Technical Manual for *MCestimate*

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Contents

1. Introduction

The analysis of competing risks has a long history in human health research, but has received limited formal attention in wildlife ecology and ecotoxicology (Heisey and Patterson 2006). Informally, however, the concept of competing risks has arisen many times in these disciplines (Abbott 1925, Ricklefs 1969). A common and accessible motivating example for defining competing risks is the concept of cause-of-death. Thus, when considering the possibility that an animal will suffer mortality in either acute or chronic response to chemical exposure, one must also consider the possibility that the animal will die due to disease, predation, or other causes, the occurrence of which will alter the rate at which animals succumb to exposure to a toxicant. Although such cause-specific failure analyses remain an important application, competing risks naturally arise in virtually all stochastic processes. The model described in this technical manual provides a unified common framework for analysis of data arising from serial observations on subjects in the presence of competing risks. The three examples below illustrate some of the diverse contexts in which such data arise.

1.1. Example: Estimating causes of avian nest failure

Most studies of nest productivity recognize multiple causes of nest failure, but focus on nest survival as the ecological process of interest. However, nests fail due to many causes, including nest predation (Martin 1995), nest parasitism (Trine 1998), interspecific competition (Radunzel et al. 1997), adverse weather (Martin 1992), nest abandonment (Traylor et al. 2004), nestling starvation (Martin 1992), and egg failure (Westemeier et al. 1998). The estimation of cause-specific nest-failure rates is a problem in competing risks (Etterson et al. 2007a, b).

1.2. Example: Distinguishing causes of mortality in toxicity tests

A common objective in wildlife toxicity testing is to estimate the mortality associated with a given chemical exposure. Sound experimental design for toxicity tests requires the use of control treatments with no chemical exposure, which are designed to allow separation of mortality due to intoxication from either natural mortality or stress associated with experimental conditions, but not exposure (USEPA 1996). Proper estimation of the portion of mortality due to the toxicant alone is a problem in competing risks and has long been of interest in toxicological research (Abbott 1925).

1.3. Example: Estimating the numbers of animals killed by contaminants and collisions

An unknown number of non-target animals are killed annually by pesticides in agroecosystems. Similarly, an important source of mortality in many bird populations is collisions with anthropogenic structures such as wind turbines, automobiles, windows, and power lines. In both cases, researchers have tried to estimate the number of animals killed by counting carcasses, but many carcasses are scavenged prior to discovery and some unscavenged carcasses remain undiscovered (Kostecke et al. 2001, Huso 2011). Carcass distribution trials, in which carcasses are placed in the field at known times and locations, are a common method used to correct for imperfect detection and scavenging (DeVault et al. 2003) and typically focus either on scavenging rates or on searcher efficiency (Morrison 2002). In the former case, the average persistence time of carcasses post-distribution is generally the parameter of interest. In the latter case, the parameter of interest is the detection probability, estimated as the proportion of distributed carcasses found by searchers. Understanding the effects of the two processes (scavenging and detection) in a simultaneous trial is a problem in competing risks.

An important barrier to the implementation of methods for estimating competing risks in animal populations has been the lack of appropriate software. In human health risk assessment and epidemiology, competing risks are traditionally modeled using extensions of classical survival analysis, with hazard functions defined as continuous-time exponential functions (Pintillie 2006). The latter methods focus on developing mathematical expressions for statistical distributions of survival times. In contrast, survival analysis in wildlife sampling and demography has developed in discrete time, and has focused on developing models for estimating probabilities of surviving a fixed period of time (typically in days, though other temporal units are equally valid). Extension of discrete-time methods for competing risks in animal populations has lagged behind the analogous methodological advances in survival analysis that are available in the human health sciences.

The program *MCestimate*, which implements the algorithms described in this technical manual within a user-friendly graphical user interface, is designed to provide some of this analytical capability within the discrete temporal framework that is typically employed for the statistical analysis of wildlife sampling data. The original motivation for the early development of *MCestimate* was the study of competing risks in nest survival estimation (Example 1, above). Because this remains an important application, and has a rich history in statistical and software development, I have continued to frame the theoretical development of *MCestimate* in terms of nest survival estimation. Existing methods for estimating nest survival parameters will also play an important role in helping to validate *MCestimate*. To this end, I present some background in existing nest survival estimation models to which *MCestimate* is equivalent under special circumstances. In these circumstances, *MCestimate* is expected to give the same answers when applied to common data. Readers only interested in the competing risks algorithms may wish to skip to Section 3, after browsing the notation that I (hopefully!) apply consistently throughout this document.

1.4 Notation

S = the probability that an arbitrary nest in the target population is successful.

t = the age (in days since the first egg is laid) that a nest fledges.

N, n = sample size variables. May be used for nests (N), observations (n) or exposure days (n), and exact meaning depends on context.

s_i = the probability that an arbitrary nest in the target population survives day i, where i is an ordinal date (by convention, i = 1 on January 1 of a non leap year). The subscript is omitted when daily survival probability is constant ($s = s_i$ for all i).

w_j = the number of times nest j is visited. The subscript j will often be omitted when it is obvious which nest is under consideration (for example when j and w_j co-occur as subscripts).

v_j = reserved indexing variable for the w_j visits to nest j (as above, j will often be assumed)

y_{sjv} = indicator variable for survival (y_{sjv} = 1 if nest j was alive on visit v. y_{sjv} = 0 otherwise).

d_{jv} = the number of days separating visits v and v + 1 to nest j.

$I_d (d_{jv})$ = scalar indicator function returning 1 if $d_{jv} = d$, 0 otherwise.

$\mathbf{X}_i$ = vector of covariates to daily survival or failure on day i.

$\boldsymbol{\beta}$ = vector of linear coefficients to survival or failure probabilities.

K = number of elements of $\mathbf{X}_i$.

k = indexing variable to elements of $\mathbf{X}_i$ and $\boldsymbol{\beta}$ (i.e., x_{ik} is the kth element of $\mathbf{X}_i$ and β_k is the kth element of $\boldsymbol{\beta}$).

