistics used in this paper: R denotes numbers released, r is the number eventually recaptured among R, and m is the number recaptured among r at a specific occasion and/or at a specific time interval.

These quantities are indexed by date and site according to the following general rules: sites as superscripts, dates as subscripts; when applicable departure is denoted on the left, arrival is denoted on the right. For example, m_{ij}^{lv} denotes the number of animals which are released on occasion i at site l, and are next recaptured on occasion j at site v. These rules for notation also apply to the model parameters. The fundamental parameters are of two types: the probabilities of surviving a time interval, denoted ϕ, and the probabilities of capture at each occasion, denoted p.

3. The Peeling-Pooling Approach

3.1 *The Reasons Why the Peeling-Pooling Method Works in the Unisite Case*

Among the assumptions of the CJS model, some relate to the experimental techniques and need not concern us. Those which have bearing on the model structure are:

- Every animal in the population has the same probability p_i of being caught in the ith sample, given that it is alive and in the population when the sample is taken.
- Every marked animal has the same probability ϕ_i of surviving from the ith to the $(i+1)$th sample and of being in the population at the time of the $i+1$ sample, given that it is alive and in the population immediately after the ith release.
- Animals behave independently.

Based on the last assumption, Burnham (1991) starts by showing that the CJS model lends itself naturally to the product multinomial formalization embodied in the data summarization called the "full m-array" (see Table 1) (Burnham et al., 1987). However, if there are no constraints on the cell probabilities of the product-multinomial—other than that they sum to one for each multinomial—then the model is saturated and no degrees of freedom are left for goodness-of-fit testing. This is where the more specific assumptions of the CJS model come into play: by rendering the cell probabilities functions of a smaller number of survival and capture parameters. Accounting for these constraints, the likelihood is factorized into one set of terms involving just parameters and minimal sufficient statistics (MSS), and another set of hypergeometric terms involving the MSS but not parameters. By application of the factorization theorem (see, for instance, Cox and Hinkley, 1974), it then becomes possible to derive a goodness-of-fit test. Additionally, due to the properties of the exponential family of distributions to which the multinomial belongs, Burnham can conclude that, because their dimensionality is that of the parameter space, the statistics in the latter term of the factorization are MSS and hence that the goodness-of-fit test is fully efficient. In fact, from a biological point of view, the peeling and pooling method of Burnham comes down to the application of one property that summarizes the assumptions of the CJS model, and, from a methodological point of view, to the repeated use of two technical tools.

Table 1
Full m-array with four occasions and one site. Each row corresponds to an independent multinomial.

		First recapture at j			
Year	Release	$j=$	2	3	4
1	R_1		m_{12}	m_{13}	m_{14}
2	$R_{2\{0\}}$			$m_{23\{0\}}$	$m_{24\{0\}}$
2	$R_{2\{1\}}$			$m_{23\{1\}}$	$m_{24\{1\}}$
3	$R_{3\{00\}}$				$m_{34\{00\}}$
3	$R_{3\{01\}}$				$m_{34\{01\}}$
3	$R_{3\{10\}}$				$m_{34\{10\}}$
3	$R_{3\{11\}}$				$m_{34\{11\}}$

Biological Property 1
All marked animals which are in the system at the same time are indistinguishable.

The useful consequences of this property are that

- all multinomials in the likelihood have proportional cell probabilities in the range of sampling dates they share, and in particular,
- all subbatches of any given release batch share the same cell probabilities.

The technical tools are the following properties of multinomial distributions.

Property 1
If $\mathbf{V}$ and $\mathbf{V}^*$ are mutually independent, multinomially distributed stochastic vectors with the same number of cells and the same values of cell probabilities, then the distribution of $\mathbf{V}+\mathbf{V}^*$ is multinomial with the same number of cells and the same cell probabilities, and the joint distribution of $\mathbf{V}$ and $\mathbf{V}^*$ conditional on $\mathbf{V}+\mathbf{V}^*$ is multivariate hypergeometric. (In fact, this result generalizes to more than two stochastic vectors.)

Property 2
If $\mathbf{V}$ and $\mathbf{V}^*$ are mutually independent stochastic vectors multinomially distributed with $\mathbf{V}=(\mathbf{W},\mathbf{U})$, where the subvector $\mathbf{U}$ of $\mathbf{V}$ has the same number of cells as $\mathbf{V}^*$ and proportional cell probabilities, then the marginal distribution of $\mathbf{W}$ is multinomial and the conditional distribution of $\mathbf{U}$ given $\mathbf{W}$ is multinomial with the same values of cell probabilities as the distribution of $\mathbf{V}^*$.

The peeling and pooling method ensues from the interplay of the above biological and methodological properties as illustrated in the diagram of Figure 1 (for details, see Burnham, 1991). It remains to be seen whether this method can be applied when observations are carried out over several sites.

3.2 *The Peeling-Pooling Method in the Case of Several Sites*

The assumptions of the AS model are similar to those of the CJS model, except that they take the sites into account. Those which have bearing on the model are:

