Survival to independence in relation to pre-fledging development and latitude in songbirds across the globe

Vladimír Remeš and Beata Matysioková

Species differ strongly in their life histories, including the probability of survival. Annual adult survival was investigated extensively in the past, whereas juvenile survival, and especially survival to independence, received much less attention. Yet, they are critical for our understanding of population demography and life-history evolution. We investigated post-fledging survival to independence (i.e. survival upon leaving the nest until nutritional independence) in 74 species of passerine birds worldwide based on 100 population level estimates extracted from published literature. Our comparative analyses revealed that survival to independence increased with the length of nestling period and relative fledging mass (ratio of fledging mass to adult body mass). At the same time, species with higher nest predation rates had shorter nestling periods and lower relative fledging mass. Thus, we identify an important trade-off in life history strategies: staying longer in the nest may improve post-fledging survival due to enhanced flight ability and sensory functions, but at the cost of a longer exposure to nest predators and increased mortality due to nest predation. Additionally, post-fledging survival to independence did not differ between species from the northern temperate zone vs species from the tropics and southern hemisphere. However, analyses of post-fledging survival curves suggest that 1) daily survival rates are not constant and improve quickly upon leaving the nest, and 2) species in the tropics and southern hemisphere have higher daily post-fledging survival rates than northern temperate species. Nevertheless, due to the accumulation of mortality risk during their much longer periods of post-fledging care, overall survival until independence is comparable across latitudes. Obtaining high-quality demographic data across latitudes to evaluate the generality of these findings and mechanisms underlying them should be a research priority.

Life histories vary across latitudes in many animal groups, including birds, amphibians, and fishes (Cardillo 2002, Vila-Gispert et al. 2002, Morrison and Hero 2003). First attempts to explain this variation focused on fecundity (Cody 1966, Lack 1968; reviewed by Roff 1992, Ricklefs 2000, Martin 2004, McNamara et al. 2008). Later studies explored other life-history traits (e.g. prenatal and postnatal growth rates; Remeš and Martin 2002, Martin et al. 2007, 2011) and their underlying physiology (Wikelksi et al. 2003, Wiersma et al. 2007). Although these studies brought significant advances in our understanding of life-history evolution, it became clear that lifespan and survival throughout the year are critical for shaping life histories (Ricklefs 1983, 2010, Perrins 1991, Roff 1992, Martin 2014). Thus, studies are needed that seek to understand the evolutionary and ecological drivers of lifespan and survival.

Annual adult survival of birds has been studied extensively and most authors agree that it is higher in the tropics and southern hemisphere as compared to northern temperate regions (Rowley and Russell 1991, Yom-Tov et al. 1992, Ghalambor and Martin 2001, McGregor et al. 2007, Lloyd et al. 2014, Martin et al. 2015; but see Karr et al. 1990; mixed evidence in Peach et al. 2001, Ricklefs et al. 2011). On the contrary, juvenile survival from fledging until the first reproduction has remained comparatively understudied until recently (Maness and Anderson 2013). Yet, its understanding is crucial for insights into population regulation (Sæther et al. 2002), life-history evolution (Ricklefs 2010, Martin 2014, 2015), and population viability and persistence (Wisdom et al. 2000, Coulson et al. 2001). Juvenile survival can be broken down into the period of dependent young cared for by parents vs independent young, and it is unclear which period is more important for overall juvenile survival. It seems that a major part of overall juvenile mortality occurs during the post-fledging period of dependence on parents (western slaty-antshrike Thamnophilus atrinucha, Tarwater et al. 2011; barn swallow Hirundo rustica, Grießbler et al. 2014). Consequently, investigations of variation in post-fledging mortality can provide new insights on population dynamics, conservation, and the evolution of life histories (Cox et al. 2014, Martin 2014, 2015). Moreover, offspring survival to independence in birds (i.e. post-fledging survival) can be influenced by parental investment before (via brood size and fledging mass; Stryský et al. 2005, Sim et al. 2013) and after fledging (Wolf et al. 1988, Ridley 2007, Grießbler and Naef-Daenzer 2010, Dybala et al. 2013). Thus,
understanding correlates of post-fledging survival is additionally important for our understanding of how carry-over effects of parenting can impact on population demography.

