



UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
Instituto de Biociências
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UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
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Efeitos de idade na sobrevivência aparente de aves de sub-bosque na floresta Amazônica

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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RESUMO

A observação de gradientes latitudinais em aspectos da história de vida de aves tem motivado o estudo da evolução e variabilidade das histórias de vida nestes organismos. Um exemplo bem documentado é a variação no tamanho da ninhada, onde aves de latitudes menores tendem a ter ninhadas menores do que os seus homólogos de latitudes altas. Uma hipótese que visa explicar esta variação propõe que a sobrevivência em latitudes tropicais é maior para compensar o tamanho da ninhada menor e evitar a extinção das populações. Esta explicação tem tido grande aceitação e apoio por parte de alguns estudos, mas tem sido questionada por outros que não encontraram taxas de sobrevivência mais elevadas em aves tropicais. De modo implícito, todos estes estudos basearam seus resultados na sobrevivência de indivíduos adultos. As populações com o tamanho da ninhada menor não poderiam crescer da mesma maneira que as populações com ninhadas maiores; portanto, se justifica acreditar que algo deve mudar com a latitude para manter o balanço em tamanho populacional. Na busca por explicações alternativas para a persistência das populações de aves tropicais com relativamente pequenos tamanhos de ninhada, surge outra hipótese que propõe que, se não houver diferenças na sobrevivência de indivíduos adultos entre latitudes, o aspecto fundamental que varia é a sobrevivência juvenil, com sobrevivência maior para os juvenis das zonas tropicais em comparação com os juvenis das zonas temperadas. No entanto, atualmente há pouca evidência que suporta esta conclusão. Os resultados contrastantes desses estudos sugerem a falta de um consenso geral sobre a hipótese de que as aves tropicais têm taxas de sobrevivência mais elevadas do que as aves de regiões temperadas, motivando a formulação de hipóteses alternativas e convidando novos testes de hipótese. Neste estudo, pretendemos a) avaliar o efeito da idade sobre a sobrevivência em aves tropicais, estimando as probabilidades anuais de sobrevivência aparentes idade-específicas para um conjunto de aves passeriformes de sub-bosque na Amazônia central brasileira; e b) contribuir para o debate sobre o gradiente latitudinal na sobrevivência de adultos, comparando nossas estimativas com estimativas de outras latitudes. Para estimar a sobrevivência idade-específica ajustamos aos nossos dados um modelo Cormack-Jolly-Seber (CJS) hierárquico para n espécies, que trata os parâmetros espécie-específicos como efeitos aleatórios, que são estimados e que descrevem todo o conjunto de espécies; para comparação de métodos, ajustamos uma versão de efeitos fixos do modelo. Para a determinação da idade das aves usamos o sistema WRP. Apresentamos uma nova variante do modelo CJS com um parâmetro de mistura para a sobrevivência de aves de idade incerta no momento da primeira captura. Encontramos efeito forte da idade na sobrevivência, com probabilidades de sobrevivência menor para os jovens do que para os adultos; evidência de efeito latitude sobre a sobrevivência, que suporta a hipótese amplamente aceita de variação na sobrevivência com a latitude; e discutimos diferenças metodológicas interessantes entre modelo de efeitos aleatórios e fixos relacionados com a precisão das estimativas e o âmbito de inferência, que nos levam a concluir que os modelos de efeitos aleatórios são os mais adequados para a nossa análise. Concluimos que não é necessário invocar uma hipótese alternativa de maior sobrevivência juvenil nos trópicos a fim de explicar o gradiente latitudinal no tamanho da ninhada.

Palavras chave: Amazônia, aves tropicais, Cormack-Jolly-Seber, idade incerta, modelo hierárquico, modelo misto de sobrevivência, sobrevivência idade-específica.



ABSTRACT

The observation of latitudinal gradients in bird life history traits has motivated the study of avian life history evolution and variability. A well-documented example is the variation in clutch size, where lower latitude birds tend to have smaller clutches than their higher latitude counterparts. A hypothesis that explains this variation proposes that survival in tropical latitudes is higher to compensate for smaller clutch size and prevent population extinctions. This explanation has had a wide acceptance and support by some studies, but has been questioned by others who have not found such higher survival rates in tropical birds. In an implicit manner, all these studies have based their results on adult survival. Populations with smaller clutch size would not be able to grow as well as populations with larger clutches; therefore one is justified to believe that something else must change with latitude. In the search for alternative explanations to the persistence of tropical bird populations with relatively small clutch sizes it has also been proposed that, if there were no differences in adult survival among latitudes, the fundamental trait that varies is juvenile survival, with higher survival rates for tropical juveniles birds than for temperate ones. However, currently there is little evidence that supports this conclusion. The contrasting results of those studies suggest a lack of a general consensus about the hypothesis that tropical birds have higher survival rates than birds of temperate regions, motivating the formulation of alternative hypotheses, and inviting further tests of the hypothesis. In our study we aim to a) assess the effect of age on survival in a tropical bird community, estimating age-specific annual apparent survival probabilities for a set of passerine understory birds from the central Brazilian Amazon; and b) contribute to the debate about the latitudinal gradient in adult survival by comparing our adult survival estimates to estimates of temperate-zone adult survival probabilities. To estimate the age-specific survival we fit to our data a hierarchical multispecies Cormack-Jolly-Seber (CJS) model for n species, that treats species-specific parameters as random effects that are estimated and that describe the whole assemblage of species; for comparison of methods, we also fit a fixed-effects version of the model. To age birds we use the cycle-based WRP system. We introduce a novel variant of CJS model with a mixture component for the survival of birds of uncertain age at the time of banding. We found strong effect of age on survival, with juveniles surviving less than adults; evidence of latitude effect on survival, that supports the widely accepted hypothesis of variation on survival with latitude; and methodological differences between random and fixed effects model related to precision of estimates and scope of inference, that lead us to conclude that random-effects models are more appropriate for our analysis. We conclude that there is no reason 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, tropical birds, Cormack-Jolly-Seber, hierarchical model



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INTRODUÇÃO GERAL

A comparação das características de histórias de vida que diferem entre as aves de latitudes tropicais e temperadas tem motivado grandemente o estudo da evolução e da variabilidade das histórias de vida de aves, e as tentativas por elucidar os mecanismos que influenciam a variação latitudinal nestas características ecológicas têm levado à formulação de várias hipóteses explicativas. Um exemplo clássico de uma característica que varia com a latitude é o tamanho da ninhada, conforme documentado inicialmente por Moreau (1944), que observou que as aves de latitudes baixas tendem a ter ninhadas menores em comparação com as aves de altas latitudes. Para explicar esta diferença no tamanho da ninhada, várias hipóteses têm sido propostas relacionadas a aspectos como variação na disponibilidade de recursos alimentares, longevidade dos adultos e predação de ninhos com a latitude (Lack 1948, Skutch 1949, 1985; Murray 1985, Martin 1987). No entanto, a explicação mais aceita até agora é a que sugere que as taxas de sobrevivência das populações de aves tropicais são mais elevadas do que nas populações temperadas, para compensar o tamanho da ninhada menor e para evitar que as populações tropicais com o tamanho da ninhada menor tenham um crescimento negativo e que, essencialmente, sejam extintas (Cody 1966, Murray 1985, Skutch 1985).

Esta hipótese de aumento da sobrevivência com a diminuição da latitude tem tido uma influência importante na teoria histórias de vida (Martin 1996, 2004), gerando vários estudos sobre a sobrevivência de aves tropicais, incluindo algumas comparações entre populações de zonas tropicais e de zonas temperadas. Vários autores oferecem apoio indireto à hipótese, alimentando sua aceitação geral (Faaborg and Arendt 1995, Johnston et al. 1997, Francis et al. 1999, Peach et al. 2001, Blake and Loiselle 2008). No entanto, apesar da sua relativamente grande aceitação, a relação entre taxas de sobrevivência e latitude é debatida por outros (Karr et al. 1990, Brawn et al. 1999). Uma das tentativas mais cuidadosas para comparar as probabilidades de sobrevivência entre aves de zonas tropicais e temperadas, intitulada “Will the dogma survive?” (Karr et al. 1990), não encontrou nenhuma evidência de variação na sobrevivência com a latitude. Enquanto o trabalho de Karr et al. (1990) é mais um chamado para uma estimativa mais cuidadosa da sobrevivência do que uma tentativa de resolver o debate, seus resultados questionam a hipótese e motivam a busca por explicações alternativas que expliquem a persistência de populações de aves tropicais com tamanhos de ninhada relativamente pequenas.

Se não houver realmente nenhum efeito da latitude na sobrevivência dos adultos, torna-se complicado explicar como as populações de aves tropicais podem manter-se estáveis, tendo ninhadas menores e sobrevivência semelhantes às das aves de região temperada. Portanto, para explicar a persistência destas populações tropicais no tempo deve existir um atributo que varie com a latitude e que compense as diferenças reprodutivas devido às diferenças em tamanhos de ninhada. Alguns estudos sugerem que o cuidado parental é maior nos trópicos (Russell 2000, Russell et al. 2004), o que resultaria em maior sobrevivência da prole. Com base nesta ideia, Tarwater et al. (2011) propôs que o aspecto fundamental que difere entre as aves tropicais e temperadas é a taxa de sobrevivência dos juvenis, sendo maior em populações tropicais. Para testar esta hipótese, Tarwater et al. (2011) estimaram a sobrevivência dos juvenis até a idade reprodutiva para uma população de passeriforme tropical de América Central (*Thamnophilus atrinucha*). Posteriormente, compararam a probabilidade de sobrevivência juvenil de *T. atrinucha* com a de juvenis de várias populações norte-americanas



de outras espécies, concluindo que a sobrevivência juvenil foi maior para a população tropical, suportando a hipótese de maior sobrevivência juvenil nos trópicos.

Em comparação com características como o tamanho da ninhada, para a qual existe abundante informação para uma ampla gama de latitudes (Cody 1966, Skutch 1985, Yom-Tov 1994, Jetz et al. 2008), existe menos informação sobre a variação da sobrevivência como função da idade (Karr et al. 1990, Martin 1996, Anders et al. 1997). Isso dificulta fazer inferências mais fortes sobre as diferenças de sobrevivência dos juvenis entre zonas tropicais e temperadas, e explica parcialmente por que Tarwater et al. (2011) usaram dados de uma única espécie tropical para as conclusões do seu trabalho. Com relação a outros estudos comparativos que usam um número maior de espécies, não encontramos estudos comparando muitas espécies que avaliem os efeitos de idade sobre a sobrevivência. A análise feita por Karr et al (1990), por exemplo, não fez distinção entre idades. Se as estimativas foram derivadas de uma mistura de adultos e juvenis, a análise pode falhar em detectar efeitos da idade na sobrevivência, como por exemplo, detectar se existe um aumento na sobrevivência dos adultos ou juvenis –ou ambos- à medida que decresce a latitude.

Portanto, os objetivos do nosso estudo são: a) avaliar o efeito da idade na sobrevivência em uma comunidade de aves tropicais, estimando as probabilidades de sobrevivência aparente anual idade-específica em um grande conjunto de aves passeriformes de sub-bosque da Amazônia central; b) contribuir para o debate sobre a relação entre gradiente latitudinal e a sobrevivência, comparando nossas estimativas de probabilidades de sobrevivência de adultos com estimativas em zonas tropicais e temperadas de outros estudos. Para atingir nossos objetivos, enfrentamos alguns desafios metodológicos relacionados à determinação da idade para aves tropicais de forma precisa, lidar com aves de idade desconhecida na primeira ocasião de captura, e trabalhar com tamanhos de amostra pequenos enquanto tentamos perder o mínimo de informação para nossas inferências de sobrevivência.

As aves em ambientes tropicais não se reproduzem em pulsos definidos como as aves das regiões temperadas, o que torna difícil determinar a idade usando o sistema de calendário anual tradicionalmente utilizado para as espécies norte-americanas (Pyle 1997, 2008). Portanto, para determinar a idade das aves em nosso estudo, utilizamos um sistema baseado nos ciclos de muda da plumagem, o sistema WRP (Wolfe et al. 2010, Johnson et al. 2011), o qual é muito conveniente para as espécies tropicais; no entanto, existe um número substancial de espécies para as quais não é possível determinar a idade com certeza na primeira ocasião de captura. Neste trabalho, incorporamos na nossa análise aqueles indivíduos com idade incerta através de uma nova variante do modelo Cormack-Jolly-Seber (CJS) usando um componente de mistura (mixture component) para a sobrevivência de aves de idade incerta no primeiro momento de captura, o que nos permitiu explorar mais informação dos nossos dados de uma forma estatisticamente rigorosa. Para estimar a sobrevivência idade-específica ajustamos aos nossos dados um modelo hierárquico CJS para múltiplas espécies, modelo que trata os parâmetros espécie-específicos como efeitos aleatórios com hiper-parâmetros que são estimados e que descrevem todo o conjunto ou comunidade de onde as amostras provem. Este método tem a vantagem de permitir lidar com tamanhos pequenos de amostras, e, portanto, com as estimativas de incerteza associadas a essas amostras. Para propósitos de comparação de métodos, ajustamos aos nossos dados outra versão do modelo CJS, na qual os parâmetros das espécie-específicos são tratados como efeitos fixos. Com este trabalho, esperamos contribuir para a compreensão das diferenças latitudinais em características de história de vida



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em aves, especificamente diferenças na sobrevivência; além disso, queremos propor novas abordagens metodológicas para fazer o máximo e melhor uso da informação para as situações em que existem aves de idade desconhecida no momento de captura e tamanhos amostrais pequenos.



ARTIGO

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Age-effects on apparent survival of Amazon forest understory birds.

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INTRODUCTION

The observation of latitudinal gradients in bird life history traits has greatly motivated the study of avian life history evolution and variability. A classic example comes from the variation in clutch size, as documented initially by Moreau (1944), who noted that lower latitude birds tend to have smaller clutches than their higher latitude counterparts. All else being equal, populations with smaller clutch size would not be able to grow as well as populations with larger clutches; therefore one is justified to believe that something else must change with latitude, and there were several hypotheses in this regard, including variation in availability of food resources, nest predation, and adult longevity (Lack 1948, Skutch 1949, 1985; Murray 1985, Martin 1987). Among these, the most widely accepted explanation—if insufficiently documented—is the idea that reproductively active tropical birds have higher survival probabilities, thus compensating the smaller clutch size with a higher number of breeding attempts, essentially avoiding negative growth and likely extinction (Cody 1966, Murray 1985, Skutch 1985).

This hypothesis of increased survival with decreasing latitude has had an important influence on avian life-history theory (Martin 1996, 2004), producing several studies about survival of tropical birds, including some comparisons between tropical and temperate zone populations. Several authors offer indirect support for the hypothesis, fueling its general acceptance (Faaborg and Arendt 1995, Johnston et al. 1997, Francis et al. 1999, Peach et al. 2001, Blake and Loiselle 2008), but some of the best available statistical assessments of latitudinal change in survival probability have debated its validity (Karr et al. 1990, Brawn et al. 1999). One of the most careful attempts at comparing tropical and temperate bird survival probability, subtitled “Will the dogma survive?” (Karr et al. 1990), actually found no evidence of latitudinal variation. While Karr et al.’s (1990) study is more of a call to more careful estimation of survival, rather than an attempt to settle the debate, their results do call



the hypothesis into question and motivate the search for alternative explanations to the persistent of tropical bird populations with relatively small clutch sizes.