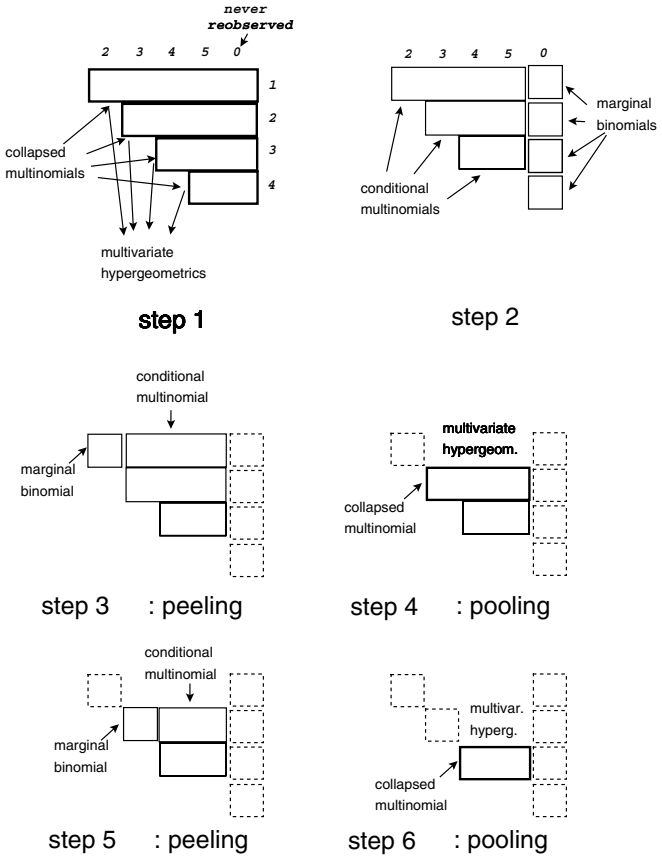

Figure 1. Schematic representation of the peeling-pooling method applied to the CJS model with 5 time intervals. Each row corresponds to a date of release, each column to a date of first reobservation, the last column being for individuals never seen again (dated 0). The multivariate hypergeometrics set aside in step 1 concern subbatches within batches, and constitute the component Test3 in Burnham et al. (1987). The other hypergeometrics set aside in the following steps constitute Test2. The shadowed binomials visible in the last step plus the last collapsed multinomial (which is in fact a binomial) together represent the parametric part of the model. There are 7 such binomials; the same number as the number of identifiable parameters in the model.

- Every animal in the population has the same probability p_i^l of being caught in the ith sample at site l, given that it is alive and at site l when the sample is taken.
- Every marked animal present at site l and time i has the same probability ϕ_i^{lm} of surviving from the ith to the $(i+1)$th sample, and of being at site m at the time of the $i+1$ sample.
- Animals behave independently.

Because the last assumption is unchanged, the likelihood is still a product multinomial, but there are many more multinomials than in the CJS model with the same number of capture occasions k. There is, in fact, one multinomial per site, date of release, and previous capture history, i.e., $(s+1)^{k-1}-1$ where s is the number of monitored sites. Also, each multinomial has more cells because the circumstances of the first reobservation of a released animal must be classified by site as well as by date. However, the key point is that biological property 1 no longer holds. It must be amended as follows.

Biological Property 2

All marked animals which are in the system at the same time and at the same site *are indistinguishable.*

Of the two consequences derived previously, only the second is maintained: all subbatches of any given release batch share the same cell probabilities. Hence, step 1 of Figure 1 can still be conducted, leading to a generalization of Test3 (Test3G) as the sum of Test3(i, l)'s (see Figure 2). But the peeling-pooling method stops there. For instance, as shown in Table 2, after peeling off the recaptures at time 2 of animals released at time 1 and site 1 (batch(1,1)), the remaining conditional multinomial does not compare to any multinomial from releases at time 2 (batch(2,1) or batch(2,2)). The pooling stage fails. The reason is that the exact location of an animal released at time 1 and not captured at time 2 is then unknown (Wintrebert, 1998). This animal could either have been at site 1 or at site 2. Because it must be at one of the two sites, it can be shown formally (see Appendix), and understood intuitively, that the conditional multinomial stemming from batch(1,1) is a mixture of those from batch(2,1) and batch(2,2). This is an important general result that can be phrased as:

Subbatch	Time (j) and location (v) of first recapture						
	$j=$	$i+1$			....	k			
	$v=$	1	..	s		1	..	s	
$R^l_{i\{h_0\}}$		$m^{l1}_{i,i+1\{h_0\}}$	..	$m^{ls}_{i,i+1\{h_0\}}$	....	$m^{l1}_{i,k\{h_0\}}$	..	$m^{ls}_{i,k\{h_0\}}$	$R^l_{i\{h_0\}}$-$r^l_{i\{h_0\}}$
.		⋮		⋮		⋮		⋮	⋮
.		⋮		⋮		⋮		⋮	⋮
$R^l_{i\{h_n\}}$		$m^{l1}_{i,i+1\{h_n\}}$	..	$m^{ls}_{i,i+1\{h_n\}}$	....	$m^{l1}_{i,k\{h_n\}}$	..	$m^{ls}_{i,k\{h_n\}}$	$R^l_{i\{h_n\}}$-$r^l_{i\{h_n\}}$

Figure 2. Test3(i,l). For each batch (i,l) of releases at time i and site l, the subbatches are indistinguishable—leading to a generalization of Test3 in the form of $(k-1)s$ contingency tables to be tested for homogeneity.

Table 2
Relationships among batches in the Arnason-Schwarz model: the conditional multinomial in bold in the first row has cell probabilities that differ from those of either of the bold conditional multinomials in rows 3 *and* 4*. However, it can be shown that the conditional multinomial in row* 1 *is a mixture of those in rows* 3 *and* 4*. (A similar statement can be made about the multinomial in row* 2.)

			Time (j) and location (v) of first recapture					
		$j=$	2		3		4	
Year	Site	Release	$v=$ 1	2	1	2	1	2
1	1	R_1^1	m_{12}^{11}	m_{12}^{12}	$\mathbf{m_{13}^{11}}$	$\mathbf{m_{13}^{12}}$	$\mathbf{m_{14}^{11}}$	$\mathbf{m_{14}^{12}}$
1	2	R_1^2	m_{12}^{21}	m_{12}^{22}	m_{13}^{21}	m_{13}^{22}	m_{14}^{21}	m_{14}^{22}
2	1	R_2^1			$\mathbf{m_{23}^{11}}$	$\mathbf{m_{23}^{12}}$	$\mathbf{m_{24}^{11}}$	$\mathbf{m_{24}^{12}}$
2	2	R_2^2			$\mathbf{m_{23}^{21}}$	$\mathbf{m_{23}^{22}}$	$\mathbf{m_{24}^{21}}$	$\mathbf{m_{24}^{22}}$
3	1	R_3^1					m_{34}^{11}	m_{34}^{12}
3	2	R_3^2					m_{34}^{21}	m_{34}^{22}

Biological Property 3
A previously released animal alive and not captured at time i behaves from this time onwards as an animal released at this same time on one or another of the s sites.

