2009

Estimating survival of precocial chicks during the prefledging period using a catch-curve analysis and count-based age-class data

Conor P. McGowan
302 Anheuser-Busch Natural Resources Bldg., Department of Fisheries and Wildlife Sciences, School of Natural Resources, University of Missouri, cpmcg00@hotmail.com

Joshua J. Millspaugh
University of Missouri, joshua.millspaugh@umontana.edu

Mark R. Ryan
302 Anheuser-Busch Natural Resources Bldg., Department of Fisheries and Wildlife Sciences, School of Natural Resources, University of Missouri

Casey D. Kruse
U. S. Army Corps of Engineers

Greg Pavelka
U. S. Army Corps of Engineers

Journal of Field Ornithology

J. Field Ornithol. 80(1):79–87, 2009 DOI: 10.1111/j.1557-9263.2009.00207.x

Estimating survival of precocial chicks during the prefledging period using a catch-curve analysis and count-based age-class data

Conor P. McGowan,[1,3] Joshua J. Millspaugh,[1] Mark R. Ryan,[1] Casey D. Kruse,[2] and Greg Pavelka[2]

[1]*302 Anheuser-Busch Natural Resources Bldg., Department of Fisheries and Wildlife Sciences, School of Natural Resources, University of Missouri, Columbia, Missouri 65211, USA*
[2]*U. S. Army Corps of Engineers, P.O. Box 710, Yankton, South Dakota 57078, USA*

Received 9 May 2008; accepted 25 September 2008

ABSTRACT. Estimating reproductive success for birds with precocial young can be difficult because chicks leave nests soon after hatching and individuals or broods can be difficult to track. Researchers often turn to estimating survival during the prefledging period and, though effective, mark-recapture based approaches are not always feasible due to cost, time, and animal welfare concerns. Using a threatened population of Piping Plovers (*Charadrius melodus*) that breeds along the Missouri River, we present an approach for estimating chick survival during the prefledging period using long-term (1993–2005), count-based, age-class data. We used a modified catch-curve analysis, and data collected during three 5-day sampling periods near the middle of the breeding season. The approach has several ecological and statistical assumptions and our analyses were designed to minimize the probability of violating those assumptions. For example, limiting the sampling periods to only 5 days gave reasonable assurance that population size was stable during the sampling period. Annual daily survival estimates ranged from 0.825 (SD = 0.03) to 0.931 (0.02) depending on year and sampling period, with these estimates assuming constant survival during the prefledging period and no change in the age structure of the population. The average probability of survival to fledging ranged from 0.126 to 0.188. Our results are similar to other published estimates for this species in similar habitats. This method of estimating chick survival may be useful for a variety of precocial bird species when mark-recapture methods are not feasible and only count-based age class data are available.

RESUMEN. **La estimación de la supervivencia de polluelos precociales durante el periodo pre-volantón usando un análisis de curva de captura y datos con clases de edades basados en conteos**
Estimar el éxito reproductivo de aves con polluelos precociales puede ser difícil debido a que los polluelos dejan el nido poco después de eclosionar y los individuos o nidadas pueden ser difíciles de seguir. Los investigadores a menudo estiman la supervivencia durante el periodo pre-volantón y aunque son efectivos, los métodos de marcaje y recaptura no son siempre factibles por razones del costo, tiempo y bienestar del animal. Usando una población amenazada de *Charadrius melodus* que se reproduce sobre el Río Missouri, presentamos un método para estimar la supervivencia de polluelos durante el periodo pre-volantón usando datos de largo plazo (1993–2005) con clases de edades, basados en conteos. Utilizamos un análisis de curva de captura modificada y datos colectados durante tres periodos de muestreo de cinco días cada uno, cerca del medio de la época reproductiva. Este método tiene algunos supuestos ecológicos y estadísticos y nuestros análisis fueron diseñados para minimizar la probabilidad de violar dichos supuestos. Por ejemplo, limitando los periodos de muestreo a solo cinco días dio el resultado razonable de que el tamaño de la población fue estable durante el periodo de muestreo. Las estimaciones de la supervivencia diaria anual variaron entre 0.825 (DE = 0.03) y 0.931 (0.02), dependiendo del año y periodo de muestreo. Estas estimaciones dependieron de la suposición de una supervivencia constante durante el periodo pre-volantón y de ningún cambio en la estructura de la edad de la población. El promedio de la probabilidad de supervivencia en la etapa pre-volantón varió desde 0.126 hasta 0.188. Nuestros resultados son similares a otras estimaciones publicadas para esta especie en hábitats similares. Este método de estimar la supervivencia de los polluelos podría ser útil para una variedad de especies de aves precociales cuando los métodos de marcaje y recaptura no son factibles y cuando solo están disponibles datos con clases de edades basados en conteos.

