

ON THE APPLICATION OF MULTIPLE SPECIES APPROACHES TO ESTIMATE SURVIVAL IN CORMACK JOLLY SEBER CAPTURE-RECAPTURE MODELS

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Understanding the survival process of wild populations can be critical in managing and conserving animal populations due to the strong impact it has on population dynamics (Lebreton et al. 1992). Within the capture-recapture literature, the Cormack Jolly Seber Model (Lebreton et al. 1992) has received much attention because of its universal approach to estimating apparent survival while accounting for imperfect capture and the few assumptions that are made in order to estimate these parameters.

The majority of demographic approaches within the capture-recapture framework have been developed for the analysis of single individual species, ignoring the biological context in which the species resides. Although models of biotic interaction are much harder to parameterize (e.g., predator-prey interactions, mutualisms, etc.), the community in which a species resides also provides information in the form of shared exposure. When species are syntopic, they are exposed to similar environments and interactions, both biotic and abiotic. However, the incorporation of this information has not typically been performed within the Cormack Jolly Seber framework.

Recent advances within the occupancy estimation literature have provided a framework to extend Cormack Jolly Seber models to multiple species using random effects (Dorazio and Royle 2005, Dorazio et al. 2006; Kery and Royle 2008, 2009; DeWan and Zipkin et al. 2010). In contrast to monitoring species individually, the multi-species approach allows for the “borrowing” of information from similar species in order to improve estimates of individual species occurrences, including rare species, or in the case of the CJS model, to improve estimates of apparent survival (DeWan and Zipkin et al. 2010). In addition, this approach provides a better understanding of the aggregated response of groups of species or the entire community to changes in the landscape or locality. This approach is based on the use of hierarchical models parameterized with random components representing individual species level demographic parameters that belong to hyperdistributions with a mean and variance that can be estimated from the entire community.

In this paper, I focus on the extension of the multi-species approach to the estimation of survival parameters within a hierarchical modeling format. In doing so, I pull on two separate modeling strategies developed for multi-species demographic inference: (1) community modeling occupancy estimation procedures developed by Dorazio and Royle (2005) and Dorazio et al. (2006) and (2) models of synchrony developed for multinomial mark-resight models (Lahoz-Monfort et al. 2011). I also demonstrate the use of additional relationships between the species within the sampling inference that can take the form of guilds, families, or even biological or ecological traits.

THE CJS MODEL AS A MULTI-SPECIES STATE-SPACE MODEL

The data observed in a capture-recapture study can be summarized in a capture-history array (\mathbf{Y}), which has dimensions $I \times J \times T$, where I is the total number of species that were captured and marked in the population, J is the total number of individuals of each species marked, and T is the number of capture occasions. Note that J and T do not have to be equal across all species, but for easier notation they are described here to be constant for all species. The elements of the three dimensional arrays are binary, and a one at position i, j, t indicates that an individual j of species i was captured at occasion t . Note $y_{1,j,t}$ is

equivalent to a standard capture history matrix used within the Cormack Jolly Seber model of analysis for species 1.

State-space models (Kalman 1960) are hierarchical models that separate an observed array of information into two components: (1) a state component that represents process variation (e.g., variation in survival) and (2) an observation component that represents error in the collection or observation of the original data (e.g., variation in capture; De Valpine and Hastings 2002, Buckland et al. 2004, Royle and Dorazio 2008, Kery and Schaub 2011). The state-space model adopted here for the multi-species CJS model of apparent survival given imperfect capture is a derivation of the single-species CJS introduced by Gimenez et al. (2007) and Royle (2008) and formulated using the model provided by Kery and Schaub (2011). The model consists of two sets of equations. The state-process equation describes the true but unobservable state of species being alive and present (i.e., apparent survival), and the observation equation describes the observation process of whether individuals were seen or not seen (i.e. capture probability).