We hypothesize following factors as potential drivers of survival to independence in passerines. As life histories often consist of suites of correlated traits, geographic region should predict post-fledging survival due to different life-history strategies of northern temperate and southern species (see above). Moreover, southern species have higher per capita feeding rates of offspring in the nest (Gill and Haggerty 2012, Martin 2015), which could carry-over to higher post-fledging survival. In addition, post-fledging parental care increases post-fledging survival (Riley 2007, Grüebler and Naef-Daenzer 2010). Consequently, if southern species, in addition to longer post-fledging care, also provide more food on a daily basis (to our knowledge, there is no study on this topic), this could lead to higher post-fledging survival in southern species. We included adult body mass as a general allometric correlate of life histories and survival (Calder 1984, Sibly 2012). We also included the length of the nestling period, because both Cox et al. (2014) and Martin (2014) showed that it predicted post-fledging survival in passerines. Moreover, we included relative body mass at fledging, which should express maturity of young and their bodily functions when leaving the nest with potential consequences for their mobility and ability to escape predators and obtain food (Remeš and Martin 2002, Cheng and Martin 2012). Furthermore, we modeled both the length of nestling period and relative body mass at fledging as functions of nest predation rates. Since nest predation can drive the evolution of these traits (Remeš and Martin 2002), it might have an indirect effect on the evolution of post-fledging survival. We used clutch size as a surrogate for the number of young in the nest that compete for food brought by parents, which could have consequences for post-fledging survival (Styrsky et al. 2005, Sim et al. 2013).

Recent studies have explored predictors of post-fledging survival within bird species (Styrsky et al. 2005, Riley 2007, Grüebler and Naef-Daenzer 2010), whereas the only study conducted across species focused mostly on North American species (Cox et al. 2014). However, no study so far analyzed post-fledging survival across a broad set of species from across the globe and its drivers. Here, we conduct such a study by analyzing post-fledging survival to independence in 74 species of songbirds (Passeriformes) based on data from the literature across diverse latitudes and life histories.

Methods

We collated data from the literature on post-fledging survival in songbirds. We included only studies that reported survival of fledglings to nutritional independence. Nutritional independence was defined as a moment beyond which fledglings obtained most of their food on their own and adults stopped feeding them. Thus, we excluded studies that 1) provided data on post-fledging survival but did not report the length of nutritional dependence, or 2) did not follow fledglings long enough so that they reached nutritional independence. The reasons were threefold. First, mortality of dependent vs independent juveniles might be caused by different factors (predation vs starvation, Sullivan 1989) due to locomotor performance and foraging skills improving with age (Weathers and Sullivan 1989) and the buffering effects of parental care (Dybala et al. 2013). Thus the presence vs absence of parental care makes the two periods biologically distinct (see additional evidence in Introduction). Second, from a biological point of view, bird species differ in whether offspring disperse at nutritional independency or delay their dispersal substantially (Droba et al. 2015), with potentially important consequences for parental care and survival strategies. Third, from a methodological point of view, dispersal of independent offspring might strongly bias estimates of juvenile survival (McKim-Louder et al. 2013). Whereas offspring in songbirds invariably stay with parents on the natal territory during post-fledging care, their dispersal behaviour upon attaining independence varies a lot across species: some species disperse almost immediately (many northern temperate species), whereas many tropical and southern species delay dispersal for a long time (e.g. tropical Sylvia warblers, Schaefer et al. 2004, or western-slaty antshrikes, Tarwater and Brawn 2010). Thus, studying offspring during one, clearly defined life-history stage (i.e. period of dependence on parents) might minimize biases in survival estimates due to dispersal. Consequently, the age of independence might provide a natural biological and methodological benchmark for standardization across species with diverse life histories and ensure minimal biases introduced into data.

We conducted a thorough literature search for data on post-fledging survival in songbirds. For North America, we used and augmented the dataset given in Martin (2014). For Australia, we obtained data on post-fledging survival as part of our research on life histories of Australian songbirds (Matysioková et al. 2011, Remeš et al. 2012). Data from other regions were obtained during an exhaustive search of the literature on songbird reproduction worldwide (see Matysioková and Remeš 2014 for detailed methods; see literature sources in Supplementary material Appendix 1). To make sure that we did not miss recent literature, we ran additional search on Web of Science on 16 October 2015 using following parameters: keywords (‘post-fledging survival’ OR ‘postfledging survival’) AND birds), timespan: 2011–2015. We obtained 76 citations and after reading their titles and abstracts we scrutinized full texts of 12 articles. However, none yielded additional data on survival until nutritional independence.

We extracted data on post-fledging period (in days), i.e. how long parents fed the young upon their leaving the nest, and post-fledging survival to independence (proportion of fledged young that survived until nutritional independence). When more than one study was available for a particular species, we took the average of published values. We obtained two or more estimates of survival to independence for 21 species (based on 47 population level estimates). Repeatability across species estimated as intraclass correlation coefficient using function ‘ICCest’ (package ‘ICC’, Wolak et al. 2012) was 0.46 (95% CI = 0.14–0.77). We did not calculate daily post-fledging survival rates, because daily survival rate upon leaving the nest rapidly improves (Naef-Daenzer et al. 2001, Sankamethawee et al. 2009, Tarwater et al. 2011) and thus is not constant over the period of dependence, which precludes statistical analysis of daily rates (for details see
Results and Supplementary material Appendix 2). Moreover, due to the nature of data extracted from literature, we were not able to employ formal survival analysis. Instead, we had to use simple proportions of fledglings that survived until independence. Thus, our analysis was not able to model detection probabilities or dispersal.

