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# Senescência atuarial em *Pithys albifrons* (Linnaeus, 1766)

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Manaus, Amazonas
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Orientador: Gonçalo Ferraz

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**Sinopse**

Avaliou-se a existência de senescência atuarial em *Pithys albifrons*, uma espécie de passeriforme tropical. A variação de sobrevivência com a idade foi analisada, selecionando-se o melhor modelo de sobrevivência para a espécie e calculando-se os principais parâmetros demográficos.

**Palavras-chave:** senescência, populações, ecologia, neotropical, Amazônia, aves

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***Só sei que nada sei***

Sócrates (470 a.C – 390 a.C)

## Resumo

Dentre as áreas de estudos que melhor se utilizam desta máxima estão os estudos sobre senescência. Aves são de especial interesse nestes estudos por serem mais longevas do que seu tamanho e taxas metabólicas prediriam. Apesar de inicialmente terem sido consideradas imunes à senescência atuarial, a partir da segunda metade do século XX, o acúmulo de informação sobre a variação das taxas de sobrevivência com a idade em aves mudou este paradigma. Os estudos sobre senescência em aves, no entanto, são limitadao, especialmente pela dificuldade em coletar dados sobre idade em aves. Este trabalho usa novos métodos de aferir idade em aves e de calcular taxas de senescência em *Pithys albifrons*, um passeriforme neotropical especializado em forragear seguindo formigas de correição. Os resultados demonstram que a senescência atuarial em *P. albifrons* é inexistente ou negligenciável. Os parâmetros demográficos estimados para *P. albifrons* demonstram que a baixa taxa de senescência não garante a essa espécie uma alta longevidade. A longevidade desta espécie é similar a espécies do mesmo peso. A baixa longevidade desta espécie está mais relacionada com o pequeno porte e com a baixa taxa de sobrevivência anual. Este trabalho apresenta evidências de ausência de sinais de senescência atuarial e de que a longevidade das espécies em passeriformes neotropicais. está mais relacionada com suas taxas de sobrevivência do que com as taxas de senescência. Estudos comparativos mais abrangentes similares ao desenvolvido para *P. albifrons* são necessários para um entendimento da senescência em aves neotropicais

## Abstract

The best way to understand biological processes that occur in humans is to use other species as comparative models. One of the areas that best uses model species are studies on senescence. Birds are of special interest in these studies since they are longer lived than its size and metabolic rates would predict. Although initially birds were considered immune to actuarial senescence, the accumulation of information in the second half of twentieth century on the variation in survival rates with age in birds changed this paradigm. The senescence studies , however, are limited, especially due the difficulty in collecting data on age of death in birds. This work use new methods of measuring age in birds and calculate senescence rates in Pithys albifrons, a neotropical passerine. The results demonstrate that actuarial senescence in P. albifrons is non-existent or negligible. The estimated demographic parameters for P. albifrons demonstrate that low senescence rate does not guarantee this species a high longevity. The longevity of this species is similar to the species of the same weight from temperate region. The low longevity of this species is more related to the small size and the low annual survival rate. This article presents evidence of a species of neotropical bird that shows no signs of actuarial senescence and that the longevity of the species is more related to their survival rates than it is with senescence rates.

# Sumário

# 1. Introdução

## 1.1. Teorias sobre Senescência

Senescência é definida como a diminuição de funções vitais com o incremento da idade (Kirkwood and Austad, 2000). Como e porque estas diminuições ocorrem é uma das principais perguntas ainda não respondidas por biólogos e médicos (Couzin, 2005). A grande questão por trás da senescência é como ela evoluiu, uma vez que aparentemente não representa uma vantagem para as espécies. Três teorias não excludentes são atualmente aceitas e todas se baseiam no fato de que a seleção natural tende a selecionar características que aumentam a eficiência reprodutiva no início da vida, independente de seus efeitos posteriores.

A Teoria do Acúmulo de Mutações, proposta por Medawar (1952), credita à senescência ao acúmulo de mutações danosas ao longo da vida. A seleção natural não evitaria essas alterações danosas pois estas apenas têm efeito danoso no fim da vida. Apesar de existirem poucas evidências empíricas que corroborem essa teoria, foi Medawar quem pela primeira vez apresentou a ideia de que a seleção natural atuaria de maneira mais ativa no início da vida.

