Modeling pair-wise dependent capture outcomes in mark-recapture experiments

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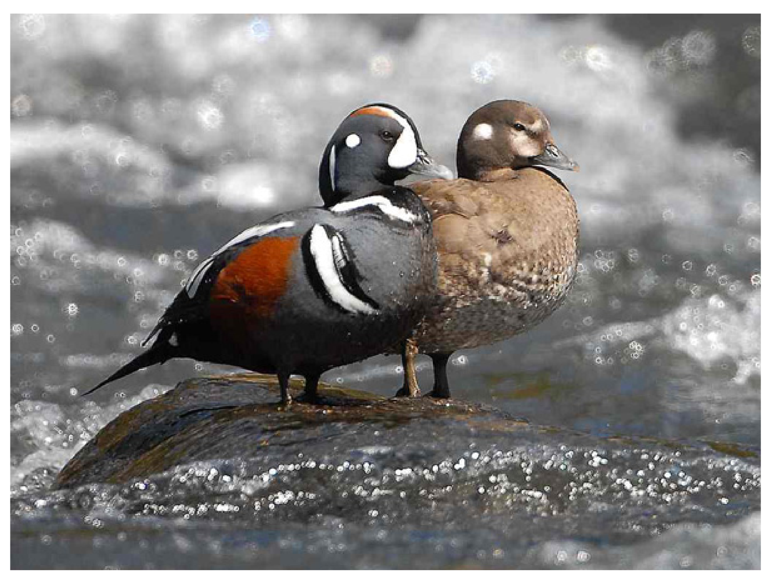
Introduction

Mark-recapture models often formulate the model likelihood as a product of individual likelihood components, thereby assuming independence among individuals. However, there exist many non-trivial situations, such as mating pairs, where we can expect to observe a dependency between individuals.

We present an extension of the multistate state-space Cormack-Jolly-Seber (CJS) model proposed by Gimenez et al (2007) that accommodates a pair-wise dependency in capture outcomes among individuals within a mating pair.

Motivation: McLeod River Harlequin Duck Study

The motivation comes from a long-term study of harlequin ducks (12 years) in the McLeod river region located Alberta, Canada. Harlequin ducks typically exhibit long term pair bonds, which are formed on the wintering grounds (West Coast) prior to their migration to the McLeod river region for reproduction. In addition to basic capture histories, this study has maintained an in-depth database of all mating pairs throughout the 12 years duration.



Harlequin duck (*Histrionicus histrionicus*) breeding pair.
Photo credit: Paul Higgins

Model Development

We assume all mating pairings are formed prior to the start of the experiment (i.e. on the wintering ground), that a linear dependence in capture outcomes exists within mating pairs (but with independence between pairs) and the process of survival is independent. We will be consider an experiment with *T* capture occasion.

For mating pair *j* there are four possible female/male pair states: alive/alive, alive/dead, dead/alive and dead/dead. Let $Z_{j,t}$ be a random state vector talking the values $(1,0,0,0)$, $(0,1,0,0)$, $(0,0,1,0)$ and $(0,0,0,1)$ to represent these states on occasion *t*. Individuals without mates will are restricted to two of the possible four states depending on sex.

The fundamental model parameters are as follows:

- $\phi^s_{j,t}$ - Survival probability for t to $t+1$ for an individual of sex $s \in \{M, F\}$ in pair j.
- $p^s_{j,t}$ - Marginal capture probability for an individual of sex $s \in \{M, F\}$ in pair j on occasion t.
- ρ - Correlation coefficient between capture outcomes for paired individuals.

Our formulation assumes that a linear dependence occurs in the capture outcomes of paired individuals only, but with independence between mating pairs. Using the definition of linear covariance the probabilities of the possible pair-wise capture outcomes for female *k* and male *l* of pair *j* will be determined as a function of ρ and $p^s_{j,t}$ (Table 1).

Table 1: Probabilities for pair-wise capture outcomes a mating pair consisting of female *k* and male *l*. A feature of the formulation is that the marginal capture probabilities for each sex will be the same as for single individuals. Pair and time specific subscripts have been removed for clarity.