Key words: catch-curve, *Charadrius melodus*, chick survival, count data, fecundity, Piping Plover, reproductive success

[3]Corresponding author. Current address: Patuxent Wildlife Research Center, U.S. Geological Survey, 12100 Beech Forest Road, Laurel, MD 20708–4017. Email: cpmcg00@hotmail.com

Estimating fecundity or reproductive success is essential for understanding the demography and management needs of any wildlife species (Williams et al. 2001). For birds, fecundity is often defined as the number of young fledged per breeding female (Ricklefs 1972). However, for species with precocial young, estimating fecundity can be difficult. Detectability of prefledging birds is often low and determining how many chicks from a brood survived or even what brood belongs to which female is difficult (Bent 1929, Lukas et al. 2004). In these cases, estimating fecundity with any meaningful measure of variance is sometimes impossible.

Due to these difficulties, researchers estimate the probability of survival during the prefledging period (hereafter: chick survival; Hitchcock and Gratto-Trevor 1997, Groen and Hemerik 2002, Colwell et al. 2007). Combining estimates of chick survival with estimates of nest survival, clutch size, and renesting rate can provide a reasonable estimate of fecundity (Noon and Sauer 1992). Mark and recapture/re-sight or radio-telemetry methods have been used in conjunction with Cormack-Jolly-Seber models to estimate chick survival for some shorebirds (Hitchcock and Gratto-Trevor 1997, Groen and Hemerik 2002, Lukas et al. 2004, Ratcliffe et al. 2005, Colwell et al. 2007), but collecting the necessary data requires substantial time, effort, and monetary expense. These methods can also be invasive and stressful to the birds, e.g., attaching radio-transmitters (Withey et al. 2001, Suedkamp Wells et al. 2003) and disturbing birds with repeated visits to collect data. Recently, Skalski et al. (2006) summarized methods for estimating demographic parameters from age, sex structure, and count data that are less data intensive. With some creativity and modification, these estimation procedures might be useful to avian biologists with access to extensive count data sets when, as is often the case in avian field research, cost, time, and animal welfare are a concern. These techniques might also prove useful when mark-recapture or radio-tracking approaches are not feasible.

There have been a number of recent attempts to develop methods for estimating survival of precocial chicks during the prefledging period (Lukas et al. 2004, Colwell et al. 2007). Here we use a modified catch-curve analysis, first described by Chapman and Robson (1960) and Robson and Chapman (1961), to estimate survival of Piping Plover (*Charadrius melodus*) chicks during the prefledging period. We used age structure data collected by the U.S. Army Corps of Engineers (USACE) from 1993–2005 (C. Kruse and G. Pavelka, unpubl. data). Our study resulted from an effort to build a predictive population model for Piping Plovers in the Great Plains that required a parameter for chick survival in riverine habitats (McGowan 2008). We focused on the catch-curve approach because it fit the data we had, and had reasonable assumptions that were satisfied by our methodological modification of our data. There may be additional alternative methods that match our data and estimation needs such as regression techniques (Skalski et al. 2006). While executing this estimation, we realized that there are a number of alternative survival estimation methods in existence that ornithologists are generally not familiar with. These methods might be useful in cases where mark-recapture/resight methods are not feasible and here we present an example (a modified catch-curve) of one such method.

Piping Plovers are listed as Threatened in the Great Plains (USFWS 1985). The USACE monitors Piping Plover populations nesting on the Missouri River system because of the effects that dam operations and water management have on nesting plovers (USFWS 2000). To date, the USACE has reported "fledge ratios" annually by dividing the number of fledglings observed at the end of the breeding season by the number of breeding females counted near the middle of the breeding season (USFWS 2000). These estimates lack an associated estimate of variance and have limited value from a demographic modeling standpoint. In addition, mark-recapture studies were not possible because of a moratorium on the use of leg bands and color bands on this species since the early 1990's due to concerns about leg injuries.

