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Authors: McGowan, Conor P., and Gardner, Beth

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Evaluating Methodological Assumptions of Catch-Curve Survival Estimation for Unmarked Precocial Shorebird Chicks

CONOR P. MCGOWAN^{1,*} AND BETH GARDNER²

¹U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL, 36849, USA

²North Carolina State University, Department of Forestry and Environmental Resources, Turner House, Campus Box 7646, Raleigh, NC, 27695-7646, USA

*Corresponding author; E-mail: cmgowan@usgs.gov

Abstract.—Estimating productivity for precocial species can be difficult because young birds leave their nest within hours or days of hatching and detectability thereafter can be very low. Recently, a method for using a modified catch-curve to estimate precocial chick daily survival for age based count data was presented using Piping Plover (*Charadrius melodus*) data from the Missouri River. However, many of the assumptions of the catch-curve approach were not fully evaluated for precocial chicks. We developed a simulation model to mimic Piping Plovers, a fairly representative shorebird, and age-based count-data collection. Using the simulated data, we calculated daily survival estimates and compared them with the known daily survival rates from the simulation model. We conducted these comparisons under different sampling scenarios where the ecological and statistical assumptions had been violated. Overall, the daily survival estimates calculated from the simulated data corresponded well with true survival rates of the simulation. Violating the accurate aging and the independence assumptions did not result in biased daily survival estimates, whereas unequal detection for younger or older birds and violating the birth death equilibrium did result in estimator bias. Assuring that all ages are equally detectable and timing data collection to approximately meet the birth death equilibrium are key to the successful use of this method for precocial shorebirds. Received 5 June 2012, accepted 24 September 2012.

Keywords.—*Charadrius melodus*, daily survival estimates, fecundity, Piping Plovers, precocial shorebirds, simulation study, validating assumptions.

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Measuring the reproductive success for individual females of a precocial bird species can be quite difficult because young leave the nest site soon after hatching. As part of assessing productivity, researchers often turn to estimating survival during the pre-fledging period (Hitchcock and Gratto-Trevor 1997; Groen and Hemerik 2002; Lukacs *et al.* 2004; Colwell *et al.* 2007). This parameter can be incorporated into population simulation models to evaluate management actions or the conservation status and needs of a species (Hitchcock and Gratto-Trevor 1997; McGowan and Ryan 2009).

A modified catch-curve approach was developed to estimate daily survival of unmarked precocial chicks using age-based count data for Piping Plovers (*Charadrius melodus*) in the Missouri River (McGowan *et al.* 2009). That study has been applied to several Piping Plover population models (McGowan and Ryan 2009; McGowan *et al.* 2011a) and the approach was also used to estimate survival of King Rail (*Rallus elegans*) chicks in the Upper Mississippi River valley (Darrah and Kremenz 2011). The

catch-curve method has seven statistical and ecological assumptions: 1) there is a stable age structure, 2) the population is stationary, 3) all animals have an equal probability of selection (equal detectability), 4) the sample is representative of the population of interest, 5) the fates of all animals are independent, 6) all ages are recorded accurately, and 7) survival probability is constant across all age classes during the sampling period (Chapman and Robson 1960; Skalski *et al.* 2005). McGowan *et al.* (2009) could not determine if any assumptions were meaningfully violated and what those violations might mean for the resulting parameter estimates.

In this paper we use a simulation model developed to mimic Piping Plovers (as a representative of shorebirds in general) and age-based count-data collection to test the effects of violating some of the assumptions of the catch-curve survival analysis method on the resulting daily survival estimates. Simulation environments are effective means to test the effects of violating assumptions because the true value of survival is known

and the true extent of assumption violation is also known. We evaluate the effects of intra-brood dependence of individuals, inaccurate aging, age dependent detection bias, unstable age structure and stationarity violations. These assumptions were selected because they are potentially problematic for precocial shorebird species and were previously insufficiently addressed (McGowan *et al.* 2009). We did not evaluate the assumption “survival probability is constant across all age classes during the sampling period” because that assumption has been previously evaluated and the assumption is unlikely to be true for Piping Plovers (Cohen *et al.* 2009; Catlin *et al.* 2011). The consequences of variable survival across age classes can be addressed by calculating survival rates for age classes separately (McGowan *et al.* 2009).

