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*RESEARCH ARTICLE*

# Age effects on survival of Amazon forest birds and the latitudinal gradient in bird survival

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## ABSTRACT

The search for explanations of the well-documented positive relationship between latitude and avian clutch size has created the expectation that tropical birds should balance their smaller clutch sizes with relatively high survival probabilities. So far, efforts to detect a latitudinal gradient in survival have found no statistical support, leading to the hypothesis that a gradient may be present in the survival of juveniles alone. Such a gradient could be masked by the data on adults when field records make no distinction between ages. We aimed to (1) assess the effect of age on survival of tropical birds by estimating age-specific annual apparent survival probabilities for a set of 40 passerine understory species from the central Brazilian Amazon and (2) test the hypothesis of a latitudinal gradient in adult survival with a meta-analysis of tropical and temperate-zone forest passerine survival probabilities at study areas from Peru to Alaska. We estimated age-specific survival using a hierarchical, multispecies Cormack-Jolly-Seber (CJS) model that treats species-specific parameters as random effects. To extend our analysis to data on birds of unknown age at the time of banding, we developed a novel CJS model with a mixture component for the survival of birds of unknown age. We found a strong effect of age on survival at our site, with juveniles having lower survival than adults. The meta-analysis of 342 survival estimates from 175 species and a latitude span of $>$60 degrees revealed a negative effect of latitude on survival, which supports the widely accepted hypothesis that, on average, tropical birds have higher annual survival than their temperate counterparts. We conclude that there is no need for an alternative latitudinal trend in juvenile survival to account for the general trend in clutch size.

*Keywords:* age-mixture survival model, age-specific survival, age uncertainty, Amazon, Cormack-Jolly-Seber, hierarchical model, tropical birds

## Efeito da idade na sobrevivência de pássaros da Floresta Amazônica e o gradiente latitudinal de sobrevivência de aves

## RESUMO

A busca por explicações para o bem documentado gradiente latitudinal do tamanho de postura em aves criou a expectativa de que as aves tropicais deveriam compensar suas posturas relativamente pequenas com probabilidades de sobrevivência altas. Até hoje, a busca empírica de um gradiente latitudinal de sobrevivência não encontrou suporte estatístico, o que gerou a hipótese de que talvez exista um gradiente que se manifesta apenas nos juvenis. Tal gradiente poderia ser mascarado pelos dados de adultos em observações de campo que não fazem distinção entre idades. Neste estudo pretendemos: a) avaliar o efeito da idade na sobrevivência de aves tropicais através da estimativa de probabilidades anuais de sobrevivência aparente de jovens e adultos em quarenta espécies de passeriformes de sub-bosque da floresta de terra firma na Amazônia Central; e b) testar a hipótese de um gradiente latitudinal de sobrevivência de adultos usando uma meta-análise de estimativas de sobrevivência de passeriformes de floresta tropical, temperada e boreal desde o Peru ao Alaska. Estimamos a probabilidade de sobrevivência específica da idade com um modelo hierárquico Cormack-Jolly-Seber (CJS) de múltiplas espécies que trata os parâmetros espécies-específicos como efeitos randômicos. Para estender nossa análise aos indivíduos de idade desconhecida no momento do anilhamento, desenvolvemos um novo modelo CJS com um componente de mistura para a sobrevivência das aves de idade incerta. Nossos resultados indicam um forte efeito da idade na sobrevivência no nosso sítio de estudo, com os jovens sobrevivendo menos que os adultos. A meta-análise de 342 estimativas de sobrevivência de 175 espécies e um intervalo de latitudes com mais de sessenta graus revelou um efeito negativo da latitude na sobrevivência, o que suporta a ideia amplamente aceite de que, em média, as aves tropicais têm sobrevivência anual mais alta que as aves de regiões temperadas. Concluímos que, para explicar o gradiente latitudinal no tamanho de postura, não há necessidade de invocar a hipótese alternativa de um gradiente latitudinal na sobrevivência de juvenis.

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*Palavras chave:* Amazônia, aves tropicais, Cormack-Jolly-Seber, incerteza de idade, modelo hierárquico, modelo de sobrevivência com mistura de idades, sobrevivência idade-específica

## INTRODUCTION

The observation of latitudinal gradients in bird life-history traits has greatly motivated the study of avian life-history diversity and evolution. A classic example is the increase of clutch size with increasing latitude, as documented by Moreau (1944), Lack (1947, 1948), Skutch (1949, 1985), and Jetz et al. (2008). There is a large body of literature on the evolution of bird life-history traits (Cody 1966, Owens and Bennett 1995, Ricklefs 2000) and on the evolutionary underpinnings of a latitudinal gradient in clutch size (Murray 1985, Martin et al. 2006, McNamara et al. 2008). Studying the evolutionary processes behind the gradient is a worthwhile endeavor, but there is a simpler problem, which also deserves attention, of how such a pattern can be maintained. Assuming that populations of temperate birds are not growing more than their tropical counterparts, the latitudinal gradient in clutch size should be matched by a gradient in the annual number of broods or in survival probability, or both. There is a widespread belief that tropical birds produce more broods per year than temperate birds (e.g., Skutch 1949; but see Martin 1996). A comparative analysis of >400 North American and European species reported a negative relationship between latitude and number of broods (Böhning-Gaese et al. 2000). Whether or not the change in number of broods suffices to maintain the clutch-size gradient, the frequent observation of fecundity–survival trade-offs (Sæther 1988, Ghalambor and Martin 2001) supports another widespread notion, that temperate birds have lower survival probabilities than their tropical counterparts (Murray 1985, Skutch 1985, Martin 1996). Here, however, the latitudinal change could take place via survival changes at different ages, and the empirical evidence deserves closer scrutiny.

The idea of higher adult survival at lower latitudes has had an important influence on avian life-history theory (Martin 1996, 2004) and is coherent with striking observations of a slower pace of life in the tropics, as measured by base metabolic rate (Wikelski et al. 2003, Wiersma et al. 2007). Several studies have offered local support for the idea, fueling its general acceptance (Faaborg and Arendt 1995, Johnston et al. 1997, Francis et al. 1999, Peach et al. 2001), but some of the most careful assessments of survival rates of tropical birds either find lower-than-expected estimates (Blake and Loiselle 2008, 2013) or debate the validity of a latitudinal trend (Karr et al. 1990, Brawn et al. 1999). Indeed, the Panama estimates obtained by Karr et al. (1990) were so similar to temperate-zone estimates that the authors subtitled their paper "Will the dogma survive?" Karr et al.'s (1990) study is more of a call to account for sampling errors in the estimation of survival rates than an attempt to settle the debate about a latitudinal trend. Nonetheless, their results did motivate the search for alternative explanations for the persistence of tropical bird populations with relatively small clutch sizes.

Under the hypothetical scenario in which adult survival probability does not change with latitude, there could still be latitudinal variation in the survival of younger birds. Russell et al. (2004) reported that postfledging Northern Hemisphere birds spend less time with their parents and become independent faster than postfledging birds from the tropical and temperate Southern Hemisphere. If this extended parental care results in increased survival of juvenile birds, it is conceivable that a latitudinal change in juvenile survival might offset the latitudinal change in clutch size. Indeed, when Tarwater et al. (2011) estimated the survival of juveniles from fledgling to 1 yr of age in a Central American population of Black-crowned Antshrikes (*Thamnophilus atrinucha*), they obtained a value of nearly 50%, which is above the range of pre-reproductive survival for 7 species of North American birds that they used for comparison. Tarwater et al. (2011) suggested that a relatively high pre-reproductive survival among tropical birds might resolve the apparent contradiction between the latitudinal trend in clutch size and the overlap of adult survival estimates across latitudes. Their reliance on a small number of species is a reflection of data availability; tropical studies of variation in survival as a function of age are rare and usually focus on single species (e.g., Anders et al. 1997, Tarwater et al. 2011), whereas information on clutch size can be mapped for thousands of species around the world (Jetz et al. 2008). The scarcity of multispecies comparisons between juvenile and adult survival leaves open the possibility that there may, after all, be a latitudinal gradient in adult survival. The analysis by Karr et al. (1990) made no distinction between ages and used temperate data predominantly from late-winter bird captures, which may lack information about first-year juvenile survival. Karr et al.'s (1990) tropical data, on the other hand, came from 2 environmentally different times of the year (dry and rainy seasons) in a relatively less seasonal environment. If their tropical estimates were derived from a mixture of juveniles and adults in which the former were relatively well represented and had lower survival probabilities than the latter, the analysis may have underestimated adult survival and failed to detect a latitudinal effect.



