ESTIMATING SURVIVAL PROBABILITIES OF UNMARKED DEPENDENT YOUNG WHEN DETECTION IS IMPERFECT

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Abstract.   We present a capture–recapture modeling approach to the estimation of survival probability of dependent chicks when only the attending adult bird is marked. The model requires that the bird's nest is found prior to hatching and that the number of eggs that hatch are counted. Subsequent data are sightings of the marked adult and a count of chicks with the adult. The model allows for imperfect detection of chicks, but the number of chicks can never exceed the number of eggs in the nest (i.e., adults cannot adopt chicks). We use data from radio-tagged adult Mountain Plovers (*Charadrius montanus*) and their unmarked chicks as an example. We present the model in terms of precocial bird species, but the method extends to many other taxa.

Key words: capture–recapture, Cormack-Jolly-Se-ber model, Mountain Plover, open population models, survival estimation.

Estimación de las Probabilidades de Supervivencia de Crías Dependientes no Marcadas cuando la Detección es Imperfecta

Resumen.   Presentamos un enfoque de captura y re-captura para modelar la estimación de la probabilidad de supervivencia de polluelos dependientes cuando sólo el adulto que atiende a los polluelos esta marcado. El modelo requiere que el nido sea encontrado antes de la eclosión y que se cuenten el número de huevos que eclosionan. Los datos subsecuentes necesarios son los avistamientos del adulto marcado y el conteo de los polluelos que se encuentran con el adulto. El modelo permite la detección imperfecta de los polluelos, pero el número de polluelos nunca puede exceder el número de huevos en el nido (i.e., los adultos no pueden adoptar polluelos). Como ejemplo, utilizamos datos de adultos marcados con radio transmisores de *Charadrius montanus* y de sus polluelos no marcados. Presentamos el modelo en términos de especies de aves precociales, pero el método también se extiende a muchas otras especies.

Survival probability of juvenile animals can be important for understanding the population dynamics of a species. Past methods of estimating survival of dependent young have assumed an accurate count of the number of chicks remaining in the brood (Flint et al. 1995, Manly and Schmutz 2001). For some species this may be a reasonable assumption, but for other species the number of chicks cannot be reliably counted after the chicks leave the nest. Imperfect counts may occur for a variety of reasons, but most often because the chicks hide when humans are present. Therefore, the counts of chicks detected are less than or equal to the total number of chicks remaining alive in the brood.

If chicks are uniquely marked, a Cormack-Jolly-Seber (CJS) model could be used to estimate survival of the chicks (Cormack 1964, Jolly 1965, Seber 1965), but young birds often cannot be uniquely marked. For example, radio transmitters may be too large, the leg structure of the young birds may not be developed enough for banding, marking may decrease survival of the chicks, or there may not be enough unique color band combinations to band both adults and young. Therefore, an estimation method which does not require uniquely marked individuals and allows for imperfect detection would be useful.

We present a likelihood-based extension to the CJS model which estimates survival of dependent young when only the adult is marked and some young may not have been counted. In theory the method may be used for broods of any number of chicks. In practice it is most useful for species that have fewer than five chicks per brood and do not show brood mixing. This method relaxes the assumption made by Flint et al. (1995) and Manly and Schmutz (2001) that all of the young must be counted at every sampling occasion, but it does not allow brood mixing as their methods do. In addition, the Manly and Schmutz (2001) estimator models heterogeneity in survival probabilities

directly, while our estimator allows a form of individual heterogeneity in survival to be modeled. Our method is designed for species with uniparental care. Cases of biparental care would require both adults to be uniquely marked and sampled nearly simultaneously.