In the absence of a low-latitude increase in adult survival, there ought to be some other trait that changes with latitude and makes up for the lost reproductive output due to small tropical clutch sizes. Some authors suggest that parental care is higher in the tropics (Russell 2000, Russell et al. 2004), which would then result in higher offspring survival. Based on this idea, Tarwater et al. (2011) proposed that the fundamental trait distinguishing tropical and temperate birds is juvenile survival, with tropical juveniles surviving better than temperate ones. To test this hypothesis Tarwater et al. (2011) estimated the survival of juveniles from fledgling to reproductive age in one Central American population of Black-crowned Antshrikes (*Thamnophilus atrinucha*). They subsequently compared *T. atrinucha* juvenile survival probability with that of juveniles from several North American populations of other species, concluding that juvenile survival was higher in the tropical population, therefore supporting to the hypothesis of higher juvenile survival in the tropics.

In comparison to traits such as clutch size, for which there is comparatively abundant information for a wide range of latitudes (Cody 1966, Skutch 1985, Yom-Tov 1994, Jetz et al. 2008), there is much less information about variation in survival as a function of age (Karr et al. 1990, Martin 1996, Anders et al. 1997). This makes it difficult to obtain stronger inference about tropical-temperate juvenile survival differences and partially explains Tarwater et al.'s (2011) reliance on data from one species alone. As for other existing comparisons with a larger number of species, we have not found studies that assess age-effects on survival. The analysis by Karr et al (1990), for example, made no distinction between ages. If their estimates were derived from a mixture of adults and juveniles where the former have particularly high and the latter particularly low survival probabilities, the analysis might fail detect an increase in adult survival with decreasing latitude.

The objectives of this study are therefore to: a) 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 b) to contribute to the debate about the latitudinal gradient in adult survival by comparing our adult estimates to estimates of tropical and temperate-zone adult survival probabilities from other studies. To meet our objectives we faced some methodological challenges related to aging tropical birds in a precise way, dealing with birds of unknown age at the first banding occasion, and managing small sample sizes while attempting to lose the minimum of information for our survival inferences.

Birds in tropical environments do not breed in defined pulses as temperate birds do, making it difficult to age them using the traditional calendar system widely used for North American species (Pyle 1997, 2008). Therefore, to age birds in our study we used the WRP cycle-based system (Wolfe et al. 2010, Johnson et al. 2011), which is very convenient for tropical species. That being said, the WRP system can only go so far, and there is a substantial



number of species for which it is hard or impossible to assess age, and we were left with a number of individuals with unknown age at first capture. We incorporated those individuals with uncertain age in the analysis by developing a novel variant of CJS model with a mixture component for the survival of birds of uncertain age at the time of banding, and were thus able to use more information from the data in a statistically rigorous manner. To estimate the age-specific survival, we used a hierarchical multi-species Cormack-Jolly-Seber (CJS) model that treats species-specific parameters as random effects, with prior distributions that are estimated and that describe the whole assemblage or community. This method has the advantage of allowing the simultaneous analysis of species with a variety of sample sizes while accounting for the influence of small sample size in the precision of estimates. With this work we hope to contribute to the understanding of latitudinal change in bird life history characters, specifically differences in survival. We also intend to propose new methodological approaches for making the maximum and best use of information for the situations when there are birds of unknown age at the time of banding and when dealing with small sample sizes.

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. The BDFFP has a tropical rainforest climate with mean annual rainfall of ca. 2,200 mm and a pronounced dry season from June to October with less than 100 mm of rain per month (Gascon & Bierregaard 2001). Our sampling area spans approximately 2,000 ha of forest, 90% of which are old-growth, with the remaining 10% being 30 to 33-year-old secondary-forest. This area is imbedded 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 seven years, with five years of sampling.

Our sampling aimed to maximize coverage of the sampling 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 two 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 two 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 to 30 mistnets at each sampled site. Mistnets were 12-meter long and 2.5-meter high, and were operated from 6 am to 12pm each day. Random sampling of sites was constrained by the distance between them, but it ensured that no site was sampled on two consecutive days. All



passerine birds captured were marked with numbered aluminum bands from the Brazilian *Centro Nacional de Pesquisas e Conservação de Aves Silvestres* (CEMAVE) obtained under permit number 14103-2.

Aging of captured birds

Temperate-zone birds are subject to sharply alternating seasons and thus have relatively short and well-defined breeding periods. Under these circumstances, each year has one pulse of reproduction, which makes it practical to age birds based on the human calendar (e.g. Pyle 1997). In contrast, tropical birds, living in comparatively stable environments, do not breed in well-defined pulses (Snow 1976) and thus are difficult to age following calendar-year approaches (Wolfe et al. 2009). One solution is to assign tropical birds to a point in their life-long sequence of plumage molt cycles (Howell et al. 2003) and estimate age based on the cycle's relation to the bird's age—that is the essence of the Wolfe-Ryder-Pyle (WRP) system, which we employed in this study (Wolfe et al. 2010). The WRP system labels individual birds with three-letter 'cycle codes' where the first letter identifies a molt cycle, e.g. 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 letter code 'U' indicates 'unknown' state either in the first or third positions. Most birds go through two different plumages during their first molt cycle, which corresponds roughly to the first year of life. The first plumage upon leaving the nest is called 'juvenile', and its replacement plumage, grown before the bird reaches sexual maturity, is called 'formative'. After the formative plumage, birds enter a sequence of approximately yearly cycles that are most often undistinguishable from each other. Aging, thus, is most effective when we can link the bird to one of the plumages of the first cycle.

For simplicity, we based our analysis on two 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 placed in the 'adult' class. 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 'adult' classes 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 age and species

Among all the species captured, we selected only passerine species that had at least one individual that was first captured as a juvenile and at least 10 captures in total. Forty species fulfilled these criteria and were included in the analysis. We subsequently built species-specific capture-history matrices, where rows correspond to individuals and columns correspond to years. This matrix arrangement implied to aggregate data that was originally in a monthly format into 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-covariate matrices containing information about the age class of individuals in every year following the initial capture. Occasionally, some individuals were classified as having different ages in different captures of the same year; when this happened, we revised the age classifications and reconciled remaining differences based on the best evidence in the full encounter history for the given year.

We estimated survival with a state-space formulation of a Cormack-Jolly-Seber (CJS) model (Royle 2008; Kéry and Schaub 2012). Under this approach, for a single species, we model both state (biological) process and observation (sampling) process as realizations of Bernoulli trials. We describe the state process using two variables, $Z_{i,t}$ and f_i . $Z_{i,t}$ is the latent variable that represents the true state of the individual i at time t , with values of 1 if the individual is alive and 0 if the individual is dead. The variable f_i is a vector containing the time at first capture for each individual i . Therefore, the state of individual i in the first capture occasion is $Z_{i,f(i)}=1$; the states on subsequent capture occasions are modelled as Bernoulli trials where an individual alive at time t will survive to time $t+1$ with probability ϕ defined by the hyper-parameter $\mu_{i,t}$, ($t = 1, \dots, T - 1$), where T is the time of the last capture occasion. In order to model the effect of age on survival we used a time-varying individual covariate with two states: juvenile and adult. Covariate values are stored in a matrix $X_{i,t}$, with $i = 1, \dots, n$, where n is the number of individuals and $t = 1, \dots, T-1$, where T is the time of the last capture occasion. The variation of $X_{i,t}$ through time for individual i is such that birds can only be juveniles for one year and never revert from adult to juvenile stage. Consequently, we can safely assume that any bird that is captured as 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:

$$\begin{aligned} Z_{i,f(i)} &= 1 \\ Z_{[i,t+1]} | Z_{[i,t]} &\sim \text{Bernoulli}(\mu_{\phi(i,t)}) \\ \mu_{\phi(i,t)} &= Z_{[i,t]} * \phi_{[X[i,t]]} \end{aligned}$$



The observation process is conditional on individual i being alive at occasion t , and is modeled with the probability $p_{i,t}$ ($t = 2, \dots, T - 1$) that individual i is recaptured at occasion t . This is formally defined as:

$$y_{i,t} \sim \text{Bernoulli}(\mu_{p(i,t)})$$
$$\mu_{p(i,t)} = Z_{[i,t-1]} * p$$

The state and the observation process are both defined only for $t \geq f_i$, since the CJS model is conditional upon first capture.

To simultaneously model age-specific survival for all species, we adopted a multi-species, or community, Cormack-Jolly-Seber (CJS) model (Lahoz-Monfort et al. 2011; Papadatou et al. 2012, Lloyd et al. 2014). This is a hierarchical extension to the classical CJS survival model for a single species, described above, which allowed us to obtain an overall mean survival estimate for each age-class in our assemblage of 40 species. Basically, in the community CJS model, every quantity above also gets an index s for species ($s=1, \dots, 40$). We fitted two variants of such a multi-species CJS model. In the first (the random-effects or truly hierarchical CJS model) we 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 in the whole community and the heterogeneity among species in the community to which our 40 study species belong. 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 ($\phi_{s,juv}$), adult survival ($\phi_{s,ad}$) and recapture probability (p_s) of species s :

$$\text{logit}(\phi_{s,juv}) \sim \text{Normal}(\mu_{\phi(juv)}, \sigma_{\phi(juv)})$$
$$\text{logit}(\phi_{s,ad}) \sim \text{Normal}(\mu_{\phi(ad)}, \sigma_{\phi(ad)})$$
$$\text{logit}(p_s) \sim \text{Normal}(\mu_p, \sigma_p)$$

Our random-effects CJS model allowed us to estimate age-specific survival and therefore, to assess the differences in survival between juveniles and adults, both for the larger community from which our species are a sample, and for each species in our 40-species dataset. The species-specific estimates are given by $\phi_{s,juv}$, $\phi_{s,ad}$, and p_s ; while the whole-community is described by the hyper-parameters $\mu_{\phi(age)}$, a community mean survival, and $\sigma_{\phi(age)}$, a community 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 multi-species CJS model—the fixed-effects model—serves a purpose of methodological comparison to the random-effects model. This is a traditional CJS model in which the species were treated as fixed effects. As in the random-effects model, this



model also provides species-specific estimates of survival and recapture probability ($\phi_{s,juv}$, $\phi_{s,ad}$, and p_s) yet, unlike the random-effects CJS model, estimates for each species are taken independently from the others, i.e. they are based exclusively on that species' data. Accordingly, the fixed-effects model has no formal description of community parameters. Although we fit 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, when we fit these models all at once using Bayesian MCMC methods as we do, we can average the species-specific estimates to obtain an estimate (along with its uncertainty) of the average survival or recapture for the particular set of studied species, though not for the community from which the study species are sampled.

As a novel feature in our CJS models, we incorporated into the model the individuals with unknown age at the time of banding by specifying a mixture model for their survival. Survival of unknown-age (*unk*) birds during the first year after banding is expressed as a weighted average of juvenile and adult survival, where the weights are exactly the proportions of juveniles (ω) 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:

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

We fit models to data in a Bayesian framework, using conventional vague (non-informative) priors for all estimated parameters. Parameter estimates, expressed as the posterior mean ± 1 posterior standard deviation, were obtained by sampling from the posterior probability distribution of each parameter with an MCMC algorithm. We ran three MCMC chains, using 500,000 iterations, with a burn-in of 100,000, and thinning of 4, giving us a posterior sample of size 300,000 for every estimated quantity. Convergence of chains was assessed using the Brooks-Gelman-Rubin statistic R_{hat} (Brooks and Gelman 1998), where values ≤ 1.1 suggest convergence. Computations were carried out with programs R (R Core Team 2015) and JAGS (Plummer 2013), connected by the R package *jagsUI* (Kellner 2015).

Analysis of survival in relation to latitude

To assess the hypothesis that survival rates increase with decreasing latitude, we compared our adult-survival estimates from Manaus (02°S), obtained under the random-effects model, with published adult-survival rates from five other regions spanning a large latitudinal gradient from North through Central and to South America (from 64°N to 02°S). For simplicity, we will refer to regions as 'sites', even though some of them refer to large expanses of land. The four northernmost sites from the literature are North American Bird Conservation Regions (BCRs; DeSante et al., 2015) that range from 64° to 30°N and were selected based on latitudinal coverage and on the presence of forest habitat, which makes them relatively comparable with our study site. The fifth site is Parque Nacional Soberanía, in



Panamá, an area of old growth forest at about 09°N (Karr et al. 1990). In total, we assembled 257 estimates of adult bird survival from 6 sites, 26 families, and 149 species. All of these, in addition to latitude, were expected to explain part of the variability in the adult apparent survival of passerines.

We combined the 257 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 analyses have been described by McCarthy & Masters, (2005), McCarthy, (2007), Lloyd et al., (2014) and Kéry and Royle (2016). 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 six sites). Furthermore, our analysis incorporated both the known component of error represented by the uncertainty associated with each estimate (i.e., the SE or the posterior SD) and the unknown component of error represented by the residual variation about the regression model. Finally, our analysis accommodated heteroskedasticity among sites in the residual errors, which is obvious especially when comparing the random-effects estimates from our Manaus study area with those from the other study areas. Our data consisted of the estimates of apparent survival $\hat{\phi}_i$ (for $i = 1, \dots, 257$), with its associated estimation error $SE_{\phi(i)}$. The regression model can be written as follows:

$$\hat{\phi}_i = \mu + \beta * lat_i + \beta_{j(i)}^{family} + \beta_{k(i)}^{family/species} + \beta_{l(i)}^{site} + \varepsilon_i + \gamma_i.$$

That is, estimate i of apparent survival ($\hat{\phi}_i$) is modeled as the sum of contributions from a grand mean or intercept (μ), a regression on latitude (β), and effects of family ($\beta_{j(i)}^{family}$), species nested within family ($\beta_{k(i)}^{family/species}$) and location ($\beta_{l(i)}^{site}$). In addition, there are two types of "error", the first being the unknown residual (ε_i) and the second term γ_i , which is also unknown, but its standard deviation is assumed to be known as the uncertainty of the estimate, i.e., the SE or the posterior SD associated with each estimate.

The model is completed by adding the following distributional assumptions about some of these terms, making them random effects:

$$\begin{aligned}\beta_j^{family} &\sim Normal(0, \sigma^{family}) \text{ (Family random effects)} \\ \beta_k^{family/species} &\sim Normal(\beta_j^{family}, \sigma^{species}) \text{ (Species random effects)} \\ \beta_l^{site} &\sim Normal(0, \sigma^{site}) \text{ (Site random effects)} \\ \varepsilon_i &\sim Normal(0, \sigma_i^{res}) \text{ (Residual)} \\ \gamma_i &\sim Normal(0, SE_{\phi,i}) \text{ (Known estimation error)}\end{aligned}$$



The first two terms account for correlations in our data due to phylogeny, where we fit 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 a standard deviation that is specific to each study, to account for violation of the usual mixed model assumption of homogeneity of variances. The final is the known component of variance with the standard deviation given by the SEs. We also note that three 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.

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 $(\mu, \beta, \sigma^{family}, \sigma^{species}, \sigma^{site}, \sigma_i^{res})$. Interesting to note, Bayesian analysis using vague priors yields very similar estimates to those obtained by the classical maximum likelihood method that is well-known by now (see for instance Kéry, 2010 or chapter 5 in Kéry and Royle, 2016).