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The objectives of the present study were therefore to (1) assess the effect of age on survival in a tropical bird community, estimating age-specific annual apparent survival probabilities in a large set of passerine understory birds from the central Brazilian Amazon; and (2) contribute to the debate about the latitudinal gradient in adult survival by comparing our adult estimates to estimates of tropical and temperate-zone survival probabilities from other studies. To meet our objectives, we faced some methodological challenges related to ageing live tropical birds in the field and to estimating survival from data on a set of species with widely varying sample sizes. Birds in tropical environments do not breed in defined pulses as temperate birds do, which makes it difficult to age them following the calendar system that is widely used for North American species (Pyle 1997). Therefore, we aged birds using a molt-cycle system that places individuals along a lifelong cycle of plumage molts (Wolfe et al. 2010, Johnson et al. 2011). This system is particularly effective in telling whether birds are within or after their first year of life, which corresponds roughly to the first molt cycle. Inevitably, though, some birds cannot be aged and we are left with an appreciable number of unknown-age individuals. We incorporated these individuals into our study by developing a novel variant of the Cormack-Jolly-Seber (CJS) model with a mixture component for the survival of birds of unknown age at the time of banding. In order to combine information from multiple species with varying sample sizes, we treated species as random effects in the CJS model. We thus built a hierarchical, multispecies CJS model that estimates not just species- and age-specific survival probabilities, but also the parameters that describe the underlying distribution of adult and juvenile survival for all species in our sample.

## METHODS

### Study Area and Sampling Design

Fieldwork was conducted near the "Cabo Frio" and "Porto Alegre" camps of the Biological Dynamics of Forest Fragments Project (BDFFP), 70 km north of Manaus, Amazonas, Brazil (Figure 1). The BDFFP has a tropical rainforest climate with mean annual rainfall of ~2,200 mm and a pronounced dry season from June to October, with <100 mm rain $mo^{-1}$ (Gascon and Bierregaard 2001). Our sampling area spans ~20 $km^2$ of forest, 90% of which is old growth, the remaining 10% being secondary forest 30–33 yr old. This area is embedded in a matrix of old-growth forest that extends hundreds of kilometers to the west, north, and east. For logistic and bird-safety reasons, we conducted fieldwork only during the dry season, between June 2009 and October 2015. We did not sample in 2010 and 2012, so our dataset spans 7 yr, with 5 yr of sampling.

Our sampling aimed to maximize coverage of the study area, while daily and randomly changing the position of sampling devices to prevent trap-aversion. To do this, we established 63 sampling sites throughout the area, 40 clustered around camp Cabo Frio and 23 around camp Porto Alegre. For logistic reasons, the 2 camps had to be accessed in separate visits, where a "visit" is a period of 9–12 days of work by one banding team. We visited Cabo Frio monthly throughout the dry season of every sampling year, and Porto Alegre twice per year in 2 consecutive dry-season months of 2013, 2014, and 2015. Within each visit, we randomly sampled one site per day, without replacement, establishing a line of 12–30 mist nets at each sampled site. Mist nets were 12 m long and 2.5 m high and were operated from 0600 hours to 1200 hours each day. Random sampling of sites was constrained by the distance between them, but it ensured that no site was sampled on 2 consecutive days. All passerine birds captured were marked with numbered aluminum bands (see Acknowledgments).

### Ageing of Captured Birds

We aged birds by assigning individuals to a stage in their lifelong sequence of plumage molt cycles (Howell et al. 2003) and described that stage using the Wolfe-Ryder-Pyle (WRP) system (Wolfe et al. 2010, 2012), which establishes a relationship between stage and age. The WRP system labels individual birds with 3-letter "cycle codes" in which the first letter identifies a molt cycle: for example, first (F), second (S), definitive (D). The second letter expresses a chronological relation to the cycle: in cycle (C), molting into cycle (P), or after cycle (A). Finally, the third letter identifies a particular plumage within the cycle mentioned in the first position: juvenile (J), formative (F), basic (B), alternate (A), or supplemental (S). The code U indicates "unknown" state, either in the first or the third position. Most birds go through 2 different plumages during their first molt cycle, juvenile and formative, which correspond roughly to the first year of life. The juvenile plumage is acquired upon leaving the nest; formative plumage replaces the juvenile and grows before the bird reaches sexual maturity. After the formative plumage, birds enter a sequence of approximately yearly cycles that are most often indistinguishable from each other. Ageing is thus most effective when we can link the bird to 1 of the 2 plumages of the first cycle.

For simplicity, we based our analysis on 2 age classes labeled "juvenile" and "adult," corresponding, respectively, to birds within their first molt cycle and birds beyond the first cycle. Every code from the set {FPJ, FCJ, FPF, FCF, FPU, FCS, FCU, FPA, FCA} was attributed to the "juvenile" class. Codes from the set {DCB, UCB, SPB, SCB, TCB, DPB, FAS, SAB, DPA, DCA} identify plumages that can only appear after the first molt cycle and thus were



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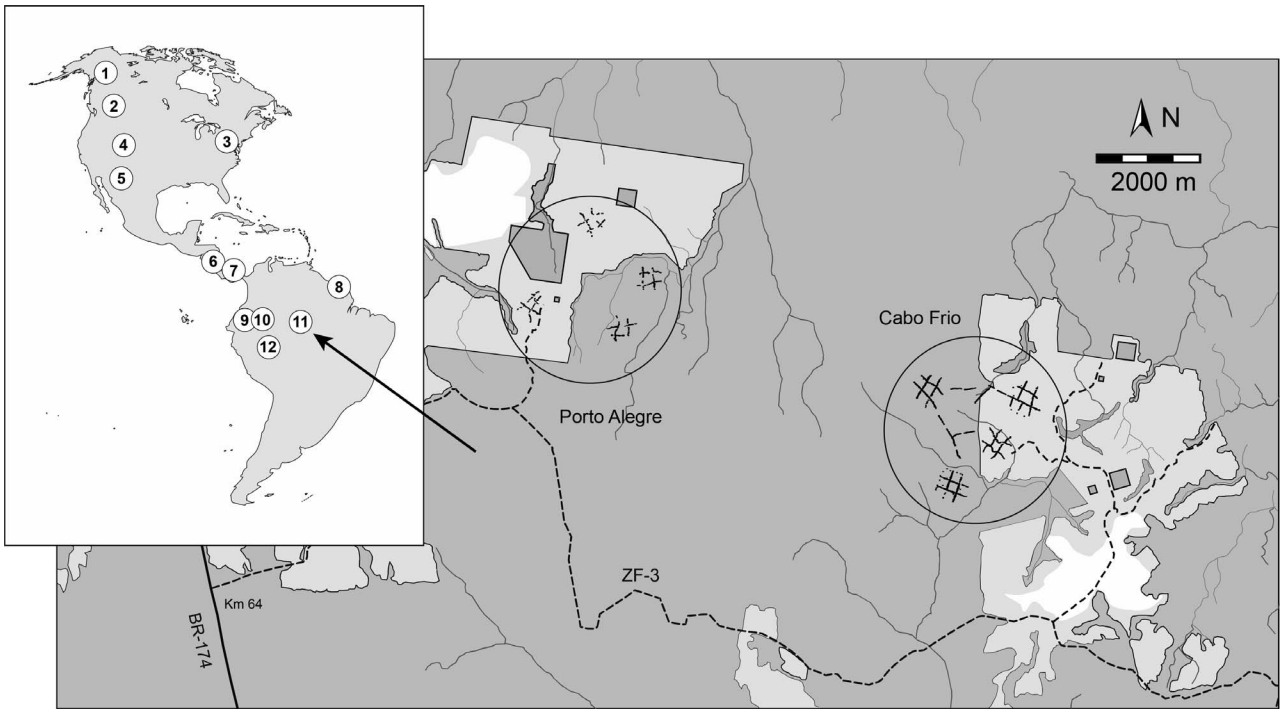