Williams (1957) se baseou nos princípios propostos por Medawar (1952) para propor a Teoria da Pleitropia Antagonística. Segundo esta teoria, a seleção natural selecionaria genes que favorecem a sobrevivência e a reprodução nos primeiros anos de vida, por mais que estes genes apresentem efeitos deletérios em estágios posteriores de vida. Uma vez que a seleção atua de maneira mais forte no início da vida, genes que provêm vantagens em idades mais jovens são favorecidos pela seleção.

A Teoria do Soma Descartável (Kirkwood, 1977), apesar de ter embasamento teórico diferente das anteriores, também segue o princípio de que a seleção atuaria mais fortemente nas idades iniciais. Esta teoria prevê que os indivíduos possuem recursos limitados, especialmente energia. A seleção natural favoreceria indivíduos que alocam esta energia em reprodução e sobrevivência nos estágios iniciais de sua vida, ao invés de investirem em reparos somáticos. A falta de reparos somáticos ao longo da vida geraria danos aos indivíduos em estágios posteriores de sua vida, como a diminuição da capacidade reprodutiva e incremento da mortalidade.

## 1.2 Senescência Atuarial

Sobrevivência é um dos principais parâmetros em ecologia de populações. Estudos que avaliam a variação da sobrevivência com a idade, também chamada senescência atuarial, são a base para o acúmulo de conhecimento nesta área. A senescência atuarial pode, por exemplo, estar relacionada com extinção local de espécies, a viabilidade de populações, além de ser influenciada por diversos fatores, como doenças (Robert et al., 2015; Vogel, 2015). Além disso, a senescência está relacionada ao continuum rápido-lento de histórias de vida, podendo jogar nova luz sobre questões como a variação latitudinal do tamanho de postura em aves (Jones *et al*., 2008; Martin, 2004). O avanço do conhecimento sobre senescência atuarial em aves, no entanto, é limitado pela dificuldade em obtenção de dados sobre as idades de morte.

O principal desafio na detecção de senescência atuarial é saber, com precisão, a idade em que os indivíduos morreram, o que exige conhecer a data de nascimento e morte dos indivíduos. Estes dados não são de fácil obtenção, especialmente em estudos que usam o método marcação e recaptura/reavistamento. A não ser que a espécie estudada possua características específicas, coletar dados de morte é uma tarefa quase impossível em aves (Bibby, 1981). Algumas aves marinhas, por exemplo, possuem alta fidelidade ao sítio reprodutivo, o que permite definir que o indivíduo está morto quando não é mais detectado no estudo (e.,g. Balbontin and Moller, 2015; McDonald, Fitzptrick and Woolfenden, 1996). Quando estas assumpções são impossíveis, os modelos da família Comarck-Jolly-Sieber (CJS) podem ser utilizados para estimar a probabilidade de sobrevivência em casos em que a detecção é imperfeita (Lebreton *et al*., 1992). Estes modelos permitem a utilização de dados em que não se sabe a data de morte dos indivíduos, além de permitir que a probabilidade de sobrevivência varie com a idade.

Estudos que utilizam modelos CJS para estimar a variação da sobrevivência com a idade necessitam que todos os indivíduos utilizados na análise tenham idade conhecida (Lebreton *et al*., 1992). Para cumprir esta premissa é necessário excluir dados de indivíduos em que não foi possível aferir uma idade ou assumir aproximações que não necessariamente condizem com a realidade (e.g. que todos os indivíduos têm a mesma idade na primeira captura: Crespin *et al*., 2006; Ruiz-Gutierrez *et al*., 2012). A exclusão de dados é um problema, pois limita estudos de senescência apenas a projetos que possuam grande base de

dados. Para contornar este problema Colchero and Clark (2012) propuseram um modelo onde é possível estimar estados latentes, de forma que possamos incluir indivíduos em que a data de nascimento é desconhecida. Neste modelo, os estados latentes são estimados em conjunto com funções paramétricas de senescência. A precisão destas estimativas aumenta quando é possível obter informações sobre a idade de alguns indivíduos (Colchero and Clark, 2012).