	$Y_l = 0$	$Y_l = 1$	Marginal (Y_k)
$Y_k = 0$	$p^{00} = 1 - p^F - p^M + \rho\sigma^F\sigma^M + p^F p^M$	$p^{m0} = p^M - \rho\sigma^F\sigma^M - p_1 p_2$	$1 - p^F$
$Y_k = 1$	$p^{f0} = p^F - \rho\sigma^F\sigma^M - p^F p^M$	$p^{fm} = \rho\sigma^F\sigma^M + p^F p^M$	p^F
Marginal (Y_l)	$1 - p^M$	p^M	

Observation and State Equations

Standard CJS models condition on first capture, setting the first capture probability to 1 since this is the only possible outcome. For mating pairs, first capture consists of three possible outcomes, which we will need to condition for when formulating the observation model. As such, the *observation equation* of the first capture occasion for the mating pair will be

$$Y_{j,t}|Z_{j,t} \sim \text{multinomial}\left(1, Z_{j,t}\begin{bmatrix} \frac{p^{fm}_{j,t}}{1-p^{00}_{j,t}} & \frac{p^{f0}_{j,t}}{1-p^{00}_{j,t}} & \frac{p^{m0}_{j,t}}{1-p^{00}_{j,t}} & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}\right) \text{ for } t = e_j,$$

where e_j is the first encounter of either member of mating pair *j*. The observation equation for subsequent captures (i.e. $e_j < t$) is

$$Y_{j,t}|Z_{j,t} \sim \text{multinomial}\left(1, Z_{j,t}\begin{bmatrix} p^{fm}_{j,t} & p^{f0}_{j,t} & p^{m0}_{j,t} & 1 - p^{fm}_{j,t} - p^{f0}_{j,t} - p^{m0}_{j,t} \\ 0 & p^F_{j,t} & 0 & 1 - p^F_{j,t} \\ 0 & 0 & p^M_{j,t} & 1 - p^M_{j,t} \\ 0 & 0 & 0 & 1 \end{bmatrix}\right) \text{ for } e_j < t \le T.$$

The *state equation* for $Z_{j,t}$ can be formulated either as multinomial or a combination of Bernoulli trials. The multinomial state equation is defined as

$$Z_{j,t+1}|Z_{j,t} \sim \text{multinomial}\left(1, Z_{j,t}\begin{bmatrix} \phi^F_{j,t}\phi^M_{j,t} & \phi^F_{j,t}(1-\phi^M_{j,t}) & (1-\phi^F_{j,t})\phi^M_{j,t} & (1-\phi^F_{j,t})(1-\phi^M_{j,t}) \\ 0 & \phi^F_{j,t} & 0 & 1-\phi^F_{j,t} \\ 0 & 0 & \phi^M_{j,t} & 1-\phi^M_{j,t} \\ 0 & 0 & 0 & 1 \end{bmatrix}\right).$$

Alternatively, for *n* total individuals the state equation will be defined as

$$X_{i,t+1}|X_{i,t} \sim \text{Bernoulli}\left(X_{i,t}\phi^s_{i,t}\right)$$

for $t \ge f_i$, where f_i is the first known instant where the individual *i* has entered the experiment. Our mating-pair state vector for occasion *t* will then be defined as

$$Z_{j,t}|X_{l,t}, X_{k,t} = \left[\; X_{k,t}X_{l,t} \quad X_{k,t}(1-X_{l,t}) \quad (1-X_{k,t})X_{l,t} \quad (1-X_{k,t})(1-X_{l,t}) \;\right],$$

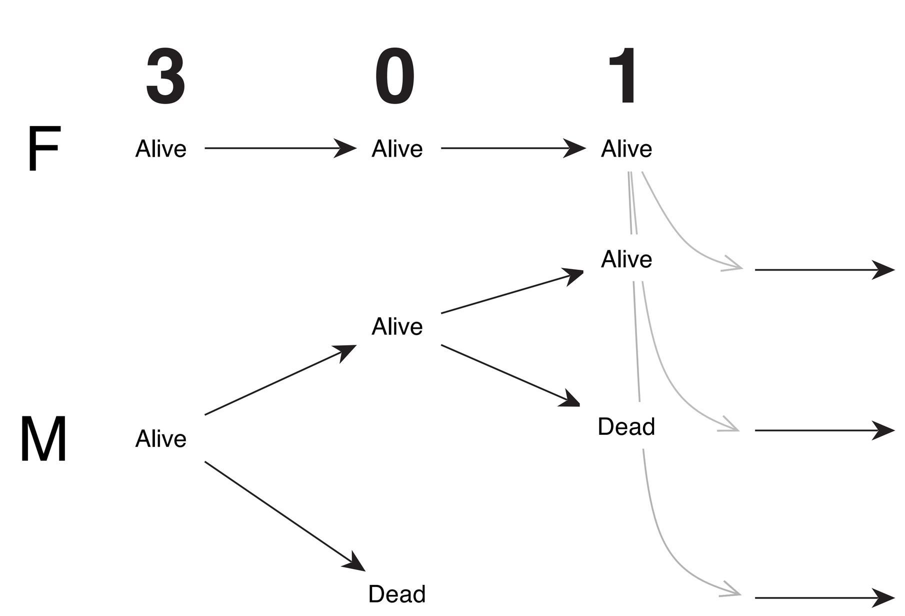
for female *k* and male *l* of mating pair *j*.