In order to estimate apparent survival from the three-dimensional capture-history array (\mathbf{Y}), a second array (\mathbf{Z}) is defined to represent the latent (i.e., unobservable) true state of individual j of species i at time t . Since the CJS model only utilizes events after the first capture, a matrix (\mathbf{F}) of the occasions at which individual j of species i is first captured (i.e., marked) is created which has dimensions equal to $I \times J$.¹ Thus, the state of individual j of species i ($z_{i,j,f_{i,j}}$) is one with probability one because the individual of the species is known to be alive. All subsequent states after $f_{i,j}$ are modeled using a Bernoulli distribution conditional on being alive and present at the previous occasion with probability $\phi_{i,j,t}$ ($t \in 1, \dots, T-1$):

$$z_{i,j,t+1}|z_{i,j,t} \sim \text{Bernoulli}(\phi_{i,j,t} \times z_{i,j,t}). \quad \text{Eq. 1}$$

Note the Markovian conditionality of $\phi_{i,j,t}$ being represented as a product with the state variable at the previous time. Thus, individuals that are dead or not present in the population are ensured to remain out of the state process for further time periods (Kery and Schaub 2011). In order to incorporate species with different numbers of marked individuals available for capture, a second “known” state matrix (\mathbf{W}) can be included within the product for the Bernoulli trial where $w_{i,j}$ indexes the presence of the marked individual j of species i in the population at the locality:

$$z_{i,j,t+1}|z_{i,j,t} \sim \text{Bernoulli}(\phi_{i,j,t} \times z_{i,j,t} \times w_{i,j}). \quad \text{Eq. 2}$$

This second “known” state matrix is required given that the capture-history array (\mathbf{Y}) has a constant second dimension equal to the maximum number of marked individuals of any of the species. Thus, for some species the extra individuals are zeros that are not incorporated into the model given that \mathbf{W} indexes real marked individuals.

Similarly to the process equation for apparent survival, capture probability ($p_{i,j,t}$) can be modeled as a realization of a Bernoulli trial with probability ($p_{i,j,t}$) conditional on the individual of the species being alive at occasion t ($t \in 2, \dots, T$):

$$y_{i,j,t}|z_{i,t} \sim \text{Bernoulli}(p_{i,j,t} \times z_{i,j,t}). \quad \text{Eq. 3}$$

¹ **R** code to create the initial captured matrix (\mathbf{F}) from the capture-history array (\mathbf{Y}) can be found in Appendix A. Likewise, **R** code to create the known presence state matrix (\mathbf{W}) can be found in Appendix B.

Because the Bernoulli trial includes the latent variable \mathbf{Z} , dead or not present individuals are not included in the observation process. Likewise, because $\mathbf{z}_{i,t}$ is conditional on the state of the individual at $\mathbf{z}_{i,t-1}$ which is conditional on $\mathbf{w}_{i,j}$, no further information is needed to incorporate species with different numbers of marked individuals.

FIXED EFFECT PARAMETERIZATION

Up to this point the multi-species state-space model does not differ in the estimation of individual species level survival or capture probabilities from a standard single-species state-space CJS model. The only difference here is the addition of a dimension representing different species of the observation matrix \mathbf{Y} , the latent state matrix \mathbf{Z} , and the initial capture matrix \mathbf{F} . The state matrix (\mathbf{W}) that indexes the presence of marked individuals of each species in the population or community should also be included if there is a different number of marked individuals for each species. Within this specification, each species can be estimated independently and separately using a fixed effect parameterization and can take the form of a constant model, time variant model, or a covariate model for both $\phi_{i,j,t}$ and $p_{i,j,t}$. For example, a regression formula can be specified for the parameter $\phi_{i,j,t}$ using the logit link:

$$\text{logit}(\phi_{i,j,t}) = \beta_{0i} + \beta_{1i} \times x_{1i,t} \dots + \beta_{Ki} \times x_{Ki,t}. \quad \text{Eq. 4}$$

where β_i represents the regression coefficients indexed by species and \mathbf{X}_i represents the regressors indexed by species. Note that not all species have to have the same regressors. Estimation using this parameterization will provide the same estimates for each species as if each species was analyzed separately using the formulation provided by Kery and Schaub (2011). An example of how to perform this parameterization in WinBUGS can be found in Appendix C.

RANDOM EFFECTS PARAMETERIZATION

Although analyzing each species independently provides estimates for survival for each species, there are several reasons for not utilizing this approach. First, the number of parameters to be estimated increases with the number of species analyzed, where when n species are included in the analysis, at least $2n$ parameters need to be estimated. Second, the estimates may have poor precision and may be unstable. This is particularly the case for species with low capture probabilities or low survival (Royle and Dorazio 2008).