We present data from radio-tagged adult Mountain Plovers (*Charadrius montanus*) and their broods from eastern Colorado as an example of the method and types of models which may be constructed. Mountain Plovers are endemic to the Great Plains region of North America. Females lay up to 3 eggs each in two or more nests in disturbed native prairie or agricultural landscapes of the western Great Plains, and in shrub semideserts to the immediate west. Mountain Plover chicks are precocial, leaving the nest within 3 hr of the last egg hatching (Graul 1973, Knopf 1996) and move with the adult up to 2 km from the nest in the first 2 days (Knopf 1996). Chicks have been reported to fledge at 33–34 days (Graul 1975) and 36 days (Miller and Knopf 1993).

METHODS

The model assumes there are k sampling occasions. Broods can be added to or removed from the data set at any occasion. Adults attending young must be uniquely marked, and that mark must be read without error each time the adult is resighted. The young do not need any type of mark. The notation used here is similar to that used by Schwarz and Stobo (1999) because our model shares some of the characteristics of their tag-misread model. Model notation is presented in Table 1.

STATISTICAL MODEL AND ASSUMPTIONS

Several assumptions underlie the model. First, broods are assumed to be independent, so that no brood influences the fate of any other brood. Here we make an assumption about broods, but inference remains at the level of individual chicks. Second, individual chicks within a brood are assumed to be exchangeable. This means that all chicks within a brood have the same survival probability at a given time. Third, survival of chicks is assumed to be equal across broods at a given age and time interval. We address some ways of relaxing these assumptions in the discussion.

To extend the CJS model to broods rather than individual birds it is necessary to switch to matrix notation to account for all of the possible outcomes of the survival and detection of chicks within a brood. For example, there are six possible ways to observe two chicks from a brood of three. One chick may have died and the remaining two chicks survived and were detected; this could happen with three different combinations of chicks. Otherwise, three chicks could have survived, but only two chicks were detected; this can also happen three ways. For example, if the encounter history (3, 2, 3, 1) is observed, the observations before the second count of three chicks provide information about detection probability because all chicks are known to be alive. Observations beyond the second three chicks provide information about survival. While this model appears similar to a multistate model, it is different in the way the detection probability is handled. Matrices used here are given in the Appendix.

Upon completion of the study each brood will have an encounter history; for example $\mathbf{h} = (3, 2, 3, 1)$ for a study with $k = 4$ sampling occasions and $m = 3$ initial chicks. The overall probability of this encounter history is

$$P[\mathbf{h}] = [1\ 0\ 0\ 0]\phi_1\mathbf{D}(\mathbf{p}_2, 2)\phi_2\mathbf{D}(\mathbf{p}_3, 3)$$

$$\times\ \phi_3\mathbf{D}(\mathbf{p}_4, 1)\begin{bmatrix}1\\1\\1\\1\end{bmatrix}$$

The row vector [1 0 0 0] is needed to denote that the brood began with three chicks. If only two of three eggs hatched the vector would be [0 1 0 0]. For computing purposes, it is most efficient to set m to the maximum number of eggs observed in any nest and use row vector to assign the number of eggs hatching from each individual nest. The final column vector [1 1 1 1]^T is required to sum over all possible outcomes of the survival and resighting processes because it is unknown how many chicks survived to the kth sampling occasion.

The likelihood function is proportional to the multinomial probability function

$$L(\phi, p\,|\,n, \mathbf{h}) \propto \prod_{i=1}^{n} P[\mathbf{h}_i].$$

The likelihood can be optimized numerically to obtain parameter estimates. We used the quasi-Newton optimization routine in SAS PROC IML (SAS Institute 2002). The variance-covariance matrix may be obtained from the numerically estimated information matrix. The variance of each parameter could also be estimated by bootstrapping on broods (Efron and Tibshirani 1993). SAS code is available from the first author.

The ϕ and p parameters can be modeled as functions of covariates through a link function as is common in general linear models (McCullagh and Nelder 1989) and in program MARK (White and Burnham 1999). It is important to note that covariates of individual chicks cannot be used with this model because individual chicks are not known uniquely. Brood-specific covariates, environmental covariates, and any form of grouping may be used to build biologically relevant models.