RESULTS

Data overview

Our data set contains 5,982 captures of 110 species from 27 families. Of these, 40 species fulfilled the conditions for inclusion in our analysis; they belong to 11 families and represent 87% (5,210) of all captures in the full data set. The number of individuals per species among the 40 species of study ranged from four (*Cyanocompsa cyanoides*) to 323 (*Pithys albifrons*) (mean = 63, median = 36; see Suppl. 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%), followed by birds of unknown age (22%), and finally by juveniles (16%). Regarding recapture, in a comparison between the three categories of age at first capture, adult individuals of all species combined were more frequently captured more than once (17%), than were juveniles (11%). Among birds that were first captured as unknown age, 18% were captured more than once.

Comparison of fixed-effects and random-effects multi-species CJS models

The fixed-effects and the random-effects multi-species CJS models produced qualitatively similar juvenile and adult survival estimates (Figs. 1, 2). The main difference between these models was in the precision of species-specific estimates (Fig. 1) and in the estimates of the heterogeneity of survival among species (σ_ϕ). All species-specific survival estimates were more precise under the random-effects than under the fixed-effects model (Fig. 1, Table S1). This difference at the species level was mirrored by the difference between two key metrics of heterogeneity: a) the random-effects standard deviation of the community survival hyper-



parameter, and b) the standard deviation 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 standard deviation 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 standard deviation under the fixed-effects than under the random-effects model. Likewise, when looking at heterogeneity metrics, the random-effects standard deviation of the community hyper-parameter for p was less than half the standard deviation 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 six captures from only 4 individuals.

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 omega \pm standard deviation across the 40 study species are almost identical (Table 1); at each species lever, all posteriors of species-specific age-mixture parameters ω were extremely wide, with values ranging from 0.30 ± 0.24 to 0.78 ± 0.15 (posterior mean \pm standard deviation) across models and species indicating that there was very little information in the data to estimate these parameters. *G. 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, for the other survival parameters the random-effects model yielded more precise 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 does 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 at the multi-species level, for both fixed- and random-effects models. The fixed-effects model resulted in ten (out of 40) species with higher juvenile than adult survival estimates (Fig. 1), but still, under a null hypothesis of no age effect, the binomial probability of a result as extreme as that is lower than 0.005. The magnitude of the difference between mean adult, $\mu_{\phi(ad)}$, and mean juvenile survival, $\mu_{\phi(juv)}$, was slightly higher under the random-effects model; nonetheless, since random-effects estimates were overall more precise, 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 and for adults. The parameter for adults, $\mu_{\phi(ad)}$, was 24% higher than its counterpart for juveniles, $\mu_{\phi(juv)}$. The 95% credibility interval for $\mu_{\phi(ad)} - \mu_{\phi(juv)}$ did not include zero, for either model (Fig. 2), evidence that juvenile survival in our study was indeed lower than adult survival. This is true even though the hyper-parameter heterogeneity is higher (14%) among juveniles than among adults. At the species-specific level, juvenile apparent survival (ϕ_{juv}) spanned the interval 0.28-0.42, while adult survival (ϕ_{ad}) spanned the interval 0.50-0.68 (Tables S1). Even though species- and age-specific survival estimates differed between models, we found that for both models the biggest differences between ϕ_{ad} and ϕ_{juv} occurred in the same three species: *Microbates collaris*, *G. spirurus* and *Dixiphia pipra*.

Latitudinal change in survival probabilities

Visual inspection of the distribution of passerine survival across the six latitudes in our analysis suggests a negative relationship between survival probability and latitude; that is, the closer one gets to the equator, the higher the survival rates (Fig. 3). Our formal examination of this relationship, using a mixed regression model, confirmed this: after accounting for non-independence in the data due to phylogeny (family and species within family), site effects, and accommodation of heteroskedasticity, we found a clear effect of latitude on survival. The magnitude of the effect was -0.001 ± 0.001 , with a 95% credibility interval from -0.002 to 0.000 (Figure 4). This amounts to an average change of 1.4 units of survival probability per 10 degrees of latitude.

DISCUSSION

We found that adult passerine birds clearly have higher apparent survival probability than post-fledgling juvenile birds, in our Manaus data set. When comparing the survival estimates for adults in our study area to estimates of adult survival from five other areas distributed over a large latitudinal gradient, we found evidence of increased survival with decreasing latitude, supporting the hypothesis that tropical birds tend to live longer than higher-latitude birds (Cody 1966, Murray 1985, Skutch 1985). These two main conclusions about age and latitude effects on 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 well-established latitudinal gradient in clutch size (Tarwater et al. 2011). 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. 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. In the following



paragraphs, 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 three weeks after fledging and increasing or stabilizing after that (Anders et al. 1997, Tarwater et al. 2011, Cox et al. 2014); however, after that initial, risky phase, it was not sufficiently clear whether survival of post-fledging first-year birds was indeed lower than that of adults. Furthermore, if such a difference exists, it is important to know its magnitude, because, among other reasons, it will help to understand whether a possible latitudinal variation in juvenile survival could help to explain life history traits as the 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—adult survival is on average 24% higher than juvenile survival in our study site.

Unfortunately we do not have access to a community-level assessment 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-one-year survival of *Thamnophilus atrinucha* in Panama (0.48 ± 0.09), which motivated the hypothesis of a latitudinal trend in juvenile survival. We can say nothing about the difference between mean juvenile survival in Panama and Manaus, but we note that *T. atrinucha*'s survival is higher, though not 'significantly' higher than our community estimate. At a finer level of comparison, within the Thamnophilidae family, we find that the random-effects ϕ_{juv} values in our study range from 0.28 ± 0.11 (*Thamnomanes ardesiacus*) to 0.42 ± 0.13 (*Willisornis poecilinotus*), being always lower than the point estimate for *T. atrinucha*. Therefore, if the fledgling-to-one-year survival estimate for *T. atrinucha* is broadly representative of Panamanian understory birds, we find no reason to suspect that juvenile survival is higher in Manaus than in Panama. Regarding the adult survival, we can compare our random-effects $\mu_{\phi(ad)}$ of 0.57 ± 0.03 with the sample average of 0.59 ± 0.10 obtained by Wolfe et al. (2014) for a sample of 31 species in a different data set from a region that includes our study area; the random-effects estimate is more precise, but beyond this there is no statistical difference.

When comparing survival probabilities across latitudes, our mixed-regression model supports the hypothesis that tropical birds have higher survival rates than temperate birds. It could be argued that the comparison between estimates from the North American Bird Conservation Regions (BCR's; DeSante et al., 2015) and estimates from our data are 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, while we tried to remove the effect of juveniles in the estimation of adult survival. There are two main reasons why we think that the comparison across approaches and the conclusion obtained are valid. First, when we exclude juveniles from our adult survival estimates, we also decrease the probability of including transient effects on adult survival, although we are aware that it is possible to encounter transient adults. However, 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. This gives us confidence that our estimates of adult survival are comparable with estimates of resident (or non-transient) survival in other studies.

The second reason that makes us confident about the validity of comparing our adult estimates with and non-transient 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). Thus, when we draw a comparison between simple CJS survival estimates in the tropics with transient-model CJS estimates from North America, our test for a latitudinal difference will be conservative. That is, we will at most underestimate the real effect of latitude. We found a latitude effect in survival probabilities, and 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 this study are based primarily on the results of the random-effects model, as explained in the results section. There are several methodological aspects that led us to rely more on the inferences from the random-effects rather than from the fixed-effects model. When comparing the results of both models, the general picture that emerges is that of a strong age-effect on survival with lower survival probability for juveniles, but there are nonetheless noticeable differences between models. 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. 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, naturally, the demographic estimates for these species are very imprecise and in some cases are hardly different from the uniform (0,1) priors used in our analysis, which indicates that there was very limited information about a parameter in the available data for a species. This is especially noticeable for 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.

In contrast, the species-specific parameter estimates for each species under the random-effects model are not only informed by the data from that species, but to some degree also by the data from all other species in the whole assemblage of species. This way, in the



random effects model the 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 (i.e., when a species has low sample size). This is sometimes referred to as "borrowing strength": the estimates for each individual species "borrow strength" from the assemblage (i.e., the community). 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), and our study provides another example for the advantages, in terms of the precision of the estimates, of random- as opposed to fixed-effects estimates for an assemblage of species.

At the multi-species or community level, we observed that the parameters describing the community average (that is, 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, both in terms of the posterior mean but also in terms of the estimation precision (i.e., the posterior standard deviation of the mean parameters). In sharp contrast, another relevant difference between the random- and fixed-effects results was that the fixed-effects sample heterogeneity of survival among species (σ_ϕ) was much higher than the community heterogeneity estimated under the random-effects model. That is, under 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 standard deviations for the parameters) contain two sources of variation: true "process" variance and sampling variance. 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 standard deviation confounds these two sources of variance and the estimation uncertainty for each individual species estimates 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 spread out posteriors of survival, especially for juveniles (Fig. S2). In consequence, when we average over species-specific variability, the sample variability is high relatively to the community-level heterogeneity. In a study of temporal variability of survival for three bird species in North America, Gould and Nichols (1998) showed how the standard deviation 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 to most studies of wildlife animal populations. The case that they studied is analogous to ours, except that they studied the variance of a parameter (survival) over time, while we studied its variance among species within a group of species.



Given these reasons, we consider the random-effects model as the most appropriate approach for our analysis. This approach results in relatively more precise species-specific estimates and on community-level inferences that separate true heterogeneity among species from the estimation uncertainty, which, again, provides relatively precise parameter estimates. The good performance of the random-effects approach at the multi-species level is particularly interesting for us, because we aim to understand the general picture of survival probability changes with age for all understory forest bird species in our study area.

Besides the random-effects approach, an important methodological aspect of our work was the field and statistical assessment of individual ages. Tropical birds are difficult to age in the field because they do not breed in well-defined and relatively short breeding seasons, as temperate birds do. Under these circumstances, one cannot easily assign birds to calendar years. The WRP system (Wolfe et al. 2010, Johnson et al. 2011) addresses this problem by placing birds within their life-long cycle of plumage molts and in particular by identifying whether birds are going through their first molt cycle. But sometimes, depending on species and individual molt traits, individuals that have more than six months are indistinguishable from individuals of any older age. Consequently, there will always be individuals of unknown age when first captured, and it is useful to employ a statistical approach to infer the distribution of ages among such unknown age birds, during the analysis.

Our mixture model approach to statistically assess age incorporates individuals with unknown age at the time of banding into the analysis of age effects. The estimates for ω (proportion of juveniles among unknown age birds) were extremely uncertain, but the approach is valuable for integrating information from all captured individuals in a statistically rigorous way. The mixture approach allows for the use of information (i.e., the data for individuals of unknown age at banding) that would otherwise have to be discarded from the analysis. Alternatively, prior to our mixture model, one might have to fit the traditional CJS model to different data sets, e.g., once assuming all doubtful birds were juveniles initially, 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. In contrast, our approach directly estimates that proportion and therefore, one single analysis is enough.

Our solution with the mixture model is a special case of a more general approach for analyzing subsets of study objects within unknown state for a particular variable of interest, when other subset 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-year olds now are 2-year 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, we believe that our new CJS mixed-model approach combined with WPR age assessment can be valuable for inferences about age-specific survival in other studies of tropical birds.

In the future, we would like to see more information about the possible variation of juvenile survival with latitude, as well as a better understanding of 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. in 1990 is still alive and well. As a consequence, we see no reason for seeking an alternative latitudinal trend in juvenile survival to account for the general trend in clutch size.



CONSIDERAÇÕES FINAIS

Os resultados do nosso trabalho indicam que existe um forte efeito de idade na sobrevivência no nosso conjunto de aves tropicais de sub-bosque da Amazônia central, observado na diferença entre os valores estimados para juvenis e adultos. Também encontramos evidências de aumento da sobrevivência com diminuição da latitude, as quais apoiam a hipótese de que as aves tropicais tendem a viver mais do que as aves de latitudes altas. Estes dois resultados principais do presente trabalho questionam a necessidade de invocar uma hipótese alternativa de maior sobrevivência juvenil nos trópicos, a fim de explicar aspectos da história de vida como o é o gradiente latitudinal no tamanho da ninhada.

As nossas conclusões biológicas baseiam-se principalmente nos resultados do modelo de efeitos aleatórios, como explicado na seção de resultados. Há vários aspectos metodológicos que nos permitiram confiar mais nos resultados deste modelo, em vez de as inferências de efeitos fixos, embora, ao se comparar os resultados de ambos os modelos, os dois chegam à conclusão de que existe um forte efeito de idade sobre a sobrevivência, com menor probabilidade de sobrevivência dos juvenis.

As estimativas espécie-específicas obtidas com o modelo de efeitos fixos são imprecisas e a heterogeneidade entre as espécies parece maior. No entanto, estes resultados refletem simplesmente incerteza nas estimativas, devido em parte ao tamanho de amostra pequeno que se tem para algumas espécies. Adicionalmente, as inferências estatísticas para o modelo de efeitos fixos se baseiam exclusivamente no conjunto de dados das espécies. Em contraste, o modelo de efeitos aleatórios permite obter estimativas mais precisas, ao separar adequadamente a variabilidade amostral da variabilidade real na população, e as estimativas para as espécies usam a informação do conjunto de dados de todas as outras espécies, através dos hiper-parâmetros ou parâmetros da comunidade estimados. O bom desempenho da abordagem de efeitos aleatórios no nível de multiespécies é interessante para nosso trabalho, uma vez que o nosso objetivo é entender o quadro geral de efeito da idade na probabilidade de sobrevivência no conjunto de aves estudadas.

Consideramos de grande utilidade o modelo de sobrevivência com mistura de idades (age-mixture survival model) apresentado, que permite incorporar na análise os indivíduos com idade incerta no momento de captura. A incerteza na determinação da idade no momento de captura é uma situação típica para muitas espécies de aves tropicais. Portanto, acreditamos que a abordagem de CJS-modelo misto proposto neste trabalho, usado em conjunto com sistema WPR para analisar ciclos de muda, tem grande potencial para permitir fazer inferências sobre a sobrevivência idade-específica em outros estudos de aves tropicais.

Por último, consideramos que é necessário ter mais estudos de sobrevivência idade-específica, principalmente estudos que analisem a variação de sobrevivência em aves tropicais durante o primeiro ano de vida. Isto permitiria fazer uma avaliação mais detalhada das hipóteses alternativas ao trade-off entre sobrevivência e tamanho de ninhada no gradiente latitudinal.



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TABLES

Table 1. Posterior mean \pm SD of juvenile apparent survival, adult apparent survival, and recapture probability parameters estimated under the random and fixed-effects multi-species CJS models. The table shows mean survival for juveniles ($\mu_{\phi(juv)}$) and adults ($\mu_{\phi(ad)}$), standard deviation of survival for juveniles ($\sigma_{\phi(juv)}$) and adults ($\sigma_{\phi(ad)}$) and, finally, recapture probability mean (μ_p) and its standard deviation (σ_p) for juveniles and adults combined. The ϕ values under the random-effects model represent community-level hyperparameters that characterize the whole community from which the 40 analyzed species form a mere sample. Values of ϕ under the fixed-effects model, on the other hand, are means and standard deviations of the 40 species-specific estimates, hence describing only the 40 species in our analysis. All σ values are given on the logit scale, while μ are yearly apparent survival probabilities (on the probability scale).