As a consequence, for each batch released before time $i-1$, the numbers of first reobservations starting at time i have a conditional multinomial distribution that is a mixture of the conditional multinomials over the same circumstances of first reobservations arising from the batches of releases at time $i-1$ at the different sites. In exploiting this property, we suggest a parallel test to Test2 of the unisite case (Burnham et al., 1987) by relying on the following property of mixtures of multinomials.

Property 3
If $\mathbf{V}$ and $\mathbf{V}^*$ are mutually independent stochastic vectors multinomially distributed, and if $\mathbf{W}$ and $\mathbf{W}^*$ are mutually independent stochastic vectors whose distributions are separately mixtures (not necessarily with the same mixing probability) of the distributions of $\mathbf{V}$ and $\mathbf{V}^*$, then the distribution of $\mathbf{W}+\mathbf{W}^*$ is itself a mixture of the distributions of $\mathbf{V}$ and $\mathbf{V}^*$.

It is thus possible to proceed as follows. The first step is to simultaneously test whether the conditional multinomials of first reobservations from time 3 onwards, from the s batches released at time 1, are mixtures of the conditional multinomials of first reobservations over the same circumstances from the s batches released at time 2. The second step is to pool the reobservations, starting at time 3 over batches released at times 1 and 2, by site of release. The third step is to repeat step 1 to compare the pooled reobservations from time 4 onwards to the reobservations over the same circumstances from the s batches released at time 3. Then, repeat steps 2 and 3 until there are no degrees of freedom left for testing for mixtures.

The tests for mixtures, which together constitute TestM, can be computed for $i = 2, \ldots, k-2$ (Figure 3). The pooling of reobservations we propose is just one possible strategy, partly inspired by the following example. Figure 4 presents the method in a manner similar to that of Figure 1.

4. Characterizations of the AS and JMV Models

The AS model is characterized by the three properties given at the beginning of Subsection 3.2. We have shown in the previous section that a necessary consequence of these conditions is that certain conditional multinomials are mixtures of other conditional multinomials (a consequence of biological property 3). However, this single property does not characterize the AS model—but rather a more general model called JMV by Brownie et al. (1993). In this section, we clarify the

Batches (time, location)	Time (j) and location (v) of first recapture						
$j=$	$i+1$			....	k		
$v=$	1	..	s		1	..	s
$(u<i,1)$	$\sum_u m_{u,i+1}^{11}$	..	$\sum_u m_{u,i+1}^{1s}$	....	$\sum_u m_{u,k}^{11}$	..	$\sum_u m_{u,k}^{1s}$
.	⋮		⋮		⋮		⋮
.	⋮		⋮		⋮		⋮
$(u<i,s)$	$\sum_u m_{u,i+1}^{s1}$	..	$\sum_u m_{u,i+1}^{ss}$	....	$\sum_u m_{u,k}^{s1}$	..	$\sum_u m_{u,k}^{ss}$
$(i,1)$	$m_{i,i+1}^{11}$	..	$m_{i,i+1}^{1s}$	....	$m_{i,k}^{11}$	..	$m_{i,k}^{1s}$
.	⋮		⋮		⋮		⋮
.	⋮		⋮		⋮		⋮
(i,s)	$m_{i,i+1}^{s1}$	..	$m_{i,i+1}^{ss}$	....	$m_{i,k}^{s1}$	..	$m_{i,k}^{ss}$

Figure 3. TestMi. The multinomial distributions of first reobservations, from the batches of releases at the different sites at occasion i (batches $(i, 1)$ to (i, s)), are bases for the mixture multinomial distributions of the first reobservations from any previous batch (batch (u, l) with $u < i$, $1 < l < s$), restricted to the same circumstances. We chose to pool the previous batches over release times at each site, but other poolings may be considered. TestMi simultaneously tests that the pooled data (first s rows) are mixtures of the bases (last s rows).

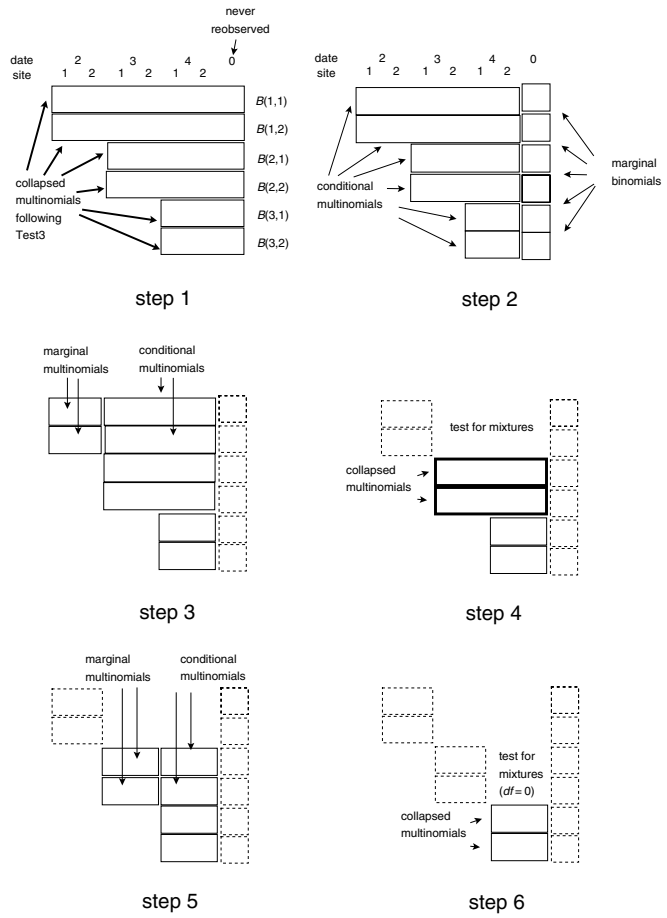

Figure 4. Schematic representation of the construction of the test for mixtures when there are 4 time intervals and 2 sites. $B(i,\ l)$ is the batch of releases at occasion i and site l. Unlike in the unisite case, the comparison of conditional multinomials across batches yields tests for mixture rather than tests for homogeneity. Each time, the current release batches play the role of bases.