Example Capture History

Modeling mating pair capture histories is more complex than a standard CJS model as we need are defining our latent states based on the fates of the two individuals in a mating pair. For example the capture history `301` indicates a mating pair that were captured together on the 1st occasion, both missed on the 2nd occasion and only the female was caught on the 3rd occasion. The marginal probability statement will be as follows

$$P(301) = \frac{p^{fm}}{1-p^{00}_{j,1}}\phi^F_{j,1}\left(\phi^M_{j,1}p^{00}_{j,2}\left(\phi^F_{j,2}\left(\phi^M_{j,t}p^{f0}_{j,3} + (1-\phi^M_{j,t})p^F_{j,t}\right)\right) + (1-\phi^M_{j,1})(1-p^F_{j,t})\phi^F_{j,2}p^F_{j,3}\right),$$

which can be broken down in terms of one female and three possible male fates:



$$P(301) =$$

$$\frac{p^{fm}_{j,1}}{1-p^{00}_{j,1}}\phi^F_{j,1}\phi^M_{j,1}p^{00}_{j,2}\phi^F_{j,2}\phi^M_{j,2}p^{f0}_{j,3}$$

$$+$$

$$\frac{p^{fm}_{j,1}}{1-p^{00}_{j,1}}\phi^F_{j,1}\phi^M_{j,1}p^{00}_{j,2}\phi^F_{j,2}(1-\phi^M_{j,2})p^F_{j,3}$$

$$+$$

$$\frac{p^{fm}_{j,1}}{1-p^{00}_{j,1}}\phi^F_{j,1}(1-\phi^M_{j,1})(1-p^F_{j,2})\phi^F_{j,2}p^F_{j,3}$$

Implementation

The overall likelihood (not shown) can be formulated by taking the product of the individual mating pair components and integrating over the possible states. Due to the complicated high-dimensionality of this type of problem we used MCMC methods and fit the model using WinBUGS.

Example (Simulation Study)

Data was simulated (*n* = 1200) with a pair-wise capture dependency between mating pairs as outlined in Table 1. The resulting data was fit with a simple CJS model using MARK and the proposed rho-CJS model using WinBUGS and uninformative priors (Table 2). Both models produced identical point estimates for survivorship and recapture probabilities, however the rho-CJS model produced slightly lower posterior standard deviations and was successfully able to estimate the correlation coefficient ρ.

Table 2: Parameter estimates from the simulation study (n = 1200) for the proposed rho-CJS model (fit with WinBUGS) and a regular CJS model (fit with MARK)

Model Parameter	True Value	Naïve CJS Estimates (MARK)		CJS with pair-wise dependent captures (WinBUGS)			
		Est	SE	Est	SD	95 % CI	
ϕ	0.800	0.7951	0.0057	0.7952	0.0056	0.7842	0.8064
ρ	0.400	-	-	0.3499	0.0297	0.2915	0.4081
p^F	0.731	0.7301	0.0112	0.7323	0.0094	0.7138	0.7500
p^M	0.818	0.8349	0.0095	0.8262	0.0083	0.8098	0.8424
p^{00}	0.118	-	-	0.1052	0.0078	0.0902	0.1207
p^{f0}	0.065	-	-	0.0685	0.0059	0.0575	0.0805
p^{m0}	0.151	-	-	0.1624	0.0084	0.1460	0.1795
p^{fm}	0.666	-	-	0.6638	0.0097	0.6449	0.6833

Discussion

The proposed rho-CJS formulation handles pair-wise dependency in capture outcomes between mating pairs. Information that is auxiliary to the capture histories of normal CJS type experiments is used to determine mating pairs. The proposed model formulation also results in individual capture history frequencies (e.g. `101`) that will be identical to a regular CJS experiment. As such, pair-wise dependency in capture outcomes of this type does not affect regular CJS type models. Our formulation however has the added advantages of being able to estimate the capture correlation within a mating pair as well as improved capture probability precision. The precision increase results from the additional zero observations introduced into the data by mates that were known to exist, but were never captured. Future model extensions will allow for pairing after the commencement of the experiment and for mate switching during the experiment. This modeling framework may have great utility for a number of long lived species where mate pairing is well known.

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