In order to extend these species-specific models of survival to a situation in which species are no longer independent, additional modeling assumptions that characterize the heterogeneity of apparent survival and capture probability among the species analyzed are needed (Royle and Dorazio 2008). As a basic model using the random effects parameterization, let $\mathbf{s}_i = \text{logit}(\phi_i)$, $\mathbf{r}_i = \text{logit}(p_i)$ and specify each as a bivariate normal distribution:

$$\begin{pmatrix} \mathbf{s}_i \\ \mathbf{r}_i \end{pmatrix} \sim N \left(\begin{pmatrix} \gamma \\ \alpha \end{pmatrix}, \Sigma \right) \quad \text{Eq. 5}$$

where γ and α are the mean logit-scale probabilities of survival and capture probability, respectively, among all species analyzed with the model, and Σ is the variance-covariance matrix that describes the variance in \mathbf{s}_i and \mathbf{r}_i among the species on the diagonal elements. For now, \mathbf{s}_i and \mathbf{r}_i are assumed independent, so the non-diagonal elements of this matrix are zero:

$$\Sigma = \begin{pmatrix} \sigma_s^2 & 0 \\ 0 & \sigma_r^2 \end{pmatrix}. \quad \text{Eq. 6}$$

Estimation using this parameterization accounts for species-level variation in survival and capture probability by estimating each parameter under a common distribution for all species. Estimates for survival or recapture between species are no longer estimated independently from other species, but rather, the parameter estimates are influenced by all individuals from all species. An example of how to perform this parameterization in WinBUGS can be found in Appendix D. Note that this parameterization can be combined with fixed effects as well, where each species has a non-shared fixed component and a shared random component. For example, one could specify survival as follows:

$$\text{logit}(\phi_{i,j,t}) = \beta_{0i} + \varepsilon_{si} \quad \text{Eq. 7}$$

where ε_{si} is normally distributed with a mean of zero and a variance of $\sigma_{\varepsilon_s}^2$. A similar expression can be used for capture probability.

RANDOM EFFECTS PARAMETERIZATION WITH GROUPING TERMS

A major advantage of the random effects parameterization found in Eq. 5 is that one can explicitly incorporate information on how species may be grouped (i.e., similar species). For example, information on the guilds, traits, or phylogenetic relationships can be incorporated by specifying group indicators on γ and/or α :

$$\gamma = \gamma_\mu + \delta_{Gi} \quad \text{Eq. 8}$$

where γ_μ specifies the common mean among all the groups, and δ_{Gi} represents the effect of being a member of the group which is distributed normally with a mean of zero and a variance of $\sigma_{\delta_G}^2$. An example of how to incorporate this information on groups of species in WinBUGS can be found in Appendix E.

RANDOM EFFECTS PARAMETERIZATION WITH CORRELATION BETWEEN ϕ AND p

The parameterization found in Eq. 5 can be extended to account for correlation between ϕ and p by expressing the non-diagonal elements of Σ as the covariance between ϕ and p . This parameterization is an extension of the multi-species occupancy model derived by Dorazio and Royle (2005) and Dorazio et al. (2006). Although within an occupancy model the correlation between occupancy (ψ) and detection probability is more biologically relevant, there is not a large penalty to including a correlation parameter in the model (i.e., increases K by one) and in some situations, the parameter might be helpful for rare species. Thus, Σ can be specified as follows:

$$\Sigma = \begin{pmatrix} \sigma_s^2 & \rho\sigma_s\sigma_r \\ \rho\sigma_s\sigma_r & \sigma_r^2 \end{pmatrix} = \begin{pmatrix} \sigma_s^2 & \text{cov}(s, r) \\ \text{cov}(s, r) & \sigma_r^2 \end{pmatrix} \quad \text{Eq. 9}$$

This parameterization can also be combined with the parameterization including grouping terms (Eq. 8). An example of how to perform this in WinBUGS can be found in Appendix F.