Model	$\mu_{\phi(juv)}$	$\mu_{\phi(ad)}$	$\sigma_{\phi(juv)}$	$\sigma_{\phi(ad)}$	μ_p	σ_p	μ_{ω}
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



FIGURE CAPTIONS

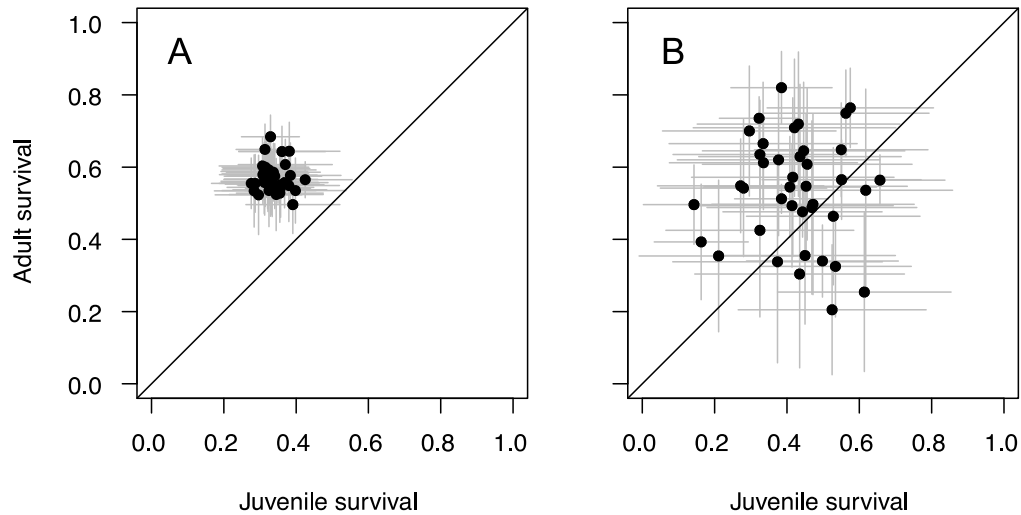


Figure 1. Plot of juvenile vs adult survival estimates for all 40 species under random-effects (A) and fixed-effects (B) models. The gray lines on each side of a point represent one standard deviation.

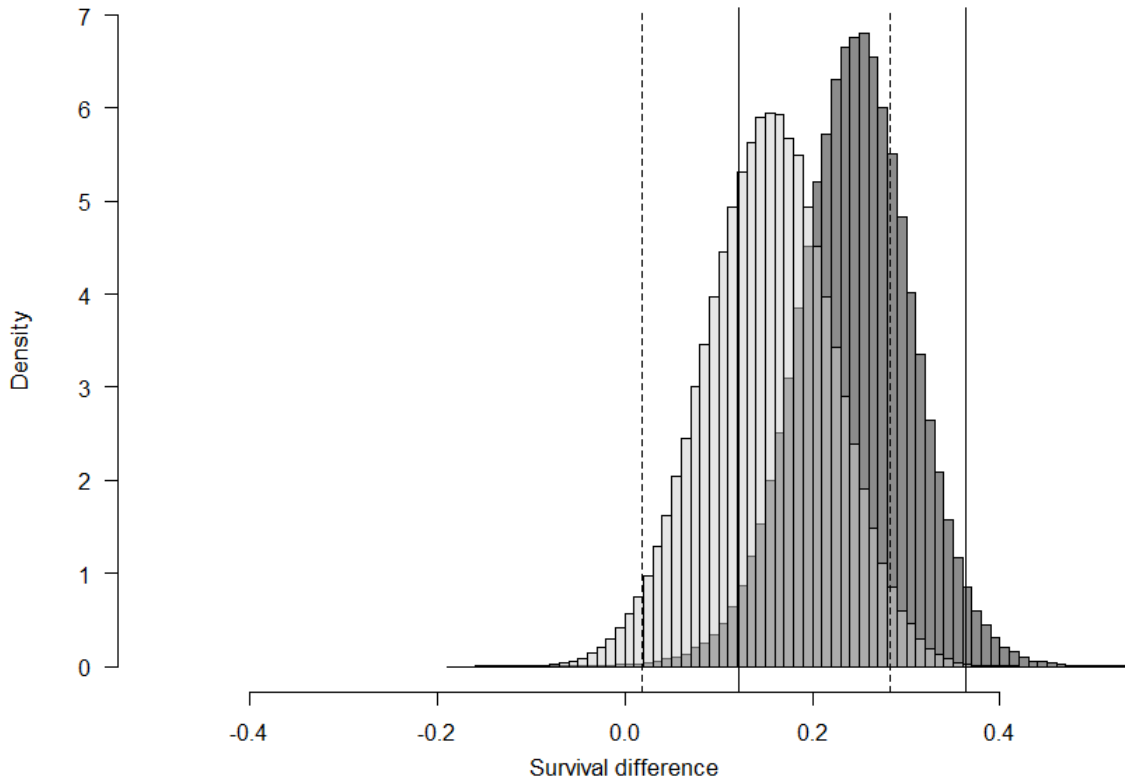


Figure 2. Posterior distributions of the difference between mean juvenile ($\mu_{\phi(juv)}$) and mean adult ($\mu_{\phi(ad)}$) apparent survival for the two models fitted to the data. Vertical lines represent the lower and upper limits of the 95% credibility intervals for this difference. Dark gray 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.

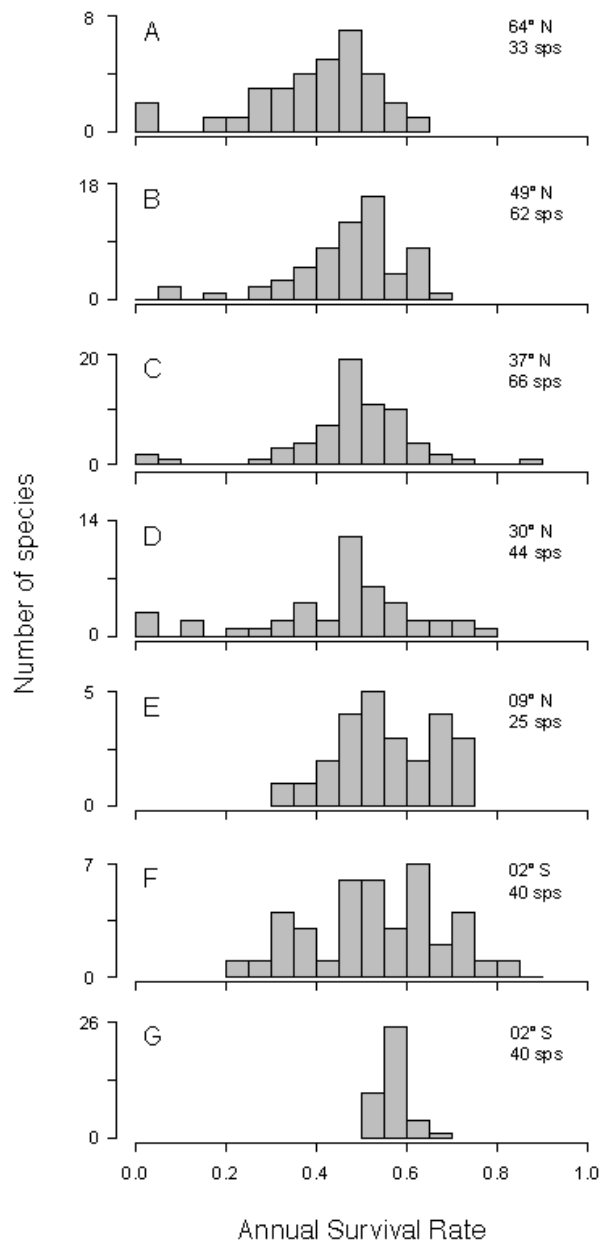


Figure 3. Comparison of the distribution of annual apparent survival rates for six samples of passerine species taken across a latitudinal gradient from North to South America. Panels A-D show non-transient survival in four North American Bird Conservation Initiative Regions: Northwestern Interior Forest (BCR4, A); Northern Rockies (BCR10, B); Southern Rockies Colorado Plateau (BCR16, C); Sierra Madre Occidental (BCR34, D). Panel E shows survival estimates from the Karr et al. (1990) analysis of Panama understory forest birds, without distinction for age or transiency. Panels F and G show adult survival from estimates obtained in this study, respectively from the fixed-effects and the random-effects models.

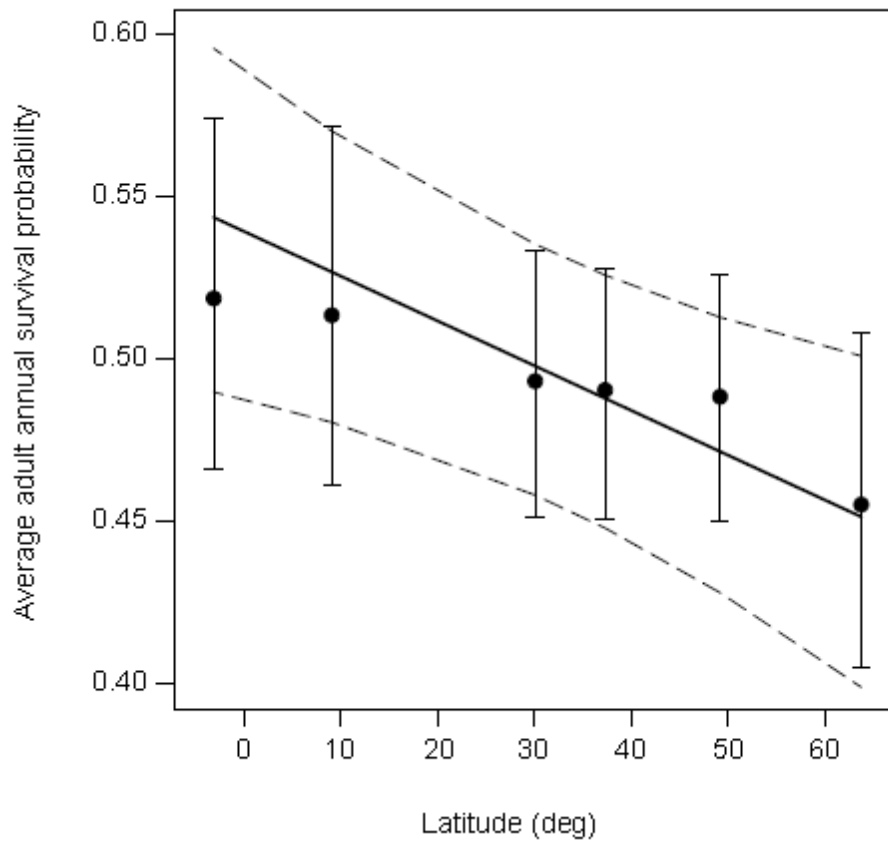


Figure 4. Estimates of average survival for the six study areas along the North-South latitudinal gradient. The dark line is the trend line from mixed-effects linear regression



- MATERIAL SUPLEMENTAR

Table S1. Species-specific posterior mean \pm SD for annual juvenile apparent survival (ϕ_{juv}), adult apparent survival (ϕ_{ad}), and recapture probability (p) under the random-effects and the fixed-effects models. N/R indicates the number of individuals captured and recaptured, respectively.

Family and species names	Random-effects model			Fixed-effects model			N/R
	ϕ_{juv}	ϕ_{ad}	p	ϕ_{juv}	ϕ_{ad}	p	
Thamnophilidae							
<i>Thamnophilus murinus</i>	0.32 \pm 0.12	0.57 \pm 0.09	0.21 \pm 0.08	0.42 \pm 0.28	0.71 \pm 0.19	0.13 \pm 0.09	36/3
<i>Thamnomanes ardesiacus</i>	0.28 \pm 0.11	0.55 \pm 0.07	0.32 \pm 0.08	0.14 \pm 0.14	0.50 \pm 0.11	0.42 \pm 0.14	96/16
<i>Thamnomanes caesius</i>	0.37 \pm 0.12	0.56 \pm 0.07	0.27 \pm 0.07	0.55 \pm 0.22	0.56 \pm 0.11	0.26 \pm 0.10	128/19
<i>Epinecrophylla gutturalis</i>	0.33 \pm 0.12	0.54 \pm 0.08	0.25 \pm 0.08	0.41 \pm 0.27	0.49 \pm 0.17	0.31 \pm 0.18	71/9
<i>Myrmotherula axillaris</i>	0.31 \pm 0.12	0.56 \pm 0.09	0.22 \pm 0.08	0.38 \pm 0.27	0.62 \pm 0.21	0.18 \pm 0.13	36/3
<i>Myrmotherula longipennis</i>	0.31 \pm 0.12	0.60 \pm 0.07	0.39 \pm 0.10	0.33 \pm 0.25	0.61 \pm 0.13	0.44 \pm 0.15	40/12
<i>Myrmotherula menetriesii</i>	0.32 \pm 0.13	0.59 \pm 0.09	0.28 \pm 0.09	0.43 \pm 0.28	0.72 \pm 0.19	0.24 \pm 0.13	20/3
<i>Hypocnemis cantator</i>	0.31 \pm 0.12	0.58 \pm 0.08	0.25 \pm 0.07	0.33 \pm 0.26	0.66 \pm 0.17	0.21 \pm 0.10	58/8
<i>Pernostola rufifrons</i>	0.39 \pm 0.13	0.50 \pm 0.08	0.35 \pm 0.09	0.50 \pm 0.21	0.34 \pm 0.10	0.52 \pm 0.17	86/15
<i>Myrmeciza ferruginea</i>	0.31 \pm 0.12	0.56 \pm 0.09	0.29 \pm 0.11	0.32 \pm 0.26	0.42 \pm 0.23	0.39 \pm 0.26	13/1
<i>Pithys albifrons</i>	0.35 \pm 0.09	0.54 \pm 0.04	0.46 \pm 0.06	0.39 \pm 0.13	0.51 \pm 0.04	0.50 \pm 0.07	323/82
<i>Gymnopathys rufigula</i>	0.35 \pm 0.12	0.59 \pm 0.06	0.38 \pm 0.08	0.44 \pm 0.22	0.48 \pm 0.07	0.46 \pm 0.12	150/30
<i>Willisornis poecilinotus</i>	0.42 \pm 0.13	0.56 \pm 0.05	0.36 \pm 0.07	0.66 \pm 0.18	0.56 \pm 0.07	0.35 \pm 0.08	167/38
Conopophagidae							
<i>Conopophaga aurita</i>	0.34 \pm 0.13	0.57 \pm 0.09	0.35 \pm 0.12	0.47 \pm 0.27	0.50 \pm 0.25	0.53 \pm 0.24	8/2
Formicariidae							
<i>Formicarius colma</i>	0.36 \pm 0.12	0.55 \pm 0.09	0.29 \pm 0.09	0.53 \pm 0.24	0.46 \pm 0.19	0.34 \pm 0.18	36/5
Furnariidae							
<i>Certhiasomus stictolaemus</i>	0.38 \pm 0.14	0.64 \pm 0.08	0.48 \pm 0.11	0.56 \pm 0.23	0.75 \pm 0.11	0.54 \pm 0.14	20/11
<i>Dendrocincla merula</i>	0.37 \pm 0.13	0.61 \pm 0.07	0.40 \pm 0.09	0.55 \pm 0.24	0.65 \pm 0.13	0.41 \pm 0.14	49/15
<i>Dendrocincla fuliginosa</i>	0.34 \pm 0.13	0.59 \pm 0.08	0.33 \pm 0.10	0.44 \pm 0.27	0.63 \pm 0.19	0.35 \pm 0.18	25/5
<i>Glyphorhynchus spirurus</i>	0.33 \pm 0.08	0.68 \pm 0.06	0.52 \pm 0.07	0.32 \pm 0.11	0.73 \pm 0.06	0.53 \pm 0.08	217/80
<i>Xiphorhynchus pardalotus</i>	0.36 \pm 0.12	0.64 \pm 0.07	0.35 \pm 0.08	0.57 \pm 0.23	0.76 \pm 0.11	0.27 \pm 0.09	80/20
<i>Xenops minutus</i>	0.33 \pm 0.12	0.57 \pm 0.08	0.26 \pm 0.09	0.45 \pm 0.28	0.64 \pm 0.19	0.21 \pm 0.14	25/3
<i>Philydor erythrocerum</i>	0.32 \pm 0.12	0.57 \pm 0.09	0.26 \pm 0.10	0.42 \pm 0.28	0.57 \pm 0.22	0.24 \pm 0.18	12/1
<i>Automolus ochrolaemus</i>	0.33 \pm 0.13	0.56 \pm 0.09	0.27 \pm 0.10	0.45 \pm 0.28	0.55 \pm 0.20	0.27 \pm 0.17	25/3
<i>Automolus infuscatus</i>	0.32 \pm 0.12	0.60 \pm 0.08	0.36 \pm 0.10	0.32 \pm 0.24	0.63 \pm 0.15	0.40 \pm 0.17	41/10