Our estimates of chick survival based on the modified catch-curve analysis could improve our understanding of the management needs of Piping Plovers in the Great Plains, especially when included in population viability analyses. This analysis allowed us to calculate a statistically rigorous and unbiased estimate of survival during the prefledging period using noninvasive methods that costs less, minimizes time needed to collect data, and minimizes disturbance to this federally protected species. The values we present are daily survival estimates and estimates of the probability of survival to fledging (approximately 20 days posthatching). They are not measures of population level fecundity or reproductive success and are not directly comparable to the widely used fledge ratio.

METHODS

The USACE monitoring efforts along the Missouri River extended from the Gavin's Point river reach at Ponca State Park in Nebraska (42° 61′ 33″ N, 96° 71′ 09″ W) to the Fort Peck Reservoir in eastern Montana (48° 00′11″ N, 106° 41′ 62″ W) (USFWS 2000). Field crews conducted surveys for Piping Plovers at all known nesting sites each week throughout the breeding season (about 20 May–15 August 1993–2005; C. Kruse and G. Pavelka, unpubl. data). During each visit to a nesting site, field crews recorded the number of chicks observed in each of five age classes: 0–5 days old, 6–10 days old, 11–15 days old, 16–20 days old, and ≥ 21 days old. Age determination was based on the known age of broods or on the size of chicks at the time of observation (Hussell and Page 1976, Cairns 1982, Miller and Knopf 1993).

The catch-curve survival approach estimates survival based on the number of individuals in each age class captured in a harvest (Chapman and Robson 1960, Robson and Chapman 1961, Skalski et al 2006), and was initially developed to use data from harvested fish to estimate survival and inform fisheries management (Skalski et al. 2006). The method has seven assumptions (Skalski et al. 2006): 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) ages are recorded accurately, and 7) survival probability is constant across all age classes during the sampling period. In an attempt to meet these assumptions, we developed a modified catch-curve analysis to apply to Piping Plovers.

The data we used were observations of individuals that were not individually marked. We created three 5-day-long capture periods to represent a harvest period. We arbitrarily used three capture periods to compare the survival estimates for different time periods in the season. The three capture periods were 26–30 June, 1–5 July, and 6–10 July. We started by identifying the approximate mid-point of the breeding season (1–5 July), and then added one capture period before and after that mid-point. We selected the capture period length of 5 days to avoid double sampling of specific sites (visited on an approximate 7-day cycle) and to avoid double sampling individuals that could grow from one age class to the next during one capture period. The 5-day capture period design was intended to reduce the risk of violating assumptions one, two, and seven, as listed above. The choice of three 5-day sampling periods at the approximate mid-point of the breeding season assumes that birth/death dynamics and age structure of the chick population at the mid-point is appropriate for use with this method. We present survival estimates for each year, and for all 13 years combined. We analyzed individual years and overall averages rather than pooling data across years because variance estimates were unrealistically small for the pooled data survival estimates.

We tallied the number of individuals observed in each age class during each 5-day period and calculated survival from these data according to Skalski et al. (2006) using:

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

where T is the sum of all the ages of all the individuals in the sample, and n is number of individuals in the sample. To calculate T, we assigned the median age to all the individuals in an age class. For example, all individuals in the 0–5 day age class were assigned an age of 2.5 days. If the average age of the individuals in an age class differs from the median value, the resulting survival estimates will be inaccurate.

To calculate the standard deviation of the survival estimates for each year, we used the delta method presented by Chapman and Robson (1960):

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

We raised the daily survival estimates to the power of 20 to predict the probability of survival to fledging; it takes approximate 20 days for a Piping Plover chick to achieve flight (Elliot-Smith and Haig 2004). To approximate a 95% CI for the estimate of survival to fledging, we raised the upper and lower bound of the daily survival rate to the power of 20 as follows:

$$95\%\ \text{C.I. for the probability of fledging} \approx (\hat{S} \pm (1.96 \times SD(\hat{S})))^{20}.$$

This procedure mimics the method recommended by Hensler and Nichols (1983) for generating a 95% C.I. for a Mayfield estimate of hatching success (Mayfield 1961).

