



Review

Post-Fledging Survival in Passerine Birds and the Value of Post-Fledging Studies to Conservation

W. ANDREW COX,^{1,2} *Department of Fisheries and Wildlife Sciences, University of Missouri, 302 ABNR, Columbia, MO 65211, USA*

FRANK R. THOMPSON III, *USDA Forest Service Northern Research Station, University of Missouri, 202 ABNR, Columbia, MO 65211, USA*

ALLISON S. COX, *Independent Researcher, 5537 N. Autumn Drive, Columbia, MO 65202, USA*

JOHN FAABORG, *Division of Biological Sciences, University of Missouri, 105 Tucker Hall, Columbia, MO 65211, USA*

ABSTRACT Conservation efforts are most effective when we have complete demographic information for a species of concern. Nevertheless, fundamental gaps in our knowledge of demography still exist for many taxa. For passerine birds, the period of time directly after young birds leave the nest and before they disperse and/or migrate (i.e., the post-fledging period) remains an understudied life stage. We reviewed the literature on survival of passerine birds during the post-fledging period to synthesize current knowledge on survival rates and the factors affecting these rates, and conducted a sensitivity analysis to explore the relationship between population growth and post-fledging survival across the range of rates reported in the literature. Fledgling age was a strong predictor of survival, with the highest mortality occurring during the first 3 weeks after birds fledged. Among species, survival ranged from 0.23 to 0.87 during the first 3 weeks post-fledging and increased with adult body mass and nestling period duration. The relatively high proportion (12 of 19; 63%) of studies that detected at least 1 habitat effect on survival indicates that management focused on post-fledging habitat can improve survival. Sensitivity analyses indicated that post-fledging survival rates less than approximately 0.4 require unrealistic overwinter survival rates of juveniles to prevent population decline, unless adult survival rates and seasonal fecundity are high. Post-fledging survival is a useful metric for monitoring passerine populations because it sets the ceiling on first-year survival, responds to habitat management, and leads to more comprehensive demographic models for songbirds. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS demography, juvenile, passerines, population modeling, post-fledging, songbird productivity, survival.

Research has clearly demonstrated that management of wildlife can be only as good as the habitat-specific demographic information available for the species of interest (Pulliam 1988). Such demographic information must cover the annual cycle (i.e., breeding season, dispersal and/or migration, winter; Norris and Marra 2007) or managers may not focus efforts on the most limiting life stages (e.g., Crouse et al. 1987) or may overlook demographic responses to stressors such as climate change (e.g., Radchuk et al. 2013). For songbirds, population growth rates are often sensitive to first-year survival (i.e., juvenile survival, or the probability of surviving from fledging to the first breeding season; Donovan and Thompson 2001, Bonnot et al. 2011), but because of the difficulty in tracking long-distance migrants or even short-distance dispersers, this period remains the least-studied of the avian life stages. As a result, studies quantifying songbird

population annual growth rates (λ) often rely on estimating first-year survival as 25–50% of annual adult survival (Ricklefs 1973, Greenberg 1980). Such an approach may provide substantially different estimates of first-year survival than empirically derived rates and may lead to inaccurate estimates of λ (Anders and Marshall 2005, Streby and Andersen 2011).

In reality, the first year of life for a passerine is composed of several separate stages and survival may vary among these stages. Fledglings initially are reliant upon their parents, and then reach the parental independence period when they are independent but have not yet dispersed or migrated (hereafter we refer to part or all of these 2 stages as the post-fledging period). The length of the post-fledging period varies substantially across and within species and depends on factors such as migratory status and biogeographic region (reviewed in Russell 2000). After the post-fledging period, individuals of migrant species will move to their wintering grounds and return the following spring to breed, usually choosing a territory away from their natal territory (Weatherhead and Forbes 1994). Similarly, most individuals of resident species disperse away from their natal territories, although some may remain to either help their parents or replace them if they die (Weatherhead and Forbes 1994).

Received: 16 June 2013; Accepted: 7 December 2013

Published: 6 February 2014

¹E-mail: wac253@mail.missouri.edu

²Current address: 103 Allwine Hall, University of Nebraska—Omaha, Omaha, Nebraska 68182, USA.

Past efforts to obtain empirical estimates of survival for the first year of life of passerines have used band recovery (e.g., Thomson et al. 1999) or mark-recapture data (e.g., Perrins 1965). However, both methods typically produce biased estimates of survival. Band recovery analyses usually violate a number of restrictive assumptions (Anderson et al. 1985), and mark-recapture methods produce only apparent survival estimates because they do not distinguish between mortality and permanent emigration. The latter method is especially problematic for first-year birds because natal dispersal rates are high and can lead to serious underestimates of survival (Zimmerman et al. 2007, Cooper et al. 2008, Faaborg et al. 2010, Gilroy et al. 2012). Additionally, these methods allow for limited assessment of ecological factors that influence first-year survival, which is critical to successfully manage populations. Although the challenges of studying the first year of life in its totality for passerines are significant, researchers have used radio transmitters to monitor survival, movement, and habitat use of birds during the post-fledging period (e.g., Anders et al. 1997, Ausprey and Rodewald 2011). A meta-analysis of transmitter effects on birds suggested that they may have a small negative effect on survival rates (Barron et al. 2010) and limited battery life precludes survival estimates across the entire first-year period. Nevertheless, these data provide an opportunity to model intrinsic and extrinsic factors that influence post-fledging survival and to determine how post-fledging survival contributes to population growth.

We searched the literature for studies on post-fledging survival of passerine birds. First, we compiled estimates of post-fledging survival across 37 passerine species and synthesized the current state of knowledge on factors that influence survival. Second, we tested whether species traits such as broad vegetation type associations (i.e., forest vs. grassland birds), adult body mass, or nestling period duration predict post-fledging survival rates among songbird species. Third, we used sensitivity analyses to demonstrate the tradeoffs among post-fledging survival and other demographic rates in sustaining a population to infer at what levels post-fledging survival may be limiting populations.

METHODS

We used the online Scopus database in November 2011 to find original, peer-reviewed studies of post-fledging survival in passerine birds. We used combinations of the keywords “post-fledging,” “survival,” “juvenile,” and “birds” and considered all resulting output for inclusion in our review. We also used the literature cited sections from the papers we found to identify other studies not captured by our search criteria. We considered only studies that used radiotelemetry, intensively followed banded individuals up to parental independence, or incorporated recapture probabilities into the analysis of recaptured banded individuals. We limited our focus to passerine species that typically breed during the year after hatching and excluded studies on captive-bred birds (e.g., Imlay et al. 2010). We used all studies that met these criteria; however, we were unable to use all studies in all

analyses because of missing information (see below for details).

Factors Influencing Survival

We could not perform a formal meta-analysis of the variables influencing post-fledging survival because required parameters, sample sizes, and a measure of error (e.g., SE or CI) were lacking in most studies. Instead, we adopted a vote-counting approach, which provides a simple percent of studies that indicate a particular variable influences survival based on the authors' model selection criteria or significance testing. The large number of variables evaluated ($n = 71$) coupled with small sample sizes for many of them (56 of the variables were tested in fewer than 5 studies) led us to place variables into 1 of 12 categories: age, habitat characteristics (e.g., vegetation type, patch size, tree density), sex, body condition or size, conspecific help or density, weather, temporal factors (e.g., year and date effects), transmitter effects, brood or clutch effects (e.g., brood and clutch size, parasitism status), parental care or quality, food availability, and post-fledging movement. We further subdivided habitat variables into categories based on the spatial scale at which they were measured (landscape, patch, territory, <territory) to identify the scales at which survival relationships with habitat characteristics were found.