METHODS

Simulating Hatching and Death

To evaluate the appropriateness of the catch-curve estimator for precocial shorebird chicks, we simulated the births (hatching) and deaths of 250 broods, with four chicks each. We assigned each brood a hatch date by drawing from a log-normal distribution with the mean/peak hatch date set at day 30. The season was set to be 90 days, broods randomly assigned a hatch date > 90 days were set to 90 days. After hatching, individuals within a brood either survived or died each day according to the following procedure.

1) We defined a mean daily survival rate (S) and a variance (s), and each day a population daily survival rate (S_d) was drawn from a beta distribution defined by that mean and variance (using the method of moments to calculate the distribution shape parameters, A and B). In the simulations, mean population daily survival was a known quantity against which estimated daily survival could be compared for accuracy.

$$S_d \sim \text{beta}(A, B),$$

2) On each day each brood was given a random number drawn from a uniform distribution between 0 and 1 to introduce randomization into the brood daily survival function. That number served as the mean daily survival rate of individuals in the brood.

$$S_d^b \sim \text{unif}(0, 1),$$

3) Then we generated a second set of random numbers for each individual in the brood from a normal distribution using the brood’s random number as the mean and predetermined variance for that simulation.

$$S_d^{b,i} \sim \text{norm}(S_d^b, s^b),$$

The intra-brood variance (S^b) could be increased or decreased to examine the sensitivity of daily survival estimates to increasing or decreasing intra-brood independence.

4) The generated number for each individual was then compared to the overall daily survival rate for that day. If the number for an individual was greater than the overall survival rate the individual died and if the number was lower it survived.

$$\text{Survive} = \begin{cases} \text{no, if } S_d^{b,i} > S_t \\ \text{yes, if } S_d^{b,i} < S_t \end{cases}$$

We kept track of each individual’s age throughout the season. If a chick reached 26 days of age it was considered fledged and its age was no longer tracked. This model was developed to mimic the hatching and death process of Piping Plover broods, but is intended to represent shorebirds more generally.

Simulating the Sampling Process

McGowan *et al.* (2009) describe in detail the method for sampling and calculating estimates of daily survival for unmarked Piping Plover chicks using a catch-curve approach (Chapman and Robson 1960) and they used 13 years of age-based count data from the U.S. Army Corps of Engineers as an example. We attempted to mimic that sampling process in our simulation model. We created three 5-day sampling periods to count the number of chicks observed and record their ages. The sampling periods were set at 5 days duration to minimize the probability that individuals would be counted on multiple visits to a site with in a single sampling window in the field study (McGowan *et al.* 2009). Sampling periods were initially set to occur near the peak hatching date of the simulated population (period 1 = days 27-31, period 2 = days 32-36, period 3 = days 37-41).

We grouped birds into age classes (0-5 days, 6-10, days, etc.) to reflect the methodology used for Piping Plovers (McGowan *et al.* 2009). The simulation simply counted the number of chicks alive in each age class during the observation window. Each individual observed in the age class was assigned the median age for that age class (i.e., 0-5 day old birds = 2.5 days, 6-10 day old birds = 8 days, etc.). With these data, we calculated the daily survival rate (Chapman and Robson 1960):

$$\hat{S} = \frac{T}{(n + T - 1)}$$

where T is the sum of all the observed ages of all the individuals, and n is the number of individuals observed.

We calculated the standard deviation of the mean daily survival rate (Chapman and Robson 1960):

$$SD(\hat{S}) = \sqrt{\hat{S} \frac{(\hat{S} - (T - 1))}{(n + (T - 1))}}$$

The simulations and sampling of simulated data were replicated 100 times each, which provided a broad range of estimates, and increasing replicate numbers to 1,000 did not appear to influence the variance estimates. All simulations were done in program R (R Development Core Team 2009).