Aferir a idade dos indivíduos capturados é um desafio, principalmente na região neotropical. O conhecimento sobre muda e plumagem na avifauna de ambientes temperados já é bastante consolidado, e uma vasta literatura sobre como determinar idades está disponível (e.g. Howell, 2010; Pyle, 1997, 2008). No neotrópico, no entanto, a literatura específica sobre o assunto é recente. O principal obstáculo em reproduzir as técnicas de determinação de idade utilizados em ambientes temperados nos trópicos é o fato destes métodos se basearem no calendário para determinar as categorias de idade. Utilizar o calendário para determinar idade em aves tropicais não é recomendado, uma vez que a maior parte das espécies nesta região não possui período reprodutivo definido (Snow, 1974; Wolfe, Pyle and Ralph, 2009). Wolfe, Ryder e Pyle (2010) propuseram um sistema (sistema WRP) que não se baseia no calendário e, portanto, pode ser utilizado independente do comportamento reprodutivo das espécies. O sistema WRP se baseia no ciclo de mudas das espécies, usando características de plumagem e presença ou ausência de mudas para determinar a classe etária do indivíduo. Sabendo identificar o ciclo de muda da espécie, a classificação aferida por meio do sistema WRP pode ser usada como proxy para determinar a idade em termos numéricos (semanas, meses) e, consequentemente, utilizar estes dados para análises de senescência.

Neste estudo, avaliamos a existência de senescência no papa-formiga-de-topete (*Pithys albifrons)*, espécie de passeriforme neotropical da família Thamnophilidae. *P. albifrons* é a espécie com maior número de capturas em nossa área de estudo (16% do número de capturas, quase duas vezes maior que a segunda espécie mais capturada, *Dixiphia pipra*). Algumas espécies de Thamnophilidae da Amazônia Central possuem seu padrão de muda e, consequentemente, sua classificação etária bem definida pelo método WRP (Johnson and Wolfe, 2014). Para analisar a variação de sobrevivência com a idade em *P. albifrons* utilizamos três funções de sobrevivência e avaliamos se os parâmetros indicam ou não a existência de senescência atuarial. Também utilizamos métodos de seleção de modelos para definir qual destas funções melhor se ajusta aos nossos dados e calculamos os principais

parâmetros demográficos para comparações com outras espécies. Para isto, combinamos o sistema WRP de classificação etária com o modelo proposto por Colchero e Clark (2012).

# 2. Objetivos

## 2.1 Objetivo Geral

- Investigar a presença senescência atuarial em *Pithys albifrons*.

## 2.2 Objetivos Específicos

- Estimar parâmetros das funções de sobrevivência para a população de *Pithys albifrons* estudada e selecionar qual função melhor explica a variação de sobrevivência com a idade nesta espécie;

- Estimar a longevidade, expectativa de vida, taxa de senescência e sobrevivência anual de *Pithys albifrons*;

# 3. Capítulo 1

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Forever young, for a price: absence of actuarial senescence in the White-plumed antbird, *Pythis albifrons*

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# Forever young, for a price: absence of actuarial senescence in the White-plumed antbird, *Pythis albifrons*

Keywords: Birds, Actuarial Senescence, Tropical, Life span, Mark-recapture models

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Introduction

Materials and Method

Results

Discussion

References

## 1.Introduction

In the last century, humans have been pursuing ways of extending the length of life ad its quality. To better understand the aging process, scientists have tried to understand senescence causes and consequences in model animals, specially other mammals and birds (Ricklefs 2008). Birds are of special interest in senescence studies once they are longer lived than what is expected for its metabolism rate and weight (Holmes and Ottinger 2003; Nussey et al. 2013). The first studies of birds life tables described constant survival for adult passerines, based in Lack's recovery of British dead birds (Lack 1943; Deevey 1947). The lack of actuarial senescence, the part of senescence studies that deal with survival, in adult birds was considered a fact and these animals were used as the main example of type II survival curves (Slobodkin 1961). At this time, data about birds survival and longevity were few and sparse. The accumulation of knowledge on birds demography was the starting point for scientists doubts about constant survival in birds.

The first article questioning the lack of actuarial senescence in birds was presented by Botkin & Miller (1974). They presented theoretical arguments indicating that constant survival rates in birds would lead to impossibly high longevities. The most remarkable cases, though, are for non-passerines, like the Royal Albatross. The high survival rates of the Royal Albatross would keep 0.1% of the population alive for at least 250 years if maintained constant during the whole lifetime. The data presented for passerines species, the Blue tit, suggests that senescence could be negligible for the estimated survival rate. Since Botkin and Miller argument, works considering age-constant survival for birds have almost disappeared while studies that consider actuarial senescence as a fact are each time more frequent (e.g. Wasser and Sherman 2010; Valcu et al. 2014). The number of available empirical evidences for passerines senescence, though, is still very limited (Nussey et al. 2013).

Actuarial senescence is hard to detect (Brunet-Rossinni and Austad 2006).