relationships between the AS and JMV models and give two useful characterizations. We start by giving a formal definition of each model:

DEFINITION 4.1: *Among the multisite models with k capture occasions and s sites, the AS model is the model for which*

- *survival-movement probabilities depend only on the time interval, site of departure, and site of arrival (notation* ϕ_i^{lm}*) and*
- *capture probabilities depend only on the occasion and site of arrival (that is, where the capture actually takes place) (notation* p_i^m*).*

The JMV model is the model for which

- *survival-movement probabilities depend only on the time interval, site of departure, and site of arrival (notation* ϕ_i^{lm}*) and*
- *capture probabilities depend only on the occasion, site of departure, and site of arrival (notation* p_i^{lm}*).*

Seber (1962) introduced a reparameterization of unisite capture-recapture models in terms of products of the forms $\alpha = \phi \times p$ and $\beta = \phi \times (1 - p)$. For instance, in the context of the CJS model, the new parameters are $\alpha_i = \phi_i \times p_{i+1}$ $(i = 1, \ldots, k - 1)$, the probabilities of being recaptured at time $i + 1$ for an individual still at risk of capture after occasion i, and $\beta_i = \phi_i \times (1 - p_{i+1})$ $(i = 1, \ldots, k - 2)$, the probabilities of remaining at risk of capture within the same batch, for an individual still at risk of capture after occasion i.

This parameterization is more convenient than the $(\phi,\ p)$ parameterization in some respects. For instance, it is well known that in the CJS model ϕ_{k-1} and p_k are not separately identifiable. This translates nicely in the (α, β) parameterization: there is no β parameter with index $k - 1$. The (α, β) parameterization extends easily to the multisite case by accounting for the sites of departure and of arrival. With this reparameterization, we have

Characterization 1

Among the multisite models with k capture occasions and s sites, the AS model is the model for which

- α*-probabilities depend only on the time interval, site of departure, and site of arrival (notation* α_i^{lm}*) and*
- β*-probabilities depend only on the time interval, site of departure, and site of arrival (notation* β_i^{lm}*) and, in addition,* $\forall i,\ 1 \le i \le k-2,\ \forall m,\ 1 \le m \le s$*, the ratio* $\beta_i^{lm}/\alpha_i^{lm}$ *does not depend on* l*.*

The JMV model is the model for which

- α*-probabilities depend only on the time interval, site of departure, and site of arrival (notation* α_i^{lm}*) and*
- β*-probabilities depend only on the time interval, site of departure, and site of arrival (notation* β_i^{lm}*).*

The JMV model has a simpler characterization than the AS model in the $(\alpha,\ \beta)$ parameterization.

Finally, we make the link with the previous section by establishing that the property of mixture along with the property of similarly distributed subbatches characterizes the JMV model.

Characterization 2

Among the multisite models with k capture occasions and s sites, the JMV model is the model such that

- *all subbatches of the same batch are distributed with the same cell probabilities and*
- *the conditional distribution of the first reobservations from batch* $(i,\ l)$ $(1 \le i \le k - 3,\ 1 \le l \le s)$*, starting at time* $i + 2$*, is a mixture of the conditional distributions of the first reobservations from the s batches* $(i + 1,\ n)$*,* $n = 1, \ldots, s$ *over the same circumstances.*

Proof. The line of reasoning followed in Section 3 and in the Appendix for the AS model is valid without change for the JMV model. Thus, the direct implication is established. It remains to establish the converse. A model obeying the conditions set in the characterization above is uniquely specified by the following parameters: the cell probabilities $\pi_{i,i+1}^{lm}$; $1 \le i \le k-1$, $1 \le l,\ m \le s$; the probabilities of ever being seen again λ_i^l, $1 \le i \le k - 2$, $1 \le l \le s$, and the mixture coefficients

Table 3

Raw component (2,1) *of Test3G for the Canada geese data. The individuals captured at occasion* 2 *and site* 1 *are sorted by location at time* 1 (*rows*), *and time and location of next recapture* (*columns*); *in both cases, row or column, a "-" sign means no capture. For instance, among the individuals captured at occasion* 2 *and site* 1, 390 *individuals had not been seen previously* (*the row heading is a "-"*) *and were next recaptured at occasion* 3 *and site* 1. *The last column is for individuals never seen again. Note that most individuals from this release batch have their last previous and next future observation* (*if any*) *at the current site* 1.

Subbatch (location at time 1)	Time (j) and location (v) of first recapture												
	$j =$	3			4			5			6			–
	$v =$	1	2	3	1	2	3	1	2	3	1	2	3	–
–		390	124	0	122	64	3	46	35	3	18	9	0	920
1		75	3	0	21	4	0	5	2	0	1	0	0	128
2		19	6	0	4	3	0	0	2	0	1	3	0	47
3		7	1	0	2	0	0	0	3	0	1	1	0	9

γ_i^{ln}, $1 \le i \le k-2$, $1 \le l \le s$, $1 \le n \le s-1$ (see Appendix). Obviously, $\alpha_i^{lm} = \pi_{i,i+1}^{lm}$, $1 \le i \le k-1$, $1 \le l,\ m \le s$. Now, if this model is indeed JMV, the demonstration in the Appendix indicates that, necessarily: $\gamma_i^{ln} = \beta_i^{ln}\lambda_{i+1}^n / (\lambda_i^l - \sum_{m=1}^s \alpha_i^{lm}), 1 \le i \le k-2, 1 \le l, n \le s$. There is a unique solution in terms of β's: $\beta_i^{ln} = \gamma_i^{ln}(\lambda_i^l - \sum_{m=1}^s \alpha_i^{lm}) / \lambda_{i+1}^n, 1 \le i \le k-2, 1 \le l, n \le s$.