Testing Estimation Assumptions

We used the simulation model to examine violations of assumptions 1, 2, 3, 5 and 6 of the catch curve method. To violate the equal detection probability, we removed 20% and 50% of the individuals from the youngest age classes and the oldest age classes in separate simulations (e.g., number of 2.5 day olds observed = $(1 - 0.2) \times N_{2.5d}$), for a total of four scenarios where detection was biased by age. To violate the independent fates assumption, we modified the intra-brood standard deviation parameter (described above) from the baseline of 0.1 to 0.2, 0.05, 0.0. These represent declining amounts of independence amongst individuals in a brood (i.e., decreasing variability within a brood). We simulated inaccurate aging for 20% and 50% of the individuals without any positive or negative bias. Meaning we subtracted or added days to the ages of randomly selected individuals (amounting to 20% or 50% of the individuals) and all bird ages were equally likely to be overestimated as underestimated. A uniform random number between zero and one was generated for each individual and if that number exceeded the 0.8 (i.e., the 20% mis-aged simulation) or the 0.5 threshold then days were added or subtracted to the actual age. The number of days to add/subtract was randomly selected from a normal distribution with mean 0.0 and a standard error of 1.0. We also introduced an aging bias where 20% of the birds were overage and underage by 2 or 4 days in separate simulations using a similar approach, but setting the mean of the normal distribution that determined the addition/subtraction as -4.0, -2.0, 2.0, or 4.0 (depending on the simulation). To examine how much the timing of the sampling with respect to the hatching/death equilibrium affects estimation accuracy, we set the three sampling periods to span days 20-35 and days 35-50. Moving the sampling window earlier or later in the season violates the stable age structure and the stationary population assumptions.

We compared the mean and the 95% confidence intervals (CI) of the daily survival estimate for each period under each scenario with the known mean survival estimate and the known 95% CI (Table 1). Also, we calculated the percent bias of each mean survival estimate by subtracting the known daily survival (u) from the estimated survival (\hat{S}), dividing by the known survival and multiplying by 100 (Table 2).

RESULTS

Our daily survival estimates from the simulated data show great variation depending

on timing of the sampling period within the season and detectability bias (Table 1, Table 2). The estimates of the middle period (days 32-36) were consistently the most accurate with large overlap in the estimated 95% CI compared to the actual daily survival estimate and CI (Table 1) and little positive or negative bias in the mean estimates (Table 2). The first period tended to result in estimates that were low and the third period returned estimates that were high with respect to the actual daily survival rate (Table 1, Table 2).

Although many of the assumption violations altered the accuracy of the resulting daily survival estimates, the 95% CI of the estimates still often fell within the range of the actual survival rate. Further, there was rarely bias in the estimates that exceeded 2% of the actual mean (Table 2). Conducting the surveys earlier in the season led to daily survival estimates that were up to 6.8% lower than the actual mean daily survival for that simulation. Inaccurate aging showed little effect on estimate accuracy, even when intentional positive or negative bias was applied (Table 1, Table 2). Variation in intra-brood independence also had little effect on estimator bias (Table 1, Table 2).

DISCUSSION

In general, our simulation study shows that the catch-curve estimator has the potential to return accurate unbiased estimates of daily survival for precocial chicks. The accuracy of resulting estimates was dependent on the timing of sampling. Too early in the season and the estimates were biased low, too late in the season and the estimates were biased high. The population must be in or near a birth/death equilibrium in order to meet the stable age structure and the stationary assumptions of the catch-curve methodology. If births exceeded deaths at the time of sampling, the proportion of young birds in the population would be inflated, whereas if the birth rate was below the death rate the proportion of older birds in the population would be inflated, biasing the resulting daily

Table 1. Daily survival estimates from simulated data of births and deaths of precocial chicks using a catch-curve estimator. We present the mean and the upper and lower bound from the actual daily survival value and the estimates from three different sampling periods with in the season (period 1 = day 27-31, period 2 = day 32-36, period 3 = day 37-41).