Our remaining analyses focused on actual values of post-fledging survival rather than the presence or absence of covariate effects on survival. Based upon our own work (Anders et al. 1997, Cox and Kesler 2012) and studies in the literature review, we assumed that fledgling age would be an important predictor of survival. Therefore, we further investigated the influence of age on post-fledging survival across passerine species by obtaining average daily survivorship for species investigated in studies that tested for an effect of age. Although a parameter estimate for the effect of fledgling age on survival was lacking in many studies, most included figures that displayed Kaplan–Meier or model-based survivorship curves as a function of fledgling age. We synthesized these data to obtain a continuous survivorship curve for each species for the duration of each study and averaged the resulting curves across passerine species. We digitized a sufficient number of points to adequately characterize each published survival curve using DigitizeIt (v.1.5.8c) software. Many studies did not present estimates of variance, so we restricted our analysis to mean survival estimates. When studies included multiple curves for different habitats (Cohen and Lindell 2004, Balogh et al. 2011, Eng et al. 2011) or different statistical assumptions (Kershner et al. 2004), we digitized each curve separately. In the 3 studies that presented daily survival rates rather than survivorship curves (Anders et al. 1997, Yackel Adams et al. 2006, Fisher and Davis 2011), we exponentiated the daily survival rates to generate a survivorship curve. We then obtained a best-fit monotonic nonlinear regression equation for each curve using the TRANSREG procedure in SAS v9.2 (2008), which recreated each survivorship curve with very little error (mean $r^2 = 0.97 \pm 0.01$ SE; $n = 32$). We used the resulting regression equation to output predicted point

estimates of survivorship for every day from fledging to the end of radiotracking for each study. When we had several curves for 1 species (i.e., from separate studies, habitats, or statistical assumptions), we averaged predicated point estimates of daily survival across all curves to obtain a single survivorship estimate for each day for the species. Finally, we calculated a simple average of rates across species to obtain an overall post-fledging survivorship curve for passerine birds.

Interspecific Variation in Post-Fledging Survival

We assessed the influence of vegetation type used during breeding, adult body mass, and duration of nestling period on post-fledging survival using a subset of the studies. We grouped North American species by 3 breeding vegetation types (i.e., grassland, forest, both) based on breeding habitats assigned in the 2009 State of the Birds Report (United States North American Bird Conservation Initiative Committee 2009); for 3 non-North American bird species we placed them into the above groups based on breeding habitat characterized in each study. We obtained most adult body mass and duration of nestling period values from the Birds of North America Online database (Poole 2005) or the Neotropical Birds database (Schulenberg 2010). We selected

values of body mass for the appropriate subspecies, season, and geographic area from these sources whenever possible and we averaged values when they were presented separately for each sex. We used the midpoint of ranges of nestling period duration when mean values were not provided and averaged nestling period durations when multiple values were presented. We searched the literature for appropriate values for species not covered by either online database (data and sources are summarized in Table 1).

We used a generalized linear model (PROC GENMOD, SAS v9.2) to assess the influence of breeding habitat vegetation association, adult body mass, and nestling period on post-fledging survival. We treated species as a repeated measure within GENMOD, which uses generalized estimating equations with an independent covariance structure to account for a lack of independence among studies of the same species. We standardized the influence of age on survival by using cumulative survival rates for the first 20–21 days post-fledging as our response variable and ran a single additive model with vegetation association, body mass, and nestling period as explanatory variables. We chose 20–21 days because this time period allowed us to include the greatest number of studies in the analysis. We derived

Table 1. Breeding habitat vegetation association, nestling period duration, body mass, and cumulative post-fledging estimates of survival used in developing correlations between species traits and post-fledging survival.

Scientific name	Breeding habitat	Nestling period (days)	Nestling period source ^a	Adult mass (g)	Adult mass source ^a	Cumulative survival ^b	Study
<i>Thamnophtilus atrinucha</i>	Forest	10.0	1	23	1	0.75	Tarwater and Brawn (2010)
<i>Hylophylax naevioides</i>	Forest	11.0	1	17	1	0.45	Styrsky et al. (2005)
<i>Empidonax virescens</i>	Forest	15.0	2	13	2	0.74	Ausprey and Rodewald (2011)
<i>Progne subis</i>	Both	28.0	2	52	2	0.87	Tarof et al. (2011)
<i>Sialia sialis</i>	Forest	18.2	2	30	2	0.76	Jackson et al. (2011)
<i>Sialia mexicana</i>	Forest	21.8	2	26	2	0.64	Wightman (2009)
<i>Catharus ustulatus</i>	Forest	13.0	2	30	3	0.68	White (2005)
<i>Hylocichla mustelina</i>	Forest	13.5	2	49	2	0.42	Anders et al. (1997)
<i>Hylocichla mustelina</i>	Forest					0.83	Fink (2003)
<i>Hylocichla mustelina</i>	Forest					0.65	Schmidt et al. (2008)
<i>Turdus assimilis</i>	Both	13.8	4	64	5	0.67	Cohen and Lindell (2004)
<i>Dumetella carolinensis</i>	Forest	10.5	2	38	2	0.77	Maxted (2001)
<i>Dumetella carolinensis</i>	Forest					0.53	Balogh et al. (2011)
<i>Anthus spragueii</i>	Grassland	11.2	2	23	2	0.38	Fisher and Davis (2011)
<i>Seiurus aurocapilla</i>	Forest	8.5	2	22	2	0.68	King et al. (2006)
<i>Seiurus aurocapilla</i>	Forest					0.42	Streby and Andersen (2011)
<i>Seiurus aurocapilla</i>	Forest					0.72	Vitz and Rodewald (2011)
<i>Helminthos vermivorum</i>	Forest	9.0	2	14	2	0.64	Vitz and Rodewald (2011)
<i>Setophaga citrina</i>	Forest	8.5	2	11	2	0.23	Rush and Stutchbury (2008)
<i>Setophaga citrina</i>	Forest					0.57	Eng et al. (2011)
<i>Icteria virens</i>	Forest	8.9	2	25	6	0.39	Maxted (2001)
<i>Calamospiza melanocorys</i>	Grassland	8.5	2	38	2	0.37	Yackel Adams et al. (2001)
<i>Calamospiza melanocorys</i>	Grassland					0.35	Yackel Adams et al. (2006)
<i>Cardinalis cardinalis</i>	Forest	9.5	2	44	2	0.44	Ausprey and Rodewald (2011)
<i>Pheucticus ludovicianus</i>	Forest	10.5	2	45	2	0.62	Moore et al. (2010)
<i>Spiza americana</i>	Grassland	9.0	2	27	2	0.60	Berkeley et al. (2007)
<i>Spiza americana</i>	Grassland	9.0				0.58	Suedkamp Wells et al. (2007)
<i>Sturnella magna</i>	Grassland	11.0	2	96	2	0.75	Kershner et al. (2004)
<i>Sturnella magna</i>	Grassland	11.0				0.66	Suedkamp Wells et al. (2007)
<i>Molothrus ater</i>	Both	10.5	2	48	7	0.33	Fink (2003)
<i>Notiomystis cincta</i>	Forest	30.0	8	35	9	0.87	Low and Pärt (2009)

^a Sources: ¹Schulenberg (2010); ²Poole (2005); ³White (2005); ⁴Cohen and Lindell (2004); ⁵Sekercioglu et al. (2007); ⁶Maxted (2001); ⁷Dunning (1993); ⁸Low and Pärt (2009); ⁹Low (2006).

^b Indicates survival for first 20–21 days post-fledging.

probabilities of surviving 20–21 days from digitized curves ($n=20$), extrapolation from daily survival rates ($n=4$), or from values published in the studies ($n=7$). We averaged probabilities when multiple values or curves were provided for a species within a study ($n=4$). We considered variables for which $P < 0.05$ to be significant.

Sensitivity Analysis: Post-Fledging Survival and Population Growth

We used a simple 2-stage population model to examine tradeoffs in demographic rates: $\lambda = P_A + P_j\beta$, where λ is the population growth rate, P_A is annual adult survival of females, P_j is survival of female fledglings to the following breeding season, and β is the number of female fledglings produced per female per breeding season (Pulliam 1988). $\lambda = 1$, <1 , and >1 for stable, declining, and growing populations, respectively. When post-fledging survival is known, P_j can be written as $P_{PF} \times P_{OW}$, where P_{PF} is post-fledging survival and P_{OW} is overwinter survival (i.e., between the end of the post-fledging period and the following breeding season). However, P_{OW} is unknown for all but a small number of passerine populations for reasons outlined above, and seasonal fecundity estimates for birds are surprisingly sparse in the literature; therefore, even with post-fledging survival estimates, building a comprehensive demographic model is difficult without relying on assumptions similar to those based on Greenberg (1980).