$o(v_j)$ = function returning the ordinal date (i) of visit v to nest j.

$a(u)$ = function returning the ordinal date (i) on which a nest is aged u (in days since the first egg was laid).

F = the number of causes of nest failure that are under study.

f = indexing variable to specific causes of failure ($1 \le f \le F$).

m_{if} = the daily probability of failure on day i due to cause f.

y_{ffjv} = indicator variable for state f (y_{ffjv} = 1 indicates nest j was in state f on visit v. y_{ffjv} = 0 otherwise).

$\mathbf{I}_f(\mathbf{X}_i)$ = indicator function that returns a vector of zeros and ones indicating which elements of $\mathbf{X}_i$ are covariates to fate f in a particular model.

2. Mathematical background (binomial nest survival)

This section provides much of the background material and history that led to the development of **MCestimate**. As such it draws heavily on the development of formal methods for estimating nest survival rates, which is the primary context that motivated **MCestimate**. However, it is not intended to be a complete history of nest survival, a much larger topic with a deeper history than can be covered here. I also provide brief treatments of some standard mathematical techniques, such as maximum likelihood and the delta method. In most of the following equations I have altered the notation used by the original authors to facilitate the subsequent introduction of the Markov transition matrices in Section 2.9.

2.1 The Mayfield estimator

The history of modern avian nest survival estimation begins with the work of Harold Mayfield (1961, 1975). Mayfield's original insight was the observation that, for most empirical samples of avian nests, drawn from a defined population, the simple proportion of successful nests would likely overestimate the probability that any given nest in the population would be successful. The reason for this positive bias is that many nests are not immediately discovered upon construction, but are nevertheless included in the sample as they are discovered, sometimes rather late in development. Therefore successful nests are more likely to be included in a sample than failed nests. These ideas are expressed mathematically below.

For simplicity, assume that, if nest j is successful, then its state on the final visit (w_j) is "successful" ($y_{sjw} = 1$), whereas if a nest fails, its state on the final visit is "failed" ($y_{sjw} = 0$). Then the number of successful nests (N_s) in the population is $N_s = \sum_{j=1}^{N} y_{sjw}$ and the simple proportion (P) of successful nests is $P = \dfrac{N_s}{N}$. Mayfield's (1961) insight was that $E\left[S\right] \leq E\left[P\right]$, where E is the expectation operator. Mayfield's (1961) proposed solution to the positive bias in $E(P)$ was to account for the duration of time each nest was under observation. To do so, he recast the problem in terms of daily survival. First, let n_j, represent the total number of days that nest j was exposed to failure following discovery (often referred to as exposure days). Then:

$$n_j = \sum_{v_j=1}^{w_j-1} d_{jv} \text{ , and:}$$

$$(2.1) \quad s = 1 - \frac{N - N_s}{\sum\limits_{j=1}^{n} n_j} \, ,$$

Equation (2.1) is commonly referred to as the Mayfield estimator. Its logic can be dissected as follows. Noting that $N - N_s$ is the number of nests that failed and that a nest can fail only once, $N - N_s$ also gives the total number of days on which a nest failed to survive. Similarly, the sum in the denominator of the ratio in Eq. (2.1) is the total number of days that nests were exposed to failure over all nests in the sample. Therefore, the ratio on the right hand side of Eq. (2.1) gives the proportion of the total number of exposure days that nests failed to survive, which is an estimator for the daily probability of failure. Its complement is an estimator for the daily probability of survival, s. At least three important assumptions underlie Eq. (2.1):

1. The precise dates of nest failure are known exactly (often equated to the assumption that $d_{jv} = 1$ for all j, v_j).
2. The rate of nest survival/failure is constant within and among nests.
3. The fates of nests (successful/failed) are correctly assigned.

While Eq. (2.1) is quite simple, and its assumptions are easily falsified, its impact on avian productivity research can hardly be overstated. It now has a long history of direct application and generalization (Johnson 2007), of which I review only a few highlights pertinent to the development of **MCestimate**. The first generalization to Mayfield's estimator (Johnson 1979) concerned assumption (1) above, that the precise dates of nest failure are known exactly. The second assumption, that nest survival is constant within and among nests has been addressed by many, with the most comprehensive treatment offered by Dinsmore et al. (2002). The third assumption, that fates are correctly assigned, has received limited attention (Manolis et al. 2000, Stanley 2004, Etterson and Stanley 2008).

2.2 Generalization of Mayfield assumption (1)

The first formal statistical treatment of the Mayfield estimator was provided by Johnson (1979) who generalized Eq. (1) to cases in which precise failure dates are unknown. In most cases, nests are not monitored every day, so that when a nest fails, its precise date of failure is known only to have occurred within the interval spanned by two visits (which I'll refer to hereafter as an observation). Johnson (1979) provided the following likelihood (though the notation is mine):

$$(2.2) \quad l\left(s \mid n_d, n_{sd} \right) = \prod_{d=1}^{\infty} \binom{n_d}{n_{sd}} \left(s^d \right)^{n_{sd}} \left(1 - s^d \right)^{n_d - n_{sd}} , \text{ where:}$$

n_d = the total number of observations lasting d days: $n_d = \sum\limits_{j=1}^{N} \sum\limits_{v=1}^{w-1} I_d \left(d_{jv} \right)$,

n_{sd} = the number of observations of length d that are successful: $n_{sd} = \sum_{j=1}^{N}\sum_{v=1}^{w-1} y_{sjv} I_d \ d_{jv}$.

Johnson (1979) further showed that the Mayfield estimator (2.1) is the maximum likelihood estimate (see below) for s when d_{jv} = 1 for all observations on all nests in the sample.