The method assumes that the age structure of the population does not change over time (Chapman and Robson 1960, Skalski et al. 2006), and we attempted to design sampling periods to account for this assumption. We believe that our 5-day sampling period was sufficiently short to meet the assumption that age structure does not change during one capture period. Factors such as weather, flooding, and water management in the Missouri River might affect average clutch initiation dates or might cause high nest failures for first clutches (Espie et al. 1999, USFWS 2000), thus resulting in a younger chick population or an older chick population in some years during the selected capture period. If there is annual variation in the timing of breeding, sampling periods may have to be adjusted each year to account for that variation. Another assumption of the catch-curve approach is that survival is constant over time. Again, a 5-day sampling period means that the survival probability has to be constant within that 5-day period, a reasonable assumption because major systemic changes in mortality factors in such a short time period would not be expected.

Another assumption of the catch-curve approach is that ages are recorded accurately. We believe that chicks in our study were aged accurately because age estimates were based on approximate hatch dates for known broods and on chick size (Hussell and Page 1976, Cairns 1982, Miller and Knopf 1993). If aging is inaccurate, survival estimates will also be inaccurate. Overestimating ages will result in survival estimates that are biased high and underestimating ages will result in survival estimates biased low. Food availability can affect growth rates of chicks (Cairns 1982, LeFer et al. 2008), and changes in growth rates might affect the ability of observers to accurately age chicks. Lumping chicks into age classes reduces the potential biases caused by growth rate variation. Furthermore field technicians used observations from known age broods to guide age class designation in the field, and this approach could be used to guide visual ageing of chicks for other species.

The statistical assumption that the population is "stationary" (Chapman and Robson 1960, Skalski et al. 2006) requires the ecological assumption of an equilibrium between births and deaths in the population during sampling periods. This assumption must be considered in determining the duration of sampling periods, but, even more importantly, in determining the timing of the sampling period. Based on published information about breeding chronology (Elliot Smith and Haig 2004) and on examination of population-level hatching asynchrony in the USACE database, we assumed that, at the peak of the breeding season, there would be a balance between births and deaths and that the stationary population assumption would be met. If sampling periods are too early, births might exceed deaths and, if too late, deaths might exceed births.

The catch-curve method for estimating survival of precocial chicks also assumes that detection probability is equal across all age classes. This may not be the case for most precocial species either because older, more mobile chicks are bolder and more likely to be seen or are faster, more independent and harder to detect. If detectability is higher for younger chicks than older chicks, estimates of survival will be biased low. If dectectability is lower for younger chicks than for higher chicks, estimates of survival will be biased high. Modifying search techniques may help insure that detection probabilities do not bias the results. In our case, field crews searched for older chicks (>10 days) by scanning sandbars and beaches using binoculars from a distance and searched for younger chicks (<10 days) by walking through breeding areas and looking for chicks hiding in the gravel and vegetation.

Another assumption is population-level hatching asynchrony, generating sufficient age differential in the chick population for the catch-curve calculations. If all chicks in the study population hatch within a 5-day period, 5-day capture periods would not effectively estimate survival. The duration of sampling periods must be determined based on the breeding biology of the focal species.

A final assumption for using catch-curve analysis is that the fates of all individuals sampled are independent (Chapman and Robson 1960, Skalski et al. 2006). For many precocial and semiprecocial bird species, this assumption is likely violated. Fates of individuals in the same brood are likely linked because they are exposed to the same predation threats and food limitations. To our knowledge, the effect of violating this assumption on survival estimates for the catch-curve method has not been addressed and, therefore, we do not know if our results are biased significantly by nonindependence. We speculate that nonindependent fates would mostly affect variance estimates and not the point estimate of survival, in much the same way that pseudo-replication affects variance estimates in experimental research. However, we assumed that, for Piping Plovers and many shorebird species, effects would be minimal because each chick in a brood is mobile and thus able to forage and escape predators. Thus, fates are somewhat independent for each chick because food acquisition and predator avoidance are the primary factors influencing survival during this life stage (Elliot-Smith and Haig 2004, LeFer et al. 2008)

RESULTS

From 1993–2005, 2376 chicks were observed from 26–30 June, 1931 chicks from 1–5 July, and 2594 chicks from 6–10 July. Average daily chick survival ranged from 0.895 in the first capture period to 0.917 in the third capture period (Table 1). Estimates of daily survival and the probability of fledging increased from the first through the third capture periods (Fig. 1). However, 95% confidence intervals for the average probability of fledging estimates for each capture period overlapped (Fig. 1). The probability of fledging ranged from 0.126 to 0.188 (Table 1), meaning that between 12.6 and 18.8% of the chicks that hatched survived to 20 days of age. The mean estimated age of chicks observed increased slightly from period one (8.9 ± 2.4 [SD] days) to period two (10.2 ± 2.3 days) and period 3 (11.1 ± 2.1 days), but these means did not differ ($\alpha = 0.05$; single factor ANOVA, $F_2 = 3.1$, $P = 0.06$; Sokal and Rohlf 1995).