**FIGURE 1.** Study area, with circles showing forest areas around camps "Porto Alegre" and "Cabo Frio," Brazil. Paved and unpaved roads are represented by continuous and dashed lines, respectively. Dark gray represents old-growth forest, with secondary forest in light gray and pasture in white. Black dots inside the circles are mist-net locations. The inset map of the Americas shows the location of the 12 sites considered in the meta-analysis: 1 = North American Bird Conservation Region (BCR) 4; 2 = BCR 10; 3 = Maryland; 4 = BCR 16; 5 = BCR 34; 6 = Costa Rica; 7 = Panama; 8 = French Guiana; 9 = Yasuní, Ecuador; 10 = Tiputini, Ecuador; 11 = Biological Dynamics of Forest Fragments Project, Manaus, Brazil; 12 = Cocha Cashu research station, Manu National Park, Peru.

attributed to the "adult" class (see Wolfe et al. 2012: fig. 1). Among the species in our study, all Furnariidae, some Tyrannidae, and some Thamnophilidae follow molt strategies that make it particularly difficult to place a bird within its first cycle. Whenever a bird could not be placed in the "juvenile" or the "adult" class with confidence, we put it in a third, "unknown" class, which corresponds to codes in the set {FAJ, UCU, UPU}. We formally dealt with age uncertainty in the unknown-age class within our statistical model, as explained in the next section.

### Analysis of Survival in Relation to Species and Age, with Age Uncertainty at Banding

Among all the species captured, we selected only passerine species that had $\geq$1 individual that was first captured as a juvenile and $\geq$10 captures in total from any number of individuals; 40 species fulfilled these criteria and were included in the analysis (see list in Supplemental Material Table S1). We subsequently built species-specific capture-history matrices, with individuals in rows and years in columns. This matrix arrangement aggregated what was originally monthly data into a yearly format, resulting in one datum per individual per year. Thus, each cell in a capture-history matrix contains a 1 or 0—depending, respectively, on whether an individual was or was not captured in a given year. In addition to the capture-history matrices, we constructed species-specific age-data matrices containing information about the age class of individuals (juvenile, adult, or unknown) in every year following the initial capture. Occasionally, some individuals were erroneously classified as having different ages in different captures of the same year; when this happened, we revised the age classifications and reconciled remaining differences by using the best evidence in the full encounter history for the given year.

We estimated survival with a state-space formulation of a CJS model (Royle 2008, Kéry and Schaub 2012); for a single species, we modeled both the biological state and the observation processes as realizations of Bernoulli trials. We describe the state process using 2 variables, $z_{i,t}$ and $f_i$, where $z_{i,t}$ is the latent variable that represents the true state of individual $i$ at time $t$, with values of 1 if the individual is alive and 0 if it is dead. The variable $f_i$ is known data and gives the time at first capture for each individual $i$. Inevitably, the state of individual $i$ in the first capture occasion is $z_{i,f(i)} = 1$; the states on subsequent capture occasions are modeled as Bernoulli trials where an individual alive at time $t$ will



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survive to time $t+1$ with the product of the alive–dead state at the previous occasion ($z_{i,t}$) and the probability $\phi_{i,t}$ ($t = 1, \ldots, T-1$), where $T$ is the time of the last capture occasion. To model the effect of age on survival, we used a time-varying individual age covariate with 2 states: juvenile and adult. The values of this covariate are partially observed and registered in the age-data matrix. Unknown values from the age-data matrix are modeled as juvenile or adult using the mixture approach explained at the end of this section. Age covariate values are stored in a matrix $X_{i,t}$, with $i = 1,\ldots, n$, where $n$ is the number of individuals and $t = 1,\ldots, T-1$, where $T$ is again the time of the last capture occasion. The variation of $X_{i,t}$ through time for individual $i$ is deterministic, such that birds can be juveniles for only 1 yr and never revert from the adult to the juvenile stage. Consequently, we can safely assume that any bird that is captured as a juvenile or unknown-age in year $t$ and survives to year $t+1$ will be an adult in year $t+1$ and all subsequent years of its life. Thus, any individual $i$ that is alive at time $t(z_{i,t} = 1)$ will survive to time $t+1$ with probability $\phi_{X[i,t]}$, where $X_{i,t}$ takes the value 1 for juveniles and 2 for adults. Formally, the state process is defined by the following equations:

$$z_i, f(i) = 1 \quad \text{[Birds are alive when banded,}$$

$$z_{[i,t+1]} | z_{[i,t]} \sim \text{Bernoulli}\left(\mu_{\phi(i,t)}\right) \quad \text{then survive according}$$

$$\text{to a Bernoulli trial,}$$

$$\mu_{\phi(i,t)} = z_{[i,t]} \times \phi_{[X[i,t]]} \quad \text{with probability that}$$

$$\text{depends on } z \text{ and phi.]}$$

The observation process is conditional on individual $i$ being alive at occasion $t$ and is modeled with the probability $p_{i,t}$ ($t = 2, \ldots, T$) that individual $i$ is recaptured at occasion $t$. This is formally defined as

$$y_{i,t} \sim \text{Bernoulli}\left(\mu_{p(i,t)}\right)$$

$$\mu_{p(i,t)} = z_{[i,t]} \times p$$

The state and the observation process are both defined only for $t \geq f_i$, because the CJS model is conditional upon first capture. Because the sample sizes for many species are small to very small, we fitted a model with constant parameters for age-specific survival and recapture probabilities.

To simultaneously model age-specific survival for all species, we adopted a multispecies CJS model (Lahoz-Monfort et al. 2011, Papadatou et al. 2012, Lloyd et al. 2014). This is a hierarchical extension to the classical CJS model with age-specific survival for a single species, described above. The multispecies approach allowed us to obtain an overall mean survival estimate for each age class in our assemblage of 40 species. In short, multispecies models attribute an index $s$ for species ($s = 1, \ldots, 40$) to every quantity in the single-species model.

We fitted 2 variants of such a multispecies CJS model. The first, the random-effects or truly hierarchical CJS model, treated the parameters of each species as random effects (i.e. as random variables drawn from a statistical distribution with hyper-parameters that describe the average species and the heterogeneity among species in the community to which our 40 study species belong). Note that by "community" we mean not just the set of species included in our analysis, but the larger, unspecified set of species of which the study species are a sample. We opted for this approach because our main interest lay in the broad pattern of age-specific survival in the community as a whole. This model makes the following random-effects assumption for the distribution of juvenile survival ($\phi_{s,\text{juv}}$), adult survival ($\phi_{s,\text{ad}}$), and recapture probability ($p_s$) of species $s$:

$$\text{logit}(\phi_s, \text{juv}) \sim \text{Normal}\left(\mu_{\phi(\text{juv})}, \sigma_{\phi(\text{juv})}\right)$$

$$\text{logit}(\phi_s, \text{ad}) \sim \text{Normal}\left(\mu_{\phi(\text{ad})}, \sigma_{\phi(\text{ad})}\right)$$

$$\text{logit}(p_s) \sim \text{Normal}(\mu_p, \sigma_p)$$

The random-effects CJS model allowed us to estimate age-specific survival and, therefore, to assess the differences in survival between juveniles and adults, at 2 hierarchical levels: the level of the community and the level of each species in our 40-species sample. The species-specific estimates are represented by $\phi_{s,\text{juv}}$, $\phi_{s,\text{ad}}$, and $p_s$, while the corresponding community-level estimates, for survival, correspond to the hyper-parameters $\mu_{\phi(\text{age})}$, a community mean survival; and $\sigma_{\phi(\text{age})}$, a community survival variance parameter. The subscript (age) denotes juvenile and adult hyper-parameters. Though perhaps biologically of less direct interest, the model also contains analogous hyper-parameters for the recapture probability $p$.