Some studies provided survival curves for a cohort of fledglings during the period of dependence. We digitized such curves (n = 25) by tracking their shape in a computer program to obtain detailed shape of the survival trajectory. We then averaged these survival curves for northern temperate and southern species (see below for the explanation of these geographic zones). Subsequently, we fit the Weibull survival model to these geographic zone-specific curves to find out whether daily mortality rate was constant across the period of dependence (Kleinbaum and Klein 2011). Weibull model has the form of $S = \exp(-\lambda t^\alpha)$, where $S$ is post-fledging survival, $\lambda$ is a parameter quantifying how fast overall survival declines with time, $t$ is time, and $P$ is the shape parameter determining how the daily mortality rate changes with time (more precisely the hazard function $h = \lambda t^{\alpha-1}$, Kleinbaum and Klein 2011). For $P > 1$ it increases, for $P < 1$ it decreases, and for $P = 1$ it is constant and thus $h = \lambda$. In the latter case the Weibull model reduces to the exponential model, which is thus its special case where $S = \exp(-\lambda t)$.

Natural logarithm of survival in both models is linear against the time axis under its proper transformation. While in the Weibull model $\ln(S)$ declines linearly with $t^\alpha$, yielding $\ln(S) = -\lambda t^\alpha$, in the exponential model as its special case $\ln(S)$ should be linear on semi-log scale, yielding $\ln(S) = -\lambda t$. Plots of both $S$ and $\ln(S)$ against time were used to visually judge model fit.

We categorized each species as either northern temperate or tropical and southern hemisphere (southern species thereafter) using 23.5°N as a cut-off latitude. We used this categorization, because tropical and southern hemisphere birds are similar in their life histories and differ from northern temperate species in a suite of life-history characteristics (Cody 1966, Rowley and Russell 1991, Yom-Tov 1994, Yom-Tov et al. 1994, Russell 2000, Ghalambor and Martin 2001, Russell et al. 2004, Martin et al. 2007). As predictors, for each species we obtained data on adult body mass (grams), nesting period duration (days), clutch size (no. of eggs), and relative fledging mass (proportion of adult body mass at fledging). Moreover, for each species we also searched data on nest predation (proportion of nests destroyed by predators) and transformed them to daily nest predation rates (d$^{-1}$) as in Remes et al. (2012). All these data were obtained from literature (complete dataset is given in Supplementary material Appendix 1, Table A1, A2, and A3).

We used phylogenetic generalized least squares to fit our models. This method accounts for shared history among species and flexibly fits a phylogenetic autocorrelation parameter $\lambda$ (Freckleton et al. 2002). We used the 'gls' function from package 'nlme' (Pinheiro et al. 2013) in the R programming environment (R Core Team). Many studies did not provide data on the number of fledged and surviving offspring, but only on the proportion of fledglings surviving to independence. That is why we were forced to use the proportion of surviving as a continuous response variable instead of more correct binomial model. We downloaded 500 phylogenetic trees for our species from birdtree.org using the Hackett backbone (Jetz et al. 2012). We calculated the Bayesian maximum credibility tree using TreeAnnotator (<http://beast.bio.ed.ac.uk/TreeAnnotator>). It has the advantage of both summarizing alternative phylogenies and providing branch lengths based on these original phylogenies. To make sure that our analyses were robust to the way alternative phylogenies were handled, we also calculated the majority rule consensus tree and imputed 'Grafen’s' branch lengths (Paradis 2012). Results using these two methods were very similar and we report only results of comparative analyses using the maximum credibility tree.

We set up several models to test our hypotheses, and their structure is apparent from Table 1, 2, and 3. Models differ in sample size, because not all variables were available for all species. In all models where geographic zone was among pre-

<table>
<thead>
<tr>
<th>Estimate</th>
<th>SE</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>21.17</td>
<td>20.32</td>
<td>-0.09</td>
</tr>
<tr>
<td>log$_{10}$ body mass</td>
<td>-4.30</td>
<td>4.80</td>
<td>-0.90</td>
</tr>
<tr>
<td>Relative fledging mass</td>
<td>-6.16</td>
<td>12.21</td>
<td>-0.50</td>
</tr>
<tr>
<td>Geographical zone (southern)</td>
<td>0.13</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>Clutch size</td>
<td>-1.28</td>
<td>1.98</td>
<td>-0.65</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Estimate</th>
<th>SE</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>33.90</td>
<td>25.87</td>
<td>-0.09</td>
</tr>
<tr>
<td>log$_{10}$ body mass</td>
<td>55.99</td>
<td>13.09</td>
<td>4.28</td>
</tr>
<tr>
<td>Relative fledging mass</td>
<td>-6.16</td>
<td>12.21</td>
<td>-0.50</td>
</tr>
<tr>
<td>Geographical zone (southern)</td>
<td>0.13</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>Clutch size</td>
<td>-1.28</td>
<td>1.98</td>
<td>-0.65</td>
</tr>
</tbody>
</table>