The conditions of characterization 1 for the JMV model are thus fulfilled. The (α, λ, γ) parameterization is just another parameterization of the JMV model.

5. Example: Wintering Locations of Canada Geese

The tests proposed in the above sections, i.e., Test3G, which generalizes Test3 of the unisite case, and the test of mixtures which we have dubbed TestM, allow assessment of the fit of the JMV model. Combined with an LRT of model AS versus JMV, they should also allow assessment of the fit of the AS model. As with the unisite models, some strategy of pooling is likely necessary because small expected values will frequently appear in some of the many cells. (For Test3G, Fisher's exact test or a Monte Carlo method are alternative solutions.) In this section, we do not intend to provide a complete discussion of the question of pooling (which deserves to be treated on its own), but nonetheless attempt to identify some guidelines for future studies through a new treatment of a pioneering example from the literature: the interannual movements among geographical locations of wintering snow geese (*Branta canadensis*). This is typical of the biological situation for which the multisite models—often used today to study transitions among states—were originally developed. This data set has been analyzed at least twice: first only partially by Hestbeck, Nichols, and Malecki (1991), then by Brownie et al. (1993). The main result of those previous analyses is that the geese tend to come back to a site previously visited in another, but not necessarily the most recent, year. This violation of the assumptions of the AS model led the authors to introduce the so-called memory models. Here we investigate whether our tests are able to detect this particular kind of departure from the assumptions of the AS model.

We use the full data set, i.e., all observations throughout three wintering regions over six years of observations. With this number of sites and time intervals, there are 12 tests 3(i, l) and 3 tests Mi. Despite the relatively large number of animals in the data set, some expected cell values in the tables making up Test3G remained low. We decided to pool until all expected cell values were greater than 2. For example, the pattern of low expected values for component (2, 1) (Table 3) led us to first pool together the columns and the rows corresponding to sites 2 and 3. To complete the pooling, a second step consisted in grouping occasions 5 and 6 within sites. The results of pooling for all the components of Test3G are given in Figure 5. Each time the major pooling step consisted of grouping the sites other than those where the animals had been observed, a "here" versus "elsewhere" alternative. To implement TestM, we used a procedure originally developed to analyze psychological data. This procedure consists of two steps: first the cell probabilities of the bases and the mixture coefficients are estimated by maximum likelihood; then the likelihood-ratio statistic G^2 is computed from the observed and expected frequencies (Yantis, Meyer, and Smith, 1991). The results for TestM are given in Figure 6. As for the difference in deviance between the AS and JMV models, it was obtained by fitting the two models with SURVIV (White, 1983). In conclusion, the JMV model is clearly rejected ($\chi^2(150) = 854.2385$, $P < 0.0001$) (see Table 4). As for the AS model, when accounting for the variability detected at the level of the JMV model, it is accepted by an analysis of deviance (Wedderburn, 1974) ($F(24, 150) = 0.74$, $P = 0.81$).

An expected advantage of contingency tables is readability, so that an alternative can be identified when the data fail to meet the requirements of the focus model. However, the present tables are relatively complex and a further, directional summarization may be helpful. To specifically address the memory phenomenon, we constructed new contingency tables, one per batch, with only those animals seen before and seen after the current occasion. Within a table, the animals are arranged according to where they were last seen (the rows) and to where they will next be seen (the columns). The associated tests "where before"–"where after" (WBWA) can easily be included as a step in a partitioning of Test3G. Table 5 presents the results of this partial test, as well as a summary of the signed contributions of each cell. Clearly,

Subbatch	Time (j) and location (v) of first recapture						
j =	3		4		5-6		-
v =	1	2-3	1	2-3	1	2-3	-
-	390	124	122	67	64	47	920
1	75	3	21	4	6	2	128
2-3	26	7	6	3	2	9	56

Test3(2,1)

Subbatch	Time (j) and location (v) of first recapture						
j =	4		5		6		-
v =	1	2-3	1	2-3	1	2-3	-
-	358	159	93	93	40	41	1135
1	169	15	50	9	9	3	272
2-3	37	34	7	19	3	4	116

Test3(3,1)

Subbatch	Time (j) and location (v) of first recapture				
j =	3		4-5-6		-
v =	1-3	2	1-3	2	-
-	145	713	116	458	1769
1-3	13	10	3	8	68
2	16	146	18	107	328

Test3(2,2)

Subbatch	Time (j) and location (v) of first recapture						
j =	4		5		6		-
v =	1-3	2	1-3	2	1-3	2	-
-	112	670	50	218	22	85	1559
1-3	26	61	5	12	7	9	163
2	23	286	12	95	6	52	553

Test3(3,2)

Subbatch	Time (j) and location (v) of first recapture				
j =	3		4-5-6		-
v =	1-2	3	1-2	3	-
-	105	136	89	72	623
1-2-3	10	22	4	5	32

Test3(2,3)

Subbatch	Time (j) and location (v) of first recapture			
j =	4-5-6			-
v =	1-2		3	-
-	91		154	473
1-2	3		6	8
3	18		83	75

Test3(3,3)

Subbatch	Time (j) and location (v) of first recapture						
j =	5		6				-
v =	1	2-3	1	2-3			-
-	150	112	57	36			643
1	224	41	54	16			391
2-3	30	27	10	6			155

Test3(4,1)