Our second variant of multispecies CJS model, the fixed-effects model, serves the purpose of methodological comparison to the random-effects model. This is the traditional age-specific CJS model in which the species



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were treated as fixed effects. Like the random-effects model, this model also provides species-specific estimates of survival and recapture probability ($\phi_{s,\text{juv}}$, $\phi_{s,\text{ad}}$, and $p_s$), yet, unlike the random-effects CJS model, estimates for each species are taken to be independent from one another (i.e. they are based exclusively on that species' data). Accordingly, the fixed-effects model has no formal description of a community. Although we fitted this model to all species at once, the estimates are identical to those that would result if we had fit a simple CJS model to each species separately. However, fitting these models all at once using Bayesian Markov chain Monte Carlo (MCMC) methods enabled us to average the species-specific estimates to obtain an estimate (along with its uncertainty) of the average survival or recapture for the set of 40 species in our sample, though not for the community from which these species were drawn.

As a novel feature in our CJS models, we extended the analysis to all individuals with unknown age at the time of banding by specifying a mixture model for their survival. The survival of unknown-age (unk) birds during the first year after banding can be expressed as a weighted average of juvenile and adult survival, where the weights are exactly the proportions of juveniles ($\omega$) and adults ($1 - \omega$) among the unknown-age individuals. Thus, survival of the unknown-age birds in the first interval after banding was modeled as

$$\phi_{s,\text{unk}} = \omega_s \times \phi_{s,\text{juv}} + (1 - \omega_s) \times \phi_{s,\text{ad}}$$

This is similar to the approach of McCrea et al. (2013) in the context of ring-recovery models. We provide BUGS-language code for the random-effects and fixed-effects models in Supplemental Material Appendix S1. We fitted models to data in a Bayesian framework, using conventional vague (noninformative) priors for all parameters. Parameter estimates are expressed as the posterior mean $\pm$ 1 posterior standard deviation (SD) and were obtained by sampling from the posterior probability distribution of each parameter with an MCMC algorithm. We ran 3 MCMC chains, using 500,000 iterations, with a burn-in of 100,000, and thinning of 4, giving us a posterior sample of 300,000 for every estimated quantity. Convergence of chains was assessed visually and using the Brooks-Gelman-Rubin R-hat statistic (Brooks and Gelman 1998), where values $\leq$1.1 suggest convergence. Computations were carried out with programs R (R Development Core Team 2017) and JAGS (Plummer 2003), connected by the R package "jagsUI" (Kellner 2016).

### Analysis of Survival in Relation to Latitude

To assess the hypothesis that survival rates decrease with increasing latitude, we combined in a meta-analysis our adult survival estimates from Manaus (02°S), obtained under the random-effects model, with published survival rates from 11 other regions, spanning a latitudinal gradient from 64°N to 11°S, starting in northwestern North America, going through our site, and ending in the Peruvian Amazon (Figure 1). For simplicity, we will refer to regions as "sites," even though some of them comprise large expanses of land. The 5 northernmost sites are in North America. They comprise one Maryland site that was used in Karr et al.'s (1990) latitudinal comparison of survival estimates, plus 4 North American Bird Conservation Regions (BCRs; DeSante et al. 2015) that range from 64°N to 30°N. The Maryland site is located far east of the north–south sequence of sites, but we decided to include it for historical reasons, because its estimates are part of a seminal work on latitudinal variation in bird survival. The BCRs were selected on the basis of latitudinal coverage along the north–south line and the presence of forest habitat, which makes them relatively comparable with our study site. Next, we obtained data from mature forest in the Limón Province of Costa Rica (Wolfe et al. 2015) and from Parque Nacional Soberanía, in Panama, an area of old-growth forest at ~09°N (Karr et al. 1990, Brawn et al. 2017). In South America, apart from our site at ~02°S (Wolfe et al. 2014, present study), we obtained tropical-forest bird survival estimates from 1 site in French Guiana (Jullien and Clobert 2000), 2 sites in Ecuador (Blake and Loiselle 2008, Ryder and Sillett 2016), and 1 site in Peru (Francis et al. 1999). In total, we assembled 342 estimates of adult bird survival from 12 sites, 28 families, and 175 species (see data and description in Supplemental Material Table S2). Location and phylogeny, in addition to latitude, were expected to explain part of the variability in the apparent survival of adult passerines.

We combined the 342 estimates of species-specific adult survival, along with their associated estimation errors, into a single regression of New World passerine adult survival on latitude. Similar meta-analyses have been described by others (Sauer and Link 2002, McCarthy and Masters 2005, Lloyd et al. 2014, Kéry and Royle 2016:679–682). Our analysis properly accounts for dependencies in the data due to both phylogeny (represented by family and species nested within family) and shared location (represented by the 12 sites). Furthermore, we incorporated both the known component of error represented by the uncertainty associated with each survival estimate (i.e. the SE or the posterior SD) and the unknown component of error represented by the residual variation about the regression model, which accounts for each estimate's own departure from the model prediction. Finally, our analysis accommodated heteroscedasticity among sites in the residual errors. Our data consisted of the estimates of apparent survival $\hat{\phi}_i$ (for $i = 1, \ldots, 342$), along with their associated estimation errors (i.e. $\text{SE}_{\phi(i)}$ or posterior SD). The regression model can be written as follows:



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$$\hat{\phi}_i = \mu + \beta \times \text{lat}_{l(i)} + \beta^{\text{family}}_{j(i)} + \beta^{\text{family/species}}_{k(i)} + \beta^{\text{site}}_{l(i)} + \varepsilon_i + \gamma_i$$

That is, estimate $i$ of apparent survival ($\hat{\phi}_i$) is modeled as the sum of contributions from a grand mean or intercept ($\mu$), a regression on latitude ($\beta$), and effects of family ($\beta^{\text{family}}_{j(i)}$), species nested within family ($\beta^{\text{family/species}}_{k(i)}$), and location ($\beta^{\text{site}}_{l(i)}$). In addition, we include the 2 components of error: the unknown residual about the regression model ($\varepsilon_i$) and the assumed known error ($\gamma_i$) of the CJS estimates, which is the SE or posterior SD of each survival estimate, treated as data in the meta-analysis. We complete the model by adding the following distributional assumptions about the 5 latter terms, making them random effects:

$$\beta^{\text{family}}_j \sim \text{Normal}(0, \sigma^{\text{family}}) \quad \text{[Family random effects]}$$

$$\beta^{\text{family/species}}_k \sim \text{Normal}(\beta^{\text{family}}_j, \sigma^{\text{species}}) \quad \text{[Species random effects]}$$

$$\beta^{\text{site}}_l \sim \text{Normal}(0, \sigma^{\text{site}}) \quad \text{[Site random effects]}$$

$$\varepsilon_i \sim \text{Normal}(0, \sigma^{\text{res}}_l) \quad \text{[Residual]}$$

$$\gamma_i \sim \text{Normal}(0, \text{SE}_{\phi,i}) \quad \text{[Known estimation error]}$$

The first 2 terms account for correlations in our data due to phylogeny, where we fitted random effects of the family, and nested species random effects. The third represents peculiarities of each site, independent of latitude. The penultimate is the residual, which has an SD that is specific to each study site, to account for violation of the usual mixed-model assumption of homogeneity of variances. The final term is the known component of variance with the SD given by the standard errors (SEs). We also note that 3 estimates obtained from the literature had missing SEs. Rather than discarding these, we formally estimated their value by putting a prior on them and estimating them as part of our Bayesian updating scheme (see Kéry and Royle 2016:169–176).

As in the analysis of survival with relation to age and species, we fitted the model in a Bayesian mode of inference using JAGS software and placing conventional vague priors on all model parameters ($\mu$, $\beta$, $\sigma^{\text{family}}$, $\sigma^{\text{species}}$, $\sigma^{\text{site}}$,$\sigma^{\text{res}}_l$). The meta-analysis is described in BUGS language in Supplemental Material Appendix S2.