MOUNTAIN PLOVER EXAMPLE

Our study was conducted in Weld County, Colorado (40°37′N, 103°58′W) during the spring and summer of 2002. Mountain Plover nests were found by locating adults and watching them until they returned to their nest. The number of eggs that hatched per nest was counted. The adult plover attending each nest was trapped and fit with a back-mounted radio just before the eggs hatched (as determined by egg flotation). Adults were located by radio-telemetry daily after the eggs hatched. The number of chicks seen with each adult was recorded. If the adult could not be located (due to adverse weather conditions for example), a "." was assigned to the encounter history for that occa-

TABLE 1.   Definitions of parameters and statistics used to estimate survival of unmarked dependent chicks.

Parameter	Definition
ϕ_i	The probability of survival of an individual chick from time i to time $i + 1$ given the chick is alive at time i and remains on the study area.
p_i	The probability that a chick will be resighted given it is alive and the adult was resighted at time i.
Statistic	
m	The maximum number of chicks in a brood.
h = $\{h_1, h_2, \cdots, h_k\}$	Number of chicks seen on each sampling occasion for a given brood. Each h_i value takes on one of the following codes: 0, 1, 2, $\cdots$, m, ".". A "." represents a brood that was not sampled on a given occasion. This is distinctly different from a zero, which indicates a brood that was sampled (i.e., the adult was seen), but no chicks were detected.
n	The number of broods sampled. This is also equal to the number of adults marked for a species with uniparental care.
D (p, h_i)	An operator that returns the appropriate capture probability matrix given the value of the encounter history at time i. See Appendix for matrix definitions.

sion. Nineteen adults and their broods were monitored for up to 40 days after hatching. An adult whose radio failed during the course of the study was removed from the analysis after the time of radio failure. Broods that fledged were also removed from analysis at the time of fledging.

We constructed models to examine several hypotheses about survival. Models included ϕ constant across time ($\phi(.)p(.)$), ϕ at the first period (day) after hatching different from subsequent $\phi(\phi(H1)p(.))$, ϕ at the first two periods after hatching equal but different from subsequent $\phi(\phi(H2)p(.))$, ϕ at the first three periods and after hatching equal but different from subsequent $\phi(\phi(H3)p(.))$. The constant ϕ model represents a situation where survival is close enough to constant that we can estimate it with a single parameter given the data available. The next three models represent either survival changing with the age of the chicks or heterogeneity in survival among chicks. These two hypotheses cannot be separated with these data and likely occur simultaneously. Detection probability was held constant in all models. Our model set is intentionally small and simple because only 19 broods were sampled. Therefore, not much information about detection probability is available to inform model selection and the chance for spurious results is high. Many other biologically reasonable models could be examined, such as trends in survival and variation in detection probability, but large model sets are dangerous with small sample sizes (Burnham and Anderson 2002). Model selection was based on information-theoretic methods and scored using Akaike's Information Criterion adjusted for small sample size (AIC_c). Parameter estimates and variances were model averaged (Burnham and Anderson 2002).

Goodness-of-fit was considered using a χ^2 test. Due to the sparsity of the data relative to the number of possible capture histories, data were pooled over five consecutive encounters, such that the highest number of chicks detected during that 5-occasion period was used as the number of chicks detected. A general time-varying model was fit to the pooled data. Expected cell counts were generated and a standard χ^2 test generated from summed (observed − expected)^2/expected values.

RESULTS

The goodness-of-fit statistics suggested the model fit the data well, except for a single encounter of a chick within one brood. Excluding the outlying value, the χ^2_{20} value was 20.5, ($P = 0.57$). The sampling protocol met the model assumptions, further supporting an adequate fit of the model to the data.