Table 2. Post-fledging period (log$_{10}$-transformed, phylogenetic signal $\lambda = 0.36$), nestling period (log$_{10}$-transformed, $\lambda = 1.00$), and relative fledging mass ($\lambda = 0.87$) in relation to adult body mass and geography, fit using phylogenetic generalized least squares models.
Table 3. Nestling period (log_{10}-transformed, phylogenetic signal λ = 0.89) and relative fledging mass (λ = 0.81) in relation to adult body mass, daily nest predation rates, and geography, fit using phylogenetic generalized least squares models.

<table>
<thead>
<tr>
<th></th>
<th>Nestling period (45 species)</th>
<th>Relative fledging mass (45 species)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>SE</td>
</tr>
<tr>
<td>Intercept</td>
<td>1.17</td>
<td>0.09</td>
</tr>
<tr>
<td>log_{10} body mass</td>
<td>0.08</td>
<td>0.04</td>
</tr>
<tr>
<td>sqrt daily nest predation rate</td>
<td>-1.09</td>
<td>0.32</td>
</tr>
<tr>
<td>Geographical zone (southern)</td>
<td>0.04</td>
<td>0.03</td>
</tr>
</tbody>
</table>

predictors, we also initially fit interactions of all predictors with the geographic zone, because we wanted to know whether relationships differed between the zones. However, none of these interactions was statistically significant, and thus we excluded them from the models. We did not do any further selection of individual variables, because stepwise procedures strongly bias parameter estimates (Whittingham et al. 2006). Variables were transformed to achieve normal distribution of residuals and the transformations used for individual variables were as follows: log_{10} (post-fledging period), log_{10} (adult body mass), log_{10} (nestling period), and square root (daily nest predation rate). We also checked that predictors were not strongly correlated and we show these relationships for key predictors here. The length of post-fledging period was not related to nestling period length (nestling period: estimate = 0.12, SE = 0.17, t = 0.73, p = 0.467; geographic zone: estimate = 0.16, SE = 0.05, t = 3.37, p = 0.001; λ = 0.60, n = 74 species). However, post-fledging period was related to relative fledging mass (relative fledging mass: estimate = -0.42, SE = 0.19, t = -2.28, p = 0.028; geographic zone: estimate = 0.17, SE = 0.05, t = 3.28, p = 0.002; λ = 0.60, n = 48 species). Finally, relative fledging mass was related to nestling period length (nestling period: estimate = 0.35, SE = 0.16, t = 2.25, p = 0.030; geographic zone: estimate = 0.05, SE = 0.04, t = 1.36, p = 0.180; λ = 0.89, n = 48 species).

Results

We obtained 25 survival curves from the literature (n = 21 species), 18 for northern temperate and 7 for southern species, respectively (Fig. 1a; sources for these curves are available in Supplementary material Appendix 1, Table A1). Fitting of the Weibull survival model to survival curves averaged for the two geographical zones showed that it provided a good fit (Fig. 1b, c) and its parameters were as follows; northern temperate species: Weibull λ_S = 0.16, P_N = 0.45; southern species: Weibull λ_S = 0.11, P_S = 0.34. These results showed that overall survival declined faster in northern temperate species than in southern species (λ_N > λ_S, Fig. 1). Moreover, estimates of both P_N and P_S showed that daily survival rate was not constant across the post-fledging period, because constant survival assumes P = 1 (see Methods). Thus, it was impossible to estimate daily survival rates that would be constant across the period of dependence (we provide further extensive analyses of this problem in Supplementary material Appendix 2). Due to the unavailability of these daily survival rates, we modeled simple post-fledging survival to independence itself.

We obtained data on post-fledging survival to independence and post-fledging period for 100 populations of 74 species of songbirds (Fig. 2). Post-fledging survival increased with the length of nestling period but not with adult body mass (Table 1). However, when relative fledging mass (ratio of fledging mass to adult body mass) was used instead, post-fledging survival increased with both relative fledging mass and the length of nestling period, and this was true for all species across geographical zones (Table 1, Fig. 3). We further showed that there was no difference in post-fledging survival to independence between southern and northern temperate species: the difference was only 5.19% (SE = 4.18) and was not statistically significant when analyzed without any other predictors (t = 1.24, p = 0.218, λ = 0.19). Similarly, geographic zones did not differ significantly in post-fledging survival.