2.3 Maximum likelihood estimation

Analysis of likelihood equations such as (2.2) proceed according to a standard technique (Edwards 1992). First, the log of the likelihood (l) over the full data set is taken, resulting in the log-likelihood (L). Then the value of s at which L reaches its maximum is calculated. In rare cases this can be done analytically, by taking the derivative of L with respect to s and solving for the value of s at which dL/ds = 0. The resulting estimate of s is the maximum likelihood estimate (MLE), and is typically denoted $\hat{s}$. In general, MLEs cannot be found analytically and must be found using a computer to perform a numerical search. The second derivative of the log-likelihood function evaluated at $\hat{s}$ contains information about the estimated sampling variance of $\hat{s}$. In particular, the negative inverse of the second derivative of L with respect to s, evaluated at $\hat{s}$ is an estimate of the sampling variance of $\hat{s}$ conditional on the available data.

In presenting the following likelihood functions, it is assumed that the MLEs are found using the above procedure generalized to the case in which the MLE is not a single value (i.e., $\hat{s}$), but rather a vector of values ($\hat{\boldsymbol{\beta}}$). The MLE is then the vector of values that jointly maximize L. The estimated covariance matrix of $\hat{\boldsymbol{\beta}}$, referred to below as $\text{cov}\ \hat{\boldsymbol{\beta}}$, is the negative inverse of the matrix of second derivatives evaluated at $\hat{\boldsymbol{\beta}}$. The variances of the elements of $\hat{\boldsymbol{\beta}}$ are along the diagonal of $\text{cov}\ \hat{\boldsymbol{\beta}}$. For more information on maximum likelihood estimation, see Edwards (1992), Williams et al. (2002) or Burnham and Anderson (2002).

2.4 Generalization of Mayfield assumption (2)

A major goal of research in avian nest ecology has been to investigate hypotheses concerning variation in $\hat{s}$. While this has been done in numerous ways beginning with Green (1977) and Johnson (1979), **MCestimate** uses methods similar to those that were articulated by Dinsmore et al. (2002), which draw from the theory of generalized linear models (Dobson 2002) and from model selection theory using Akaike's Information Criterion (AIC, Burnham and Anderson 2002).

The probability that a nest, active on day i, survives to day i + 1, can be specified as a linear function in the log-odds (or logit) of daily survival:

(2.3) $\ln\left(\dfrac{s_i}{1-s_i}\right) = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + ... + \beta_K x_K$

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In Eq. (3), x_1, x_2, ...,x_K represent values of variables (covariates) thought to influence nest survival (s_i) on day i. For example, these could be ordinal date (i), nest height above ground, age of the nest since the first egg was laid, etc. By convention, $x_1 = 1$ and β_1 represents an intercept parameter. Equations like (2.3) are more succinctly expressed in matrix notation. Thus let:

$\boldsymbol{\beta}$ = column-vector of K linear coefficients (β_k)

$\mathbf{X}_i$ = row-vector of variables thought to influence s_i, where the first element of $\mathbf{X}_i$ is always 1.

Then Eq. (2.3) can be rewritten:

$$(2.4) \quad \ln\left(\frac{s_i}{1-s_i}\right) = \mathbf{X}_i\boldsymbol{\beta}$$

The basic estimation problem is no longer to obtain maximum likelihood estimates for s_i, but rather for $\boldsymbol{\beta}$. This is done by using the inverse logit function (Eq. 2.5 below) and substituting the resulting expression for s_i into the likelihood (2.6, below).

$$(2.5) \quad s_i = \frac{\exp \mathbf{X}_i\boldsymbol{\beta}}{1+\exp \mathbf{X}_i\boldsymbol{\beta}}$$

The basic likelihood function employed by Dinsmore et al. (2002) is a generalization of Johnson's (1979) likelihood, Eq. (2.2) to allow nest survival to vary among days within a nest (again the notation is my own, but the equation is that of Dinsmore et al. 2002).

$$(2.6) \quad l\left(\boldsymbol{\beta} \mid w_j, y_{sjv}, d_{jv}\right) \propto \prod_{j=1}^{n}\left[\left(\prod_{i=o\,1}^{o\,w-1\,-1} s_i\right)\left(1-\prod_{i=o\,w-1}^{o\,w\,-1} s_i\right)^{1-y_{sjw}}\left(\prod_{i=o\,w-1}^{o\,w\,-1} s_i\right)^{y_{sjw}}\right]$$

2.5 AIC and model selection

Different hypotheses about influences on s_i can be formulated by specifying different variables in the linear component of Eq. (2.3) and finding the MLEs as described above. The fitted models, representing alternative hypotheses, can then be compared using Akaike's Information Criterion (AIC, Burnham and Anderson 2002), where the smallest value of AIC corresponds to the best model (hypothesis) among all models tested.

$$(2.7) \quad \mathrm{AIC} = -2L\left(\hat{\boldsymbol{\beta}}\right) + 2K$$

In Eq. (2.7), the log-likelihood (L) is evaluated at the maximum likelihood solution ($\hat{\boldsymbol{\beta}}$). Both Dinsmore et al. (2002) and **MCestimate** actually use a sample-size corrected version of AIC (AIC$_c$, Burnham and Anderson 2002):

$$(2.8) \quad \text{AIC}_{\text{c}} = -2L\left(\hat{\boldsymbol{\beta}}\right) + 2K\left(\frac{n}{n-K-1}\right)$$

In Eq. (2.8) n is the sample size for nest-survival estimation. Dinsmore et al. (2002) used the total number of observation days over all nests for n:

$$n = \sum_{j=1}^{N}\sum_{v=1}^{w-1} d_{jv}$$

MCestimate uses a slightly modified calculation provided by Rotella et al. (2004) in which n is calculated as the sum of the total number of successful observation days over all nests and the total number of failed nests.

$$n = \sum_{j=1}^{N}\sum_{v=1}^{w-1} \left(d_{jv}\left(y_{sj,v+1}\right) + 1 - y_{sj,v+1}\right)$$

2.6 Fledging rates

Mayfield's original motivation, to better estimate the overall probability (S) that a nest will fledge at least one young, remains an important goal in nest-survival estimation. When s is invariant, then:

$$(2.9) \quad \hat{S} = \hat{s}^{t}$$

When s is assumed to vary, then:

$$(2.10) \quad \hat{S} = \prod_{i=a_1}^{a_t - 1} \hat{s}_i$$

2.7 Variance

2.7.1 Variance of homogeneous daily survival rates

For a single estimated MLE (e.g., $\hat{s}$), its variance $\text{var}\left(\hat{s}\right)$ is estimated as the negative inverse of the second derivative of the log-likelihood function, evaluated at $\hat{s}$ (Edwards 1992). For the Mayfield estimator, this quantity is available as a simple formula:

$$(2.11) \quad \text{var}\left(\hat{s}\right) = \frac{\hat{s}\left(1-\hat{s}\right)}{\sum_{j=1}^{n}\sum_{v=1}^{w-1} d_{jv}},$$

When the MLE must be estimated numerically, the variance is generally not available in simple form, though it can be estimated numerically.