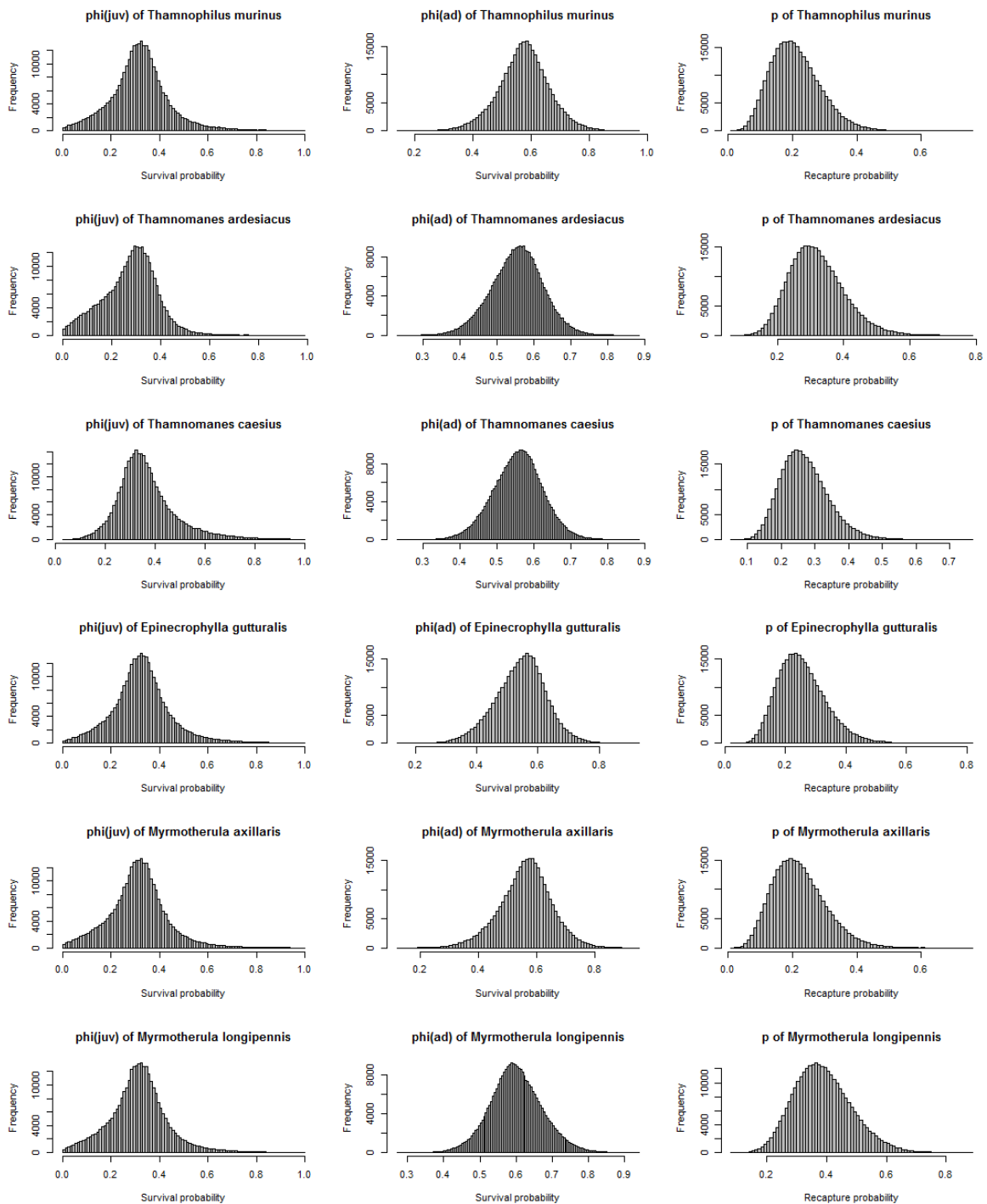
Table S1. (Cont.)

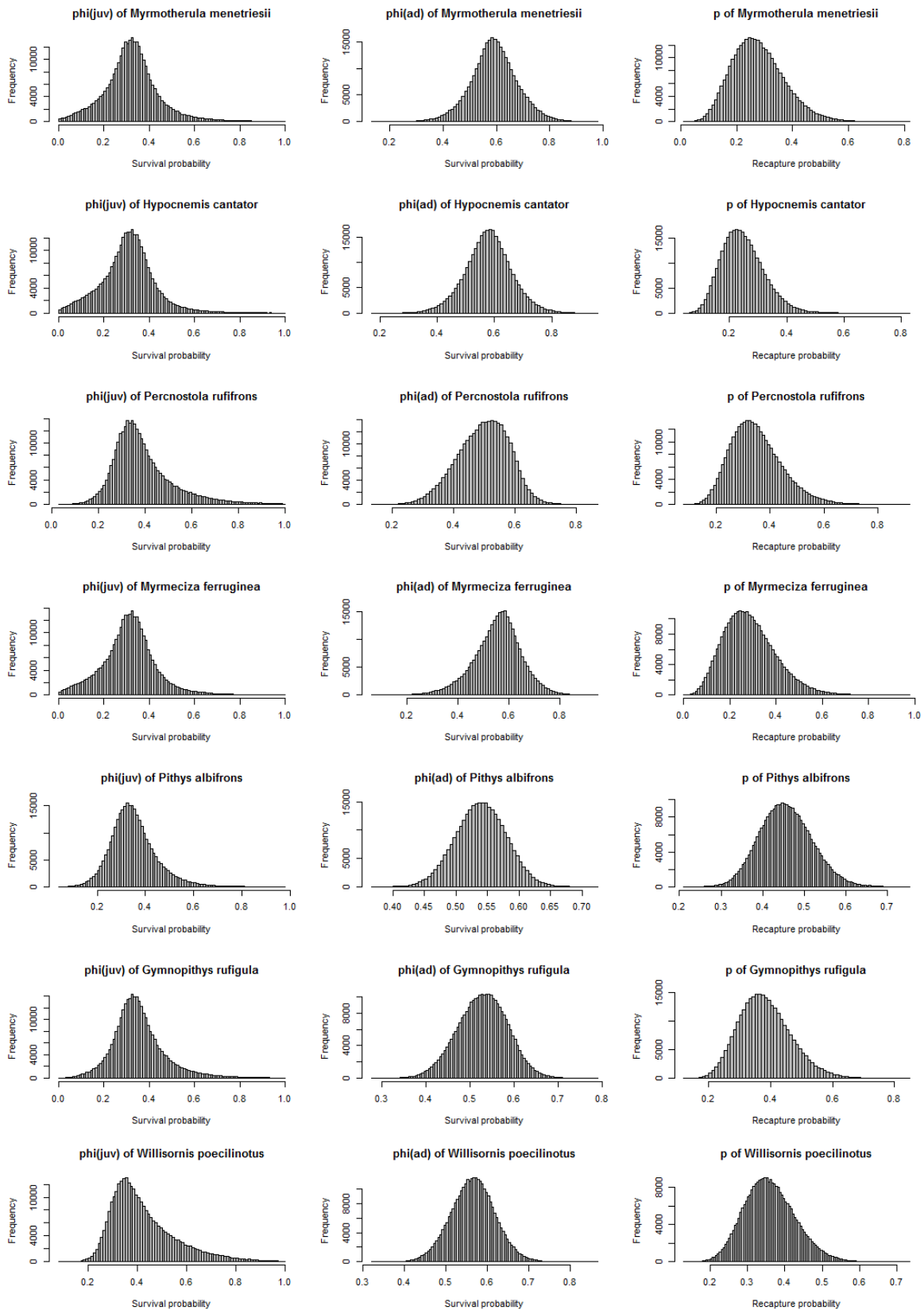
Family and species names	Random-effects model			Fixed-effects model			N/R
	ϕ_{juv}	ϕ_{ad}	p	ϕ_{juv}	ϕ_{ad}	p	
Tyrannidae							
<i>Mionectes macconnelli</i>	0.28±0.11	0.53±0.10	0.22±0.08	0.21±0.22	0.35±0.21	0.39±0.25	71/5
<i>Platyrinchus saturatus</i>	0.31±0.12	0.58±0.09	0.38±0.12	0.28±0.23	0.54±0.19	0.60±0.23	10/3
<i>Platyrinchus coronatus</i>	0.33±0.13	0.57±0.09	0.25±0.08	0.46±0.29	0.61±0.21	0.23±0.14	31/4
<i>Myiobius barbatus</i>	0.31±0.12	0.59±0.08	0.42±0.11	0.27±0.23	0.55±0.13	0.58±0.18	31/9
<i>Attila spadiceus</i>	0.32±0.13	0.53±0.10	0.22±0.10	0.43±0.29	0.30±0.26	0.23±0.23	14/0
Pipridae							
<i>Corapipo gutturalis</i>	0.35±0.13	0.54±0.09	0.29±0.09	0.45±0.25	0.35±0.19	0.49±0.24	36/6
<i>Lepidothrix serena</i>	0.29±0.10	0.55±0.08	0.33±0.10	0.16±0.13	0.39±0.16	0.60±0.23	50/8
<i>Manacus manacus</i>	0.40±0.14	0.53±0.09	0.38±0.10	0.53±0.21	0.32±0.14	0.65±0.21	33/9
<i>Dixiphia pipra</i>	0.31±0.08	0.65±0.07	0.21±0.04	0.38±0.14	0.82±0.10	0.15±0.04	306/42
<i>Ceratopipra erythrocephala</i>	0.30±0.12	0.52±0.11	0.15±0.07	0.37±0.29	0.34±0.28	0.10±0.15	46/0
Troglodytidae							
<i>Pheugopedius coraya</i>	0.38±0.14	0.55±0.10	0.32±0.11	0.61±0.23	0.25±0.22	0.52±0.24	11/2
<i>Cyphorhinus arada</i>	0.33±0.13	0.55±0.09	0.25±0.10	0.47±0.29	0.49±0.24	0.28±0.23	15/1
Poliotilidae							
<i>Microbates collaris</i>	0.31±0.12	0.60±0.08	0.34±0.10	0.30±0.24	0.70±0.18	0.36±0.17	22/5
Turdidae							
<i>Turdus albicollis</i>	0.34±0.12	0.58±0.07	0.38±0.10	0.41±0.24	0.54±0.14	0.47±0.17	50/12
Thraupidae							
<i>Tachyphonus surinamus</i>	0.34±0.13	0.52±0.10	0.26±0.10	0.52±0.26	0.20±0.18	0.45±0.25	22/2
Cardinalidae							
<i>Cyanocompsa cyanoides</i>	0.38±0.14	0.57±0.09	0.40±0.13	0.62±0.24	0.54±0.28	0.65±0.22	4/2



Figure S1. Species-specific posterior distributions of juvenile apparent survival (ϕ_{juv}), adult apparent survival (ϕ_{ad}), and recapture probability (p) under the random-effects model.