## RESULTS

### Data Overview

For the years 2009–2015, our dataset contains 5,982 captures of 110 species from 27 families. Of these, 40 species fulfilled the conditions for inclusion in the analysis; they belong to 11 families and represent 87% (5,210) of all captures in the full dataset. The number of individuals per species ranged from 4 (*Cyanocompsa cyanoides*) to 323 (*Pithys albifrons*) (mean = 63, median = 36; see Supplemental Material Table S1 for details), totaling 2,514 individuals across the 40 species. The distribution of ages at first capture for the 2,514 individuals shows a preponderance of adults (62%, $n$ = 1,559), followed by birds of unknown age (22%, $n$ = 553) and finally by juveniles (16%, $n$ = 402). Regarding recapture, in a comparison between the 3 categories of age at first capture, adult individuals of all species combined were captured more than once more frequently (17%, $n$ = 265) than were juveniles (11%, $n$ = 44). Among birds that were first captured as unknown-age, 18% ($n$ = 99) were captured more than once.

### Comparison of Fixed-effects and Random-effects Multispecies CJS Models

The fixed-effects and the random-effects multispecies CJS models both revealed higher survival of adults than of juveniles (Figures 2 and 3). The main difference between these models was in the precision of species-specific estimates (Figure 2) and in the estimates of the heterogeneity of survival among species ($\sigma_\phi$). All species-specific survival estimates were more precise under the random-effects than under the fixed-effects model (Figure 2 and Supplemental Material Table S1). This difference at the species level was matched by the difference between 2 key metrics of heterogeneity among species: (1) the random-effects SD of the community survival hyper-parameter and (2) the SD of the 40 species-specific, fixed-effects survival estimates. The community hyper-parameter in the random-effects model suggested much less heterogeneity among species than the sample SD in the fixed-effects model (Table 1). This was true for both juvenile and adult birds.

Recapture probability estimates showed a pattern not unlike that in the survival estimates, where species-specific posterior distributions of $p$ had a larger SD under the fixed-effects than under the random-effects model. Likewise, when looking at heterogeneity metrics, the random-effects SD of the community hyper-parameter for $p$ was less than half the SD of the $p$ estimates for the sample of 40 species under the fixed-effects model (Table 1). Species-specific estimates of recapture probability $p$ ranged from 0.10 to 0.65, depending on model and species. *Ceratopipra erythrocephala* showed the lowest $p$ under both models, while *Glyphorynchus spirurus* and *C. cyanoides* had the highest $p$, respectively, for the random-effects and the fixed-effects models. Estimates for *C. cyanoides* were particularly imprecise because they were based on 6 captures of only 4 individuals.



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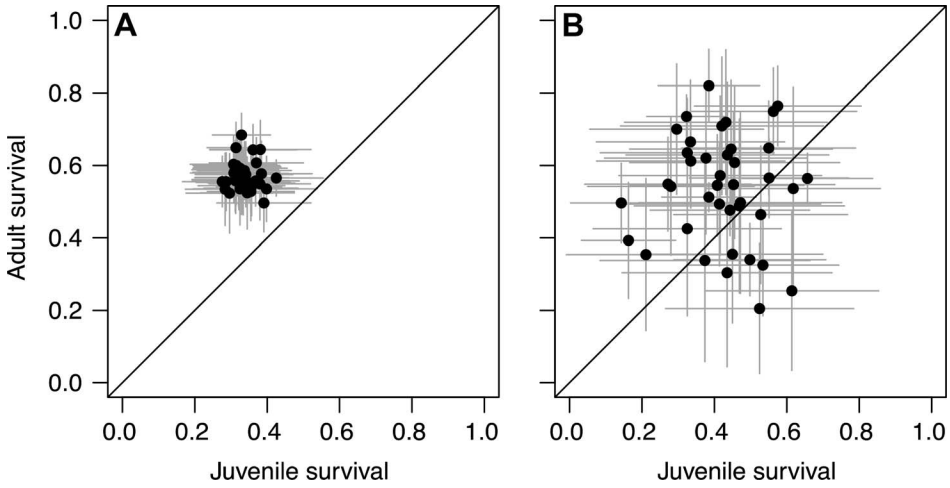



**FIGURE 2.** Plot of juvenile vs. adult survival estimates for all 40 species under random-effects (**A**) and fixed-effects (**B**) models. Gray lines = SD.

When contrasting models, we found relatively small differences between estimates of ω, the proportion of juveniles among birds with unknown age at first capture. Values of the posterior distribution of the mean ω ± SD across the 40 study species are identical to the second decimal place (Table 1); at the species level, all posteriors of the age-mixture parameter ω were extremely wide, with values ranging from 0.30 ± 0.24 to 0.78 ± 0.15 across models and species, indicating that there was limited information in the data to estimate these parameters. *Glyphorynchus spirurus* was the species with the highest and most precise ω estimate under both models. Overall, despite a similar lack of precision in the ω estimates, the random-effects model yielded more precise survival estimates than the fixed-effects model, while simultaneously allowing a more general inference (i.e. not restricted to the 40 species in the sample, as is the fixed-effects model), but allowing formal inference about the bird community as a whole.

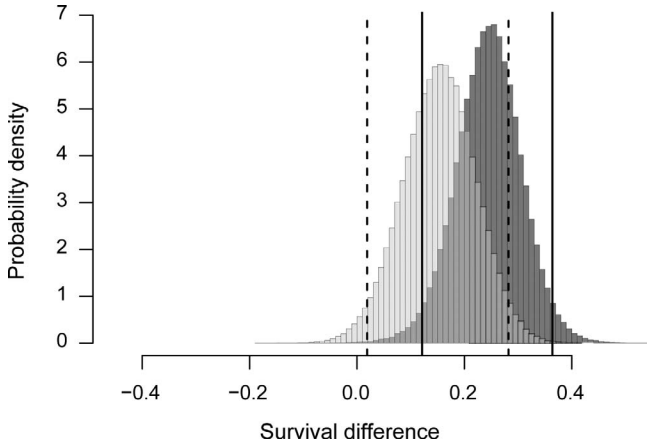



**FIGURE 3.** Posterior distributions of the difference between mean juvenile ($\mu_{\phi(juv)}$) and mean adult ($\mu_{\phi(ad)}$) apparent survival for the 2 models fitted to the data. Vertical lines represent the lower and upper limits of the 95% credibility intervals for this difference. Dark gray bars and solid lines correspond to the mean hyper-parameter values for the random-effects model. Light gray bars and dashed lines correspond to the sample average values for the fixed-effects model.

## Age Differences in Survival Probability

Estimates of apparent survival probability were consistently higher for adults than for juveniles at the species-specific and multispecies levels, for both fixed- and random-effects models. The fixed-effects model resulted in 10 (out of 40) species with higher juvenile than adult survival estimates (Figure 2), but still, under a null hypothesis of no age effect, the binomial probability of $\leq$10 successes out of 40 draws is $<$0.005. The magnitude of the difference between mean adult survival, $\mu_{\phi(ad)}$, and mean juvenile survival, $\mu_{\phi(juv)}$, was slightly higher under the random-effects model. Because the random-effects estimates were more precise overall, we will focus on random-effects model results for the remainder of this section.