Figure 1. Survival curves extracted from literature (n = 25 curves of 21 species) and their modeling using the Weibull model. (a) Survival curves of northern temperate (n = 18 curves of 14 species) and southern species (n = 7 curves of 7 species). (b) Their averages for individual days plotted against days post-fledging and fit with Weibull model curves. Scatter in later days post-fledging is caused by sparse data (i.e. few species had such long periods of post-fledging care, see panel (a)). (c) Fit of the Weibull model on the time scale where it should be linear as detailed in Methods (i.e. time raised to the Pth power). ‘Southern’ denotes species from the tropics and southern hemisphere.
species with the same body mass can differ by 10 d in their pressure fledged earlier and in lower body mass. This early us, species under stronger nest predation (Table 3, Fig. 5).

mass decreased with increasing daily nest predation rates, relationship was not statistically significant in the nestling for the allometric effect of adult body mass (although this compared to northern temperate species when controlled relative fledging mass were all greater in southern species as time, the length of nestling and post-fledging periods and these relationships are available in Table 1.

Figure 2. Distribution of post-fledging survival to independence (median northern temperate = 67.1%, southern = 68.6%) and post-fledging period length (median northern temperate = 22.0 d, southern = 33.7 d) in species of songbirds worldwide (n = 74 species), split by the geographical zone. ‘Southern’ denotes species from the tropics and southern hemisphere.

survival when controlled for the length of post-fledging period (geographic zone: estimate = 5.33, SE = 4.67, t = 1.14, p = 0.257; post-fledging period: estimate = −0.96, SE = 12.18, t = −0.08, p = 0.938; λ = 0.19). At the same time, the length of nestling and post-fledging periods and relative fledging mass were all greater in southern species as compared to northern temperate species when controlled for the allometric effect of adult body mass (although this relationship was not statistically significant in the nestling period; Table 2, Fig. 4).

Both the length of nestling period and relative fledging mass decreased with increasing daily nest predation rates (Table 3, Fig. 5). Thus, species under stronger nest predation pressure fledged earlier and in lower body mass. This early fledging can bring significant survival benefit. For example, species with the same body mass can differ by 10 d in their nestling period, even when accounting for the geographic zone (Supplementary material Appendix 1). At the same time, daily nest predation rates ranged from 0.1% d⁻¹ in species with long nestling periods to 5.2% d⁻¹ in species with short nestling periods. Consequently, for example exposure to additional daily nest predation probability of 5% for additional 10 d would mean depredation of additional 40% of nests (or the probability of depredation = 0.4 for each nest), a substantial cost to nest survival. Hence there is a clear trade-off between the benefits of fledging early (lower probability of nest depredation) vs late (higher survival to independence).

Discussion

We showed that post-fledging survival to independence in songbirds worldwide increased with the length of nestling period and relative fledging mass. At the same time, nestling period was shorter and relative fledging mass was lower in species with higher nest predation rates. Thus, there was a clear trade-off between benefits of staying in the nest longer (higher post-fledging survival) vs shorter (lower probability of nest depredation). Furthermore, post-fledging survival was not related to adult body mass, clutch size (surrogate of the number of young), or the length of post-fledging period, and it did not differ significantly between northern temperate and southern species (i.e. species in the tropics and southern hemisphere). However, daily post-fledging survival rate improved faster, and was consequently on average higher, in southern species than in northern temperate species.

Cox et al. (2014) and Martin (2014) recently demonstrated higher post-fledging survival in species with longer nestling periods. Here we show that this relationship is true for survival to independence in songbirds worldwide. Moreover, we show that post-fledging survival to independence is higher in species where nestlings leave the nest at higher relative body mass (in relation to adult body mass) and that these two predictors have additive effects. Both of these relationships can be explained by improved development of locomotor abilities and other bodily functions (e.g. sensory capabilities) in better-developed fledglings. Locomo-

Figure 3. Post-fledging survival to independence in relation to the length of nestling period (days, log₁₀-transformed) and relative fledging mass (ratio of fledging mass to adult body mass) in songbirds worldwide, split by the geographical zone. ‘Southern’ denotes species from the tropics and southern hemisphere. Raw data and ordinary least squares regression lines are shown. Phylogenetic statistical analyses of these relationships are available in Table 1.
Anava et al. 2001, Bonnevie 2004). The difference in fledging age of a mere 1 to 2 d can have strong survival consequences in small passerines (Wolf et al. 1988). These ideas are supported by a general observation that predation is a major source of mortality during post-fledging care (Sullivan 1989, Sim et al. 2013) and a host of birds, mammals, and reptiles were found or suspected to be responsible (Table 4 in Shipley et al. 2013). At the same time, we know that high predation on nests selects for early fledging in low relative body mass (Bosque and Bosque 1995, Reméš and Martin 2002, this study). Thus, we identify an important trade-off: offspring of species that stay longer in the nest can attain larger body mass (Reméš and Martin 2002), longer wings (Cheng and Martin 2012), and subsequent higher post-fledging survival (Cox et al. 2014, Martin 2014, this study). However, this is at a cost of being exposed for longer time to time-dependent mortality caused by nest predators (Reméš and Martin 2002, Roff et al. 2005, Reméš 2007, this study). An interesting alternative explanation is that these relationships are not driven by the development of locomotor abilities of fledglings, but and sensory abilities are certainly critical, as fledglings of virtually all songbirds leave the nest with poor flying abilities and spend their first days outside the nest in the vegetation surrounding the nest (Woolfenden and Fitzpatrick 1984, 1985).