We therefore examined the relationship between post-fledging survival and population growth by assuming that $P_{OW} < P_A$. We partitioned P_j into P_{PF} and P_{OW} , held λ constant at 1, and varied P_{PF} across the range of reported values for passerine birds from our literature review to determine values of P_{OW} . We repeated this for 3 values of β (1, 2, 3) that spanned a reasonable range of seasonal production of female juveniles given equal sex ratios (e.g., DeCocco et al. 2000, Whitehead et al. 2000, Mahony et al. 2006), and at 3 levels of P_A (0.5, 0.6, 0.7). We interpreted values of $P_{OW} > P_A$ to mean that P_{PF} was too low to support a stable population. We consider this to be a conservative assessment because P_{OW} is likely less than P_A because juvenile birds may be excluded from high quality wintering habitat (Sherry and Holmes 1996), which can reduce survival (Marra and Holmes 2001).

RESULTS

We found 45 studies of post-fledging survival for 35 passerine species that met our criteria for inclusion, plus 1 study (Naef-Daenzer et al. 2001) that provided a combined estimate for 2 species. Several studies investigated multiple species, which resulted in 53 total data points for this study (Appendix A). Most survival estimates were generated from radiotelemetry data ($n=31$), but others also used banded individuals meeting our criteria (see Methods section; $n=17$) or both methods ($n=5$).

We excluded 1 study (Whittaker and Marzluff 2009) from the vote-count analysis because of the large number of potentially non-independent tests that were performed (i.e., the influence of habitat aggregation and 3 land-cover classes

on survival were assessed for 2 age classes of 4 species at 7 spatial scales, a total of 224 statistical tests). We placed 68 variables into the 12 defined categories ($n=223$ total tests) for the vote-counting analysis. An effect of age on survival was most frequently detected, and in all but 1 case (purple martin [*Progne subis*]; Tarof et al. 2011) survival improved as fledglings aged (Fig. 1). Habitat characteristics were investigated more than any other covariate category, with relatively few significant relationships detected with survival (Fig. 1). However, this was partially because of a large number of univariate tests performed in some studies (e.g., 15 tests in Berkeley et al. 2007). Overall, 12 of 19 (63%) investigations of habitat effects on post-fledging survival detected at least 1 effect. Habitat effects on survival were detected in 1 of 6 (17%) tests at the landscape scale, 4 of 20 (20%) tests at the patch scale, 0 of 6 (0%) tests at the territory scale, and 9 of 29 (31%) tests at scales smaller than the territory. Temporal (e.g., seasonal, year) and body condition effects on survival were frequently studied and effects were detected in $>33\%$ of tests for both categories (Fig. 1). Brood effects (e.g., brood size, parasitism status) on survival were frequently tested but rarely detected. We found varying support for the remaining covariate categories, all of which had a relatively small number of tests ($n < 11$; Fig. 1).

We used 24 studies (22 used radiotagged birds, 2 used both radiotagged and leg banded birds; see Appendix A) to derive an average survivorship curve for passerines. Across species, mortality rates were high during the first 10 days post-fledging but declined with time. Survival remained relatively constant after day 20 (day 20 survival: 0.58 ± 0.03 , $n=17$ species; day 50 survival: 0.55 ± 0.05 , $n=8$ species; Fig. 2, see Appendix A for studies used). Because larger birds can carry longer lasting radios and have higher survival rates than smaller birds (Fig. 3A), the survivorship curve for all species could have been positively biased. However, 10 of 18 species were studied longer than 30 days after fledging (well after the flattening of the curve) and had an average weight of 36.8 g (range: 11–96 g), whereas all of the species in the analysis had an average weight of 35.0 g (range: 11–96 g). Therefore, the subset of species studied 30–50 days after fledging was well representative of all birds in the analysis, and we interpret the

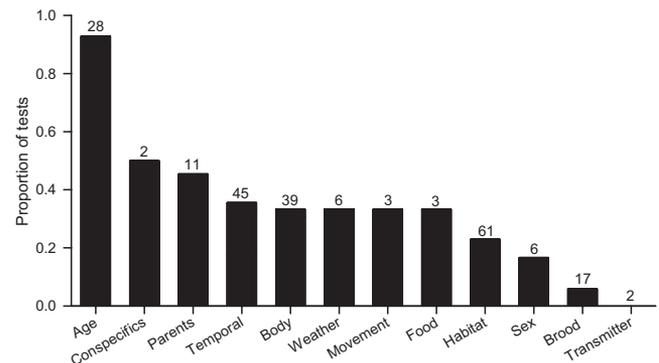


Figure 1. Proportion of tests from 45 studies of passerine post-fledging survival that detected a covariate effect. Numbers above bars indicate total number of tests performed across studies.

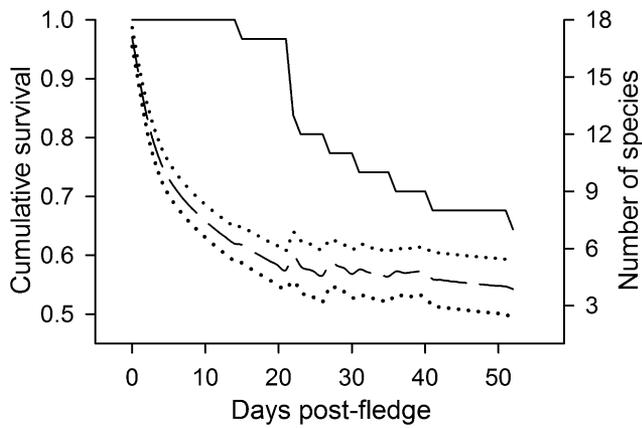


Figure 2. Mean cumulative post-fledging survival (dashed line) \pm standard error (dotted line) for passerine birds. The solid line represents the number of species each daily survival value is based on.

flattening of the survival curve to be a biological phenomenon rather than a sampling artifact.

We found 31 studies (24 used radiotagged birds, 5 used leg bands, 2 used both) that qualified for inclusion in our quantitative analysis of interspecific variation of post-fledging survival (Table 1). We found no collinearity between body mass and duration of the nestling period (tolerance = 0.93; Allison 1999), indicating that both could be included in the model. Examination of a $Q-Q$ residual plot and a Shapiro–Wilk test for normality of residuals ($W = 0.94$; $P = 0.09$) both indicated adequate fit. We found 20–21-day post-fledging survival increased with adult body mass ($\beta = 0.003 \pm 0.001$ SE; $P = 0.02$; $n = 31$; Fig. 3A and duration of nestling period ($\beta = 0.017 \pm 0.003$ SE; $P < 0.01$, $n = 31$; Fig. 3B). However, post-fledging survival was not related to breeding habitat vegetation association (i.e., forest, grassland, both; $P_{\text{forest}} = 0.09$, $P_{\text{grassland}} = 0.60$; $n = 31$).

The sensitivity analysis revealed that P_{PF} had a strong influence on whether $P_{\text{OW}} > P_{\text{A}}$ at all levels of P_{A} and β (Fig. 4). When P_{A} was relatively low (e.g., 0.5; Fig. 4A), $P_{\text{PF}} < 0.33$ resulted in unrealistic P_{OW} values even when $\beta = 3$. As P_{A} increased (e.g., Fig. 4B–C), P_{PF} could be somewhat lower (approx. 0.2) without resulting in unrealistic P_{OW} values. Regardless of the values chosen for P_{A} and β , the slopes of the P_{OW} curves increased dramatically when P_{PF} values were < 0.4 (Fig. 4A–C).