Passeriformes' actuarial senescence evidences come mainly from birds with special characteristics, like fidelity to the reproductive site, and from long term studies with huge databases (e.g. Dhont 1988; McDonald, Fitzpatrick and Woolfenden 1996; Vleck, Vleck and Palacios 2011). Comparative studies regarding birds senescence, then, use another demographic measures as proxy for actuarial senescence. The most widely used measure to make comparisons about senescence is maximum lifespan. Studies using maximum lifespan elucidated several patterns about animals life history. One of the most remarkable findings is the positive relation of lifespan with weight (Wasser and Sherman 2010). Lighter bird species are expected to have smaller longevity and, consequently, smaller senescence rate than heavier ones. This assumption, though, is made assuming that all species show actuarial senescence, which may not be so true. In this work we provide empirical evidence for lack of senescence in a tropical passerine, the White-plumed-antibrd (*Pithys albifrons*). We used a recently described aging system for birds, the WRP system, which is suitable for tropical species, and a model for estimate age-varying survival with incomplete data.

## 2.Materials and Methods

### 2.1. Study area and sampling design

Fieldwork was conducted near the *Cabo Frio* camp 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 at *Cabo Frio* spans approximately 625 ha of forest, two thirds of which are old-growth, with the remaining third 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 2011 and 2013, so our dataset spans seven years, with five years of sampling.

Our sampling design observes the two main principles of coverage and randomness. We seek to have as much coverage of the sampling area as possible, while randomly changing the position of our sampling devices to prevent avoidance of sampling points by birds. To do this, we established 40 sampling points throughout the area, and randomly selected a subset of these for sampling in each visit. Each year we visited *Cabo Frio* monthly throughout the dry season, staying for nine to twelve consecutive days per visit. On each day, we randomly selected one point (without replacement within the visit), and sampled this point with twelve to twenty mist nets. Sampling effort varied slightly through time because we had more resources, a larger crew, and more sampling points in the later years. The maximum number of points was 40, but we started out with twelve in 2009. The temporal variation in effort is accounted for in the analyses as variation in recapture probability. We worked with 12-m long and 2.5-meter high mist nets with a mesh of 36 mm. 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.

**2.2 Focal species**

The White-plumed-antbird (*Pithys albifrons*), is a medium-small (14-24 g) Amazon-forest antbird, from the family Thamnophilidae. *P. albifrons* is often the most frequently captured species in mistnet samples of rainforest birds from the northern part of the Amazon river basin. In our dataset, it corresponds to 16% of all captures, which is more than twice as many captures as the next most-captured species. *P. albifrons* has peculiar foraging, breeding and plumage molt traits. Being an obligate ant-follower, it forages exclusively around army ant swarms. While foraging, white-plumed antbirds appear to be socially subordinate to other ant-

following species because they stay mostly on the edges of the swarm (Willis, 1978); nonetheless, they makes frequent forays into the center of the flock, where they are often attacked by larger, dominant species, such as *Gymnopithys rufigula* and *Dendrocincla merula* (Willis, 1981). With respect to breeding, as far as the evidence goes, *P. albifrons* does not have a regular breeding period, appearing able to take advantage of favorable food and climate conditions to reproduce at any time of the year (Johnson, Stouffer and Bierregard 2012). Its plumage molt is peculiar because it is protracted, as is typical of species with a relatively stable resource supply (Howell, 2003). *P. albifrons* can take up to ten months to complete a molt (Johnson and Wolfe 2012).

### 2.3 Bird aging

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). Tropical birds, living in relatively stable environments, do not breed in well-defined pulses (Snow 1974) 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 codes where the first letter identifies a molt cycle (e.g. first, second, definitive), the second letter expresses a chronological relation to the cycle (in cycle, molting into cycle, or after cycle), and the third letter identifies a particular plumage within the cycle mentioned in the first code (e.g. juvenile, formative, definitive). Many birds, including *P. albifrons*, 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.

One can identify four WRP codes in *P. albifrons* (Johnson and Wolfe 2012). The first code is FPJ (First cycle, pre-juvenile molt) and corresponds to the two-month period after hatching, when the bird is growing its first feathers. Once this period is over, birds fall under the FCJ code (First cycle, juvenile) when, roughly between two and five months of age, they show no signs of molt but have recognizably young feathers. FCJ’s are fully-fledged individuals, which may receive some parental care. At about five-months old, *P. albifrons* starts molting into its formative plumage and enters the FPF (First cycle, pre-formative molt) stage, which can last up to seven months. However, both males and females grow the fully-formed white crest, or plume, which gives the species its common name, during the first two months of the FPF stage. Because the pre-formative plumage of *P. albifrons* is indistinguishable from subsequent plumages. Once the crest is formed, at seven months of age, we are no longer able to tell the bird’s aging from its plumage, and classify it as an FAJ, for ‘after the first cycle juvenile plumage’.