AN APPLICATION OF THE MULTI-SPECIES CJS MODEL

To examine how effective this modeling strategy is, I created a simulated dataset for 10 species with 10 occasions of capture. These 10 species were randomly assigned to 1 of 3 groups (e.g., guilds) in order to estimate true apparent survival. Each species apparent survival was simulated with a unique random number from a uniform distribution with the upper and lower bounds differing depending on group membership. Group one was simulated with bounds of 0.1 and 0.3, group two was simulated with bounds of 0.3 and 0.7, and group three was simulated with bounds of 0.5 and 0.9. Capture probability was also simulated to differ between species; however, this difference was not a function of group membership. Instead, two of the 10 species were simulated at random with a random number from a uniform distribution bounded by 0.05 and 0.15, and the other eight were simulated by a uniform bounded by 0.1 and 1. This method was chosen to ensure that at least two species would have capture probabilities less than 0.15. All capture histories were simulated under the constant CJS model (i.e., $p(\cdot)\phi(\cdot)$). Additionally, the number of new individuals marked on each sample occasion for each species was simulated using a random number bounded by 20 and 60. The function to create the simulated dataset can be found in Appendix G.

To assess how well the multi-species model performed compared to standard estimation approaches, each species was first analyzed using the multinomial single species CJS model found in program MARK (White and Burnham 1999) using the R (R Development Core Team 2012) package RMARK (Laake 2012). The parameter estimates and confidence limits were then stored in R for comparisons. Using the same simulated dataset, the species were combined into a three-dimensional array and analyzed using four of the multi-species parameterizations found above: (1) the fixed effects parameterization, (2) a random effects parameterization for survival and a fixed effects parameterization for capture probability, (3) a random effects parameterization of survival with group membership and a fixed effects parameterization for capture probability, and (4) a random effects parameterization of survival with group membership and a random effects parameterization for capture probability. Using the parameter estimates for each species in each parameterization of the CJS model, total bias in survival was estimated as:

$$\text{Total Bias} = \sum_{i=1}^n |\widehat{\phi}_i - \phi_i| \quad \text{Eq. 10}$$

where $\widehat{\phi}_i$ is the parameter estimate for apparent survival for species i , ϕ_i is the true apparent survival for species i , and n is the total number of species. Also, mean bias was calculated for each group, where mean bias is the quotient of total bias for the group divided by the number of species.

RESULTS

Of the five models used to analyze the simulated dataset, the best fit was the parameterization using random effects with grouping terms for survival and with fixed effects with capture probability (Table 1). The single-species multinomial model performed in MARK estimated survival for species from groups two and three (i.e., apparent survival of at least 0.3 or higher) with relatively low bias (mean bias of 0.05 and 0.005, respectively), and performed relatively well for species belonging to group 1 if the capture probability was high (Figure 1); however, when both survival and capture probability were low, the model performed poorly. For one species (Species 1 in Figure 1), the model provided both a severely biased estimate (bias=0.119) and a confidence interval with deceptively low coverage (Figure 1).

TABLE 1. Average bias in apparent survival for each group of species and total bias for each parameterization of the CJS model.

Model	Group 1	Group 2	Group 3	Total
Multinomial CJS	0.06922	0.046902	0.005194	0.497194
Fixed Effects	0.043864	0.04679	0.00617	0.37203
Random Survival	0.040683	0.042909	0.005225	0.342592
Random Survival with Groups	0.033408	0.046219	0.009674	0.325046
Random Survival with Groups and Random Capture	0.046644	0.046661	0.011184	0.395572

The fixed parameterization of the multi-species CJS model also provided reasonable estimates for species from groups two and three with relatively low bias (Table 1), and often the estimates and credible intervals were very similar to the ones derived using the multinomial model in MARK (Figure 1a). However, similarly to the multinomial CJS, the fixed effects parameterization performed poorly for species in group 1 with low capture probability (Figure 1a). However, the coverage of the credible interval for Species 1 in Figure 1a was much closer to the real parameter than the single species multinomial model performed in MARK (Figure 1a).

Allowing apparent survival to be a random effect coming from a hyperdistribution generally improved parameter estimates and reduced bias (Table 1). More importantly, the coverage of the credible interval for Species 1 included the real parameter used to simulate the data. However, precision for many species remained low (e.g., Species 3 in Figure 1b). When a grouping term was added to the model for the random hyperdistribution for apparent survival, bias was further reduced and precision was generally increased for most estimates (Table 1 and Figure 1c). However, the credible interval for Species 1 no longer included the true estimate. Finally, when both apparent survival and capture probability were treated as random effects, with survival being governed by group membership, bias increased beyond any of the multi-species parameterizations used in this study. Similarly, the precision of many estimates was reduced and the coverage of the credible interval did not include the true parameter for Species 1.