DISCUSSION

We provide the first quantitative summary of studies of the post-fledging period for passerine birds. The age of post-fledging birds was the most frequently detected factor influencing post-fledging survival, and most mortality occurred during the first 3 weeks (Fig. 2). No other covariate category influenced survival in $> 50\%$ of the tests performed, but covariate effects on survival were detected in $\geq 23\%$ of the tests for 9 of 12 (75%) covariate categories (Fig. 1). Post-fledging survival differed markedly across species, but increased with adult body mass and with the duration of the

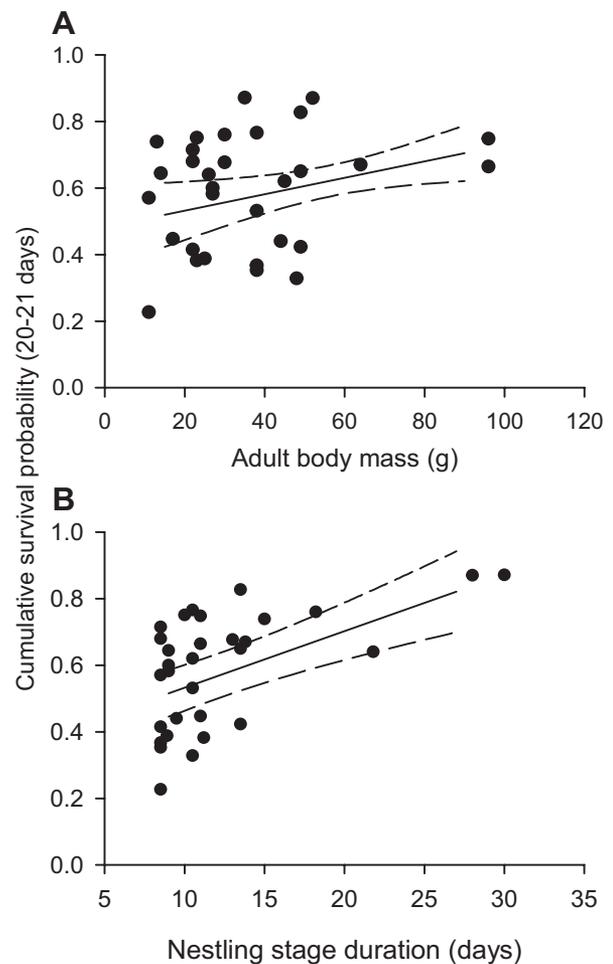


Figure 3. Relationship between post-fledging survival (20–21 days after fledging) and (A) adult body mass and (B) nestling-stage duration for passerine birds. Filled circles indicate raw data and solid lines indicate model-based estimates with nestling stage duration held constant at its mean value in (A) and adult body mass held constant at its mean in (B). Dashed lines indicate 95% confidence intervals.

nestling stage (Fig. 3). Sensitivity analyses suggested that when post-fledging survival was < 0.4 , small improvements in post-fledging survival greatly relaxed unrealistic assumptions about overwinter survival for juvenile birds.

The vote-counting approach allows for the use of studies that do not present estimates of effect sizes of variables. We felt this inclusive approach was appropriate considering the small number of post-fledging survival studies for passerines. However, vote-counting does have limitations because it does not take into account the power of a study when determining whether the effect of a variable is detected (Borenstein et al. 2009). As such, the approach can provide evidence of the importance of particular effects if they are frequently detected, but drawing conclusions about covariates that are infrequently found to influence a response variable is difficult (i.e., effects may actually exist that are not detected because of inadequate sampling). Given the conservative nature of this approach, we believe that the relatively frequent detection of a suite of covariates is

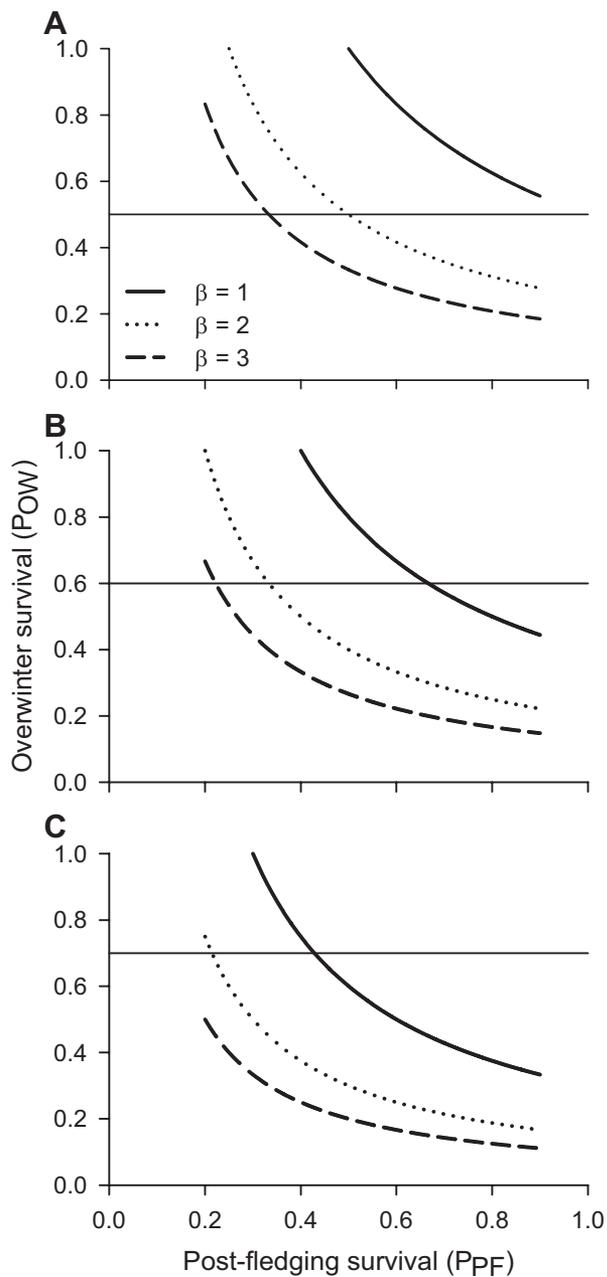


Figure 4. Relationship between post-fledging survival (P_{PF}) and overwinter survival P_{OW} for stable populations ($\lambda = 1$) at 3 levels of seasonal fecundity (β) and 3 levels of adult survival (P_A , indicated by horizontal lines): $P_A = 0.5$ (A), 0.6 (B), or 0.7 (C). We interpret $P_{OW} > P_A$ to mean that P_{PF} is too low to support a stable population.

demonstrative of the complex nature of factors that ultimately determine survival for young birds.

Most factors we found to influence survival are outside the direct control of managers. Within species, intrinsic factors such as parental quality (e.g., Rush and Stutchbury 2008) or the duration of parental care (e.g., Gruebler and Naef-Daenzer 2008) can improve survival, whereas environmental influences such as drought (Yackel Adams et al. 2006) or high temperatures during the nestling period (Greño et al. 2008) can reduce it. Nonetheless, intrinsic factors that affect

post-fledging survival may be indirectly tied to habitat quality. For example, higher nestling body condition (e.g., Vitz and Rodewald 2011) and mass (e.g., Suedkamp Wells et al. 2007), which can be influenced by features of habitat quality such as high food availability (Wilkin et al. 2009), were often associated with improved post-fledging survival. This might indicate that benefits obtained while in the nest may continue to improve survival after fledging (e.g., Mitchell et al. 2011) and that in the absence of detailed post-fledging survival data, managers may be able to improve post-fledging survival by providing habitat that improves nestling condition. We caution against making such an assumption, however, because habitat that is high quality for nestling growth and nest survival may be low quality for post-fledging survival to the point that overall productivity is greatest where nest productivity is lowest (Shiple et al. 2013).

Encouragingly, the relatively high proportion (63%) of studies that detected direct habitat effects suggests that management focused on post-fledging habitat can improve survival. That post-fledging survival is often influenced by factors at the patch or smaller spatial scales suggests that it may be a more tractable component of management plans than other life-cycle stages (e.g., migratory or wintering grounds management). For example, studies of forest dwelling passerines found positive correlations between vegetation density and post-fledging survival (e.g., Fink 2003, King et al. 2006, Ausprey and Rodewald 2011, Vitz and Rodewald 2011), probably because of the increased cover from predators that dense vegetation provides. Forest passerines that have recently fledged often select habitats with high vegetation density (e.g., Anders et al. 1998, Ausprey and Rodewald 2011) further supporting the idea that dense vegetation occurring naturally or created by management activities may benefit young birds.