Figure 4. The length of nestling period (days, log_{10}-transformed), relative fledging mass (ratio of fledging mass to adult body mass), and the length of post-fledging period (days, log_{10}-transformed) in relation to adult body mass (grams, log_{10}-transformed) in songbirds worldwide, split by the geographical zone. 'Southern' denotes species from the tropics and southern hemisphere. Raw data and ordinary least squares regression lines are shown. Phylogenetic statistical analyses of these relationships are available in Table 2.

Figure 5. The length of nestling period (days, log_{10}-transformed) and relative fledging mass (ratio of fledging mass to adult body mass) in relation to daily nest predation rates (d^{-1}, square root-transformed) in songbirds worldwide, split by geographic zone. 'Southern' denotes species from the tropics and southern hemisphere. Raw data and ordinary least squares regression lines are shown. Phylogenetic statistical analyses of these relationships are available in Table 3.
but by a shared predator community between nests and fledglings. Accordingly, low predation on both nests and fledglings would lead to high nest survival, long nesting periods, high relative fledging mass, and high post-fledging survival (and vice versa). This alternative can be tested by 1) video-monitoring of nests, and 2) radio-tracking of fledglings on the same study sites.

Overall survival to independence did not differ between songbird species in the northern temperate zone and southern species, but daily post-fledging survival rate improved faster, and was consequently on average higher, in southern species than in northern temperate species (Fig. 1 and Supplementary material Appendix 2). Higher daily survival rate upon fledging in southern species might be caused by more food delivered by parents on a daily basis or higher quality of few fledglings (e.g. longer wings, Martin 2015). The lack of difference in overall survival to independence between these two groups of species is likely caused by different length of post-fledging period of parental care, which is much longer in southern species (Russell 2000, Russell et al. 2004, this study). Thus it seems that mortality accumulates for a longer period of time in southern species and resulting overall survival until independence is similar across latitudes. However, this fact might have significant consequences for juvenile survival until 1 yr of age and thus for overall demography. If juvenile birds survive to independence at a similar rate across latitudes, but post-fledging period of care is longer in the tropics and southern hemisphere, less time remains for species living here before they reach the next breeding season. Consequently, their overall juvenile survival from fledging until 1y of age might be higher (Tarwater et al. 2011). Thus, extended parental care after fledging (Russell et al. 2004, this study), heavier fledglings (this study, but see Martin 2015), and longer wings at fledging (Martin 2015) might be key ‘southern secrets’ (sensu Russell 2000) leading to high juvenile survival and thus enabling tropical and southern hemisphere birds to balance their populations even with small clutch sizes. Of course, contributing factors will be high adult survival (see Introduction) and long breeding seasons enabling frequent re-nesting (Stutchbury and Morton 2001). Conjectures outlined above can be evaluated only with high-quality data on parental care and offspring behavior and survival after fledging and thus obtaining such data across latitudes should be a research priority.

Acknowledgements – This study would not be possible without hard work of generations of field ornithologists. We are obliged to N. Friedman for comments on the first draft of the manuscript and to T. Koutný for help with digitizing survival curves. K. Weidinger, M. Krist, and E. Kolářová commented on selected parts of the manuscript and their insights were much appreciated. Three reviewers and the Editor provided very valuable comments and suggestions that significantly improved this work. This study was supported by an internal grant from Palacký Univ. (Prf_2016_004).

References


Supplementary material Appendix 2

Remeš, V. and Matysioková, B. Survival to independence in relation to pre-fledging development and latitude in songbirds across the globe. Journal of Avian Biology 000: 000-000.

Prepared by V. Remeš

The purpose of this Appendix 2 is to show that daily post-fledging mortality rate in passerines is not constant: It generally strongly declines upon fledging. This represents a challenge for statistical analysis of post-fledging survival derived from literature data, where original survival histories of individuals are not available. More importantly, it means that it is not possible to express “daily mortality/survival rate” by a single number for a given species and thus precludes analyses based on daily rates.

I follow this general outline:

1) Extraction of survival curves from literature
2) Fitting of survival models to these average curves
3) Inferring survival parameters for all species
4) Comparing survival parameters between geographic regions
5) Conclusions
1) Extraction of survival curves from literature

I found and digitized 25 survival curves (n = 21 species) that fulfilled my criteria when selecting post-fledging survival studies (see the main article). These included 18 curves (n = 14 species) for Northern Temperate species and 7 curves (n = 7 species) for Southern species. Following figure (Fig. S1) shows individual curves (left panel) and their averages for individual days, separately for the two geographic regions (right panel). Scatter in later days in the right panel is caused by sparse data (i.e., few species have such long periods of post-fledging care; see the left panel).