The age effect on survival is made clear by a comparison of the posterior distributions of the hyper-parameters that give the mean community survival for juveniles, $\mu_{\phi(juv)}$, and for adults, $\mu_{\phi(ad)}$. The 95% credible interval for the difference $\mu_{\phi(ad)} - \mu_{\phi(juv)}$ did not include zero, for either model (Figure 3), evidence that juvenile survival at our site was indeed lower than adult survival. The odds of survival were 2.7× higher for adults than for juveniles. The difference between adults and juveniles is evident even though the heterogeneity hyper-parameter is higher (14%) among juveniles than among adults (i.e. species differed more among each other in terms of juvenile than adult survival). At the species-specific level, point estimates of



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**TABLE 1.** Posterior mean (± SD) juvenile apparent survival, adult apparent survival, and recapture probability estimated with the random-effects and fixed-effects multispecies Cormack-Jolly-Seber models. Shown are mean survival for juveniles ($\mu_{\phi(juv)}$) and adults ($\mu_{\phi(ad)}$), standard deviation (SD) of survival for juveniles ($\sigma_{\phi(juv)}$) and adults ($\sigma_{\phi(ad)}$), and recapture probability mean ($\mu_p$) and its SD ($\sigma_p$) for juveniles and adults combined. The $\phi$ values for the random-effects model represent community-level hyper-parameters that characterize the whole community from which the 40 analyzed species form a mere sample. Values of $\phi$ for the fixed-effects model, on the other hand, are for the 40 species-specific estimates, hence describing only the 40 species in our analysis. All $\sigma$ values are given on the logit scale, while $\mu$ values are yearly apparent survival probabilities (on the probability scale).

| Model | $\mu_{\phi(juv)}$ | $\mu_{\phi(ad)}$ | $\sigma_{\phi(juv)}$ | $\sigma_{\phi(ad)}$ | $\mu_p$ | $\sigma_p$ | $\mu_\omega$ |
|---|---|---|---|---|---|---|---|
| Random-effects | 0.33 ± 0.06 | 0.57 ± 0.03 | 0.50 ± 0.42 | 0.36 ± 0.15 | 0.30 ± 0.04 | 0.61 ± 0.15 | 0.51 ± 0.04 |
| Fixed-effects | 0.39 ± 0.06 | 0.55 ± 0.04 | 1.66 ± 0.24 | 1.32 ± 0.22 | 0.35 ± 0.04 | 1.33 ± 0.20 | 0.51 ± 0.04 |

juvenile apparent survival ($\phi_{juv}$) spanned the interval 0.28–0.42, while adult survival ($\phi_{ad}$) spanned the interval 0.50–0.68 (Supplemental Material Table S1). Even though species- and age-specific survival estimates differed between random-effects and fixed-effects models, we found that for both models the biggest differences between $\phi_{ad}$ and $\phi_{juv}$ occurred in the same 3 species: *Microbates collaris*, *G. spirurus*, and *Dixiphia pipra*.

### Latitudinal Change in Survival Probabilities

Visual inspection of the distribution of passerine survival across the 12 latitudes in the meta-analysis suggests a negative relationship between survival probability and latitude; that is, the closer one gets to the equator, the higher survival rates get (Figure 4). Our formal examination of this relationship, using a meta-analysis that combines our own estimates with those from 11 other published studies in a mixed regression model, confirmed the visual impression: even after accounting for nonindependence in the data due to phylogeny (family and species within family), site effects, and accommodation of heteroscedasticity, we found a clear effect of latitude on survival. The magnitude of the effect was –0.002 ± 0.001, with a 95% credible interval from –0.004 to –0.001 (Figure 5). The slope of this relationship amounts to an expected survival of 0.58 ± 0.03 at the equator and of 0.45 ± 0.03 at 60° latitude; the odds of survival at 60° are 0.6× as high as for the equator.

## DISCUSSION

We found that adult passerine birds in our Manaus dataset clearly have higher apparent survival probability than postfledging juveniles. When comparing the survival estimates for adults in our study site to estimates of forest passerine adult survival from 11 other sites distributed over a large latitudinal gradient, we also found evidence of increased survival with decreasing latitude, supporting the idea that tropical birds tend to live longer than higher-latitude birds (Murray 1985, Skutch 1985, Martin 1996). These 2 main conclusions about age and latitude effects on forest passerine survival suggest that it is not necessary to invoke an alternative hypothesis of higher juvenile survival in the tropics in order to account for the persistence of the well-established latitudinal gradient in clutch size. That is, if clutch size decreases with latitude and adult survival stays constant, a corresponding increase in juvenile survival could help explain how tropical populations persist despite their reduced clutch sizes (Tarwater et al. 2011). On the other hand, if the survival probability of tropical adults is higher than the survival of both tropical juveniles and adults from other latitudes, then it appears that variation in adult survival alone is still a reasonable candidate for explaining the latitudinal variation in clutch size. Below, we discuss the biological implications and methodological underpinnings behind the observed age and latitude effects on survival.

It is well known that survival of juveniles varies throughout the first weeks of life, being lowest during the first 3 wk after fledging and subsequently increasing (Anders et al. 1997, Tarwater et al. 2011, Cox et al. 2014, Naef-Daenzer and Grüebler 2016); however, after that initial, risky phase, it was not sufficiently clear whether survival of postfledging first-year birds was indeed lower than that of adults. Furthermore, if such a difference exists, it is important to know its magnitude, because it will help us understand whether a possible latitudinal variation in juvenile survival may explain the persistence of a latitudinal gradient in clutch size. In fact, if there were no clear difference in survival rates between tropical and temperate birds, as suggested by Karr et al. (1990), and if juvenile tropical birds had relatively high survival, as suggested by Tarwater et al. (2011), we would expect a relatively small difference in survival probabilities between juveniles and adults in tropical latitudes. This expectation is at odds with our finding of a clearly positive effect of age on survival and with the considerable magnitude of that effect (the odds of adult survival are more than twice as high as those of juvenile survival).

We are not aware of community-level assessments of juvenile survival for temperate-zone passerines. Nonetheless, we can contrast our community-level, random-effects estimate of $\mu_{\phi(juv)}$ for Manaus (0.33 ± 0.06) to Tarwater et al.'s (2011) estimate of fledgling-to-1-yr survival of Black-



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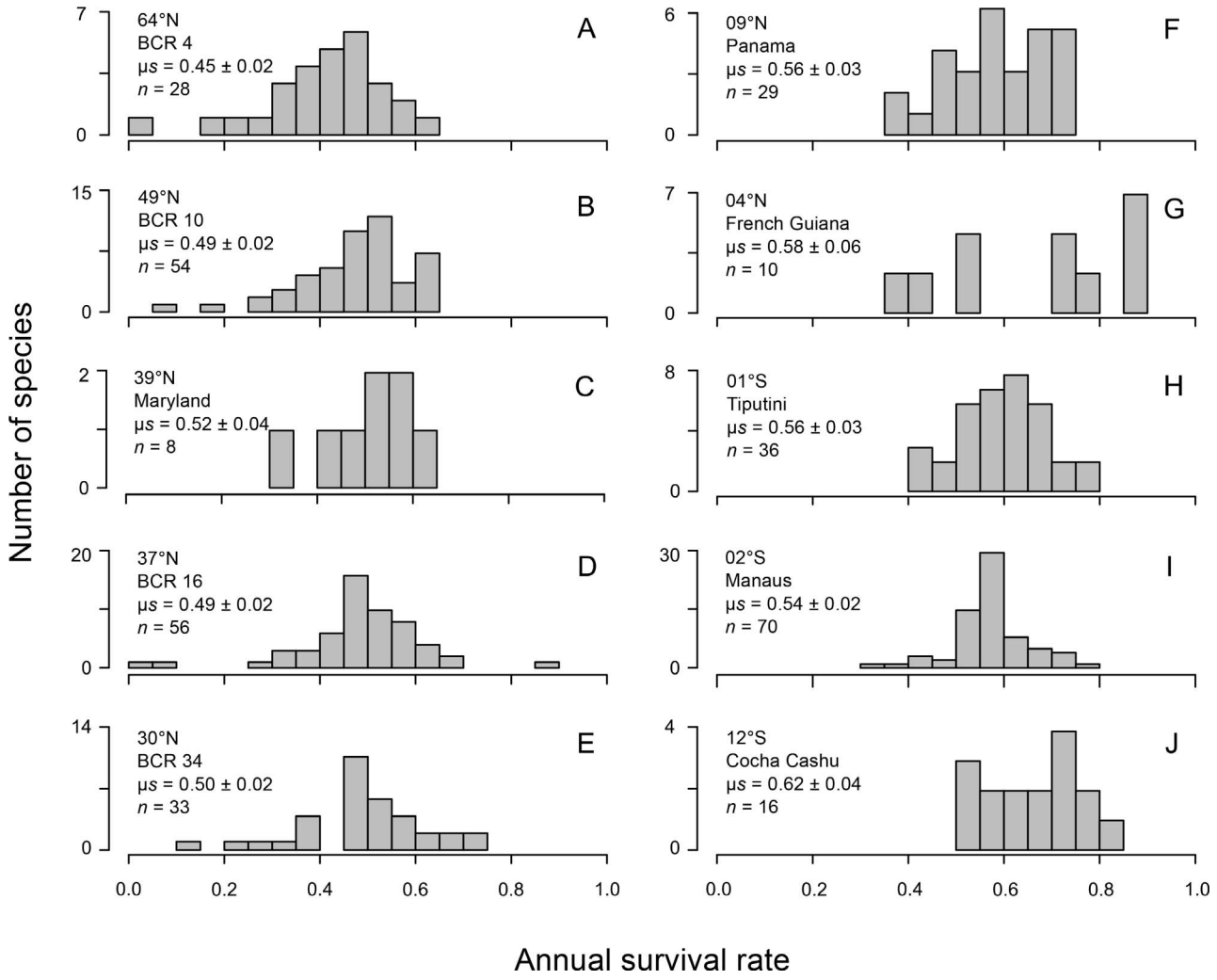