2.7.2 Variance of heterogeneous daily survival rates

When the estimated quantity is a vector of parameters (e.g., $\hat{\boldsymbol{\beta}}$), the covariance matrix, $\mathrm{cov}\ \hat{\boldsymbol{\beta}}$, is estimated as the negative inverse of the Hessian matrix (the matrix of second derivatives of the log-likelihood, evaluated at $\hat{\boldsymbol{\beta}}$). To get the variance of the $\hat{s}_i$ from $\mathrm{cov}\ \hat{\boldsymbol{\beta}}$ we can use the delta method (Seber 1982). In the general case, let $\hat{\boldsymbol{\theta}}$ represent an MLE (scalar or vector) and $f(\hat{\boldsymbol{\theta}})$ represent some function of $\hat{\boldsymbol{\theta}}$. Then the variance of the function $f(\hat{\boldsymbol{\theta}})$ is calculated from the estimated variance of $\hat{\boldsymbol{\theta}}$ as:

$$(2.12) \quad \mathrm{var}\ f\ \hat{\boldsymbol{\theta}}\ = \left[\frac{df\ \hat{\boldsymbol{\theta}}}{d\hat{\boldsymbol{\theta}}} \right] \mathrm{cov}\ \hat{\boldsymbol{\theta}}\ \left[\frac{df\ \hat{\boldsymbol{\theta}}}{d\hat{\boldsymbol{\theta}}} \right]^{\mathrm{T}}$$

For the case of variable daily survival rates, $\hat{s}_i$, $\hat{\boldsymbol{\theta}} = \hat{\boldsymbol{\beta}}$, and $f\ \hat{\boldsymbol{\theta}}\ = f\ \hat{\boldsymbol{\beta}}$ is given by Eq. (2.5). Therefore (for derivation of Eq. 2.13 below, see Section 4.1):

$$(2.13) \quad \frac{df\ \hat{\boldsymbol{\beta}}}{d\hat{\boldsymbol{\beta}}} = \frac{d\hat{s}_i}{d\boldsymbol{\beta}} = \hat{s}_i\ 1 - \hat{s}_i\ \mathbf{X}_i\ , \text{ and:}$$

$$(2.14) \quad \mathrm{var}\ \hat{s}_i\ = \hat{s}_i\ 1 - \hat{s}_i\ \mathbf{X}_i \mathrm{cov}\ \hat{\boldsymbol{\beta}}\ \hat{s}_i\ 1 - \hat{s}_i\ \mathbf{X}_i^{\mathrm{T}}$$

2.7.3 Variance of fledging rates under homogeneous daily survival

The delta method can also be extended to overall fledging rates. It first requires calculation of the derivative of the overall fledging rate (S) with respect to the estimated survival rates. In the simple homogenous case (Eq. 2.9 above), the equation is:

$$(2.15) \quad \mathrm{var}\ \hat{S}\ = \left[\frac{d\hat{S}}{d\hat{s}} \right] \mathrm{var}\ \hat{s}\ \left[\frac{d\hat{S}}{d\hat{s}} \right] = \left[t\hat{s}^{t-1} \right] \mathrm{var}\ \hat{s}\ \left[t\hat{s}^{t-1} \right]$$

2.7.4 Variance of fledging rates under heterogeneous daily survival

When the overall fledging rate is a function of variable survival rates ($\hat{s}_i$), which are in turn functions of β, a relatively simple formula can still be found, but with a little more effort. First, from Eq. (2.10), note that:

$$\ln\ \hat{S}\ = \sum_{i=a\ 1}^{a\ t\ -1} \ln\ \hat{s}_i\ .$$

Therefore:

$$\frac{d \ln \hat{S}}{d\hat{s}_i} = \sum_{i=a\,1}^{a\,t\,-1} \frac{d \ln \hat{s}_i}{d\hat{s}_i} = \sum_{i=a\,1}^{a\,t} \frac{1}{\hat{s}_i}.$$

Therefore:

$$\frac{d\hat{S}}{d\hat{s}_i} = \hat{S} \frac{d \ln \hat{S}}{d\hat{s}_i} = \hat{S} \sum_{i=a\,1}^{a\,t\,-1} \frac{1}{\hat{s}_i}.$$

Remembering Eq. (2.13) above, and applying the chain rule:

$$\frac{d\hat{S}}{d\boldsymbol{\beta}} = \frac{d\hat{S}}{d\hat{s}_i} \frac{d\hat{s}_i}{d\boldsymbol{\beta}} = \hat{S} \sum_{i=a\,1}^{a\,t\,-1} \mathbf{X}_i \left(1-\hat{s}_i\right)$$

Therefore, under variable $\hat{s}_i$:

$$(2.16) \quad \text{var}\left(\hat{S}\right) = \hat{S} \sum_{i=a\,1}^{a\,t\,-1} \mathbf{X}_i \left(1-\hat{s}_i\right) \text{cov}\left(\hat{\boldsymbol{\beta}}\right) \hat{S} \sum_{i=a\,1}^{a\,t\,-1} \mathbf{X}_i^{\mathrm{T}} \left(1-\hat{s}_i\right)$$