Many passerine species may benefit from heterogeneous habitat at an appropriate (and likely species-specific) spatial scale to balance the habitat needs of nesting adults against those of recently fledged young, which can differ markedly (Anders et al. 1998, Marshall et al. 2003, Vitz and Rodewald 2006). However, data on post-fledging survival and resource selection is not available for most passerine species, which precludes us from knowing which species may need heterogeneous habitat to maximize productivity in both the nesting and post-fledging components of the breeding season. There is also insufficient data on the degree to which landscape-scale habitat features influence post-fledging survival, which is somewhat surprising given the influence of matrix habitat on within-patch songbird nest survival (e.g., Robinson et al. 1995, Lloyd et al. 2005). Research that places post-fledging survival within the context of habitat amount and connectivity at the landscape scale may offer further insights into management strategies for songbird productivity.

Among species, adult body mass and the duration of the nestling stage were both positively associated with post-fledging survivorship to 20–21 days, which is consistent with life-history theory (see Stearns 1992, Cheng and

Martin 2012). Clearly, mechanisms that affect the positive relationship between body mass and overall longevity in passerines (Lindstedt and Calder 1976) may also affect post-fledging survival. Species that nest in cavities or other locations that reduce the risk of nest predation (e.g., stitchbird [*Notiomystis cincta*], eastern bluebird [*Sialia sialis*], purple martin) can remain in the nest longer, which may improve flight capacity (Dial 2003) and thus improve predator evasion or food procurement after fledging. However, despite the statistical significance of the relationship between body mass and nestling stage duration, variation in survival rates was high, likely because of the suite of biotic and abiotic factors that can influence survival. As such, we caution against the use of post-fledging survival values in demographic models unless they are empirically derived from the population of interest.

Barron et al. (2010) performed a comprehensive meta-analysis of the avian literature and determined that transmitters have a small negative effect on survival. Deriving an effect size (e.g., a percentage decline in survival between tagged and untagged birds) from their work was not possible (D. G. Barron, Washington State University, personal communication), and the difficulties associated with estimating survival for untagged birds have led to few studies that directly compare the survival of tagged and untagged birds (see results for summary of papers that consider transmitter effects on post-fledging survival). As a result, we caution that the average survival curve we present is based on survival rates that may be biased low to an unknown but likely small extent because of transmitter effects on survival. Nevertheless, the nearly ubiquitous improvement in survival with age suggests that the first 3 weeks after fledging are critical (Fig. 2), and that most of the other factors affecting survivorship are operating during that time period. This is encouraging because post-fledging survival studies are often limited temporally by battery life of transmitters or the researcher's ability to resight fledglings. Transmitters are currently available for 10-g birds with expected battery life >3 weeks (e.g., NTQB-1; Lotek Wireless, Newmarket, Ontario, Canada). Therefore, future radiotelemetry studies on even very small passerines will be able to estimate survival rates and test for factors affecting survival during the most critical portion of the post-fledging period. Survival rates clearly level off after 20 days and thereafter, young birds maintain a relatively high survival rate similar to adults during the late breeding season. We did not have data to determine whether survival rates for young birds remains similar to adults during migration when most mortality for migrant species occurs (Sillert and Holmes 2002) or during the winter for resident birds, but we feel it is not likely to be the case for several reasons. First-year birds of migratory species often take different migratory pathways than adults (Johnson 1973, Ralph 1981), make up a disproportionate percentage of vagrants (i.e., birds that are lost; reviewed in Newton 2008), and may have comparatively low fat deposits required for crossing large bodies of water (Woodrey and Moore 1997). Mitchell et al. (2012) found evidence that young birds make suboptimal breeding ground departure

decisions with respect to weather when compared to adults, and first-year birds are often competitively excluded from high quality habitats on the wintering grounds (Sherry and Holmes 1996, Latta and Faaborg 2002), which may reduce overwinter survival for young birds (Marra and Holmes 2001). Furthermore, differential mortality between juveniles and adults during migration has been observed in a non-passerine species (Strandberg et al. 2010).

The arbitrary valuation of first-year survival as half of adult survival that has been used in past demographic models will usually be inaccurate because many populations are not stable, which was an explicit assumption of the derivation of the half adult survival calculation (Greenberg 1980). But because so much remains unknown about survival from the time a young bird leaves the breeding grounds until it breeds the following year, obtaining estimates of post-fledging survival still leaves us with an incomplete understanding of passerine demography. Nevertheless, sensitivity analyses such as ours (Fig. 4) can identify when post-fledging survival estimates would require unrealistic overwinter survival rates and provide managers with a possible mechanism driving population declines. Furthermore, the sensitivity analysis suggests that when post-fledging survival rates are low (e.g., <0.4, which was true for 11 of 50 [22%] published rates), even small improvements in survival can rapidly reduce rates of overwinter survival required for lambda to remain at 1.

Clearly, demographic models for passerine birds remain a work in progress. Fortunately, recent work offers promise in obtaining unbiased first-year survival estimates. First, quantification of dispersal probabilities disentangles emigration from mortality and provides unbiased first-year survival values. For example, Gilroy et al. (2012) incorporated empirically derived dispersal probabilities into mark-recapture survival estimates for Cape Sable seaside sparrows (*Ammodramus maritimus mirabilis*) and estimated first-year survival to be 0.34 ± 0.08 CL, roughly twice the apparent survival produced when emigration rates and dispersal were not integrated into the analysis. In addition, new radiotelemetry transmitters that emit signals >1 year after application (e.g., Biotrack CTx connectivity tags; Biotrack, Dorset, United Kingdom) may help other researchers quantify dispersal probabilities and produce unbiased overwinter survival estimates. Second, advances in integrated population models allow researchers to estimate unobserved demographic parameters such as overwinter survival, essentially by using observed demographic parameters in conjunction with population count data to solve for unobserved demographic parameters (e.g., chapter 11 in Kéry and Schaub 2012). Although both improvements are data intensive and rely on their own sets of assumptions, they offer opportunities to refine our current understanding of passerine demography.

MANAGEMENT IMPLICATIONS

We recommend that post-fledging resource selection and evaluation of factors that influence post-fledging survival for passerines become an integral part of management plans for

species of conservation concern. The majority of post-fledging mortality occurs during the first 3 weeks after fledging, so management efforts should focus on actions that improve survival during this time period. Although many species appear to respond positively to increased vegetation density, managers should consult the literature for species-specific recommendations on habitat features that promote post-fledging survival. We recommend that researchers avoid the use of the half adult survival assumption, as well as the use of post-fledging estimates derived from a population other than the one of interest when building demographic models for songbirds because inter-population variation in important demographic parameters can be extensive (Fredriksen et al. 2005, Balogh et al. 2011) and the arbitrary use of demographic parameters may provide misleading population projections. Instead, we recommend that researchers perform elasticity analyses (e.g., Fletcher et al. 2006, McNew et al. 2012) to examine the degree to which growth rates are sensitive to post-fledging and/or first-year survival. Ultimately, acquiring data on post-fledging survival across space and time is imperative if we are to maximize the productivity of breeding songbirds.

ACKNOWLEDGMENTS

We thank members of the University of Missouri Avian Ecology lab and T. Martin for the discussions that led to this paper. Funding was provided by the United States Department of Agriculture Forest Service Northern Research Station and the Department of Interior's Northeast Climate Science Center, under United States Geological Survey funding. Several anonymous reviewers provided feedback that greatly improved the quality of the manuscript.