DISCUSSION

Although this study only provided one simulation to compare aspects of the different formulations of the CJS model, some generalizations can still be made. First, although the state-space formulation of the CJS model (Gimenez et al. 2007) is different than the multinomial formulation of the CJS model (Lebreton et al. 1992) implemented in programs like MARK and CAPTURE, the estimates of the state-space model, and the extension developed here for multiple species, can provide relatively similar estimates and credible intervals. However, one should note that the interpretation of these estimates and intervals is slightly different than in a likelihood analysis. In particular, the posterior expected values derived are a combination of both the likelihood and the prior used in the analysis. In an analysis where a subjective prior is used, the interpretation of the credible interval is much clearer (i.e., personal belief probabilities); however, when a diffuse prior is used, as in this study, the interpretation of this interval is not as clear and may not have the same properties as a confidence interval (Lele and Denis 2009). Nonetheless, it is clear that the fixed parameterization of multi-species CJS model will give equivalent estimates as the single-species CJS model and similar estimates to the multinomial likelihood model.

Second, the simulation used in this study shows how known information about species relationships can be incorporated into an analysis for multiple species. Such an approach has been advocated for other models

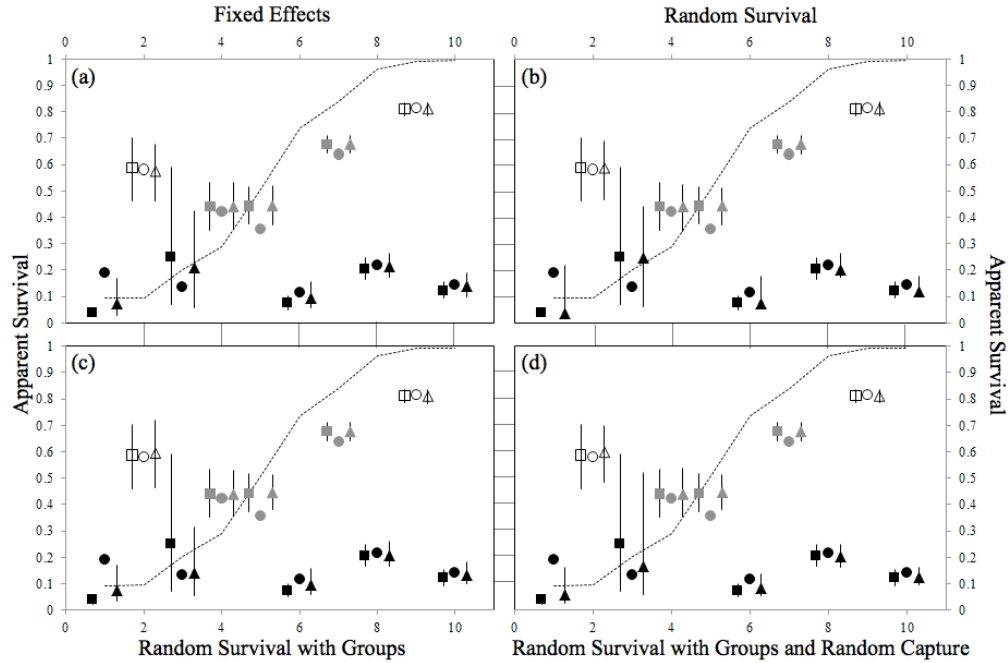


FIGURE 1. True apparent survival (circles), parameter estimates for apparent survival from the multinomial single-species CJS model (squares in all panels) and different parameterization of the multi-species CJS model (triangles). Panel a shows estimates from the fixed effects model, panel b shows estimates from the random survival model, panel c shows estimates from the model with random effects for survival including group membership, and panel d shows the estimates for the model with both random survival and random capture. All multinomial estimates are shown with 95% confidence intervals, and all multi-species CJS estimates are shown with 95% credible intervals. Colors of the symbols reflect group membership: black is group one, grey is group two, and clear is group three. Each panel also shows the true capture probability used to simulate the dataset as a dashed line.

as well (Sauer and Link 2002). Based on the simulation done in this study, one would expect reduced bias in parameter estimates and greater precision as these grouping relationships become more applicable to demographic parameter of interest and as the number of species within a group increases. A number of different grouping characteristics could be proposed: functional groups, traits, generalist vs. specialists, phylogenetic groups, etc. Thus, if several different grouping structures are hypothesized to carry predictive weight, one could assess the influence of different hierarchical formulations. However, one also must be careful not to create too many hierarchies so that the ratio of information content to the complexity of the model remains high (Lele and Denis 2009).