2.8 Confidence limits

Standard practice in linear modeling for generating confidence limits around estimated parameters is to choose a tolerable Type I error rate (α) and find the associated z-score from a standard normal distribution corresponding to 100 $(1-\alpha)$% coverage (two-tailed). A common choice is $z = 1.96$, corresponding to an approximate 95% coverage ($\alpha = 0.05$). Confidence limits can then be generated as $\hat{s} \pm z \sqrt{\text{var}\left(\hat{s}\right)}$. However, both logic and experience suggest that this procedure will often produce confidence limits outside the range [0, 1]. Thus, a better practice is to adopt the generalized linear modeling approach to nest survival estimation (Eqs. 2.3 – 2.5, above) and use $\text{cov}\left(\hat{\boldsymbol{\beta}}\right)$ to generate $100(1-\alpha)$% confidence limits around the logit (Eq. 2.3). The resulting confidence limits can then be transformed to the probability scale using the inverse logit (Eq. 2.5), and the resulting limits will always lie in the interval [0, 1]. Because the mapping from the logit to the probability space is one-to-one, the resulting coverage rate for the probabilities is equal to that of the confidence interval on the logit (Rao 1973). This procedure still requires the use of the delta method to calculate confidence limits on the logit. In this case $\hat{\boldsymbol{\theta}} = \hat{\boldsymbol{\beta}}$ and $f\left(\hat{\boldsymbol{\beta}}\right) = \text{logit}\left(\hat{s}_i\right) = \ln\left(\frac{\hat{s}_i}{1-\hat{s}_i}\right) = \mathbf{X}_i \hat{\boldsymbol{\beta}}$, and $\dfrac{df\left(\hat{\boldsymbol{\beta}}\right)}{d\hat{\boldsymbol{\beta}}} = \mathbf{X}_i$. Therefore:

$$(2.17) \quad \text{var}\left(\text{logit}\left(\hat{s}_i\right)\right) = \mathbf{X}_i \text{cov}\left(\hat{\boldsymbol{\beta}}\right) \mathbf{X}_i^{\mathrm{T}}.$$

Thus confidence limits [l, u] around the logit can be generated as follows:

(2.18) $\quad [l,u] = \left[\mathrm{logit}\ \hat{s}_i\ - z_i\sqrt{\mathbf{X}_i \mathrm{cov}\ \hat{\boldsymbol{\beta}}\ \mathbf{X}_i^{\mathrm{T}}}, \mathrm{logit}\ \hat{s}_i\ + z_i\sqrt{\mathbf{X}_i \mathrm{cov}\ \hat{\boldsymbol{\beta}}\ \mathbf{X}_i^{\mathrm{T}}}\right].$

Finally, back-transformed confidence limits around $\hat{s}_i$, $[L, U]$ are:

(2.19) $\quad [L,U] = \left[\dfrac{e^l}{1+e^l}, \dfrac{e^u}{1+e^u}\right].$

2.9 Binomial nest survival as a Markov chain

Etterson and Bennett (2005) showed that the basic likelihood function of Johnson (1979) could be formulated as a product of cell probabilities in Markov transition matrices. The notation used below differs from Etterson and Bennett (2005), but the mathematical expressions are equivalent. Let:

(2.20) $\quad \mathbf{M} = \begin{bmatrix} s & 1-s \\ 0 & 1 \end{bmatrix}$ and

$\qquad \mathbf{Y}_{jv} = \left[y_{sjv}, 1 - y_{sjv}\right]$

Using the above notation a probability model for an arbitrary observation on a nest can be formulated as follows:

(2.21) $\quad \mathrm{Pr}\ \left(y_{j,v+1} \mid s, y_{jv}, d_{jv}\right) = \mathbf{Y}_{jv}\mathbf{M}^{d_{jv}}\mathbf{Y}_{j,v+1}^{\mathrm{T}}$

The corresponding likelihood for all observations on all nests is:

(2.22) $\quad l\ \left(s \mid\ y_{jv}, d_{jv}\right) \propto \prod_{j=1}^{n}\prod_{v=1}^{w_j-1}\ \mathbf{Y}_{jv}\mathbf{M}^{d_{jv}}\mathbf{Y}_{j,v+1}^{\mathrm{T}}$

Eq. (2.22) is equivalent to Eq. (2.2), except that the binomial coefficients are omitted (they don't affect the solution). Similarly, when $d_{jv} = 1$ for all j, v, the MLE corresponding to Eq. (2.22) is the original Mayfield estimator (Eq. 2.1).

To investigate variation in daily survival, we must have different matrices ($\mathbf{M}_i$) for each day, where s_i is as defined in Eqs. (2.3 – 2.5). Thus:

$\qquad \mathbf{M}_i = \begin{bmatrix} s_i & 1-s_i \\ 0 & 1 \end{bmatrix}$

The full likelihood over all observations on all nests is:

(2.23) $\quad l\ \left(\boldsymbol{\beta} \mid\ y_{jv}, d_{jv}\right) \propto \prod_{j=1}^{n}\prod_{v=1}^{w_j-1}\left(\mathbf{Y}_{jv}\left(\prod_{i=o_v}^{o_{v+1}-1} \mathbf{M}_i\right)\mathbf{Y}_{j,v+1}^{\mathrm{T}}\right)$

Eq.(2.23) is equivalent to Eq. (2.6).

Standard errors and confidence limits for these binomial (success/fail) models can be calculated exactly as described in Sections 2.7 and 2.8.

3. Competing risks (multinomial nest survival)

With the Matrix notation of Markov chain transition matrices developed above, the generalization of survival methods to handle competing risks is straightforward. For simplicity, the equations below are all presented with two causes of failure, but all equations immediately generalize to an arbitrary number of failure categories. The transition matrix for this probability model was originally published by Etterson et al. (2007).