Model $\phi(H1)p(.)$ was selected as the best model by AIC_c (Table 2). Models $\phi(H2)p(.)$ and $\phi(H1)p(.)$ both had considerable support ($\Delta AIC_c < 2$). Model $\phi(.)p(.)$ had essentially no support from the data. The model-averaged estimate of survival probability for the first day after hatching was 0.88 ± 0.05. The model averaged survival estimates increase each day after hatching up to the fourth day at which survival was modeled as constant and equaled 0.98 ± 0.01 (Table 3).

DISCUSSION

Allowing for imperfect detection of chicks is important for species whose chicks are difficult to detect. Previous methods assumed that all chicks in a brood were counted each time the adult was resighted. This is very difficult for some species, such as the Mountain Plover, where the chicks hide when alerted by the adult (Sordahl 1991).

The model presented here does not allow for brood mixing. Therefore, the adult bird is assumed to be caring only for young from the nest it was tending. This is a reasonable assumption for many species, but is

TABLE 2.   Summary of model selection results for Mountain Plovers in Weld County, Colorado in 2002. Maximized log likelihoods, number of parameters (K), sample size (n), ΔAIC_c and Akaike weights for models listed by order of AIC_c from best to worst approximating model. ΔAIC_c is the difference between model i and the best approximating model.

Model	Log-likelihood	K	n	ΔAIC_c[a]	AIC_c weight
$\phi(H1)p(.)$	−447.42	3	19	0.00	0.49
$\phi(H3)p(.)$	−448.03	3	19	1.22	0.27
$\phi(H2)p(.)$	−448.16	3	19	1.48	0.23
$\phi(.)p(.)$	−452.34	2	19	6.99	0.01

[a] The lowest AIC_c value in the analysis was 902.44.

less so for other species, such as waterfowl. Flint et al. (1995) and Manly and Schmutz (2001) present methods for dealing with brood mixing, but assume that all chicks are detected.

Our model allows for adults to be marked in any way that allows for individual identification. The example Mountain Plover data used radio-tagged adults, which allowed adults to be located easily and therefore increased capture probability. This resulted in precise estimates of survival of the young. In situations where adults are only banded, our model remains applicable but precision will likely be worse if the adults are difficult to resight.

In some species there may be dependence in fate across broods. In Mountain Plovers, males and females independently brood clutches and raise young from separate nests. Some clutches may therefore be highly related. One would expect the survival of chicks in a clutch to be more similar to closely related clutches than to distantly related clutches. Using a bootstrapped variance (Efron and Tibshirani 1993) can help account for the lack of independence within broods.

Survival probability may vary among chicks within a brood. If this is true, then one would expect the chicks with the lowest survival probability to die first and the chicks with the highest survival probability to die last. The result appears much like increasing survival probability with age of chicks. Therefore, an age or heterogeneity model may be constructed in the same manner as was done with models H1–H4 in our example. Unfortunately, when chicks are not individually marked, there is no information to separate these two hypotheses. These age/heterogeneity models fit Mountain Plover survival well and would likely be useful for other species. Mountain Plovers show increased survival with time since hatch up to at least 4 days of

age suggesting either an age differences or individual heterogeneity in survival.

The pooling for the goodness-of-fit test was admittedly *ad hoc,* but it appeared to provide useful information about model fit. Much of capture-recapture statistics suffers from problems with goodness-of-fit testing and our model is no exception. One could generalize Test 2 and Test 3 from Burnham et al. (1987) to examine data for this model, but it would result in very small expected values in most cells and therefore the test would be unreliable. Our goal in this paper was to present a new model structure applicable to avian studies, not to expand goodness-of-fit theory. Therefore, we feel the fit statistic used here was adequate.

The model can estimate the survival of young in broods of any number, but in practice smaller broods (<5 young per brood) will produce better estimates. As the broods get larger, the number of possible outcomes with nearly the same probability becomes large. This results in the likelihood surface flattening and estimation being unreliable without very large sample sizes. With simulated broods similar to that of the Mountain Plover, the estimator performs well.