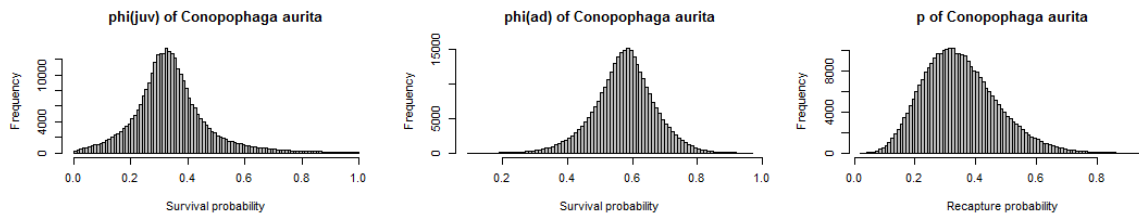
Family *Thamnophilidae*



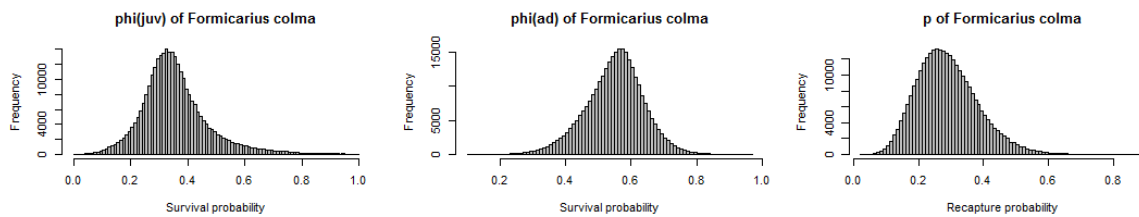




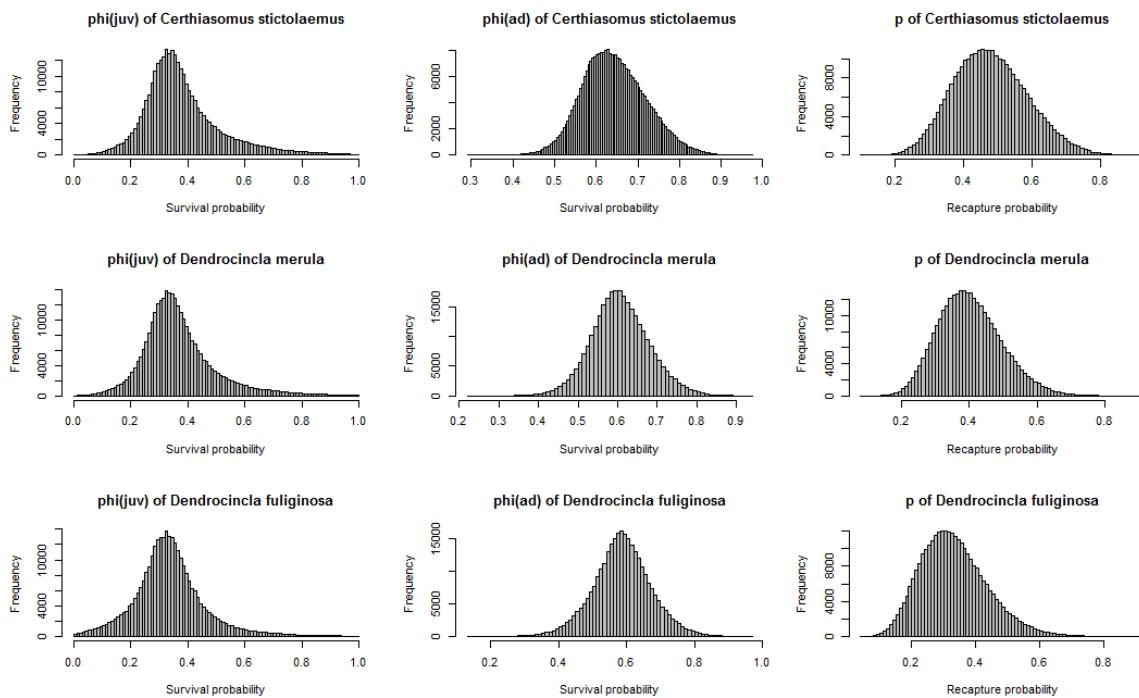
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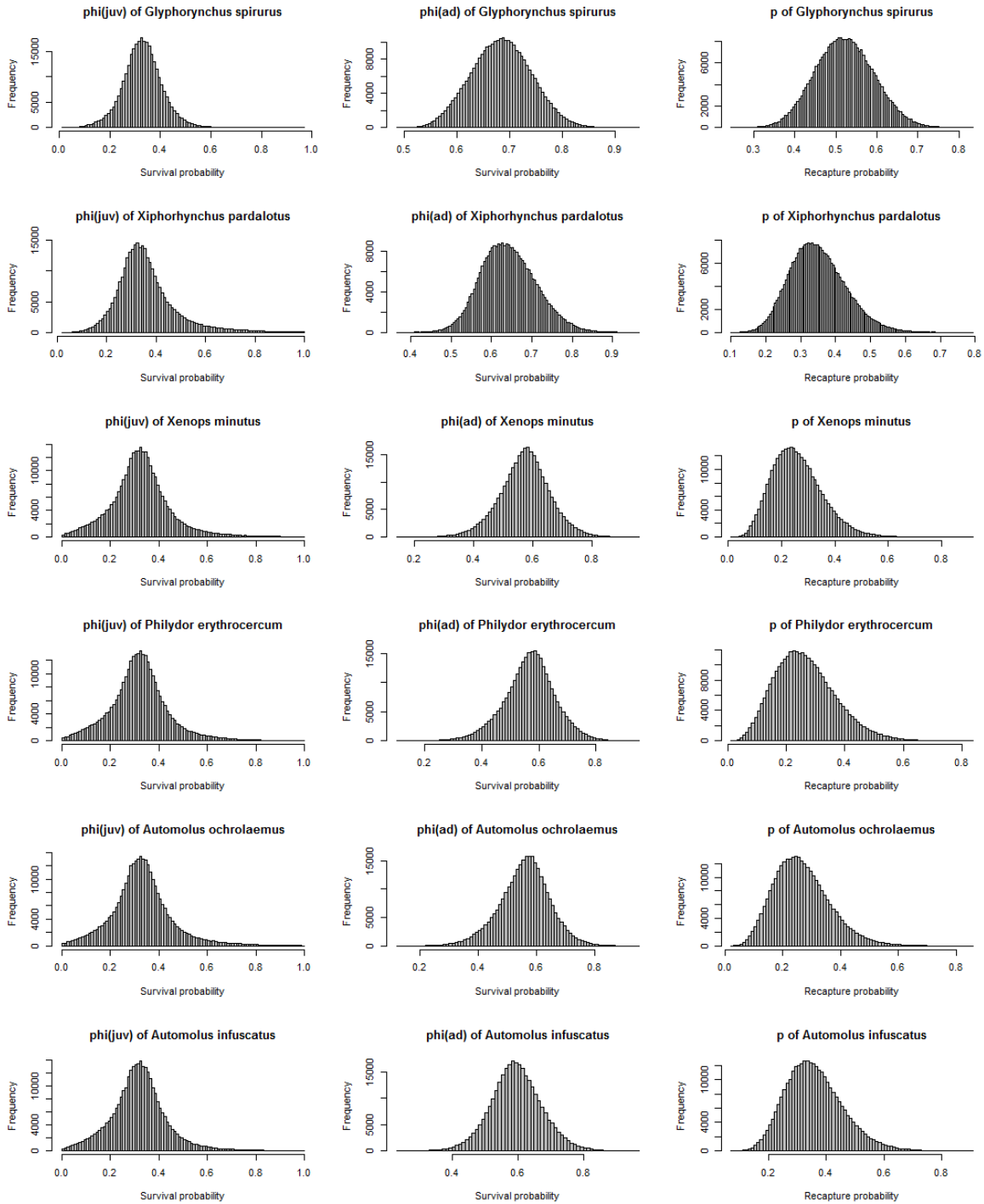


Family Formicariidae



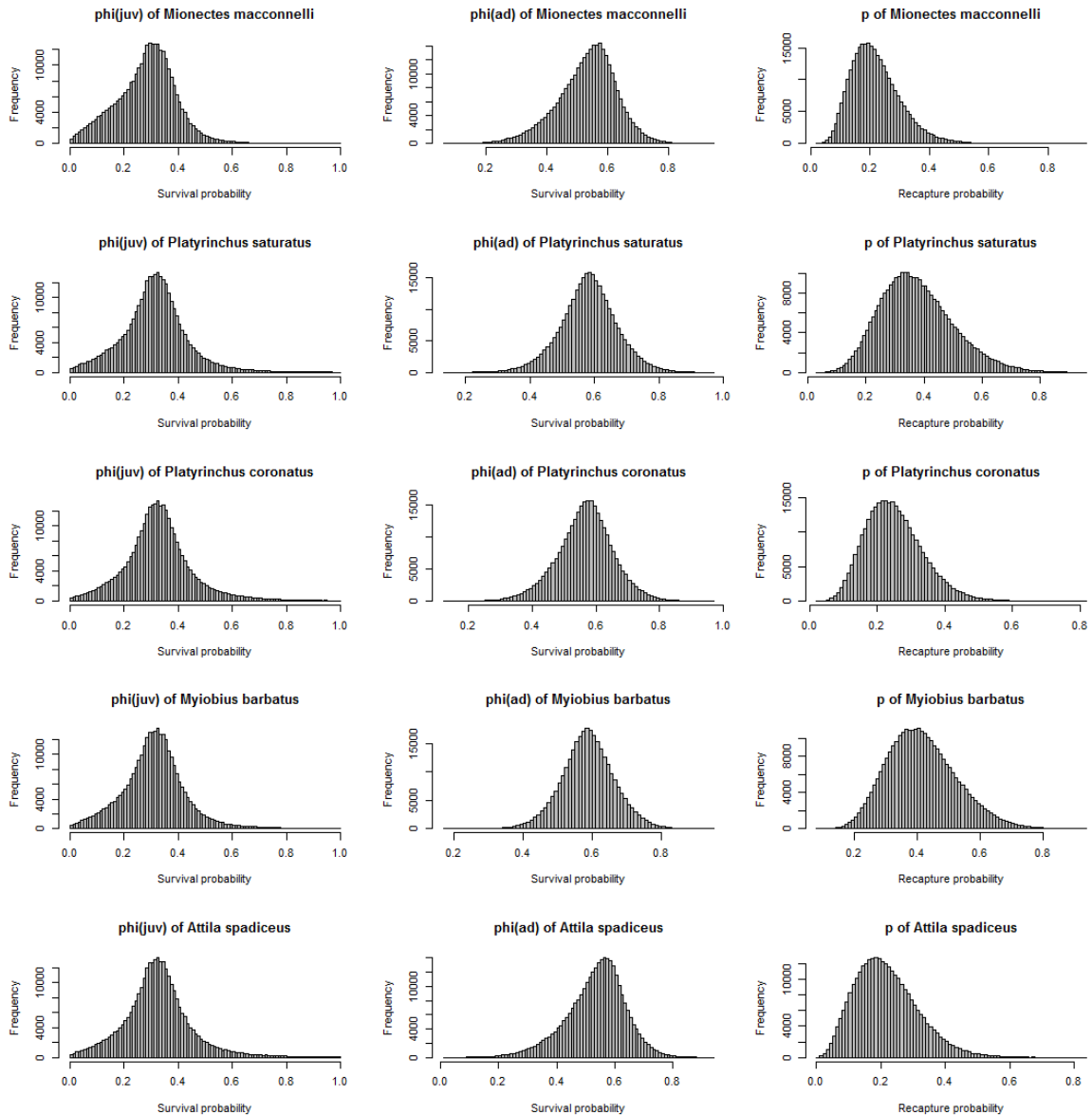
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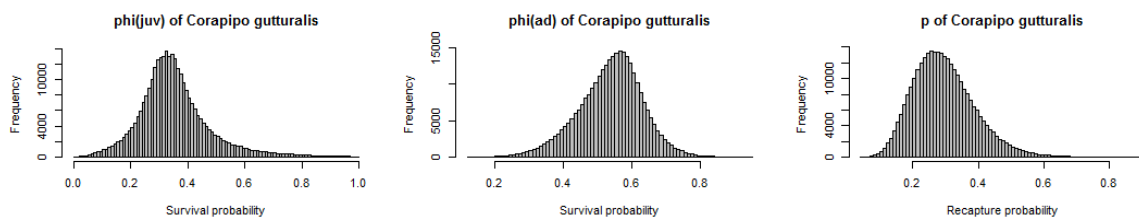


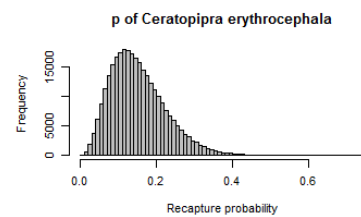
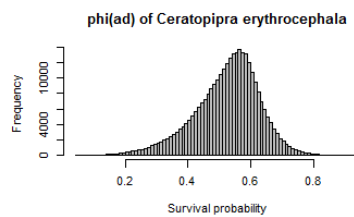
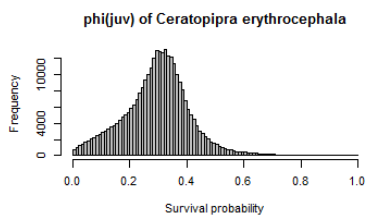
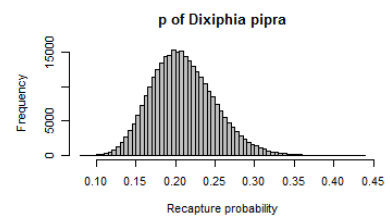
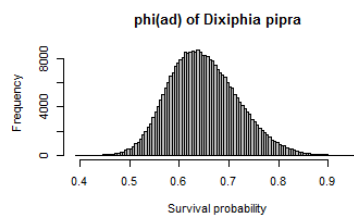
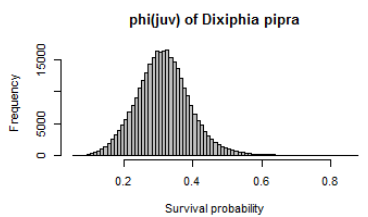
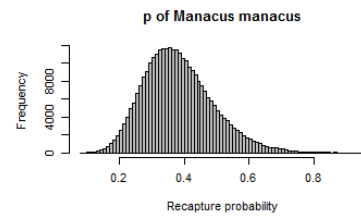
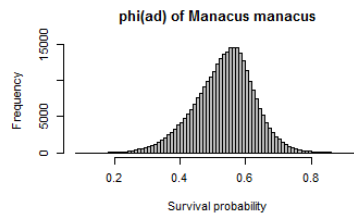
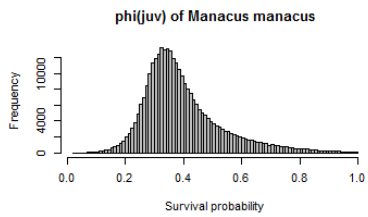
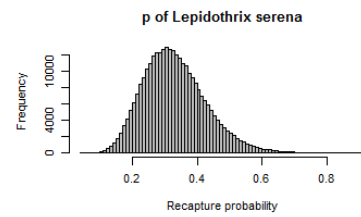
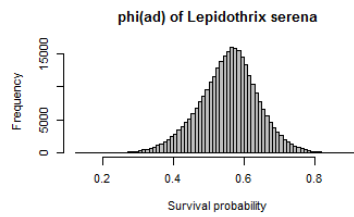
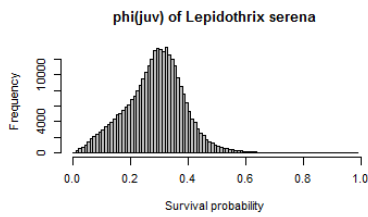


Family Tyraniidae

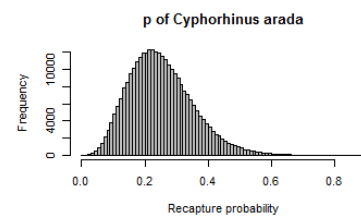
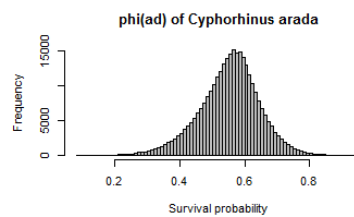
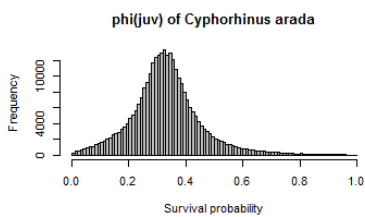
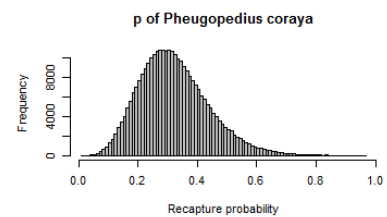
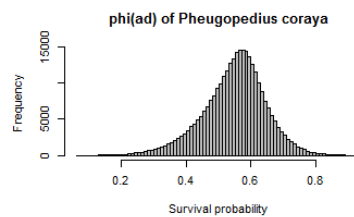
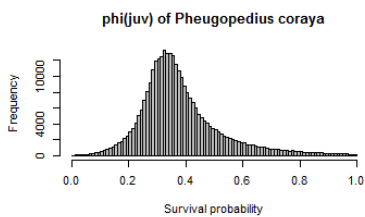