Catch-curves for individual years generally showed indistinct patterns, but sample sizes in some years were small (Table 1). Daily chick survival estimates during the 26–30 June period ranged from 0.825 in 1997 ($N = 12$) to 0.931 in 1993 ($N = 28$). For the 1–5 July period, daily chick survival ranged from 0.864 in 1994 ($N = 13$) to 0.931 in 1993 ($N = 20$). For the 6–10 July period, daily chick survival ranged

Table 1. Daily probability of survival, standard deviation of daily survival, and the probability of survival to fledging for Piping Plover chicks along the Missouri River from 1993–2005 estimated using a modified catch-curve analysis with three 5-day time (capture) periods.

Year	*N*[a]	T[b]	Survival	SD	Probability of fledging[c]
Period 1: 26–30 June					
1993	28	364	0.931	0.049	0.239
1994	51	388	0.886	0.045	0.089
1995	25	189	0.887	0.065	0.092
1996	9	54	0.871	0.119	0.063
1997	12	52	0.825	0.114	0.022
1998	88	936	0.915	0.030	0.169
1999	36	402	0.920	0.046	0.188
2000	335	4007	0.923	0.015	0.202
2001	218	2219	0.911	0.019	0.155
2002	216	1583	0.880	0.022	0.078
2003	474	4190	0.899	0.014	0.118
2004	475	4070	0.896	0.014	0.110
2005	409	3506	0.896	0.015	0.111
Mean			0.895	0.028	0.126
Period 2: 1–5 July					
1993	20	257	0.931	0.058	0.240
1994	13	76	0.864	0.099	0.053
1995	11	113	0.919	0.086	0.183
1996	22	142	0.871	0.073	0.063
1997	0	0			
1998	42	330	0.889	0.049	0.096
1999	34	404	0.924	0.046	0.208
2000	134	1537	0.920	0.023	0.190
2001	291	3217	0.917	0.016	0.178
2002	554	6685	0.924	0.011	0.204
2003	347	4120	0.923	0.014	0.199
2004	252	2265	0.900	0.019	0.122
2005	211	2383	0.919	0.019	0.185
Mean			0.909	0.022	0.160
Period 3: 6–10 July					
1993	29	269	0.906	0.055	0.138
1994	26	155	0.861	0.069	0.050
1995	15	183	0.929	0.069	0.229
1996	6	63	0.926	0.117	0.217
1997	15	187	0.930	0.068	0.236
1998	107	1228	0.921	0.026	0.191
1999	147	1366	0.903	0.024	0.131
2000	201	2568	0.928	0.018	0.223
2001	326	3350	0.912	0.016	0.157
2002	322	4129	0.928	0.014	0.224
2003	455	5781	0.927	0.012	0.220
2004	470	5555	0.922	0.012	0.198
2005	475	6110	0.928	0.012	0.224
Average			0.917	0.019	0.188

[a]Number of chicks observed.
[b]Sum of all the ages of all chicks observed (in days).
[c]Probability of fledging calculated by raising the daily survival to the power of 20.

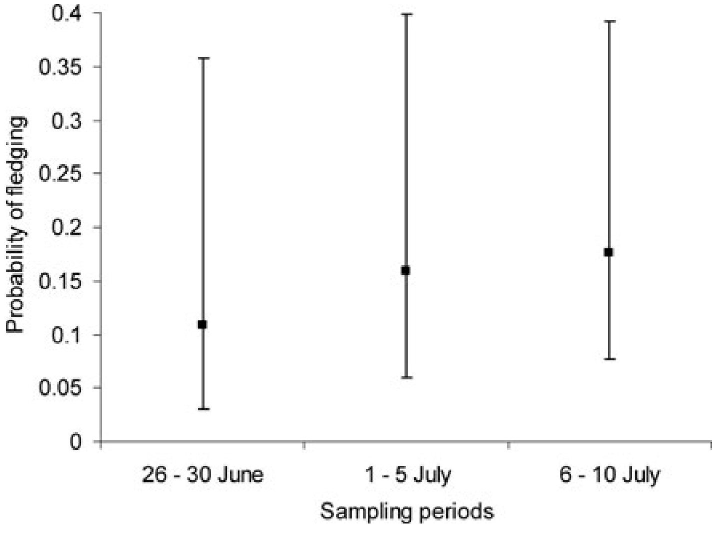

Fig. 1. Comparison of estimates of the probability of survival to fledging (and 95% confidence intervals) for Piping Plover chicks in the Missouri River system during the periods from 26–30 June, 1–5 July, and 6–10 July 1993–2005.