**FIGURE 4.** Comparison of the distribution of annual apparent survival rates for 10 samples of passerine species taken across a latitudinal gradient from North to South America. Two samples included in the meta-analysis, from Costa Rica and Ecuador, are omitted because they include only one estimate each. A, B, D, and E show nontransient survival in 4 North American Bird Conservation Regions (BCRs): (**A**) Northwestern Interior Forest (BCR 4); (**B**) Northern Rockies (BCR 10); (**D**) Southern Rockies Colorado Plateau (BCR 16); and (**E**) Sierra Madre Occidental (BCR 34). Survival estimates in the other panels are for (**C**) birds of any age, transient or not, in Maryland (Karr et al. 1990); (**F**) birds of any age, transient or not (Karr et al. 1990), and adult birds (Brawn et al. 2017) in Panama; (**G**) adult birds in the Nouragues field station, French Guiana (Jullien and Clobert 2000); (**H**) nontransient birds in the Tiputini Biodiversity Station, Ecuador (Blake and Loiselle 2013); (**I**) nontransient birds (Wolfe et al. 2014) and adult birds in a random-effects model (present study) at the Biological Dynamics of Forest Fragments Project, near Manaus, Brazil; and (**J**) nontransient birds in the Cocha Cashu research station, Manu National Park, Peru (Francis et al. 1999). Text inside each panel shows latitude in degrees, site name, average survival probability for the site without the effect of latitude ($\mu s$), and number of estimates ($n$) used in the meta-analysis.

crowned Antshrikes in Panama (0.48 ± 0.09). We can say nothing about the difference between mean juvenile survival in Panama and Manaus, but we note that fledgling-to-1-yr survival in Black-crowned Antshrikes is higher than our estimate of mean juvenile survival, even though it falls within its 95% credible interval. At a finer level of comparison, within the Thamnophilidae, we find that the random-effects $\phi_{juv}$ values in our study range from 0.28 ± 0.11 for Dusky-throated Antshrikes (*Thamnomanes ardesiacus*) to 0.42 ± 0.13 for Common Scale-backed Antbirds (*Willisornis poecilinotus*), being always lower than the point estimate for Black-crowned Antshrikes in Panama. Therefore, if the fledgling-to-1-yr survival estimate for Black-crowned Antshrikes is broadly representative of Panamanian understory birds, it gives us no reason to suspect that juvenile survival is higher in Manaus than in Panama. We are reassured that our estimates offer a reasonable representation of the Manaus



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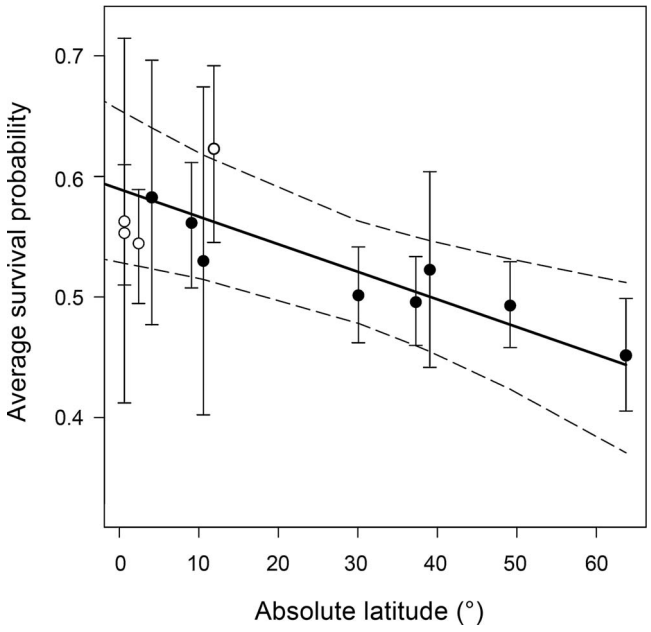



**FIGURE 5.** Estimates of average survival probability for the 12 study sites along the north–south latitudinal gradient. Dark line is the trend line from mixed-effects linear regression. Filled circles are from the Northern Hemisphere and empty circles are from the Southern Hemisphere; their latitudes are shown by their absolute value.

region, not just because they encompass 40 species but also because they broadly agree with previous results from the same area. There are no other estimates of juvenile survival from Manaus, but our random-effects mean adult survival ($\mu_{\phi(ad)}$) of 0.57 ± 0.03 is close to the sample average of 0.59 ± 0.10 obtained by Wolfe et al. (2014) for survival in a sample of 31 species in a different dataset from a region that includes our study area. In conclusion, we believe that our results appropriately represent our site, but we found no evidence to suggest an increase in juvenile survival with decreasing latitude. Further studies of juvenile survival over a latitudinal gradient are needed to determine whether juvenile survival, like adult survival, varies with latitude.

In the latitudinal analysis, our mixed-regression model supports the idea that tropical-forest birds have higher survival rates than temperate-forest birds. Following a reviewer's suggestion, we fitted a model with interaction between latitude and a categorical classification of migration modes, into short, medium, and long distance (Supplemental Material Appendix S2). The negative effect of latitude on survival holds across migration modes without statistical distinction between the slopes (Supplemental Material Figure S1). Because the survival data span a period of 39 yr, we also fitted 2 additional models with an effect of estimate time on survival: one with an additive effect of time and the other with an interaction between time and latitude (Supplemental Material Appendix S2). We measured time as the midyear of the time span of data contributing to each estimate. In both cases, the main effect of latitude remained negative (with credibility interval excluding zero) and the credibility intervals for the effect of time, with or without interaction, included zero. We conclude that neither migration mode nor time period acts as a confounding factor in our description of the latitudinal variation in survival.

It could be argued that the comparison between estimates from the North American BCRs (DeSante et al. 2015) and estimates from our data is misleading because the former estimate survival using models that account for transient individuals in the data and try to remove their effect from a resident individual survival estimate, whereas we tried to remove the effect of juveniles in the estimation of adult survival. Studies by Blake and Loiselle (2013; Tiputini), Wolfe et al. (2014; Manaus), and Francis et al. (1999; Cocha Cashu) also tried to remove the effect of transients. There are 2 main reasons why we consider the comparison across approaches—and, especially, the conclusion of a latitudinal gradient obtained—valid. First, when we exclude juveniles from our adult survival estimates, we also decrease the probability of including transient effects on adult survival. This holds despite the possibility of there being transient adults. Indeed, if being captured only once is a fair indication of an individual's transiency, we found a higher proportion of transient individuals (captured only once) among juveniles than among adults in our dataset. More specifically, 17% of adults and 11% of juveniles at first capture were recaptured one or more times. The second reason why we are confident about the validity of comparing our adult estimates with nontransient estimates from other localities is that, if our estimates of adult survival are biased low because they are drawn from a set of animals that includes transient individuals, then the true adult survival should be even higher than we are estimating (Pradel et al. 1997). In fact, an exploratory analysis of our data using a transients model without age revealed an average nontransient survival probability that is higher than our random-effects mean adult survival probability. Thus, when we draw a comparison between simple CJS survival estimates in the tropics with transient-model CJS estimates on higher latitudes, our test for a latitudinal difference will be conservative. That is, we will at most underestimate the real effect of latitude. We did find a latitude effect in survival probabilities; therefore, if we had considered transients as well, we would expect to find an even higher latitudinal trend than reported in our analysis.