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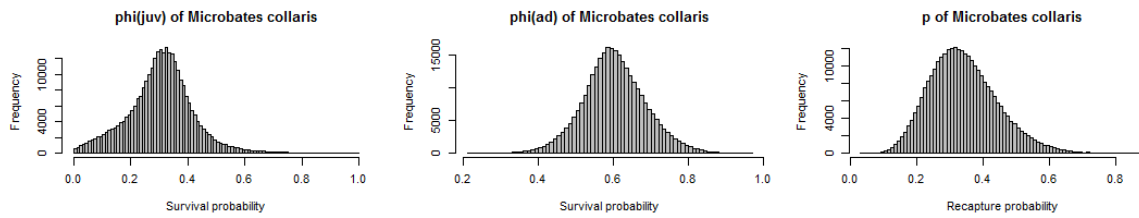


Family Troglodytidae

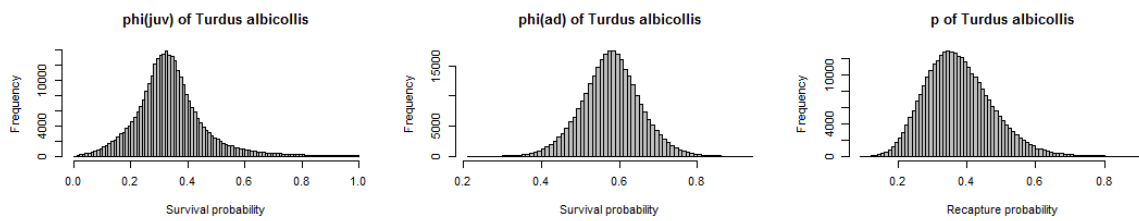




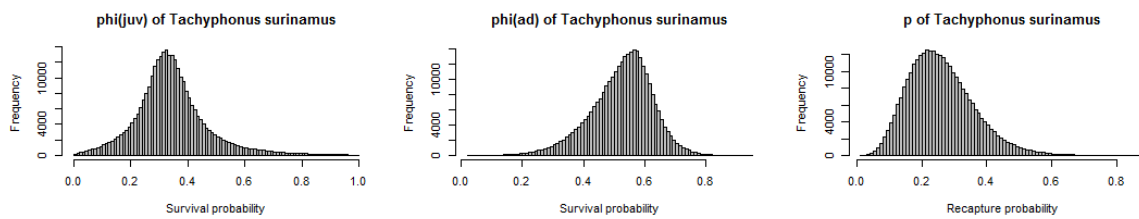
Family Polioptilidae



Family Turdidae



Family Thraupidae



Family Cardinalidae

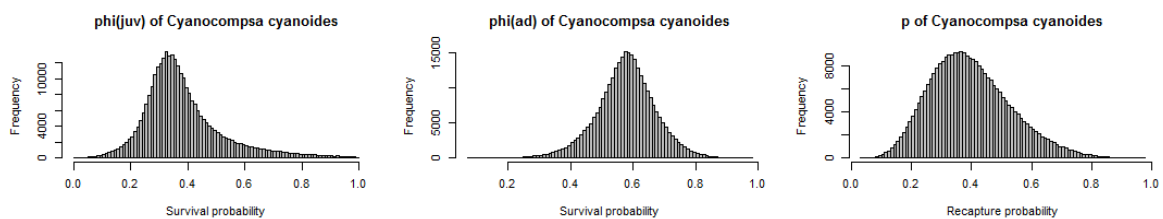
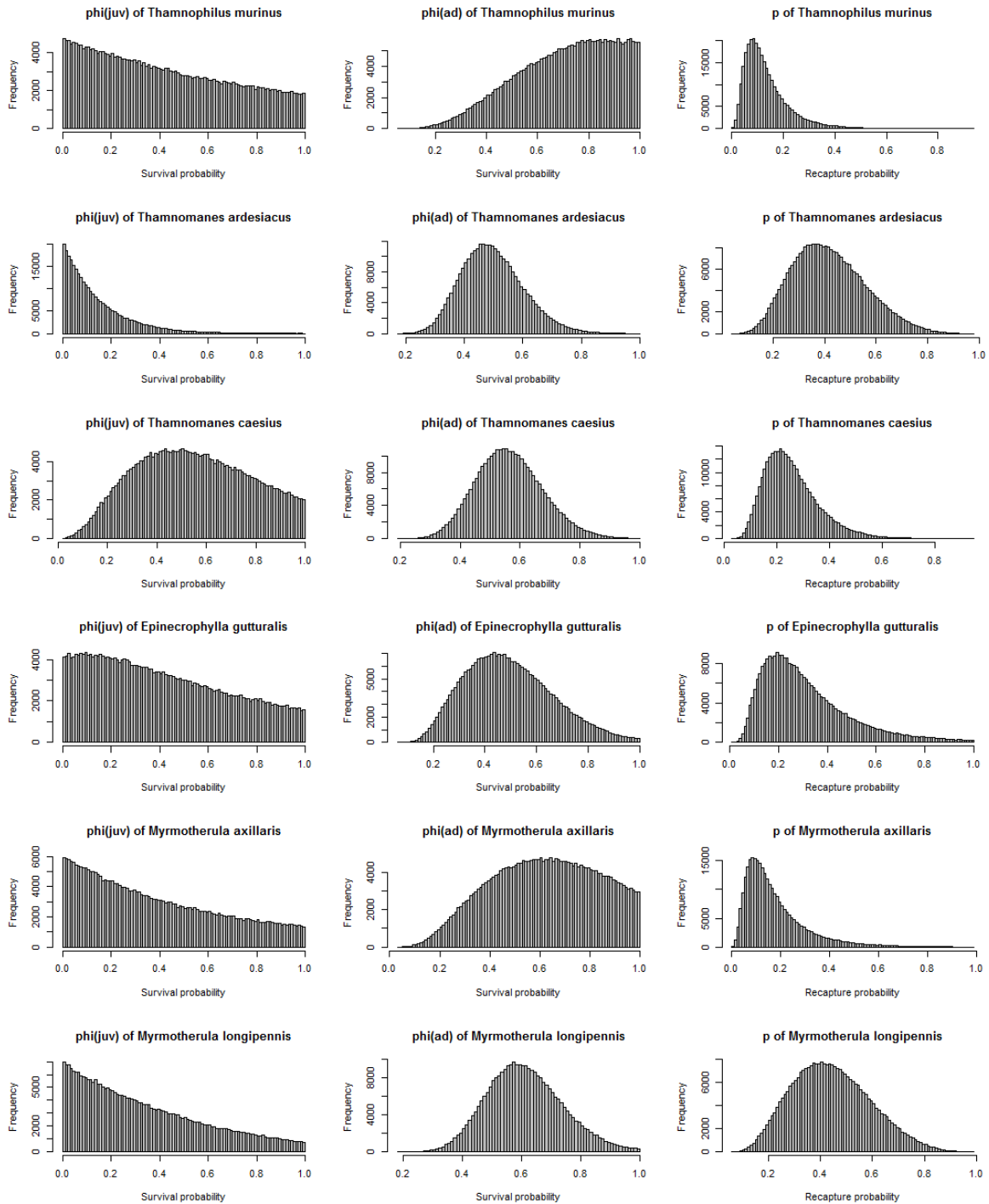
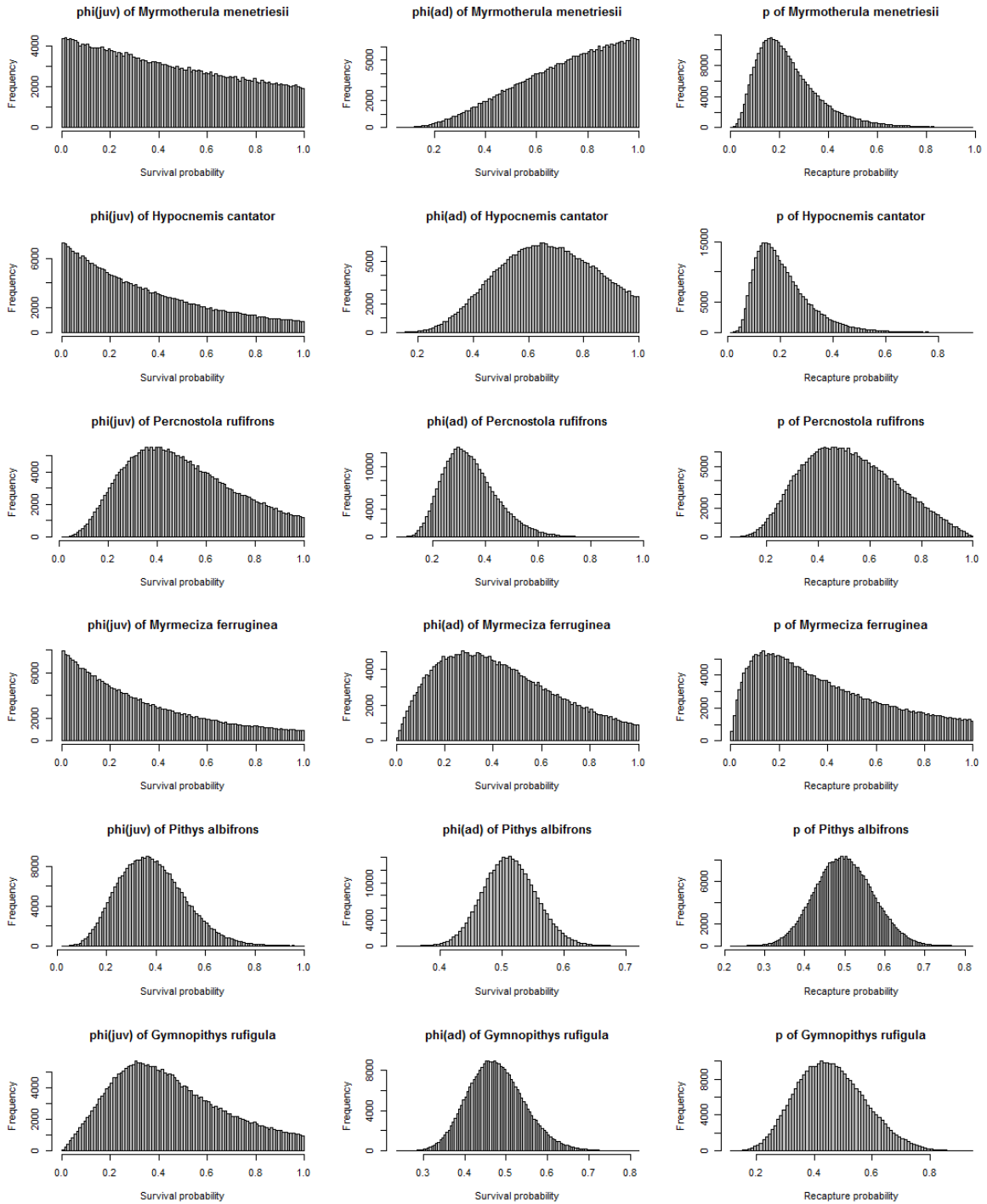




Figure S2. Species-specific posterior distributions of juvenile apparent survival (ϕ_{juv}), adult apparent survival (ϕ_{ad}), and recapture probability (p) under the fixed-effects model.

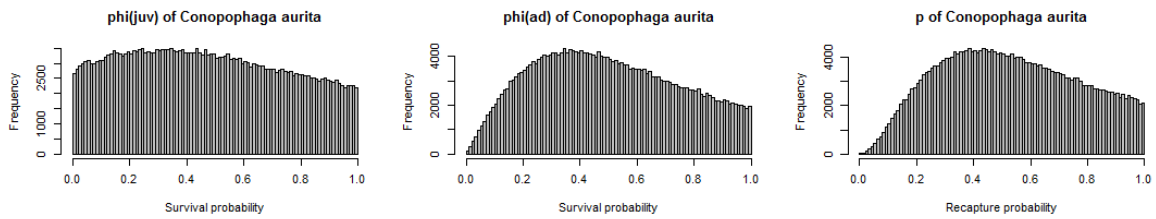
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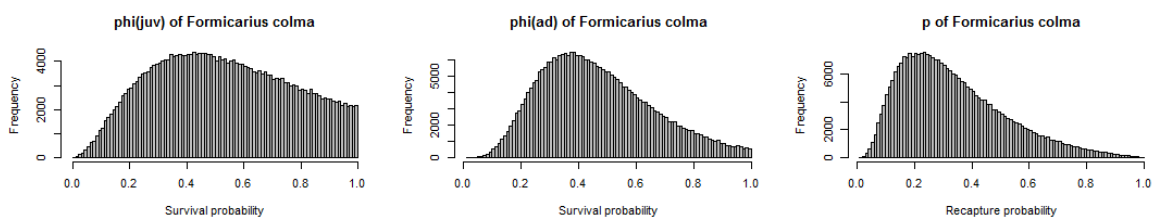