A standard CJS model estimates apparent survival, the probability that an individual remains alive and available for recapture. We suggest that the estimator presented here gives true survival in many situations, such as with the Mountain Plover, because chicks have little or no chance of surviving if they leave the adult. As long as the chick is with the adult, it remains available for recapture because the adult may be found with telemetry.

We presented the model in the language of avian biology, and Mountain Plover chicks were the motivation for the development of the model, but the model applies to a wide array of taxa for which young stay

TABLE 3.   Model-specific and model-averaged estimates of survival ± SE for individual Mountain Plovers for days 1, 2, 3 and 4+ after hatching.

Model	Day 1	Day 2	Day 3	Day 4+
$\phi(.)p(.)$	0.97 ± 0.01	0.97 ± 0.01	0.97 ± 0.01	0.97 ± 0.01
$\phi(H1)p(.)$	0.86 ± 0.05	0.98 ± 0.01	0.98 ± 0.01	0.98 ± 0.01
$\phi(H2)p(.)$	0.90 ± 0.03	0.90 ± 0.03	0.98 ± 0.01	0.98 ± 0.01
$\phi(H3)p(.)$	0.91 ± 0.03	0.91 ± 0.03	0.91 ± 0.03	0.98 ± 0.02
Model-averaged estimate	0.88 ± 0.05	0.94 ± 0.04	0.96 ± 0.03	0.98 ± 0.01

near the adult and are hard to detect, including bear cubs and other species.

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APPENDIX

It is necessary to use matrix notation to describe all possible outcomes of the survival and capture processes. We follow a notation similar to that of Schwarz and Stobo (1999). See Table 1 for definitions of parameters and statistics

ϕ_i an $m + 1 \times m + 1$ matrix with elements describing all possible outcomes of the survival process. Rows represent the number of chicks alive at encounter occasion i and columns represent the number of chicks alive at $i + 1$.

$$\begin{bmatrix} \phi_i^m & \binom{m}{m-1}\phi_i^{m-1}(1-\phi_i) & \binom{m}{m-2}\phi_i^{m-2}(1-\phi_i)^2 & \cdots & \binom{m}{0}(1-\phi_i)^m \\ 0 & \phi_i^m & \binom{m-1}{m-2}\phi_i^{m-2}(1-\phi_i) & \cdots & \binom{m-1}{0}(1-\phi_i)^{m-1} \\ 0 & 0 & \phi_i^{m-2} & \cdots & \binom{m-2}{0}(1-\phi_i)^{m-2} \\ \vdots & \vdots & & & \vdots \\ 0 & 0 & \cdots & 0 & 1 \end{bmatrix}$$

$\mathbf{p}_i$ an $m + 1 \times m + 1$ matrix with elements describing all possible outcomes of the detection process:

$$
\begin{bmatrix}
p_i^m & 0 & 0 & \cdots & 0 \\
0 & 0 & & & \\
0 & & \ddots & & \vdots \\
\vdots & & & & \\
0 & & & & 0
\end{bmatrix} \text{ if } h_i = m,
$$

$$
\begin{bmatrix}
\binom{m}{m-1} p_i^{m-1}(1 - p_i) & 0 & 0 & \cdots & 0 \\
0 & p_i^{m-1} & 0 & \cdots & 0 \\
0 & 0 & 0 & \cdots & 0 \\
\vdots & & & \ddots & \ddots & \vdots \\
0 & & & \cdots & & 0
\end{bmatrix} = \text{mif } h_i = m - 1,
$$

$\cdots \mathbf{p}_i$ matrices follow this pattern for all other values of h_i.

$$
\begin{bmatrix}
1 & 0 & \cdots & 0 & 0 \\
0 & 1 & & 0 & 0 \\
\vdots & & \ddots & & \vdots \\
0 & 0 & & 1 & 0 \\
0 & 0 & \cdots & 0 & 0
\end{bmatrix} \text{ if } h_i \text{ is observed } (\cdot).
$$