I also digitized an average survival curve shown in Fig. 2 in Cox et al. (2014, J. Wildl. Manag. 78:183–193), which represents all species included in that study across all geographic regions. Although there was some overlap in studies included, Cox et al. (2014) used different criteria when selecting studies on post-fledging survival for their metaanalysis, and thus their average survival curve provides partly independent material for the present analyses (their curve is depicted below in Fig. S3).

2) Fitting of survival models to these average curves

Several models can be fitted to survival trajectories and I followed general guidelines given in Kleinbaum and Klein (2011, Survival Analysis: A Self-Learning Text, Third Edition. Springer). I fitted following two models to average survival curves:

i) Weibull model of the form $S = \exp(-\lambda t^p)$, where $S$ is post-fledging survival, $\lambda$ is a parameter quantifying how fast overall survival declines with time, $t$ is time, and $P$ is the shape parameter determining how the daily mortality rate changes with time (more precisely the hazard function $h = \lambda Pt^{p-1}$, see Kleinbaum and Klein 2011). For $P>1$ it increases, for $P<1$ it decreases, and for $P=1$ it is constant and thus $h = \lambda$. In the latter case the Weibull model reduces to the Exponential model, which is thus its special case where $S = \exp(-\lambda t)$.

Natural logarithm of survival in both models is linear against the time axis under its proper transformation. While in the Weibull model ln(S) declines linearly with $t^p$, yielding $\ln(S) = -\lambda t^p$, in the Exponential model as its special ln(S) should be linear on semi-log scale, yielding $\ln(S) = -\lambda t$. Plots of both S and ln(S) against time will be used to visually judge model fit.

ii) Power model of the form $S = at^k$, where $a$ and $k$ are parameters, and $t$ is time. The power model is not often used in survival analyses, but it provides a convenient way to model non-linear curves. This model is linear on a log-log scale, yielding $\ln(S) = \ln(a) - k \ln(t)$. When fitting this model, I assumed $a = 1$, meaning $S =$
100% at the age of 1 day, which was set as fledging day, making this assumption a logical necessity. I again used plots of both $S$ and $\ln(S)$ against time to judge model fit.

Following figure (Fig. S2) shows that both Weibull and Power models fit the average survival curves reasonably well, whereas the Exponential model (special case of Weibull assuming constant daily mortality rate) provides very poor fit (panel A). Note how non-linear the empirical survival trajectories are on the semi-log panel (panel B), and how the Exponential model provides very poor fit. If the Exponential model were a good approximation of the post-fledging survival trajectories in passerines, the empirical survival trajectories would be linear on the semi-log plot, as the estimated Exponential fits are (panel B). On the contrary, empirical survival trajectories and their fits are reasonably linear on the appropriate time scales for both Power ($\ln$(time), panel C) and Weibull model (time raised to the $P^{\text{th}}$ power, panel D).

The same findings are true for the average survival curve (Fig. S3) from Cox et al. (2014; their Fig. 2).
The estimates of the parameters of the Weibull and Power models are as follows (Table 1):

<table>
<thead>
<tr>
<th></th>
<th>Weibull $\lambda$</th>
<th>Weibull $P$</th>
<th>Power $k$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern Temperate spp.</td>
<td>0.158</td>
<td>0.452</td>
<td>0.198</td>
</tr>
<tr>
<td>Southern spp.</td>
<td>0.112</td>
<td>0.342</td>
<td>0.106</td>
</tr>
<tr>
<td>All spp. (based on Cox et al. 2014)</td>
<td>0.152</td>
<td>0.381</td>
<td>0.163</td>
</tr>
</tbody>
</table>

For the Weibull model, all $P$ estimates are $<< 1$, showing that daily survival rate is not constant but increases with days post-fledging (i.e., daily mortality rate decreases). Additionally, both $\lambda_N > \lambda_S$ and $P_N > P_S$, meaning that overall survival declines faster in Northern Temperate than in Southern species (see Fig. S2). Similarly, for the Power model $k_N > k_S$ has the same consequence. Thus, these two models converge on the observation that the decline of overall survival is faster in Northern Temperate passerines as compared to Southern passerines.

Note: As the wording might be confusing, I provide 3 different statements how to describe these results: i) overall survival declines faster in Northern Temperate species than in Southern species, ii) daily survival rate improves faster in Southern species than in Northern Temperate species, or iii) daily mortality rate declines faster in Southern species than in Northern Temperate species. These three statements could be used interchangeably when describing the results presented above.
3) Inferring survival parameters for all species

I then estimated Weibull $\lambda$ and Power $k$ for all species in my sample. For all species, I used average age of independence and average post-fledging survival, both calculated from the original studies (see the main article). Thus, for all species I had only two data points: the start of the survival curve (fledging time, survival 100%) and its end (empirically observed survival at and age of independence). Calculations were as follows.