3.1. Homogeneous failure rates

$$(3.1) \quad \mathbf{M} = \begin{bmatrix} s & m_1 & m_2 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

In Equation (3.1) and all subsequent similar matrices, note the constraints that:

$$1 = s + \sum_{f=1}^{F} m_f$$

$$0 \le s, m_f \le 1$$

The state vectors ($\mathbf{Y}$) are of the form:

$$\mathbf{Y}_{jv} = \begin{bmatrix} y_{sjv} & y_{1jv} & y_{2jv} \end{bmatrix}$$

With $\mathbf{M}$ and $\mathbf{Y}_{jv}$ modified as above, the likelihood for the case in which nest failure rates (m_f) are constant is virtually identical to Eq. (2.22).

$$(3.2) \quad l\left(m_1, m_2 \mid y_{jv}, d_{jv} \right) \propto \prod_{j=1}^{n} \prod_{v=1}^{w_j-1} \mathbf{Y}_{jv} \mathbf{M}^{d_{jv}} \mathbf{Y}_{j,v+1}^{\mathrm{T}}$$

3.2. Heterogenous failure rates

For variable m_{if}, we must generalize the linear models notation introduced by Dinsmore et al. (2002) (Eqs. 2.3 – 2.5). Recognizing that the ability to model competing risks will immediately beg the question of what factors influence competing risks, it makes more sense to model the failure rates (m_{if}) as functions of covariates than the survival rate. This will require extension of the logit (Eq. 2.3) to multiple fates. Let:

(3.3) $\mathbf{X}_{if} = \mathbf{I}_f\ \mathbf{X}_i \bullet \mathbf{X}_i$, where the • operator represents the element-wise (dot) product.

By convention (as above) the first non-zero element of $\mathbf{X}_{if}$ will always be 1, corresponding to an intercept parameter for that failure rate. Then, for a given failure rate, its multinomial logit (relative to daily survival) is defined as:

(3.4) $\ln\left(\dfrac{m_{if}}{s_i}\right) = \mathbf{X}_{if}\boldsymbol{\beta}$

The inverse function of (3.4) is:

(3.5) $m_{if} = \dfrac{\exp\ \mathbf{X}_{if}\boldsymbol{\beta}}{1 + \displaystyle\sum_{g=1}^{F} \exp\ \mathbf{X}_{ig}\boldsymbol{\beta}}$

And

(3.6) $s_i = \dfrac{1}{1 + \displaystyle\sum_{g=1}^{F} \exp\ \mathbf{X}_{ig}\boldsymbol{\beta}}$

Again, the likelihood function is virtually identical to Eqs. (2.23):

(3.7) $l\ \boldsymbol{\beta}\mid\ y_{jv}, d_{jv}\ \propto \displaystyle\prod_{j=1}^{n}\prod_{v=1}^{w_j-1}\left(\mathbf{Y}_{jv}\left(\prod_{i=o\ v}^{o\ v+1\ -1}\mathbf{M}_i\right)\mathbf{Y}_{j,v+1}^{\mathrm{T}}\right)$

In Eq. (3.7) $\mathbf{M}_i$ is as defined in Eq. (3.1), except that s, m_1 and m_2 are replaced by s_i, m_{i1} and m_{i2}, as defined in Eqs. (3.4 and 3.5):

(3.8) $\mathbf{M}_i = \begin{bmatrix} s_i & m_{i1} & m_{i2} \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$

3.3 Fledging rates and overall probabilities of failure

As with the binomial model it is of interest to know the overall probabilities that a nest will fledge or fail due to the various identified causes. These are trivial to calculate under the Markov notation. In the case of homogeneous failure rates (using the matrix $\mathbf{M}$ from Eq. 3.1), we can define a new matrix $\mathbf{S}_t$:

(3.9) $\mathbf{S}_t = \mathbf{M}^t$

The cell entries of $\mathbf{S}_t$ corresponding to particular probabilities in $\mathbf{M}$ give the overall probabilities that a nest is in a given state after t days . Thus, for example, the entry in the first row and first column of $\mathbf{S}_t$ gives the overall survival probability after t days. Similarly, the entry in the first row and second column of $\mathbf{S}_t$ gives the overall probability that a nest has suffered the first fate (corresponding to f = 1) after t days, and so on.

For the case of heterogenous failure rates (m_{if}, $\mathbf{M}_i$), we use the product operator and define the sequence of age-specific matrices.

$$(3.10) \quad \mathbf{S}_t = \prod_{i=a\,1}^{a\,t-1} \mathbf{M}_i = \mathbf{M}_{a\,1}\,\mathbf{M}_{a\,2}\,\mathbf{M}_{a\,3}\,...\mathbf{M}_{a\,t-1}$$

3.5 Variance

Variances in the competing risks models are calculated in similar fashion to the binomial models, using the delta method (Eq. 2.12) and the estimated covariance matrix of MLEs. However, the inverse multinomial logit (expit, Eq. 3.4 3.5) complicates the calculation of the derivatives for the failure rates (for derivation see Section 4.2). For this section, I assume the generalized linear model framework is used and provide the formulae only for those cases. Formulae for the homogeneous rates are obtained as special cases in which $\mathbf{X}_{if}$ =1 for all f.

3.5.1. Daily probabilities

$$(3.11) \quad \frac{\partial \hat{m}_f}{\partial \hat{\boldsymbol{\beta}}} = \mathbf{X}_i \hat{m}_f \bullet \left(\mathbf{I}_f\; \mathbf{X}_i\; -\sum_g \mathbf{I}_g\; \mathbf{X}_i\; \hat{m}_{ig} \right)$$

For completeness it is worth noting the partial derivative with respect to the daily survival rate (s_i):

$$(3.12) \quad \frac{\partial \hat{s}_i}{\partial \boldsymbol{\beta}} = -\hat{s}_i \mathbf{X}_i \bullet \sum_g \mathbf{I}_g\; \mathbf{X}_i\; \hat{m}_g$$

Application of the delta method (Eq. 2.12) is now possible, with $\hat{\boldsymbol{\theta}} = \hat{\boldsymbol{\beta}}$ and $f\,\hat{\boldsymbol{\theta}}\, = f\,\hat{\boldsymbol{\beta}}$ is Eq. (3.4), with derivatives as shown in Eqs (3.11 – 3.12).