from 0.861 in 1994 ($N = 26$) to 0.928 in 2000 ($N = 201$) and 2005 ($N = 475$). More individuals were observed from 2000–2005 than from 1993–1999. There was no pattern in survival estimates across years or sampling periods. There were few significant differences among annual estimates, in part because confidence intervals for the survival estimates in the 1990's were large due to small sample sizes.

DISCUSSION

To our knowledge, our analysis represents the first attempt to estimate survival of precocial chicks using a catch-curve approach. However, count-based survival estimation methods have recently been used by ornithologists (Beissinger and Peery 2007). An advantage of catch-curve analysis is that survival and variance can be estimated using count data. If sampling periods are designed well, chick survival during the pre-fledging period can be estimated using data collected in just a few days with one visit to a site for counting and aging chicks. In our example, we could have used data collected in just five days each year and still obtained a reasonable, unbiased point estimate of daily chick survival and variance. Even with three sampling periods per year, only 15 days of field work were needed to collect the data we used. Studies involving mark-recapture or radio-tracking methods would likely require much more time to obtain the needed data. Catch-curve techniques have a long history of use in fisheries and wildlife science (Skalski et al. 2006), and we believe they provide investigators with an opportunity to use existing databases to obtain demographic information.

Despite these advantages, several assumptions of catch-curve analysis may potentially limit its use (Chapman and Robson 1960, Skalski et al. 2006). For example, survival estimates could be affected by early- or late-season mortality factors that would not be detected using a mid-season sampling period. If there is evidence for high mortality at some point in the breeding season (e.g., flooding that destroyed almost all Piping Plover nests and killed most chicks along the Missouri River in 1997), estimating a separate survival estimate for that time period might be necessary (i.e., determine when the mortality event occurs and then estimate survival for that period and the rest of the season separately). However, if high mortality events are stochastic and unpredictable, catch-curve analysis may not be appropriate.

In addition, survival estimates might be biased low if surveys are conducted too early and biased high if conducted too late in the season. In our study, as the breeding season progressed, a greater proportion of observed chicks were older because fewer 1–5 day old chicks were being added to the population. In 2005, 51.2% of the nests monitored hatched on 25 June or earlier in the season, and 62.0% of the nests hatched by 1 July (C. Kruse and G. Pavelka, unpubl. data). At the start of the third capture period in 2005, 62% of the chicks in our study had already aged past the first age class. As fewer chicks are added to the population, proportionally more are in the older age classes, making survival probabilities appear higher. As a result, it is important to select an appropriate capture period for surveying the chick population. In retrospect, an ideal capture period for our study would probably have been from 28 June–2 July.

Catch-curve analyses generates one survival estimate for chicks from the point of hatching to the point of fledging, implying a constant survival during that period. Recent nest survival analyses have shown that daily nest survival varies with both nest age and date (Dinsmore et al. 2002, Shaffer 2004), and evidence suggests that the survival probability of chicks also changes with age (Colwell et al. 2007). As chicks age, thermal stress is less likely, predation threats change, and so do energy requirements (Schekkerman and Visser 2001, Elliot-Smith and Haig 2004, Colwell et al. 2007). We did not attempt to account for these potential violations of the constant survival assumption. We cannot determine if mortality is greater during the early or late stages or what factors affect survival at different stages of chick growth. However, we assumed that these estimates of survival represented the average daily survival of individuals throughout the prefledging period. Even where age-dependent survival patterns have been documented, like avian nest survival, biologists recommend using the average survival rate at the median age to incorporate the parameter into a predictive population models (Shaffer and Thompson 2007). Detailed information about age-dependent survival patterns might enhance management decisions. However, such information is not often used in population projection models. If there is sufficient evidence for differential survival related to age of the chicks, calculating two or more survival estimates might be possible. In our study, for example, given the available data, we could have calculated one daily survival estimate from 0–10 days and another for 11–21 days.