Finally, an interesting finding in this study is the increased bias of a model parameterized with random effects for both apparent survival and capture probability. In additional simulations not included in this analysis, this trend was found in a large number of the 100 simulations assessed. Therefore, careful consideration of the consequences of treating demographic parameters as random must be made, especially when these parameters have a hierarchical effect on the estimation of other parameters (e.g., capture probability on apparent survival). Undoubtedly, this finding deserves greater attention, especially since it is relevant to other models such as multi-species occupancy models (Dorazio and Royle 2005, Dorazio et al. 2006, Dorazio et al. 2010). However, treating detection (a parameter related to capture probability) as random is a requirement of these models in order to estimate community size. In the models provided in this

study, the only penalty in expressing capture probability as fixed is the additional parameters required to estimate the model.

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APPENDIX A. R function to create a matrix of first capture events (F) for each individual of each species for the multi-species CJS model.

```
make.F<-function(x) { #where x is a 3-dimensional array of capture histories
  get.first <- function(x) min(which(x!=0))
  if(length(dim(x))>2) {
    n.species<-dim(x)[1]
    n.ind<-dim(x)[2]
    F<-array(dim=c(n.species,n.ind))
    for(i in 1:n.species) {
      tmp<-rowMeans(x[i,,])
      n.zero<-n.ind-length(tmp[tmp>0])
      F[i,]<-c(apply(x[i,1:(n.ind-n.zero)],1,get.first),rep(dim(x)[3]-
1,n.zero))
    }
  }
  return(F)
}
F<-make.F(Y) #Create first capture matrix
```

APPENDIX B. R function to create a matrix of individual presences (W) for each species for the multi-species CJS model.

```
make.W<-function(x) { #where x is a 3-dimensional array of capture histories
  W<-array(dim=dim(x)[1:2])
  for(i in 1:dim(x)[1]) {
    tmp<-rowMeans(x[i,,])
    W[i,]<-c(rep(1,length(tmp[tmp>0])),rep(0,dim(x)[2]-length(tmp[tmp>0])))
  }
  return(W)
}
W<-make.W(Y)
```

APPENDIX C. WinBUGS model to perform a fixed effects parameterization of the multi-species CJS model.

```
model {  
  # Priors and constraints  
  for(i in 1:n.species){ #Loop over all species  
    for(j in 1:nind){ #Loop over all individuals  
      for(t in f[i,j]:(n.occasions-1)){ #Loop over capture events  
        phi[i,j,t]<-mean.phi[i] #Constant survival for each species  
        p[i,j,t]<-mean.p[i] #Constant capture prob for each species  
      } #end t  
    } # end j  
  } #end i  
  for(i in 1:n.species){ #Loop over species  
    mean.phi[i]~dunif(0,1) #Diffuse prior  
    mean.p[i]~dunif(0,1) #Diffuse prior  
  } #end i  
  # Likelihood  
  for(i in 1:n.species){ #Loop over species  
    for(j in 1:nind){ #Loop over individuals  
      z[i,j,f[i,j]]<-1 #Latent state at first capture  
      for(t in (f[i,j]+1):n.occasions){ #Loop over captures  
        #State Process  
        z[i,j,t]~dbern(eff.mul[i,j,t]) #Bernoulli for survival  
        eff.mul[i,j,t]<-mul[i,j,t]*w[i,j] #Only for indiv. captured once  
        mul[i,j,t]<-phi[i,j,t-1]*z[i,j,t-1] #Only for indiv alive and present  
        #Observation process  
        y[i,j,t]~dbern(mu2[i,j,t]) #Bernoulli for capture  
        mu2[i,j,t]<-p[i,j,t-1]*z[i,j,t] #Only for indiv. alive and present  
      }#end t  
    } #end j  
  } #end i  
} #end model
```