3.5.2. Overall rates

Using Eq. (3.10):

$$(3.13) \quad \mathbf{S}_1 = \mathbf{M}_{a\,1}\;,\; \text{and, for arbitrary } t > 1:$$

$$(3.14) \quad \mathbf{S}_t = \mathbf{S}_{t-1}\mathbf{M}_{a\,t-1}$$

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First, given a matrix of the form (3.8), define $\dfrac{d\mathbf{M}_i}{d\beta_k}$ as the matrix of element-wise derivatives of $\mathbf{M}_i$ with

respect to the kth element of $\boldsymbol{\beta}$ (β_k). These can be obtained from Eqs. (3.11 3.12). Second, define: $\dfrac{d\mathbf{S}_t}{d\beta_k}$

inductively as follows:

$$(3.15) \quad \frac{d\mathbf{S}_1}{d\beta_k} = \frac{d\mathbf{M}_{a\,1}}{d\beta_k} \quad \text{and, for arbitrary } (t > 1), \text{ we apply the product rule for matrices:}$$

$$(3.16) \quad \frac{d\mathbf{S}_t}{d\beta_k} = \mathbf{S}_{t-1}\frac{d\mathbf{M}_{a\,t-1}}{d\beta_k} + \frac{d\mathbf{S}_{t-1}}{d\beta_k}\mathbf{M}_{a\,t-1}$$

The matrix $\dfrac{d\mathbf{S}_t}{d\beta_k}$ gives the required derivatives, which can be used with the delta method, to calculate

the desired variances.

3.6. Confidence limits

Confidence limits on the multinomial probabilities are more difficult to estimate than for binomial probabilities. However, the multinomial case is a direct generalization of the binomial case. The method used by *MCestimate* was described in detail by Sambamoorthi et al. (1994). In contrast to the binomial model, in the multinomial case the expected coverage rate is not exact. Instead, it is a minimal bound on the expected coverage rate. In other words, the true expected error rate is less than or equal to the nominal error rate and the true expected coverage rate is greater than or equal to the nominal coverage rate. Thus the confidence intervals provided by *MCestimate* are, on average, conservative.

As with the binomial case, generation of confidence limits begins with the logit. However, in the multinomial case there are F logits that must be considered as well as the survival probability. The logits for the estimated failure probabilities are given by Eq. (3.4). For each of the logits, upper and lower confidence limits can be calculated as described in Section 2.8 above. Let $\mathbf{L}_i$ and $\mathbf{U}_i$ represent column-vectors of F lower and upper confidence limits around the logits calculated individually for each logit. Thus, for a specific fate, f:

$$(3.17) \quad \mathbf{L}_{if} = \mathbf{X}_{if}\hat{\boldsymbol{\beta}} - z\sqrt{\mathbf{X}_{if}\,\text{cov}\,\hat{\boldsymbol{\beta}}\,\mathbf{X}_{if}^{\text{T}}} \text{ , and:}$$

$$(3.18) \quad \mathbf{U}_{if} = \mathbf{X}_{if}\hat{\boldsymbol{\beta}} + z\sqrt{\mathbf{X}_{if}\,\text{cov}\,\hat{\boldsymbol{\beta}}\,\mathbf{X}_{if}^{\text{T}}} \text{ .}$$

In Equations (3.17 3.18) z is the two-tailed z-score from a standard normal distribution and $\mathbf{L}_{if}$ and $\mathbf{U}_{if}$ are the fth elements of $\mathbf{L}_i$ and $\mathbf{U}_i$, respectively. Now, let $\mathbf{C}_i$ represent an f x 2 matrix with $\mathbf{L}_i$ as column 1 and $\mathbf{U}_i$ as column 2. Further, let $\mathbf{F}_i$ represent a 2^f x f matrix consisting of all possible f-tuples generated

by drawing one element from each row of $\mathbf{C}_i$. The 2^f rows of $\mathbf{F}_i$ form the basis for deriving simultaneous confidence intervals around the estimated probabilities. However, one additional step is needed. Let $\mathbf{P}_i$ represent a matrix of dimension 2^f x $(f+1)$ generated by applying the inverse multinomial logit (Eq. 3.5 and 3.6) to each row of $\mathbf{F}_i$. For example, let $\mathbf{F}_i(r,f)$ represent the entry in the rth row and f^{th} column of $\mathbf{F}_i$. Then the rth row of $\mathbf{P}_i$ is generated as follows:

$$(3.19) \quad \mathbf{P}_i\ r,1\ = \frac{1}{1+\displaystyle\sum_{f=1}^{F}\exp\ \mathbf{F}_i\ r,f}\ , \text{ and:}$$

$$(3.20) \quad \mathbf{P}_i\ r,f+1\ = \frac{\exp\ \mathbf{F}_i\ r,f}{1+\displaystyle\sum_{f=1}^{F}\exp\ \mathbf{F}_i\ r,f}\ .$$

Sambamoorthi et al. (1994) showed that the column-wise minima and maxima of $\mathbf{P}_i$ are conservative (with respect to the nominally specified α) simultaneous confidence intervals on the estimated probabilities (s_i and m_{if}).

4. Appendix: useful derivatives

4.1. The derivatives of the binomial logit

Let $s_i = \dfrac{\exp\ \mathbf{X}_i\boldsymbol{\beta}}{1+\exp\ \mathbf{X}_i\boldsymbol{\beta}}$

Then, by the quotient rule:

$$\frac{\partial s_i}{\partial \boldsymbol{\beta}} = \frac{1+\exp\ \mathbf{X}_i\boldsymbol{\beta}\ \dfrac{\partial}{\partial\boldsymbol{\beta}}\ \exp\ \mathbf{X}_i\boldsymbol{\beta}\ -\exp\ \mathbf{X}_i\boldsymbol{\beta}\ \dfrac{\partial}{\partial\boldsymbol{\beta}}\ 1+\exp\ \mathbf{X}_i\boldsymbol{\beta}}{1+\exp\ \mathbf{X}_i\boldsymbol{\beta}\ ^2}$$

Therefore:

$$\frac{\partial s_i}{\partial \boldsymbol{\beta}} = \frac{1+\exp\ \mathbf{X}_i\boldsymbol{\beta}\ \exp\ \mathbf{X}_i\boldsymbol{\beta}\ \mathbf{X}_i -\exp\ \mathbf{X}_i\boldsymbol{\beta}\ \exp\ \mathbf{X}_i\boldsymbol{\beta}\ \mathbf{X}_i}{1+\exp\ \mathbf{X}_i\boldsymbol{\beta}\ ^2}$$