Subbatch	Time (j) and location (v) of first recapture				
j =	6				-
v =	1	2-3			-
-	62	31			317
1	176	31			404
2	31	35			167
3	2	4			31

Test3(5,1)

Subbatch	Time (j) and location (v) of first recapture				
j =	5		6		-
v =	1-3	2	1-3	2	-
-	91	398	38	117	1040
1	30	51	15	24	157
2	42	376	23	115	888
3	11	18	2	8	63

Test3(4,2)

Subbatch	Time (j) and location (v) of first recapture				
j =	6				-
v =	1-3	2			-
-	63	234			748
1	39	55			244
2	44	346			974
3	9	19			112

Test3(5,2)

Subbatch	Time (j) and location (v) of first recapture				
j =	5		6		-
v =	1-2	3	1-2	3	-
-	92	130	73	60	694
1-2	10	6	2	2	40
3	6	60	7	37	126

Test3(4,3)

Subbatch	Time (j) and location (v) of first recapture				
j =	6				-
v =	1-2	3			-
-	85	72			504
1-2	17	6			52
3	21	90			145

Test3(5,3)

Figure 5. Components of Test3G after pooling for the Canada geese data. Within each table, the individuals are arranged by location of previous capture in rows, and next capture in columns; in both cases, row or column, a "-" sign means no capture. For example, among the individuals released at occasion 3 and site 3 (Test3(3,3)), 154 individuals had not been seen before time 3 (the row heading is a "-") and were next seen at occasions 4, 5, or 6 at site 3.

whatever the present location of an animal, there is a strong positive relationship between where it has last been seen and where it will next be seen again. Thus, TestWBWA strongly supports the hypothesis of memory in the choice of a wintering region. Using TestWBWA to estimate the residual deviance in an analysis of deviance, the difference in deviance between AS and JMV is not significant ($F(24,\ 26) = 0.22,\ P = 1$). This confirms that JMV does not represent an improvement over AS in this particular case.

6. Discussion

If, from a biological point of view, the AS model appears as the natural generalization to several sites of the CJS model, then—as already noted by Brownie et al. (1993)—from a methodological point of view the JMV model is a better candidate for the title. Brownie et al. (1993) have pointed out the similarity of the moment estimators of CJS and JMV models. We add that characterization 1 convincingly relates JMV, rather than AS, to CJS. However, there are also limits

Batches (time, location)	Time (j) and location (v) of first recapture											
$j =$	3			4			5			6		
$v =$	1	2	3	1	2	3	1	2	3	1	2	3
$(u < 2, 1)$	36	18	0	13	6	0	6	5	1	5	2	0
$(u < 2, 2)$	36	158	2	22	92	3	7	32	2	3	22	0
$(u < 2, 3)$	11	30	18	3	10	10	0	8	3	2	5	3
$(2, 1)$	491	134	0	149	71	3	51	42	3	21	13	0
$(2, 2)$	159	869	15	63	335	10	41	164	3	18	74	2
$(2, 3)$	14	101	158	8	47	48	7	16	18	1	14	11

TestM2

Batches (time, location)	Time (j) and location (v) of first recapture								
$j =$	4			5			6		
$v =$	1	2	3	1	2	3	1	2	3
$(u < 3, 1)$	162	77	3	57	47	4	26	15	0
$(u < 3, 2)$	85	427	13	48	196	5	21	96	2
$(u < 3, 3)$	11	57	58	7	24	21	3	19	14
$(3, 1)$	564	200	8	150	116	5	52	46	2
$(3, 2)$	125	1017	36	53	325	14	29	146	6
$(3, 3)$	7	45	178	11	27	39	1	21	26

TestM3

Batches (time, location)	Time (j) and location (v) of first recapture					
$j =$	5			6		
$v =$	1	2	3	1	2	3
$(u < 4, 1)$	207	163	9	78	61	2
$(u < 4, 2)$	101	521	19	50	242	8
$(u < 4, 3)$	18	51	60	4	40	40
$(4, 1)$	404	175	5	121	58	0
$(4, 2)$	132	843	42	64	264	14
$(4, 3)$	19	89	196	12	70	99

TestM4

Figure 6. Components of TestM for the Canada geese data. In each table, the three upper rows are mixtures, the three lower rows are bases (see Figure 3 for details). For instance, given that TestM3 relates to occasion 3, "196" in the middle of its second row means that 196 individuals had been released earlier at site 2 (row $(u < 3, 2)$), were not captured at occasion 3 (their location then is unknown), and were next recaptured at site 2 and occasion 5 ($v = 2$, $j = 5$). The animals captured at occasion 3 appear in the bottom rows (the bases).

Table 4
Results of the goodness-of-fit test to the AS model for the Canada geese data

Summary of Test3G results			
Component	Chi-square	*df*	*P*-level
Test3(2,1)	39.5658	12	<0.0001
Test3(2,2)	38.5977	8	<0.0001
Test3(2,3)	18.3610	4	0.0010
Test3(3,1)	118.4752	12	<0.0001
Test3(3,2)	59.7354	12	<0.0001
Test3(3,3)	49.6930	4	<0.0001
Test3(4,1)	90.1297	8	<0.0001
Test3(4,2)	64.9801	12	<0.0001
Test3(4,3)	76.6404	8	<0.0001
Test3(5,1)	62.3343	6	<0.0001
Test3(5,2)	53.7470	6	<0.0001
Test3(5,3)	88.1583	4	<0.0001
Test3G	760.4179	96	<0.0001
Summary of TestM results			
Component	Chi-square	*df*	*P*-level
TestM2	34.6852	27	0.1470
TestM3	36.0371	18	0.0070
TestM4	23.0983	9	0.0060
TestM	93.8206	54	0.0006
Likelihood ratio test between the JMV and the AS models			
	Chi-square	*df*	*P*-level
	101.282	24	<0.0001

to the correspondence between the unisite and multisite situations. If the number of occasions k is greater than three, the moment-type estimators of the JMV model analogous to those of the CJS model (see Appendix in Brownie et al., 1993) are not maximum likelihood estimators. This is most probably linked to the fact that, apart from the binomial case, the minimal sufficient statistics for mixtures of multinomials is of greater dimensionality than the set of parameters—as can be easily verified using proportional likelihood equivalence classes (see Cox and Hinkley, 1974, p. 24). Then the marginal totals cease to be sufficient.