APPENDIX D. WinBUGS model to perform a random effects parameterization of the multi-species CJS model with no grouping or correlation.

```
model {
  # Priors and constraints
  for(i in 1:n.species){ #Loop over all species
    for(j in 1:nind){ #Loop over all individuals
      for(t in f[i,j]:(n.occasions-1)){ #Loop over capture events
        logit(phi[i,j,t])<-s[i] #Note the logit transformation
        logit(p[i,j,t])<-r[i]
      } #end t
    } #end j
    s[i] ~ dnorm(gamma, tau.s) #Random effect distribution
    r[i] ~ dnorm(alpha, tau.r)
  } #end i
  gamma<-log(phi.mean)-log(1-phi.mean) #anti-logit transformation
  phi.mean~dunif(0,1)
  p.mean~dunif(0,1)
  alpha<-log(p.mean)-log(1-p.mean)
  tau.s<-pow(sigma.s,-2) #Precision to std.
  tau.r<-pow(sigma.r,-2)
  sigma.s~dunif(0,5) #Prior for std.
  sigma.r~dunif(0,5)
  # Likelihood
  for(i in 1:n.species){ #Loop over species
    for(j in 1:nind){ #Loop over individuals
      z[i,j,f[i,j]]<-1 #Latent state at first capture
      for(t in (f[i,j]+1):n.occasions){ #Loop over captures
        #State Process
        z[i,j,t]~dbern(eff.mul[i,j,t]) #Bernoulli for survival
        eff.mul[i,j,t]<-mul[i,j,t]*w[i,j] #Only for indiv. captured once
        mul[i,j,t]<-phi[i,j,t-1]*z[i,j,t-1] #Only for indiv alive and present
        #Observation process
        y[i,j,t]~dbern(mu2[i,j,t]) #Bernoulli for capture
        mu2[i,j,t]<-p[i,j,t-1]*z[i,j,t-1] #Only for indiv. alive and present
      }#end t
    } #end j
  } #end i
} #end model
```

APPENDIX E. WinBUGS model to perform a random effects parameterization of the multi-species CJS model with grouping.

```
model {
  # Priors and constraints
  for(i in 1:n.species){ #Loop over all species
    for(j in 1:nind){ #Loop over all individuals
      for(t in f[i,j]:(n.occasions-1)){ #Loop over capture events
        logit(phi[i,j,t])<-s[i] #Note the logit transformation
        logit(p[i,j,t])<-r[i]
      } #end t
    } #end j
    s[i] ~ dnorm(gamma[i], tau.s) #Note the new index for gamma
    gamma[i]<-mu.gamma+b.group[group[i]] #model for groups
    r[i] ~ dnorm(alpha, tau.r)
  } #end i
  phi.mean~dunif(0,1)
  mu.gamma<-log(phi.mean)-log(1-phi.mean) #anti-logit transformation
  p.mean~dunif(0,1)
  alpha<-log(p.mean)-log(1-p.mean)
  for(k in 1:n.group){b.group[k]~dnorm(0,tau.group)} #Loop over groups
  tau.s<-pow(sigma.s,-2) #Precision to std.
  tau.r<-pow(sigma.r,-2)
  tau.group<-pow(sigma.g,-2)
  sigma.s~dunif(0,5)
  sigma.r~dunif(0,5)
  sigma.g~dunif(0,5)
  # Likelihood
  for(i in 1:n.species){ #Loop over species
    for(j in 1:nind){ #Loop over individuals
      z[i,j,f[i,j]]<-1 #Latent state at first capture
      for(t in (f[i,j]+1):n.occasions){ #Loop over captures
        #State Process
        z[i,j,t]~dbern(eff.mul[i,j,t]) #Bernoulli for survival
        eff.mul[i,j,t]<-mul[i,j,t]*w[i,j] #Only for indiv. captured once
        mul[i,j,t]<-phi[i,j,t-1]*z[i,j,t-1] #Only for indiv alive and present
        #Observation process
        y[i,j,t]~dbern(mu2[i,j,t]) #Bernoulli for capture
        mu2[i,j,t]<-p[i,j,t-1]*z[i,j,t] #Only for indiv. alive and present
      }#end t
    } #end j
  } #end i
} #end model
```