LITERATURE CITED

- Allison, P. D. 1999. Logistic regression using SAS: theory and application. SAS Institute, Cary, North Carolina, USA.
- Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson. III. 1997. Juvenile survival in a population of Neotropical migrant birds. *Conservation Biology* 11:698–707.
- Anders, A. D., J. Faaborg, and F. R. Thompson. III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile wood thrushes. *Auk* 115:349–358.
- Anders, A. D., and M. R. Marshall. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology* 19:66–74.
- Anderson, D. R., K. P. Burnham, and G. C. White. 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. *Journal of Animal Ecology* 54:89–98.
- Ausprey, I. J., and A. D. Rodewald. 2011. Postfledging survivorship and habitat selection across a rural-to-urban landscape gradient. *Auk* 128:293–302.
- Balogh, A. L., T. B. Ryder, and P. P. Marra. 2011. Population demography of gray catbirds in the suburban matrix: sources, sinks and domestic cats. *Journal of Ornithology* 152:717–726.
- Barron, D. G., J. D. Brawn, and P. J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* 1:180–187.
- Berkeley, L. I., J. P. McCarty, and L. L. Wolfenbarger. 2007. Postfledging survival and movement in dickcissels (*Spiza americana*): implications for habitat management and conservation. *Auk* 124:396–409.
- Bonnot, T. W., F. R. Thompson, III, and J. J. Millsbaugh. 2011. Extension of landscape-based population viability models to ecoregional scales for conservation planning. *Biological Conservation* 144:2041–2053.
- Borenstein, M., L. V. Hedges, J. P. T. Higgins, and H. R. Rothstein. 2009. Introduction to meta-analysis. John Wiley and Sons Ltd., Chichester, United Kingdom.
- Brown, W. P., and R. R. Roth. 2004. Juvenile survival and recruitment of wood thrushes *Hylocichla mustelina* in a forest fragment. *Journal of Avian Biology* 35:316–326.
- Cheng, Y., and T. E. Martin. 2012. Nest predation risk and growth strategies of passerine species: grow fast or develop traits to escape risk? *American Naturalist* 180:285–295.
- Cohen, E. B., and C. A. Lindell. 2004. Survival, habitat use, and movements of fledgling white-throated robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. *Auk* 121:404–414.
- Cooper, C. B., S. J. Daniels, and J. R. Walters. 2008. Can we improve estimates of juvenile dispersal distance and survival? *Ecology* 89:3349–3361.
- Cox, A. S., and D. C. Kesler. 2012. Reevaluating the cost of natal dispersal: post-fledging survival of red-bellied woodpeckers. *Condor* 114:341–357.
- Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead seas turtles and implications for conservation. *Ecology* 68:1412–1423.
- DeCecco, J. A., M. R. Marshall, A. B. Williams, G. A. Gale, and R. J. Cooper. 2000. Comparative seasonal fecundity of four Neotropical migrants in middle Appalachia. *Condor* 102:653–663.
- Dial, K. P. 2003. Evolution of avian locomotion: correlates of flight style, locomotor modules, nesting biology, body size, development, and the origin of flapping flight. *Auk* 120:941–952.
- Donovan, T. M., and F. R. Thompson. III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications* 11:871–882.
- Dunning, J. B. Jr. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, Florida, USA.
- Eng, M. L., B. J. M. Stutchbury, D. M. Burke, and K. A. Elliott. 2011. Influence of forest management on pre- and post-fledging productivity of a Neotropical migratory songbird in a highly fragmented landscape. *Canadian Journal of Forest Research* 41:2009–2019.
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merford, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson III, and N. Warnock. 2010. Conserving migratory land birds in the New World: do we know enough? *Ecological Applications* 20:398–418.
- Fauth, P. T., D. G. Krementz, and J. E. Hines. 1991. Ectoparasitism and the role of green nesting material in the European starling. *Oecologia* 88: 22–29.
- Fink, M. L. 2003. Post-fledging survival of juvenile wood thrush in fragmented and contiguous landscapes. Dissertation, University of Missouri, Columbia, USA.
- Fisher, R. J., and S. K. Davis. 2011. Post-fledging dispersal, habitat use, and survival of Sprague's pipits: are planted grasslands a good substitute for native? *Biological Conservation* 144:263–271.
- Fletcher, R. J., R. R. Koford, and D. A. Seaman. 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. *Journal of Wildlife Management* 70:145–157.
- Fredriksen, M., M. P. Harris, and S. Wanless. 2005. Inter-population variation in demographic parameters: a neglected subject? *Oikos* 111: 209–214.
- Gilroy, J. J., T. Virzi, R. L. Boulton, and J. L. Lockwood. 2012. A new approach to the “apparent survival” problem: estimating true survival rates from mark-recapture studies. *Ecology* 93:1509–1516.
- Green, D. J., and A. Cockburn. 2001. Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology* 70:505–514.
- Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493–504 in A. Keast, and E. S. Morton, editors. *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, D.C., USA.
- Greño, J. L., E. J. Belda, and E. Barba. 2008. Influence of temperatures during the nestling period on post-fledging survival of great tit *Parus major* in a Mediterranean habitat. *Journal of Avian Biology* 39: 41–49.
- Grübler, M. U., and B. Naef-Daenzer. 2008. Fitness consequences of pre- and post-fledging timing decisions in a double-brooded passerine. *Ecology* 89:2736–2745.