The biological conclusions we reached in the present study are based primarily on the results of the random-effects model, as explained above. There are several methodological reasons that led us to rely more on the



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random-effects than the fixed-effects model. When comparing the results of both models, the general picture that emerges is of a strong age effect on survival with lower juvenile survival probability, but there are nonetheless noticeable differences between each model's results. First, at the species-specific level, the estimates for all parameters for individual species under the fixed-effects model are less precise than those under the random-effects model (Supplemental Material Figures S2 and S3). This is so because in the fixed-effects model, parameter estimates for each species are informed exclusively by the data from the species itself and not by the data from any other species. The sample sizes for many species are fairly small; hence, the demographic estimates for these species are very imprecise and in some cases hardly distinguishable from the uniform (0,1) priors used in the analysis—a reflection of the limited amount of information available. This is especially noticeable with juvenile survival, for which the sample sizes (the number of birds that were juvenile at the moment of banding) were particularly low for some species.

By contrast, species-specific parameter estimates under the random-effects model are not only informed by each species' data, but to some degree also by the data from all other species in the dataset. In the random-effects model, information is shared among all species via the hyper-parameters, which are common to all of them and which do inform the species-specific estimates to some degree, especially when the information content of the data for a particular species is low because of small sample size. This is sometimes referred to as "borrowing strength": the estimates for each species "borrow strength" from the information on all species in the data. Other works have also demonstrated how precision in species-specific parameter estimations can be improved when using random-effects models (Sauer and Link 2002, Zipkin et al. 2009); our results provide yet another clear example.

At the multispecies level, we observed that parameters describing the aggregate of species (i.e. the sample mean of the individual species' estimates in the fixed-effects model and the community mean hyper-parameter in the random-effects model) were rather similar, in terms of the posterior mean and of estimation precision (i.e. the posterior SD of the mean parameters). In sharp contrast, a relevant difference between the random- and fixed-effects results was that the fixed-effects sample heterogeneity of survival among species ($\sigma_\phi$) was much higher than the community heterogeneity estimated under the random-effects model. That is, according to the fixed-effects estimates, we would conclude that species are much more dissimilar to each other in their survival and recapture probability than under the random-effects model. However, we must be careful with this conclusion, because it is well known that in the fixed-effects approach, the heterogeneity parameters (i.e. the sample SDs for the parameters) contain 2 sources of variation: true "process" variance and sampling variance. In our study, the former is the true variability in, say, survival probability, from species to species, while the latter is the estimation uncertainty associated with each estimate of that survival probability.

In the fixed-effects model, the sample SD confounds these 2 sources of variance, and the estimation uncertainty for each individual species inflates the estimate of the variance among species. The estimation uncertainty is considerable and the species-specific fixed-effects survival estimates have much lower precision, which is evident in the broad posteriors of survival, especially for juveniles (Supplemental Material Figure S3). In consequence, when we average over species, the sample variability is high in relation to the community-level heterogeneity. In a study of temporal variability of survival for 3 bird species in North America, Gould and Nichols (1998) showed how the SD of estimates under a fixed-effects model was an overestimate of the true variability of survival over years, due to the sampling variation (i.e. estimation uncertainty) that is inherent in most studies of wildlife animal populations. Their case is analogous to ours, except that they studied the variance of a parameter (survival) over time, whereas we studied its variance among species within a group of species.

Besides the random-effects approach, an important methodological aspect of our work was the field and statistical assessment of individual ages. The WRP system (Wolfe et al. 2010, Johnson et al. 2011) is extremely useful for assessing the age of birds that do not breed in well-defined and relatively short breeding seasons; but sometimes, depending on species and individual molt traits, birds that just turned 6 mo old are indistinguishable from individuals of any older age. Our mixture-model approach to statistically assessing age incorporates individuals with unknown age at the time of banding into the analysis of age effects. The estimates for $\omega$ (proportion of juveniles among unknown-age birds) were extremely uncertain, but the approach is valuable for formally integrating information from *all* captured individuals in a statistically rigorous way. The mixture approach allows for the use of information about individuals of unknown age at banding that would otherwise have to be discarded from the analysis. One alternative to our mixture model would be to fit the traditional CJS model to different datasets (e.g., once assuming all unknown-age birds were juveniles, once assuming they were all adults, and perhaps once assuming any arbitrary mixture proportion). Drawing conclusions from such a multitude of sets of inferences would be more complicated. By contrast, our approach directly estimates the mixture proportion and, therefore, a single analysis is enough. Yet another alternative would be to completely discard the data associated with unknown-age captures



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and fit a random-effects CJS with a binary effect of age, without age uncertainty. We did just this in an exploratory analysis and found that inference about adult individuals was virtually unchanged. Inference about juveniles, however, became more uncertain, based on a smaller dataset and apparently more influenced by the flat prior (Supplemental Material Figure S4). We thus consider our new model a useful solution to exploit all the available data.

Our mixture model is a special case of a more general approach for analyzing subsets of study objects with an unknown state for a particular variable of interest, when other subsets of objects in the same analysis can be unambiguously assigned a value for that same variable. In such cases, the parameters for the unknown state become identifiable by the use of a mixture parameter, which assesses the proportion of unknown individuals belonging to each known state of the variable. In the case of age, we know that age class is a deterministically dynamic state variable—where all 1-yr-olds now are 2-yr-olds next year—which makes identifiability more certain. The logic behind the mixture model allowed us to gain precision in our survival estimates. The limits to precise age determination in the field will be a persistent problem in the study of not-so-seasonal tropical areas; for this reason, our new CJS mixed-model approach can be a valuable aid for drawing inferences about age-specific survival based on WRP age assignments from other tropical sites.

It will be useful to attain more information about the possible variation of juvenile survival with latitude, as well as about the influence of transiency in age-specific survival estimates. But for the time being, given the clear difference between adult and juvenile survival in Manaus and the broad latitudinal trend in survival given by the mixed regression, we are convinced that the "dogma" identified by Karr et al. (1990) no longer deserves to be considered dogma. There is a real latitudinal trend in forest passerine survival in the Americas, which may contribute to the persistence of latitudinal differences in clutch size. To what extent the variation in survival is sufficient to sustain the variation in clutch size and how the variation in survival evolved should be questions for future study.

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**Ethics statement:** All passerine birds captured were marked with numbered aluminum bands from the Centro Nacional de Pesquisas e Conservação de Aves Silvestres (CEMAVE) of Brazil (permit no. 14103-2). Capture and handling procedures were in accordance with the Bander's Code of Ethics from the North American Banding Council and performed under permit from Sistema Nacional de Anilhamento/CEMAVE (registration no. 2216909). We worked under permit no. 007/2014 from the Comitê de Ética no Uso de Animais of Brazil's Instituto Nacional de Pesquisas da Amazônia.

**Author contributions:** G.F., A.P.M., and M.K. conceived the idea of the study. G.F. supervised the research and formulated the sampling design. G.F., A.P.M., P.V.M., and M.K. conducted the research. A.P.M. and P.V.M. collected the data. A.P.M., M.K., and G.F. wrote the paper. M.K. designed the analytical methods. A.P.M. and M.K. analyzed the data. This study was presented as a master's thesis by A.P.M. at Universidade Federal do Rio Grande do Sul, under a CNPq MSc grant. It is contribution no. 730 of the BDFFP Technical Series.

**Data deposits:** Capture data are deposited at Brazil's Sistema Nacional de Anilhamento de Aves Silvestres and at the Landbird Monitoring Network of the Americas (LaMNA).

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