The main result of this article is that the combined use of Test3G and TestM makes possible an assessment of the fit of the JMV model. However, this model is not as interesting to biologists as it may be to methodologists. It would thus be very useful to translate the constraint on the β's that differentiates AS from JMV in terms of properties of the m_{ij}^{lm}'s or of some other statistics. So far, our attempts have been unsuccessful. Pending progress, the ability to fit the JMV model is thus critical, and development of current software in this respect is highly desirable. If the JMV model could be fitted routinely, the goodness-of-fit test to the JMV model, combined with the comparison of models JMV and AS, would be a way to validate the analyses of the many ongoing multistate studies.

As proposed, the tests 3G and M are somewhat raw and could probably be made more specific by partitioning and pooling to improve both their ease of interpretation and their efficiency. In this article, we have attempted to render Test3G more informative for the Canada goose example. A subtest of Test3G, which we named TestWBWA, apparently captured most of the lack of fit in our example, i.e., probably most of the variability due to "memory." As we believe that the memory model is often a biologically more plausible alternative to the AS model than is JMV, we believe that the strategy for partitioning should yield tests sensitive to the memory model alternative. Partitioning should reflect a biologically important alternative even when dealing with states instead of sites. Beyond that, a general remark is that the meaning of the states depends on the particular study and that, contrary to occasions, they have no a priori compelling ordering. Hence, it may be necessary to develop different strategies of partitioning and pooling, corresponding to broad classes of data.

The methods described in this article are implemented in the software program `u-care` version 2.0 available at the web address `ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR`, directory `u-careV2.0`.

Table 5

Contingency tables making up test "where before" vs. "where after" for the Canada geese data. Each component WBWA(i,l) contains the animals seen at occasion i and site l (the current location) that had been seen at least once previously and were seen at least once later. They are arranged according to their most recent capture location (the rows) and to their next capture location (the columns). For example, 19 *in WBWA*(5,2) *means that among the animals captured at occasion* 5 *and site* 2, 19 *had been previously captured at site* 3 (*third row*) *and were next recaptured at site* 2 (*second column*). *The associated p-value of Fisher's exact test for homogeneity is given below each table. A symbol* (+) (*resp.* (−)) *following an observed number means that the corresponding cell has a relative positive* (*resp. negative*) *contribution to the chi-square test for homogeneity greater than* 2 *per cent*

$i =$	2	3	4	5
$l = 1$	102 (+) 9 (−) 0 24 (−) 14 (+) 0 10 (−) 5 (+) 0 $P < 0.0001$	228 (+) 26 (−) 1 45 (−) 49 (+) 2 2 (−) 4 (+) 2 (+) $P < 0.0001$	278 (+) 57 (−) 0 (−) 39 (−) 29 (+) 2 1 (−) 2 (+) 0 $P < 0.0001$	176 (+) 31 (−) 0 31 (−) 35 (+) 0 2 2 2 (+) $P < 0.0001$
$l = 2$	13 (+) 8 (−) 0 31 (−) 253 3 1 10 2 (+) $P < 0.0001$	21 (+) 39 (−) 1 32 (−) 433 9 (−) 4 43 12 (+) $P < 0.0001$	44 (+) 75 (−) 1 52 (−) 491 13 0 (−) 26 13 (+) $P < 0.0001$	38 (+) 55 (−) 1 39 (−) 346 (+) 5 4 19 5 (+) $P < 0.0001$
$l = 3$	0 0 0 1 (+) 2 (+) 0 (−) 1 (−) 10 27 $P = 0.0160$	0 0 0 0 (−) 3 (+) 6 (−) 2 16 (−) 83 $P = 0.3204$	3 (+) 1 1 (−) 1 7 (+) 7 (−) 4 (−) 9 (−) 97 $P < 0.0001$	2 (+) 5 (+) 1 (−1) 1 9 (+) 5 (−) 1 (−) 20 (−) 90 (+) $P < 0.0001$

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Résumé

L'identification d'un modèle qui ajuste les données est une étape critique d'une analyse de capture-recapture. Pour les modèles multisites (aussi dits multi-états) un tel test n'était pas disponible. Nous en proposons un sous la forme de tables de contingence à tester pour homogénéité ou mélange pour le modèle JMV qui est une généralisation du modèle de référence d'Arnason-Schwarz (AS). Pour ce dernier modèle nous suggérons de compléter le test précédent par le test du rapport de vraisemblance entre les deux modèles. L'examen d'un exemple nous conduit de plus à proposer un partitionnement qui met en avant le rôle du modèle à mémoire (Brownie et al., 1993) comme alternative biologiquement plus plausible au modèle AS.

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Appendix

The Mixture Property of the Arnason-Schwarz Model

In this appendix, we establish the mixture property, stated as the consequence of biological property 3 in the main text, for batch (i, l) (the mixture), and batches $(i + 1, 1)$ to $(i + 1, s)$ (the bases). Let α_i^{lm} denote the product $\phi_i^{lm} p_{i+1}^m$, β_i^{lm} the product $\phi_i^{lm}(1 - p_{i+1}^m)$, and $\pi_{ij}^{lm} = E(m_{ij}^{lm} \mid R_i^{lm})/R_i^{lm}$ the cell probability. Then:

Theorem A1: *The Arnason-Schwarz model implies that* π_{ij}^{lm}, *cell probability, is of the form* $\delta_l' \prod_{u=i}^{j-2} B_u A_{j-1} \delta_m, j > i$ *with* $\delta_l = (0, \ldots, 1, 0, \ldots)'$ (1 *at position* l) *and* $A_i = (\alpha_i^{lm})_{1<l,m<s}$, $i = 1, \ldots, k-1$; $B_i = (\beta_i^{lm})_{1<l,m<s}$, $i = 1, \ldots, k-2$.