Simulation	Actual			Period 1			Period 2			Period 3		
	lower	mean	upper	lower	mean	upper	lower	mean	upper	lower	mean	upper
Baseline	0.907	0.919	0.931	0.896	0.904	0.913	0.916	0.922	0.929	0.926	0.931	0.937
Age dependant detection bias												
80% detection of younger age classes	0.907	0.919	0.931	0.900	0.909	0.917	0.919	0.926	0.932	0.928	0.933	0.939
50% detection of younger age classes	0.910	0.921	0.933	0.908	0.917	0.926	0.925	0.931	0.938	0.932	0.937	0.943
80% detection of older age classes	0.907	0.921	0.934	0.889	0.899	0.908	0.911	0.918	0.926	0.922	0.928	0.935
50% detection of older age classes	0.906	0.919	0.932	0.876	0.888	0.899	0.900	0.909	0.918	0.912	0.921	0.929
Intra-brood independence bias												
Within brood variance = 0	0.907	0.919	0.931	0.900	0.907	0.915	0.919	0.925	0.931	0.928	0.933	0.938
Within brood variance = 0.05	0.904	0.919	0.934	0.898	0.906	0.914	0.917	0.923	0.930	0.927	0.932	0.938
Within brood variance = 0.2	0.908	0.919	0.931	0.891	0.901	0.910	0.912	0.919	0.927	0.922	0.929	0.936
Within brood variance = 0.4	0.908	0.920	0.932	0.881	0.893	0.904	0.904	0.914	0.923	0.916	0.924	0.932
Incorrect aging												
20% mis-aged (no +/- bias)	0.909	0.920	0.931	0.897	0.905	0.914	0.917	0.923	0.930	0.926	0.932	0.937
50% mis-aged (no +/- bias)	0.908	0.920	0.932	0.898	0.906	0.915	0.917	0.924	0.930	0.926	0.932	0.938
20% mis-aged by -2 days	0.907	0.920	0.932	0.893	0.902	0.910	0.914	0.921	0.928	0.925	0.931	0.937
20% mis-aged by -4 days	0.908	0.920	0.933	0.890	0.899	0.908	0.912	0.918	0.925	0.923	0.929	0.935
20% mis-aged by +2 days	0.906	0.920	0.934	0.900	0.908	0.917	0.918	0.924	0.931	0.926	0.932	0.938
20% m isaged by +4 days	0.907	0.921	0.934	0.902	0.910	0.918	0.919	0.925	0.932	0.927	0.933	0.939
Birth and death equilibrium												
Sampling periods days 35-50	0.907	0.920	0.933	0.923	0.929	0.935	0.928	0.934	0.940	0.930	0.937	0.943
Sampling periods days 20-35	0.907	0.920	0.933	0.842	0.857	0.873	0.883	0.893	0.903	0.910	0.917	0.924

Table 2. Percent bias of simulated catch-curve daily survival estimates from three different sampling periods compared to the known mean daily survival under different violations of the catch-curve assumptions.

Scenario	Actual	Period 1		Period 2		Period 3	
		Estimate	% biased	Estimate	% biased	Estimate	% biased
Baseline (all assumptions met)	0.919	0.904	-1.630	0.922	0.326	0.931	1.310
80% detection of younger age classes	0.919	0.909	-1.090	0.926	0.762	0.933	1.520
50% detection of younger age classes	0.921	0.917	-0.434	0.931	1.090	0.937	1.740
80% detection of older age classes	0.921	0.899	-2.390	0.918	-0.326	0.928	0.760
50% detection of older age classes	0.919	0.888	-3.370	0.909	-1.090	0.921	0.218
Within brood variance = 0	0.919	0.907	-1.310	0.914	-0.544	0.933	1.520
Within brood variance = 0.05	0.919	0.906	-1.410	0.923	0.435	0.932	1.410
Within brood variance = 0.2	0.919	0.901	-1.960	0.919	0	0.929	1.090
Within brood variance = 0.4	0.920	0.893	-2.930	0.914	-0.652	0.924	0.435
20% mis-aged (no +/- bias)	0.920	0.905	-1.630	0.923	0.326	0.932	1.300
50% mis-aged (no +/- bias)	0.920	0.906	-1.520	0.924	0.435	0.932	1.300
20% mis-aged by -2 days	0.920	0.902	-1.960	0.921	0.109	0.931	1.200
20% mis-aged by -4 days	0.920	0.899	-2.280	0.918	-0.217	0.929	0.978
20% mis-aged by +2 days	0.920	0.908	-1.300	0.924	0.435	0.932	1.300
20% mis-aged by +4 days	0.921	0.910	-1.190	0.925	0.434	0.933	1.300
Sampling periods days 35-50	0.920	0.929	0.978	0.934	1.520	0.937	1.850
Sampling periods days 20-35	0.920	0.857	-6.850	0.893	-2.930	0.917	-0.326