APPENDIX F. WinBUGS model to perform a random effects parameterization of the multi-species CJS model with grouping and correlation.

```

model {
  # Priors and constraints
  for(i in 1:n.species){ #Loop over all species
    for(j in 1:nind){ #Loop over all individuals
      for(t in f[i,j]:(n.occasions-1)){ #Loop over capture events
        logit(phi[i,j,t])<-s[i] #Note the logit transformation
        logit(p[i,j,t])<-r[i]
      } #end t
    } #end j
    s[i] ~ dnorm(gamma[i], tau.s) #Note the new index for gamma
    gamma[i]<-mu.gamma+b.group[group[i]] #model for groups
    mu.r[i]<-alpha+(rho*sigma.r/sigma.s)*(s[i]-gamma[i]) #Note relation est.
    r[i]~dnorm(mu.r[i],var.r)
  } #end i
  var.r<-tau.r/(1.-pow(rho,2)) #Note variance specification
  for(k in 1:n.group){b.group[k]~dnorm(0,tau.group)}
  phi.mean~dnorm(0,1)
  mu.gamma<-log(phi.mean)-log(1-phi.mean)
  p.mean~dunif(0,1)
  alpha<-log(p.mean)-log(1-p.mean)
  sigma.s~dunif(0,5)
  sigma.r~dunif(0,5)
  tau.s<-pow(sigma.s,-2)
  tau.r<-pow(sigma.r,-2)
  tau.group<-pow(sigma.g,-2)
  sigma.g~dunif(0,5)
  rho~dunif(-1,1) #Prior for correlation
  # Likelihood
  for(i in 1:n.species){ #Loop over species
    for(j in 1:nind){ #Loop over individuals
      z[i,j,f[i,j]]<-1 #Latent state at first capture
      for(t in (f[i,j]+1):n.occasions){ #Loop over captures
        #State Process
        z[i,j,t]~dbern(eff.mul[i,j,t]) #Bernoulli for survival
        eff.mul[i,j,t]<-mul[i,j,t]*w[i,j] #Only for indiv. captured once
        mul[i,j,t]<-phi[i,j,t-1]*z[i,j,t-1] #Only for indiv alive and present
        #Observation process
        y[i,j,t]~dbern(mu2[i,j,t]) #Bernoulli for capture
        mu2[i,j,t]<-p[i,j,t-1]*z[i,j,t] #Only for indiv. alive and present
      }#end t
    } #end j
  } #end i
} #end model

```

APPENDIX G. R script to simulate multi-species capture histories for species belonging to three groups.

```
sim.multisp.cjs.group<-function(n.species,n.occasions,n.groups=3){
  group<-sample(1:n.groups,n.species,replace=TRUE)
  phi<-rep(NA,n.species)
  for(i in 1:n.species){
    if(group[i]==1){phi[i]<-runif(1,0.1,0.3)}
    if(group[i]==2){phi[i]<-runif(1,0.3,0.7)}
    if(group[i]==3){phi[i]<-runif(1,0.5,0.9)}
  }
  p<-sample(c(runif(2,0.05,0.15),runif((n.species-2),.1,1)))
  marked<-matrix(rep(NA,n.species*(n.occasions-1)),ncol=(n.occasions-1))
  for(i in 1:n.species){marked[i,]<-round(runif((n.occasions-1),20,60))}
  params<-matrix(c(phi,p),byrow=TRUE,ncol=n.species)
  rownames(params)<-c("phi","p")
  W<-vector("list", (n.species+3))
  tmp<-0:n.species
  names(W)[1]<-"All"
  for(i in 2:(n.species+1)){
    names(W)[i]<-do.call(paste,c("SP",as.list(tmp[i]),sep=""))
    W[[i]]<-sim.cjs(n.occasions,marked[i-1,],phi[i-1],p[i-1])
  }
  colnames(params)<-names(W)[2:(n.species+1)]
  W[[n.species+2]]<-params
  names(W)[n.species+2]<-"Params"
  names(W)[n.species+3]<-"Groups"
  W$Groups<-group
  max.row<-rep(NA,n.species)
  for(i in 2:(n.species+1)){max.row[i-1]<-nrow(W[[i]])}
  max.row<-max(max.row)+1
  TMP<-vector("list", (n.species))
  for(i in 1:n.species){
    TMP[[i]]<-matrix(rep(NA,max.row*n.occasions),ncol=n.occasions)
    TMP[[i]][1:nrow(W[[i+1]]),]<-W[[i+1]]
    TMP[[i]][(nrow(W[[i+1]])+1):max.row,]<-0
  }
  Y<-array(dim=c(n.species,max.row,n.occasions))
  for(i in 1:n.species){Y[i,,]<-TMP[[i]]}
  W$All<-Y
  z<-W
}
```