Our survival estimates are similar to, although slightly lower than, estimates reported by LeFer et al. (2008) who used a modified Mayfield approach (Mayfield 1961, Flint et al. 1995) to estimate survival for a small number of chicks in the Missouri River. LeFer et al.'s (2008) daily survival estimates ranged from 0.853 to 0.985, whereas our estimates ranged from 0.825 to 0.931. Our results show a slight increase in survival and fledging probability from the first through the third capture period. This may reflect some real change in survival probability over the season, but may also reflect sampling differences in the capture periods. For example, the second period (1 July–5 July) included a 1-day holiday when field crews did not work. Overall, there were > 400 fewer chicks observed during this capture period than in the other two periods and, in 1997, field crews did not observe any chicks in any age class during the second capture period. Nonbiological factors such as holidays might impact survival estimates and must be considered when designing capture periods for catch-curve survival analyses.

Despite potential limitations, the use of catch-curves to estimate chick survival in precocial species may have benefits. For example, our estimates could be used in combination with nest survival data, and in a Piping Plover population viability analysis, to generate variable fecundity estimates (Noon and Sauer 1992). Although the estimates come with caveats and should be used with appropriate caution to avoid violating the assumptions we have discussed, this approach could be useful for inexpensively estimating chick survival for some precocial species. Catch-curve analysis may also be useful where short field surveys are conducted to count and age chicks in a population regardless of developmental mode (i.e., colonial seabirds). The catch-curve approach might be ideal for estimating survival during the prefledging period for species that breed in remote, hard-to-access regions where time and access are limited, such as monitoring penguin populations in the Antarctic or shorebird populations in the Arctic. It may also be useful to estimating annual survival for species where individuals can be aged based on appearance and plumage such as many species of gulls. Lastly, the catch-curve approach may be appropriate when observer disturbance is a concern, for example, endangered species.

As Conroy (2006) cautioned, researchers should not use count-based methodology "in lieu of other, more robust approaches." Researchers should continue using robust approaches when feasible (William et al. 2001). However, when only count data are available and survival estimates over a large area are needed, these methods provide an alternative and may provide useful insight into demographic properties provided assumptions are reasonable and robust to departures. In addition, count data collected over many years, for example, data collected by management agencies that remain largely unused or underused, may be ideally suited for this type of survival analysis approach (Skalski et al. 2006).

ACKNOWLEDGMENTS

We thank the U. S. Fish and Wildlife Service, U. S. Geological Survey, and the Missouri Cooperative Fish and Wildlife Research Unit for financial and logistical support. We thank the U. S. Army Corps of Engineers for access to and use of the Piping Plover reproductive success database. We are grateful to M. A. Larson for assistance with data analysis and study design, and to M. A. Larson, J. S. Rikoon, F. R. Thompson III, S. J. Dinsmore, G. Ritchison, three anonymous reviewers, and the University of Missouri Avian Ecology Lab for reviewing this manuscript and helping us improve this study.

LITERATURE CITED

BEISSENGER, S. R., AND M. Z. PEERY. 2007. Reconstructing the historic demography of an endangered seabird. Ecology 88: 296–305.

BENT, A. C. 1929. Life histories of North American shorebirds, part 2. U.S. National Museum Bulletin, Washington, D.C.

CAIRNS, W. E. 1982. Biology and behavior of breeding Piping Plovers. Wilson Bulletin 94: 531–545.

CHAPMAN, D. G., AND D. S. ROBSON. 1960. Analysis of a catch-curve. Biometrics 16: 354–368.

COLWELL, M. A., S. J. HURLEY, J. N. HALL, AND S. J. DINSMORE. 2007. Age-related survival and behavior of Snowy Plover chicks. Condor 109: 638–647.

CONROY, M. J. 2006. Wildlife demography: analysis of sex, age and count data. Auk 123: 1205–1206.

DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. Ecology 83: 3476–3488.

ELLIOTT-SMITH, E., AND S. M. HAIG. 2004. Piping Plover (*Charadrius melodus*). In: The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY, Retrieved from the Birds of North America Online-http://bna.birds.cornell.edu.bna/species/002

ESPIE, R. H. M., P. C. JAMES, AND R. M. BRIGHAM. 1998. The effects of flooding on Piping Plover (*Chardrius melodus*) reproductive success at Lake Diefenbaker, Saskatchewan, Canada. Biological Conservation 86: 215–222.