survival estimate low or high. We argue that if a constant daily survival probability is assumed, the days just after the peak of hatching in the population would be in birth/death equilibrium because there is a temporary stable age distribution and the population is stationary. Our simulation data indicate that peak hatching occurred on day 30 and the mean day of death was 35, supporting the equilibrium assertion. Researchers that intend to use this approach should consider using pilot studies to examine phenology of the species being studied and perhaps consider a small mark recapture study to generate initial estimates of daily survival (if literature values are not available) to help identify the best possible sampling periods. Often, past reproductive monitoring data may be a useful source of information on nest initiation and perhaps nest survival. Also, simulation studies, in combination with field based pilot studies or historic datasets, might be helpful to identify the best sampling periods.

Age dependent detection bias and inaccurate aging had the expected result on daily survival estimates. These effects may have been exacerbated if the inaccurate aging was applied to whole broods instead of individual chicks independently. However, even when 20% of the younger or older chicks were not

detected, the 95% CI of the daily survival estimates from the middle sampling period greatly overlapped with the actual daily survival estimate CI (Table 1) and the bias was less than 1% for the middle sampling period. Likewise, the middle period daily survival estimates for the simulations with 2 or 4 day positive or negative bias in aging estimates show extensive overlap in the estimated 95% CI and the actual CI and the daily survival estimate bias was small. We conclude that grouping individuals into age classes alleviated the effects of detection bias and inaccurate aging on the accuracy of daily survival estimates. Linking the fates of individuals within a brood did not seem to greatly affect the accuracy of the catch-curve daily survival estimates. Linked fates may not be a large problem in shorebird species where broods are small, and seldom exceeding four chicks. Other precocial taxa, such as waterfowl, with much larger broods may be more susceptible to violations of the independent fates assumption.

From these simulations, we conclude that, if used carefully, the catch-curve approach will return accurate and unbiased estimates of daily survival for precocial shorebird species and perhaps other precocial species. We did not consider how multiple simultaneous assumption violations would affect the resulting daily

survival estimates. In those cases some assumption violations might offset each other (a positive bias combined with a negative bias) or multiple assumptions might compound and increase bias. The sources of bias should be carefully considered and the possible effects on the parameter estimates should be evaluated under any circumstances. The effect of a 1-2% positive or negative bias of course depends on how the estimates are being used in a science or management context. When translating daily survival into an estimate of survival to fledging, by multiplying the daily estimate out over the number of days to fledging, a 1-2% bias could result in a large difference in pre-fledging survival. That difference can further translate into a discrepancy in predicted population viability, depending on the population's sensitivity to changes in pre-fledging chick survival. For example, a 1% negative bias in daily survival, dropping daily survival from 0.92 to 0.91 and using a 25 day pre-fledging period, resulted in a 2% increase in the probability of extinction and a 0.5% decrease in predicted population growth rate 50 years into the future. We did these viability simulations using the McGowan and Ryan (2009) population viability model. If using the estimates to incorporate parameters into a population projection model, we highly recommend applying parametric uncertainty principles into the simulations to account for unknown estimator biases (e.g., McGowan *et al.* 2011b). Like McGowan *et al.* (2009), we are not promoting this methodology as an equivalent alternative to more statistically robust mark and recapture based approaches to survival estimation. However, we do argue that the catch-curve approach is a viable alternative in some monitoring contexts when mark recapture approaches are not possible due to excessive cost or animal welfare concerns. Further, a simulation based approach, such as the one presented here, is an effective way to test estimator assumptions and evaluate any potential biases in data collection.

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