In particular, we have

Proposition A1:

$$\pi_{i,i+1}^{lm} = \alpha_i^{lm}$$

and given that

Lemma: $AB = \sum_{v=1}^{s} A\delta_v \delta_v' B = A \sum_{v=1}^{s} \delta_v \delta_v' B$, *where* s *is the common number of columns of* A *and rows of* B, we also have:

Proposition A2:

$$\pi_{ij}^{lm} = \sum_{v=1}^{s} \beta_i^{lv} \pi_{i+1,j}^{vm} \quad \forall j > i+1$$

Proof.

$$\begin{aligned}
\pi_{ij}^{lm} &= \delta_l' \prod_{u=i}^{j-2} B_u A_{j-1} \delta_m \\
&= \delta_l' B_i \prod_{u=i+1}^{j-2} B_u A_{j-1} \delta_m \\
&= \sum_{v=1}^{s} \delta_l' B_i \delta_v \delta_v' \prod_{u=i+1}^{j-2} B_u A_{j-1} \delta_m \\
&= \sum_{v=1}^{s} \beta_i^{lv} \pi_{i+1,j}^{vm}.
\end{aligned}$$

□

We now consider the probability λ_i^l that an animal belonging to batch (i, l) is ever reobserved: $\lambda_i^l = \sum_{j=i+1}^{k} \sum_{m=1}^{s} \pi_{ij}^{lm}$.

A generalization of the recurrence relationship for the lambdas as given in (Burnham 1991, p. 27) is

Theorem A2:

$$\lambda_i^l = \sum_{m=1}^{s} \alpha_i^{lm} + \sum_{m=1}^{s} \beta_i^{lm} \lambda_{i+1}^m$$

Proof.

$$\begin{aligned}
\lambda_i^l &= \sum_{j=i+1}^{k} \sum_{m=1}^{s} \pi_{ij}^{lm} \\
&= \sum_{m=1}^{s} \pi_{i,i+1}^{lm} + \sum_{j=i+2}^{k} \sum_{m=1}^{s} \pi_{ij}^{lm} \\
&= \sum_{m=1}^{s} \alpha_i^{lm} + \sum_{j=i+2}^{k} \sum_{m=1}^{s} \sum_{v=1}^{s} \beta_i^{lv} \pi_{i+1,j}^{vm} \\
&= \sum_{m=1}^{s} \alpha_i^{lm} + \sum_{v=1}^{s} \beta_i^{lv} \sum_{j=i+2}^{k} \sum_{m=1}^{s} \pi_{i+1,j}^{vm} \\
&= \sum_{m=1}^{s} \alpha_i^{lm} + \sum_{v=1}^{s} \beta_i^{lv} \lambda_{i+1}^v.
\end{aligned}$$

□

It is now possible to demonstrate that

THEOREM A3: *The survivors from batch* $(i,\ l)$*—i.e., those released at site* l *and time* i*, that are captured at the different sites from time* $i+2$ *to time* k $(m_{i,j}^{l,v},\ j = i+2,\ldots,k,\ v = 1,\ldots,s)$*—are distributed according to a multinomial, which is a mixture of the* s *multinomials arising from the recaptures at the same times and at the same sites as those of the survivors of the* s *batches released at time* $i+1$ *at the different sites.*

Proof. The cell probabilities of the multinomial distributions for batch $(i,\ l)$ and for the batches $i+1$ are respectively:

batch$(i,\ l)$	$\pi_{i,i+1}^{l,1}$	$\ldots$	$\pi_{i,i+2}^{l,1}$	$\ldots$	$\ldots$	π_{ik}^{ls}	$1-\lambda_i^l$
batches i+1	$\pi_{i+1,i+2}^{1,1}$	$\ldots$	$\pi_{i+1,i+2}^{1,k}$	$\ldots$	$\ldots$	$\pi_{i+1,s}^{1,k}$	$1-\lambda_{i+1}^1$
	$\vdots$					$\vdots$	$\vdots$
	$\pi_{i+1,i+2}^{s,1}$	$\ldots$					

The corresponding conditional distributions after restriction to the observations made from $i+2$ to k are:

batch$(i,\ l)$	$\pi_{i,i+2}^{l,1}$	$\ldots$	π_{ik}^{ls}	$\times \frac{1}{\lambda_i^l - \sum_{m=1}^{s} \alpha_i^{lm}}$
batches i+1	$\pi_{i+1,i+2}^{1,1}$	$\ldots$	$\pi_{i+1,s}^{1,k}$	$\times \frac{1}{\lambda_{i+1}^1}$
	$\vdots$		$\vdots$	$\vdots$
	$\pi_{i+1,i+2}^{s,1}$	$\ldots$		

From $\pi_{ij}^{lm} = \sum_{n=1}^{s} \beta_i^{ln} \pi_{i+1,j}^{nm}$ (see above), it follows that:

$$\frac{\pi_{ij}^{lm}}{\lambda_i^l - \sum_{m=1}^{s} \alpha_i^{lm}} = \sum_{n=1}^{s} \left(\frac{\beta_i^{ln} \lambda_{i+1}^n}{\lambda_i^l - \sum_{m=1}^{s} \alpha_i^{lm}} \right) \frac{\pi_{i+1,j}^{nm}}{\lambda_{i+1}^n},$$

$$\forall m \in [1,s], j \in [i+2,k]$$

where, according to Theorem A2, $\sum_{n=1}^{s} \left(\frac{\beta_i^{ln} \lambda_{i+1}^n}{\lambda_i^l - \sum_{m=1}^{s} \alpha_i^{lm}} \right) = 1$. □