- Grüebler, M. U., and B. Naef-Daenzer. 2010. Brood overlap and male ornamentation in the double-brooded barn swallow. *Behavioral Ecology* 21:513–519.
- Hochachka, W., and J. N. M. Smith. 1991. Determinants and consequences of nestling condition in song sparrows. *Journal of Animal Ecology* 60:995–1008.
- Hovick, T. J., J. R. Miller, R. R. Koford, D. M. Engle, and D. M. Debinski. 2011. Postfledging survival of grasshopper sparrows in grasslands managed with fire and grazing. *Condor* 113:429–437.
- Imlay, T. I., J. F. Crowley, A. M. Argue, J. C. Steiner, D. R. Norris, and B. J. M. Stutchbury. 2010. Survival, dispersal, and early migration movements of captive-bred juvenile eastern loggerhead shrikes (*Lanius ludovicianus migrans*). *Biological Conservation* 143:2578–2582.
- Jackson, A. K., J. P. Froneberger, and D. A. Cristol. 2011. Postfledging survival of eastern bluebirds in an urbanized landscape. *Journal of Wildlife Management* 75:1082–1093.
- Johnson, N. K. 1973. Spring migration of the western flycatcher, with notes on seasonal changes in sex and age ratios. *Bird-Banding* 44:205–220.
- Kershner, E. L., J. W. Walk, and R. E. Warner. 2004. Postfledging movements and survival of juvenile eastern meadowlarks (*Sturnella magna*) in Illinois. *Auk* 121:1146–1154.
- Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS. Academic Press, San Diego, California, USA.
- King, D. I., R. M. Degraaf, M. L. Smith, and J. P. Buonaccorsi. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *Journal of Zoology* 269:414–421.
- Krementz, D. G., J. D. Nichols, and J. E. Hines. 1989. Postfledging survival of European starlings. *Ecology* 70:646–655.
- Latta, S. C., and J. Faaborg. 2002. Demographic and population responses of Cape May warblers wintering in multiple habitats. *Ecology* 83:2502–2515.
- Lindstedt, S. L., and W. A. Calder. 1976. Body size and longevity in birds. *Condor* 78:91–94.
- Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. *Ecological Applications* 15:1504–1514.
- Low, M. 2006. Sex, age and season influence morphometrics in the New Zealand stitchbird (or Hihi; *Notiomystis cincta*). *Emu* 106:297–304.
- Low, M., and T. Pärt. 2009. Patterns of mortality for each life-history stage in a population of the endangered New Zealand stitchbird. *Journal of Animal Ecology* 78:761–771.
- Magrath, R. D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *Journal of Animal Ecology* 60:335–351.
- Mahony, N. A., P. G. Krannitz, and K. Martin. 2006. Seasonal fecundity of sagebrush Brewer's sparrow (*Spizella breweri breweri*) at the northern edge of its breeding range. *Auk* 123:512–523.
- Marra, P. P., and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *Auk* 118:92–104.
- Marshall, M. R., J. A. DeCecco, A. B. Williams, G. A. Gale, and R. J. Cooper. 2003. Use of regenerating clearcuts by late-successional bird species and their young during the post-fledging period. *Forest Ecology and Management* 183:127–135.
- Maxted, A. M. 2001. Post-fledging survival, dispersal, and habitat use in two migratory shrubland bird species. Thesis, Purdue University, West Lafayette, Indiana, USA.
- McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2012. Demography of greater prairie-chickens: regional variation in vital rates, sensitivity values, and population dynamics. *Journal of Wildlife Management* 76:987–1000.
- Middleton, H. A., and D. J. Green. 2008. Correlates of postfledging survival, the timing of dispersal, and local recruitment in American dippers. *Canadian Journal of Zoology* 86:875–881.
- Mitchell, G. W., C. G. Guglielmo, N. T. Wheelwright, C. R. Freeman-Gallant, and D. R. Norris. 2011. Early life events carry over to influence pre-migratory condition in a free-living songbird. *PLoS ONE* 6: e28838.
- Mitchell, G. W., A. E. M. Newman, M. Wikelski, and R. D. Norris. 2012. Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. *Journal of Animal Ecology* 81:1024–1033.
- Moore, L. C., B. J. M. Stutchbury, D. M. Burke, and K. A. Elliott. 2010. Effects of forest management on postfledging survival of rose-breasted grosbeaks (*Pheucticus ludovicianus*). *Auk* 127:185–194.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730–738.
- Newton, I. 2008. The migration ecology of birds. Academic Press, San Diego, California, USA.
- Norris, D. R., and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* 109:535–547.
- Perrins, C. M. 1965. Population fluctuations and clutch-size in the great tit, *Parus major* L. *Journal of Animal Ecology* 34:604–647.
- Poole, A. editor. 2005. The birds of North America online. Cornell Laboratory of Ornithology, Ithaca, New York, USA.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Radchuk, V., C. Turlure, and N. Schtickzelle. 2013. Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology* 82:275–285.
- Ralph, C. J. 1981. Age ratios and their possible use in determining autumn routes of passerine migrants. *Wilson Bulletin* 93:164–188.
- Reed, W. L., M. E. Clark, P. G. Parker, S. A. Raouf, N. Arguedas, D. S. Monk, E. Snajdr, V. Nolan, Jr., and E. D. Ketterson. 2006. Physiological effects on demography: a long-term experimental study of testosterone's effects on fitness. *American Naturalist* 167:667–683.
- Ricklefs, R. E. 1973. Fecundity, mortality, and avian demography. Pages 366–434 in D. S. Farner, editor *Breeding biology of birds*. National Academy of Sciences, Washington, D.C., USA.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- Rush, S. A., and B. J. M. Stutchbury. 2008. Survival of fledgling hooded warblers (*Wilsonia citrina*) in small and large forest fragments. *Auk* 125:183–191.
- Russell, E. 2000. Avian life histories: is extended parental care the southern secret? *Emu* 100:377–399.
- Sankamethawee, W., G. A. Gale, and B. D. Hardesty. 2009. Post-fledgling survival of the cooperatively breeding puff-throated bulbul (*Alophoixus pallidus*). *Condor* 111:675–683.
- SAS Institute Inc. 2008. SAS/STAT 9.2 user's guide. SAS Institute, Cary, North Carolina, USA.
- Schmidt, K. A., S. A. Rush, and R. S. Ostfeld. 2008. Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. *Journal of Animal Ecology* 77:830–837.
- Schulenberg, T. S. editor. 2010. Neotropical birds. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Sekercioglu, C. H., S. R. Loarie, F. Brenes Oviedo, P. R. Ehrlich, and G. C. Daily. 2007. Persistence of forest birds in the Costa Rican agricultural countryside. *Conservation Biology* 21:482–494.
- Sherry, T. W., and R. T. Holmes. 1996. Habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77:36–48.
- Shipley, A. A., M. T. Murphy, and A. H. Elzinga. 2013. Residential edges as ecological traps: postfledging survival of a ground-nesting passerine in a forested urban park. *Auk* 130:501–511.
- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.
- Strandberg, R., R. H. G. Klaassen, M. Hake, and T. Alerstam. 2010. How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. *Biology Letters* 6:297–300.
- Streby, H. M., and D. E. Andersen. 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. *Ecosphere* 2:art78. doi: 10.1890/ES1810-00187.00181
- Stromborg, K. L., C. E. Grue, J. D. Nichols, G. R. Hepp, J. E. Hines, and H. C. Bourne. 1988. Postfledging survival of European starlings exposed as nestlings to an organophosphorus insecticide. *Ecology* 69:590–601.
- Styrsky, J. N., J. D. Brawn, and S. K. Robinson. 2005. Juvenile mortality increases with clutch size in a neotropical bird. *Ecology* 86:3238–3244.

- Suedkamp Wells, K. M., M. R. Ryan, J. J. Millsbaugh, F. R. Thompson III, and M. W. Hubbard. 2007. Survival of postfledging grassland birds in Missouri. *Condor* 109:781–794.
- Sullivan, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeotus*). *Journal of Animal Ecology* 58:275–286.
- Tarof, S. A., P. M. Kramer, J. R. Hill III, J. Tautin, and B. J. M. Stutchbury. 2011. Brood size and late breeding are negatively related to juvenile survival in a neotropical migratory songbird. *Auk* 128:716–725.
- Tarwater, C. E., and J. D. Brawn. 2010. The post-fledging period in a tropical bird: patterns of parental care and survival. *Journal of Avian Biology* 41:479–487.
- Tarwater, C. E., R. E. Ricklefs, J. D. Maddox, and J. D. Brawn. 2011. Pre-reproductive survival in a tropical bird and its implications for avian life histories. *Ecology* 92:1271–1281.
- Thomson, D. L., S. R. Baillie, and W. J. Peach. 1999. A method for studying post-fledging survival rates using data from ringing recoveries. *Bird Study* 46:S104–S111.
- United States North American Bird Conservation Initiative Committee. 2009. The State of the Birds, United States of America, 2009. U.S. Department of Interior, Washington, D.C., USA.
- Vitz, A. C., and A. D. Rodewald. 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. *Biological Conservation* 127:477–486.
- Vitz, A. C., and A. D. Rodewald. 2011. Influence of condition and habitat use on survival of post-fledging songbirds. *Condor* 113:400–411.
- Weatherhead, P. J., and M. R. L. Forbes. 1994. Natal philopatry in passerine birds: genetic or ecological influences. *Behavioral Ecology* 5:426–433.
- White, J. D. 2005. Post-fledging survival, resource selection, and dispersal of juvenile Swainson's thrushes in central coastal California. Dissertation, University of Missouri, Columbia, USA.
- Whitehead, M. A., S. H. Schweitzer, and W. Post. 2000. Impact of brood parasitism on nest survival parameters and seasonal fecundity of six songbird species in southeastern old-field habitat. *Condor* 102: 946–950.
- Whittaker, K. A., and J. M. Marzluff. 2009. Species-specific survival and relative habitat use in an urban landscape during the postfledging period. *Auk* 126:288–299.
- Wightman, C. S. 2009. Survival and movements of fledgling western bluebirds. *Southwestern Naturalist* 54:248–252.
- Wilkin, T. A., L. E. King, and B. C. Sheldon. 2009. Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. *Journal of Avian Biology* 40:135–145.
- Woodrey, M. S., and F. R. Moore. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114: 695–707.
- Wolf, L., E. D. Ketterson, and V. Nolan, Jr. 1988. Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? *Animal Behaviour* 36:1601–1618.
- Woolfenden, G. E. 1978. Growth and survival of young Florida scrub jays. *Wilson Bulletin* 90:1–18.
- Yackel Adams, A. A., S. K. Skagen, and R. D. Adams. 2001. Movements and survival of lark bunting fledglings. *Condor* 103:643–647.
- Yackel Adams, A. A., S. K. Skagen, and J. A. Savidge. 2006. Modeling post-fledging survival of lark buntings in response to ecological and biological factors. *Ecology* 87:178–188.
- Zimmerman, G. S., R. J. Gutiérrez, and W. S. Lahaye. 2007. Finite study areas and vital rates: sampling effects on estimates of spotted owl survival and population trends. *Journal of Applied Ecology* 44:963–971.

Associate Editor: David King.

Appendix A. Summary of studies and covariate categories used in this review of post-fledging survival in passerine birds. Type B refers to studies that used banded birds, R indicates studies that used radiotags, and BR indicates studies that used both. We used Y to indicate that ≥ 1 test detected an effect of a covariate within a category and N to indicate that at least 1 test was conducted for the category and no effects were found. Empty cells indicate that no tests for the category were performed.