FLINT, P. L., K. H. POLLOCK, D. THOMAS, AND J. S. SEDINGER. 1995. Estimating prefledge survival: allowing for brood mixing and dependence among brood mates. Journal of Wildlife Management 59: 448–455.

GROEN, N. M., AND L. HEMERIK. 2002. Reproductive success and survival of Black-tailed Godwits (*Limnosa limnosa*) in a declining population in The Netherlands. Ardea 90: 239–248.

HENSLER, G., AND J. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93: 42–53.

HITCHCOCK, C. L., AND C. GRATTO-TREVOR. 1997. Diagnosing a shorebird local population decline with a stage structure population model. Ecology 78: 522–534.

HUSSELL, D. J. T., AND G. W. PAGE. 1976. Observations on the breeding biology of Black-bellied Plovers on Devon Island, NWT, Canada. Wilson Bulletin 88: 632–653.

LE FER, D., J. D. FRASER, AND C. D. KRUSE. 2008. Piping Plover chick foraging, growth and survival in the Great Plains. Journal of Wildlife Management 72: 682–687.

LUKAS, P. M., V. J. DREITZ, F. L. KNOPF, AND K. P. BURNHAM. 2004. Estimating survival of unmarked dependent young when detection is imperfect. Condor 106: 926–931.

MAYFIELD, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73: 255–261.

MCGOWAN, C. P. 2008. Incidental take and endangered species demography. Ph.D. dissertation, University of Missouri, Columbia, MO.

MILLER, B. J., AND F. L. KNOPF. 1993. Growth and survival of Mountain Plovers. Journal of Field Ornithology 64: 500–506.

NOON, B. R., AND J. R. SAUER. 1992. Population models for passerine birds: structure, parameterization, and analysis. In: Wildlife 2001: populations (D. R. McCullough, AND R. H. Barrett, eds.). pp. 441–464. Elsevier Applied Science, London.

RATCLIFFE, N., S. SCHMITT, AND M. WIFFIN. 2005. Sink or swim? Viability of a Black-tailed Godwit population in relation to flooding. Journal of Applied Ecology 42: 834–843.

RICKLEFS, R. E. 1972. Fecundity, mortality and avian demography. In: Breeding biology of birds (D. S. Farner, ed.). pp. 366–435. National Academy of Sciences, Washington, D.C.

ROBSON, D. S., AND D. G. CHAPMAN. 1961. Catch-curves and mortality rates. Transactions of the American Fisheries Society 90: 181–189.

SCHEKKERMAN, H., AND G. H. VISSER. 2001. Prefledging energy requirements in shorebirds: energetic implication of self-feeding precocial development. Auk 118: 944–957.

SEUDEKAMP WELLS, K. M., B. E. WASHBURN, J. J. MILLSPAUGH, M. R. RYAN, AND M. W. HUBBARD.

2003. Effects of radio transmitters on fecal glucocordicoid levels in captive Dickcissels. Condor 105: 805–810.

SHAFFER, T. L. 2004. A unified approach to analyzing nest success. Auk 121: 526–540.

SHAFFER T. L., AND F. R. THOMPSON III. 2007. Making meaningful estimates of nest survival with model-based methods. Studies in Avian Biology 34: 84–95.

SKALSKI, J. R., K. L. RYDING, AND J. J. MILLSPAUGH. 2006. Wildlife demography: analysis of sex, age and count data. Elsevier Academic Press, Burlington, MA.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. W. H. Freeman and Company, New York.

U. S. FISH AND WILDLIFE SERVICE. 1985. Endangered and threatened wildlife and plants; determination of endangered and threatened status for the Piping Plover: a final rule. Federal Register 50: 50726–50734.

U. S. FISH AND WILDLIFE SERVICE. 2000. Formal biological opinion of the Missouri River main stem reservoir system. U.S. Fish and Wildlife Service, Denver, CO.

WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2001. Analysis and management of animal populations. Academic Press, New York.

WITHEY, J. C., T. D. BLOXTON, AND J. M. MARZLUFF. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. In: Radio tracking and animal populations (J. J. Millspaugh, AND J. M. Marzluff, eds.). pp. 43–75. Academic Press, New York.