And:

$$(4.1) \quad \frac{\partial s_i}{\partial \boldsymbol{\beta}}\ \frac{\exp\ \mathbf{X}_i\boldsymbol{\beta}}{1+\exp\ \mathbf{X}_i\boldsymbol{\beta}}\ \frac{1}{1+\exp\ \mathbf{X}_i\boldsymbol{\beta}}\ \mathbf{X}_i = s_i\ 1-s_i\ \mathbf{X}_i$$

4.1. The derivatives of the multinomial logit

Let $m_{if} = \dfrac{\exp\ \mathbf{X}_{if}\boldsymbol{\beta}}{1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}}.$

Then, by the quotient rule:

$$\frac{\partial m_{if}}{\partial \boldsymbol{\beta}} = \frac{\left(1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}\right)\dfrac{\partial}{\partial \boldsymbol{\beta}}\ \exp\ \mathbf{X}_{if}\boldsymbol{\beta}\ -\exp\ \mathbf{X}_{if}\boldsymbol{\beta}\ \dfrac{\partial}{\partial \boldsymbol{\beta}}\left(1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}\right)}{\left(1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}\right)^{2}}$$

$$\frac{\partial m_{if}}{\partial \boldsymbol{\beta}} = \frac{\left(1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}\right)\exp\ \mathbf{X}_{if}\boldsymbol{\beta}\ \mathbf{X}_{if}-\exp\ \mathbf{X}_{if}\boldsymbol{\beta}\left(\mathbf{X}_{ig}\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}\right)}{\left(1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}\right)^{2}}$$

$$\frac{\partial m_{if}}{\partial \boldsymbol{\beta}} = \frac{\exp\ \mathbf{X}_{if}\boldsymbol{\beta}}{1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}}\left(\frac{\mathbf{X}_{if}\left(1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}\right)}{1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}}-\frac{\left(\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}\ \mathbf{X}_{ig}\right)}{1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}}\right)$$

$$\frac{\partial m_{if}}{\partial \boldsymbol{\beta}} = \frac{\exp\ \mathbf{X}_{if}\boldsymbol{\beta}}{1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}}\left(\mathbf{X}_{if}-\frac{\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}\ \mathbf{X}_{ig}}{1+\sum\limits_{g=1}^{F}\exp\ \mathbf{X}_{ig}\boldsymbol{\beta}}\right)$$

$$\frac{\partial m_{if}}{\partial \boldsymbol{\beta}} = m_{if}\left(\mathbf{X}_{if}-\sum\limits_{g=1}^{F}m_{ig}\mathbf{X}_{ig}\right)$$

Noting that, by Eq. 3.3, $\mathbf{X}_{if}=\mathbf{I}_{f}\ \mathbf{X}_{i}\ \bullet\mathbf{X}_{i}$

$$\frac{\partial m_{if}}{\partial \boldsymbol{\beta}} = m_{if}\left(\mathbf{I}_{f}\ \mathbf{X}_{i}\ \bullet\mathbf{X}_{i}-\sum\limits_{g=1}^{F}m_{ig}\mathbf{I}_{g}\ \mathbf{X}_{i}\ \bullet\mathbf{X}_{i}\right)$$

And finally:

$$(4.2) \qquad \frac{\partial m_{if}}{\partial \boldsymbol{\beta}} = \mathbf{X}_i m_{if} \bullet \left(\mathbf{I}_f \ \mathbf{X}_i \ - \sum_{g=1}^{F} \mathbf{I}_g \ \mathbf{X}_i \ m_{ig} \right)$$

To obtain the derivatives with respect to daily survival (s_i) under the multinomial logit, let

$$s_i = \frac{1}{1 + \sum_{g=1}^{F} \exp \ \mathbf{X}_{ig} \boldsymbol{\beta}_g}.$$

Then, by the quotient rule:

$$\frac{\partial s_i}{\partial \boldsymbol{\beta}} = - \frac{\frac{\partial}{\partial \boldsymbol{\beta}} \left(1 + \sum_{g=1}^{F} \exp \ \mathbf{X}_{ig} \boldsymbol{\beta} \right)}{\left(1 + \sum_{g=1}^{F} \exp \ \mathbf{X}_{ig} \boldsymbol{\beta} \right)^2} = - \frac{\sum_{g=1}^{F} \exp \ \mathbf{X}_{ig} \boldsymbol{\beta} \ \mathbf{X}_{ig}}{\left(1 + \sum_{g=1}^{F} \exp \ \mathbf{X}_{ig} \boldsymbol{\beta} \right)^2}$$

And:

$$\frac{\partial s_i}{\partial \boldsymbol{\beta}} = - \frac{\mathbf{X}_i \bullet \sum_{g=1}^{F} \exp \ \mathbf{X}_{ig} \boldsymbol{\beta} \bullet \mathbf{I}_g \ \mathbf{X}_i}{\left(1 + \sum_{g=1}^{F} \exp \ \mathbf{X}_{ig} \boldsymbol{\beta} \right)^2} = -\mathbf{X}_i \bullet \frac{1}{1 + \sum_{g=1}^{F} \exp \ \mathbf{X}_{ig} \boldsymbol{\beta}} \bullet \sum_{g=1}^{F} \frac{\exp \ \mathbf{X}_{ig} \boldsymbol{\beta} \bullet \mathbf{I}_g \ \mathbf{X}_i}{1 + \sum_{g=1}^{F} \exp \ \mathbf{X}_{ig} \boldsymbol{\beta}}$$

Substituting back in the daily survival and failure probabilities:

$$(4.3) \qquad \frac{\partial s_i}{\partial \boldsymbol{\beta}} = -s_i \mathbf{X}_i \bullet \sum_{g=1}^{F} m_{ig} \mathbf{I}_g \ \mathbf{X}_i$$

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