Common name	Family	Scientific name	Reference	Type	Age	Conspecifics	Parents	Weather	Temporal	Body	Movement	Food	Habitat	Sex	Brood	Transmitter	Effects	
																	Effects	Effects
Western slaty-antshrike	Thamnophilidae	<i>Thamnophilus atrinucha</i>	Tarwater and Brawn (2010)	B	Y				Y	Y				N				
Western slaty-antshrike	Thamnophilidae	<i>Thamnophilus atrinucha</i>	Tarwater et al. (2011)	BR														
Spotted antbird	Thamnophilidae	<i>Hylophylax naevioides</i>	Styrsky et al. (2005)	B	Y				N	N			Y	Y				
Acadian flycatcher ^a	Tyrannidae	<i>Empidonax virens</i>	Ausprey and Rodewald (2011)	R	Y				Y	N								
Brown thornbill	Acanthizidae	<i>Acanthiza pusilla</i>	Green and Cockburn (2001)	B	Y		N		Y	Y		N						
Sitcbird	Notiomystidae	<i>Notiomystis cinerea</i>	Low and Pärt (2009)	B	Y	Y				Y								
Florida scrub-jay	Covidae	<i>Apelocoma coarctatus</i>	Woolfenden (1978)	B	Y					N								
Purple martin	Hirundinidae	<i>Progne subis</i>	Tarof et al. (2011)	BR	Y		Y		Y			Y						
Barn swallow	Hirundinidae	<i>Hirundo rustica</i>	Grüebler and Naef-Daenzer (2008)	R	Y		Y											
Barn swallow	Hirundinidae	<i>Hirundo rustica</i>	Grüebler and Naef-Daenzer (2010)	R														
Great tit and coal tit	Paridae	<i>Parus major/Parus ater</i>	Naef-Daenzer et al. (2001)	BR	Y				Y	Y								
American dipper	Cinclidae	<i>Cinclus mexicanus</i>	Middleton and Green (2008)	B	Y				N	N								
Puff-throated bulbul	Pycnonotidae	<i>Alophopus pallidus</i>	Sankamthawee et al. (2009)	B	Y	N			Y	N			N					N
Eastern bluebird ^a	Turdidae	<i>Sialia sialis</i>	Jackson et al. (2011)	R	Y				Y	N								
Western bluebird	Turdidae	<i>Sialia mexicana</i>	Wightman (2009)	R	Y					N								
Swainson's thrush ^a	Turdidae	<i>Catharus ustulatus</i>	White (2005)	R	Y		N	Y	N	N								
Swainson's thrush	Turdidae	<i>Catharus ustulatus</i>	Whittaker and Marzluff (2009)	R	Y					Y								
Wood thrush ^a	Turdidae	<i>Hylocichla mustelina</i>	Anders et al. (1997)	R	Y				N	N								
Wood thrush ^a	Turdidae	<i>Hylocichla mustelina</i>	Fink (2003)	R	Y				N	N			Y					
Wood thrush	Turdidae	<i>Hylocichla mustelina</i>	Brown and Roth (2004)	B	Y				Y	N								
Wood thrush ^a	Turdidae	<i>Hylocichla mustelina</i>	Schmidt et al. (2008)	R	Y				Y	N			Y					
Common blackbird	Turdidae	<i>Turdus merula</i>	Magrath (1991)	B						Y								
White-throated thrush ^a	Turdidae	<i>Turdus assimilis</i>	Cohen and Lindell (2004)	R						Y								
American robin	Turdidae	<i>Turdus migratorius</i>	Whittaker and Marzluff (2009)	R	Y				N	N								
Gray catbird ^a	Mimidae	<i>Dumetella carolinensis</i>	Maxed (2001)	R	Y		N			N								
Gray catbird ^a	Mimidae	<i>Dumetella carolinensis</i>	Balogh et al. (2011)	R	Y				N	N								
European starling	Sturnidae	<i>Sturnus vulgaris</i>	Stromborg et al. (1988)	B	Y				N	N								
European starling	Sturnidae	<i>Sturnus vulgaris</i>	Krements et al. (1989)	B					N	Y								
European starling	Sturnidae	<i>Sturnus vulgaris</i>	Fauth et al. (1991)	B	N			N	Y	N								
Sprague's pipit ^a	Motacillidae	<i>Anthus spragueii</i>	Fisher and Davis (2011)	R	Y					N			Y					
Ovenbird ^a	Parulidae	<i>Seturus auricapilla</i>	King et al. (2006)	R	Y				Y	Y			Y					
Ovenbird	Parulidae	<i>Seturus auricapilla</i>	Strey and Andersen (2011)	R	Y				Y	Y			Y					
Ovenbird ^a	Parulidae	<i>Seturus auricapilla</i>	Vitz and Rodewald (2011)	R	Y				Y	Y			Y					
Worm-eating warbler ^a	Parulidae	<i>Helminthos vermivorum</i>	Rush and Rodewald (2008)	B	Y		Y		N	N			N					
Hooded warbler	Parulidae	<i>Setophaga citrina</i>	Eng et al. (2011)	BR	Y				Y	Y			N					
Hooded warbler ^a	Parulidae	<i>Setophaga citrina</i>	Maxted (2001)	R	Y				Y	Y			Y					
Yellow-breasted chat ^a	Parulidae	<i>Icteria virens</i>	Whittaker and Marzluff (2009)	R	Y					N			Y					
Spotted towhee	Emberizidae	<i>Pipilo maculatus</i>	Yackel Adams et al. (2001)	R					Y	Y								
Lark bunting	Emberizidae	<i>Calamospiza melanocorys</i>	Yackel Adams et al. (2006)	R	Y			Y	Y	N								
Lark bunting ^a	Emberizidae	<i>Calamospiza melanocorys</i>	Yackel Adams et al. (2006)	BR	Y			N	Y	N								
Grasshopper sparrow ^a	Emberizidae	<i>Ammodramus saccannorum</i>	Hovick et al. (2011)	B	Y					Y								
Song sparrow	Emberizidae	<i>Melospiza melodia</i>	Hochachka and Smith (1991)	B						Y								
Song sparrow	Emberizidae	<i>Melospiza melodia</i>	Whittaker and Marzluff (2009)	R					Y	Y			Y					
Song sparrow	Emberizidae	<i>Melospiza melodia</i>	Wolf et al. (1988)	B						Y								
Dark-eyed junco	Emberizidae	<i>Junco hyemalis</i>	Reed et al. (2006)	B						Y								
Dark-eyed junco	Emberizidae	<i>Junco hyemalis</i>	Whittaker and Marzluff (2009)	R						Y								
Dark-eyed junco	Emberizidae	<i>Junco hyemalis</i>	Sullivan (1989)	B	Y				N	N								
Yellow-eyed junco	Emberizidae	<i>Junco phaeonotus</i>	Ausprey and Rodewald (2011)	R	Y				N	N			Y					
Northern cardinal ^a	Cardinalidae	<i>Cardinalis cardinalis</i>	Moore et al. (2010)	R	Y				N	N								
Rose-breasted grosbeak ^a	Cardinalidae	<i>Phoenicurus ludovicianus</i>	Berkeley et al. (2007)	R	Y				N	N								
Dickcissel ^a	Cardinalidae	<i>Spiza americana</i>	Suedkamp Wells et al. (2007)	R	Y				N	Y								
Dickcissel ^a	Cardinalidae	<i>Spiza americana</i>	Suedkamp Wells et al. (2004)	R	Y				N	N								
Eastern meadowlark ^a	Icteridae	<i>Sturnella magna</i>	Suedkamp Wells et al. (2007)	R	Y				N	N								
Eastern meadowlark ^a	Icteridae	<i>Sturnella magna</i>	Suedkamp Wells et al. (2007)	R	Y				N	N								
Brown-headed cowbird ^a	Icteridae	<i>Molothrus ater</i>	Fink (2003)	R	N				N	N		N						

^a Study was used to derive overall passerine post-fledging survival curve.