Weibull model: When estimating Weibull $\lambda$, it is necessary to supply the shape parameter $P$. Thus, I used i) one global $P$ value derived for all species (based on Cox et al. 2014 curve), and ii) region-specific $P$ values (i.e., $P_N$ for Northern Temperate species and $P_S$ for Southern species). I estimated $\lambda = -\ln(S) / AI^P$, where $AI$ is age of independence and other symbols are as above.

Power model: I estimated $k = -[\ln(S) / \ln(AI)] = -\ln(AI)/S$, where symbols are as above.

Following figure (Fig. S4) shows survival curves fitted for all species using the Weibull and Power models. Thin lines with a dot at the end are estimated survival curves for individual species, where the dot denotes empirically observed survival for a given age of independence. Thick lines are averages for Northern Temperate and Southern species, respectively.

4) Comparing survival parameters between geographic regions

Finally, I tested whether Weibull $\lambda$ or Power $k$ differ significantly between Northern Temperate and Southern species of passerines, while controlling for nesting period length, the main predictor of post-fledging survival (see the main article). These tests yielded similar results when run without the nesting period length.

The prediction is that if survival in Northern Temperate species declines faster than in Southern species, then for Weibull model $\lambda_N > \lambda_S$ and for Power model $k_N > k_S$. I ran these tests using phylogenetic generalized least squares models as in the main article.

Results of these phylogenetic analyses ($n = 78$ species) are as follows (Table 2):

<table>
<thead>
<tr>
<th></th>
<th>Weibull $\lambda$ (global $P$)</th>
<th>Weibull $\lambda$ (geogr. specific $P$)</th>
<th>Power $k$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate (SE) t (p)</td>
<td>Estimate (SE) t (p)</td>
<td>Estimate (SE) t (p)</td>
</tr>
<tr>
<td>Intercept</td>
<td>0.77 (0.09) 0.72 (0.09)</td>
<td>0.84 (0.06)</td>
<td></td>
</tr>
<tr>
<td>Geography (South)</td>
<td>-0.05 (0.02) -2.4 (0.019)</td>
<td>0.01 (0.02) 0.51 (0.610)</td>
<td>-0.04 (0.02) -1.89 (0.063)</td>
</tr>
<tr>
<td>$\log_{10}$ Nestling period</td>
<td>-0.36 (0.08) -4.69 (&lt;0.001)</td>
<td>-0.35 (0.08) -4.56 (&lt;0.001)</td>
<td>-0.40 (0.06) -6.70 (&lt;0.001)</td>
</tr>
</tbody>
</table>
1) There is a clear effect of the length of the nestling period: overall survival declines more slowly in species with longer nestling periods. This agrees with the observation in the main article that long nestling periods are associated with high survival to independence across species and latitudes.

2) The effect of geography is apparent in the Weibull model with global P (one shape of the curve) and to a lesser extent ($p = 0.06$) in the Power model. Northern Temperate species have higher parameters (Weibull $\lambda$ and Power $k$) than Southern species, which means that overall survival declines faster in passerine species living north of the Tropic of Cancer.

On the other hand, the effect of geography was not significant in the Weibull model with P specific for Northern Temperate vs. Southern species (see Table 1 above for these estimates). However, I suggest that this absence of the effect of geography on Weibull $\lambda$ with region-specific P is caused by the fact that the difference between geographic regions was already captured by different shape parameter P ($P_N = 0.452$ in Northern Temperate spp, $P_S = 0.342$ in Southern spp., see Table 1). Following figure (Fig. 5S) demonstrates this effect. The same difference between two survival curves can be caused by different P with the same $\lambda$ (red lines) or by different $\lambda$ with the same P (blue lines). Lambda and P values in Fig. 5S are real values estimated above. This confusion stems from the fact that it is not possible to estimate both parameters based on data available here. Also, it is a common practice in survival analysis to model $\lambda$ while keeping P fixed (see Kleinbaum and Klein 2011). I thus suggest that the Weibull model with global P and the Power model provide more correct insight into differences between geographic regions.

Thus, a tentative conclusion from these analyses is that overall survival declines faster in Northern Temperate species than in Southern species. However, since age of independence is much higher in Southern species, post-fledging mortality in these species accumulates for a longer time and this might result in similar survival to independence, as shown in the main article.

5) Conclusions

It is important to stress that all these analyses are very preliminary and depend on a number of assumptions. However, they clearly demonstrate that:

1) It is **not possible to analyse post-fledging survival in passerines using daily survival rates**, because daily survival rate increases upon fledging (i.e. daily mortality declines).
2) Only high-quality demographic data across latitudes can confirm whether there really are systematic differences between temperate and tropical passerines in: i) overall survival to independence, and ii) the shape of survival trajectories.