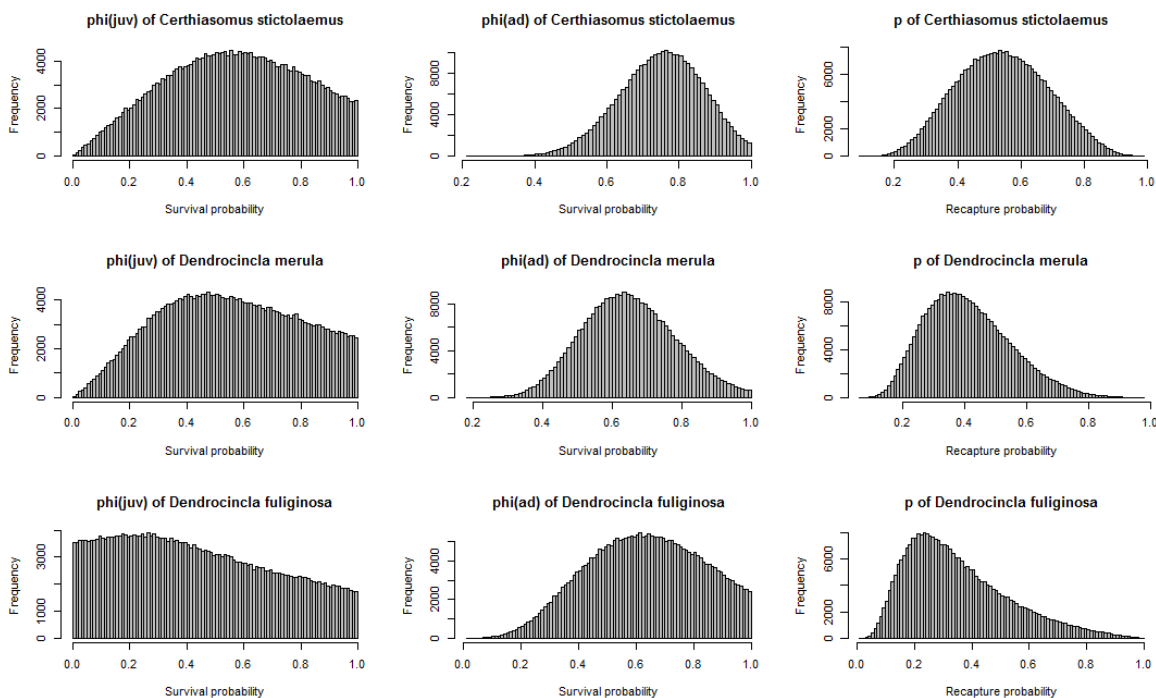
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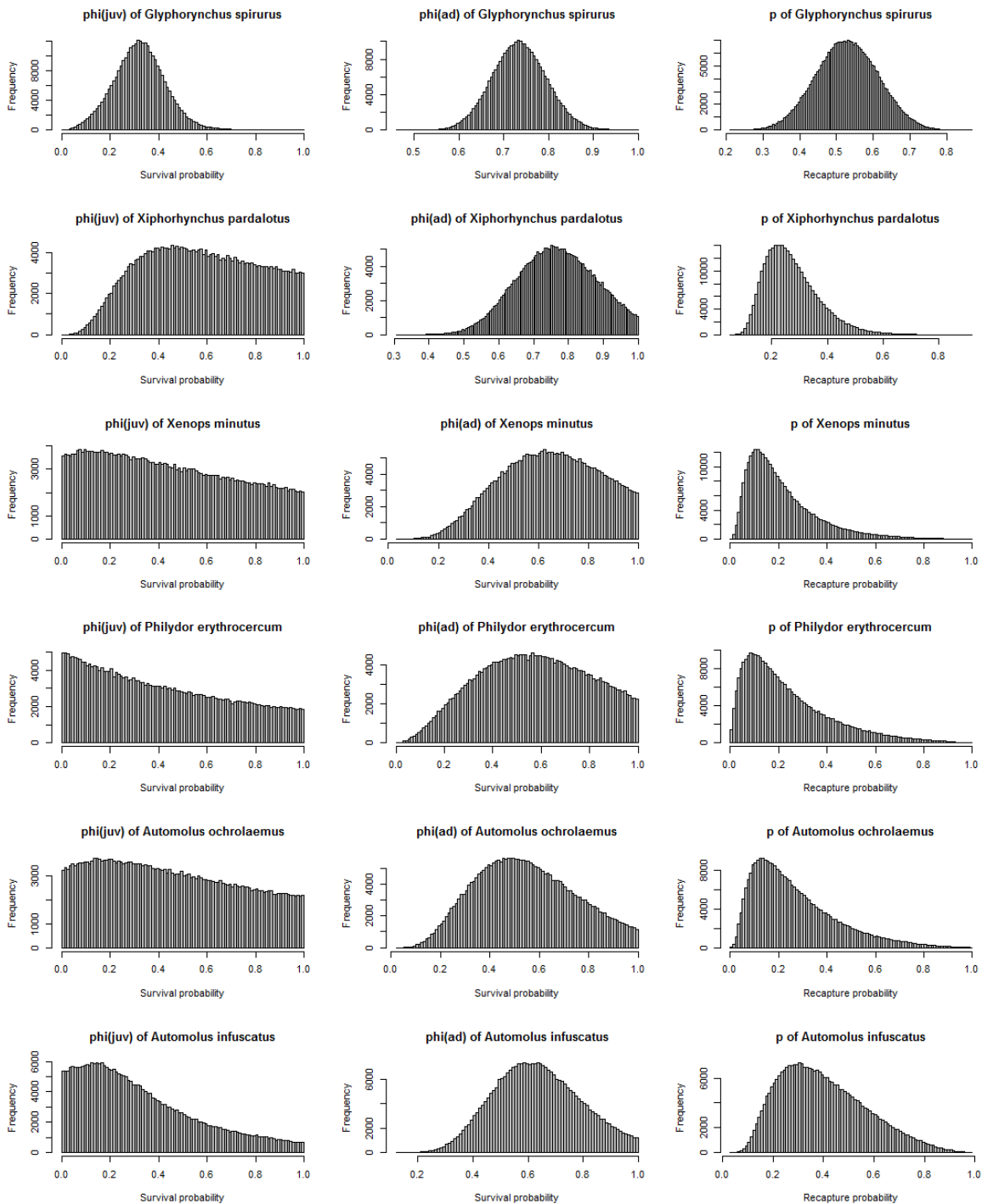


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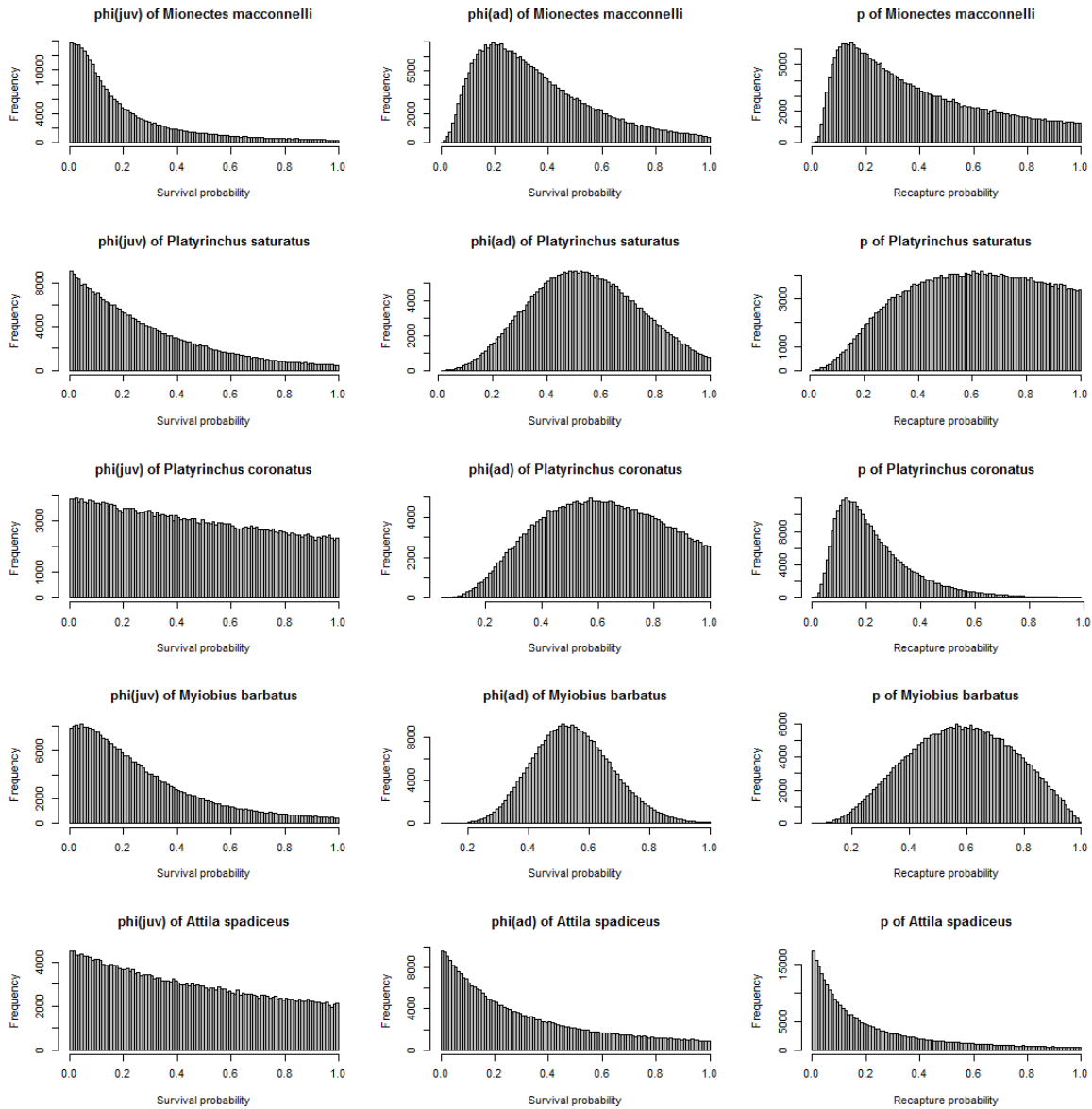
Family Furnariidae



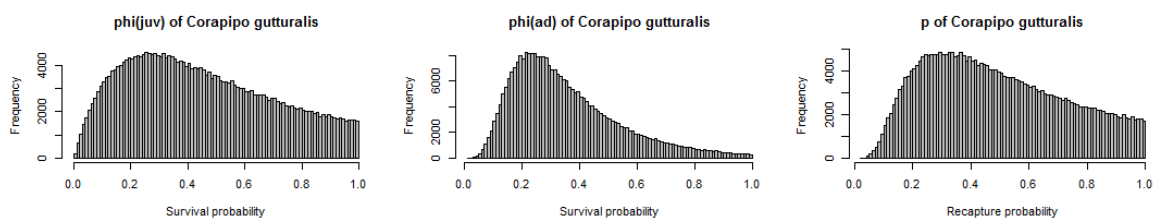


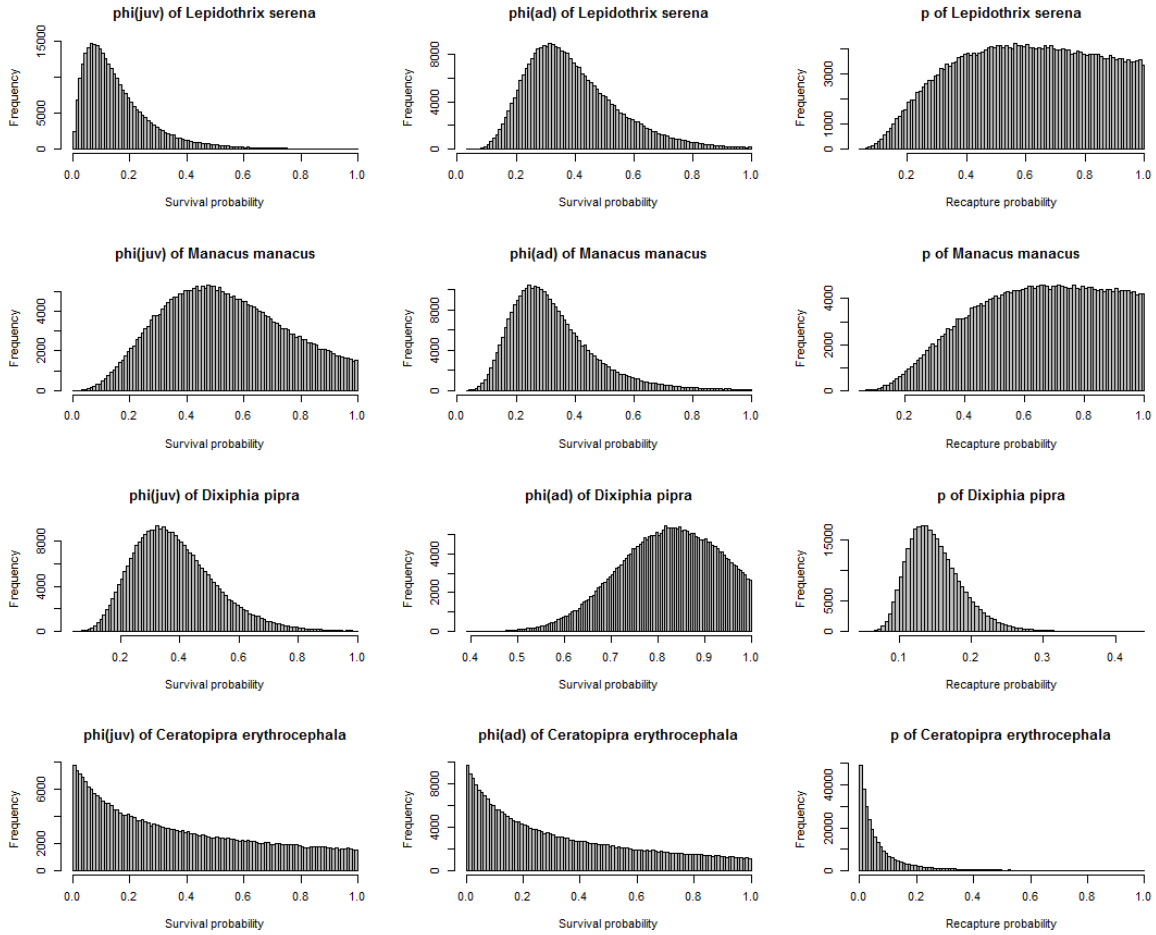


Family Tyraniidae

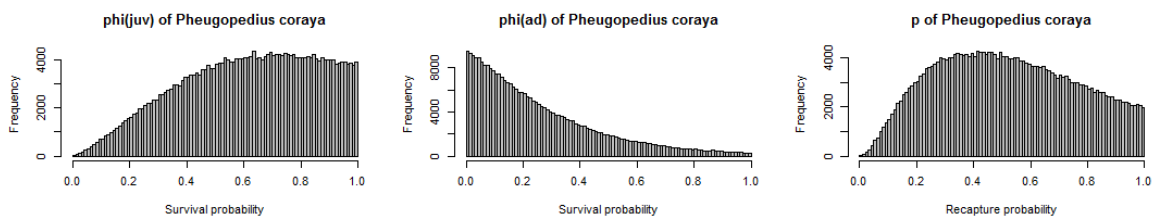


Family Pipridae



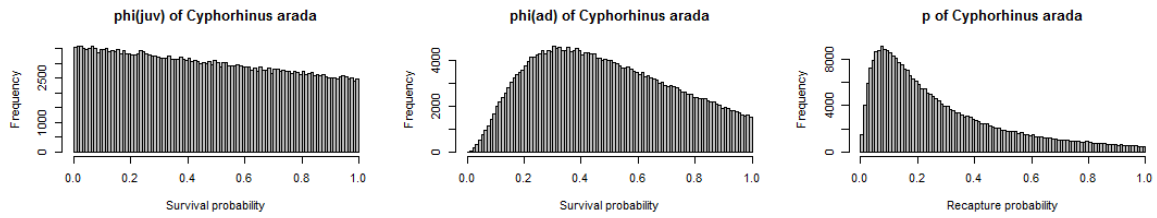


Family Troglodytidae

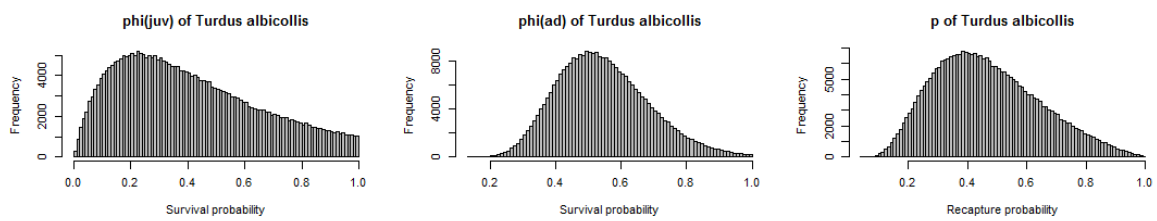




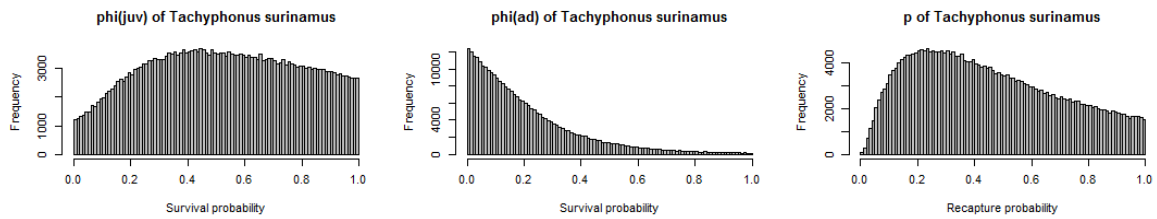
Family Polioptilidae



Family Turdidae



Family Thraupidae



Family Cardinalidae