### 2.4 Survival analysis

In order to fit survival functions to data and look for evidence of senescence, we organized *P. albifrons* mist-net captures in a capture-history matrix, where rows correspond to individuals and columns correspond to months, or sampling occasions. Table cells take the values ‘1’ or ‘0’ depending on whether an individual was or was not captured in a given month, respectively. In an ideal world, we would know the hatching and death dates for every

individual in the data; however, this was not possible in our study for three main reasons: a) our observation technique is imperfect and we inevitably miss many individuals that are alive and available for capture at a given occasion; b) many individuals hatch before the beginning and/or die after the end of our study period; and finally, c) our knowledge of molt cycles provides an approximation of the hatching date only for individuals that were first captured younger than seven months old. To addressed the combined problems of missing data, censored/truncated records, and uncertainty about age, we employed the Bayesian approach introduced by Colchero and Clark (2012), which accounts for recapture failure and estimates times of hatching and death for all individuals while fitting a variety of parametric survival functions to the data.

The inclusion of age in our analyses offered two technical challenges: scarcity of very young (< 3 months) birds, and lack of precision in age assignments. The first challenge led us to focus on birds that lived at least ten months, into the beginning of the FPF stage, when *P. albifrons* reportedly reaches sexual maturity (Willis 1981). Younger birds are either less than three months old, with very low mobility and subject to nest-predation, or between three and ten months, learning to forage and moving about with low-quality feathers. In either case, birds younger than ten months are subject to a peculiar suit of threats and face a high mortality rate for reasons that have nothing to do with senescence (Tarwater et al. 2011). If we had more information about very young birds we would fit a model to recover the 'bathtub' pattern of initial decrease and subsequent increase in mortality; however, with only 1.6% of birds first captured in the first three months of life, we felt justified to focus on survival after the tenth month. As for the second challenge, Colchero and Clark's (2012) approach to modeling age-specific mortality is implemented in the R package BaSTA (Colchero et al. 2012), which takes age information in the form of precise birth or hatching

dates. Because our age information is not precise, i.e. a bird with an FCJ code may be anywhere between two and five months of age, we could not use BaSTA in its original form, but adapted its R code by setting limits to the Gibbs sampler in such a way that birds in the FPJ, FCJ, and first two months of the FCF stage were given random hatching dates within the interval that is biologically acceptable (see code in Supplementary Materials B).

We compared age-variant and age-invariant mathematical descriptions of survival in our data by fitting the constant-survival exponential model and the two main age-varying survival models used in population biology: Gompertz and Weibull (Ricklefs & Scheuerlein 2002). The Gompertz model specifies an exponential rise in mortality rate with age; while the Weibull, originally meant for studying failure rates in mechanical systems but now frequently used in senescence studies, describes mortality rate as a power function of time (Table 1). Both models have two parameters ($\beta_0, \beta_1$) in their simplest parametrization, but can be extended with a third parameter ($m_0$), which represents baseline mortality. We do not report on the extended versions of the Gompertz and Weibull models because we could not obtain numerical convergence when trying to fit them. We ran all our analysis in R, using non-informative priors for all model parameters. Every model was fit with three MCMC chains, using 800,000 iterations, a burn-in of 100,000, and thinning of 100. To evaluate the convergence of the MCMC chains we used the Gelman-Rubin diagnosis (Gelman & Rubin 1992); and to compare model we used the Deviance Information Criterion (DIC) in a form adjusted for models with latent states (Celeux et al. 2006).

**Table 1.** Survival models fitted in this study with $\mu(x)$ showing age-specific mortality rate expressions for each model as a function of parameters $\beta_0$ and $\beta_1$. 'Condition for constant $\mu$' shows the parameter values that result in constant mortality rate.

| | $\mu(x)$ | Condition for constant $\mu$ |
|---|---|---|
| Gompertz | $e^{\beta_0+\beta_1 x}$ | $\beta_1 = 0$ |
| Weibull | $\beta_0\beta_1(\beta_1 x)^{\beta_0-1}$ | $\beta_0 = 1$ |
| Exponential | $\beta_0$ | $-\infty < \beta_0 < \infty$ |

Note: Note that parameters$\beta$, $\beta_0$, and $\beta_1$ may take different values and mathematical meanings for different models.

**2.5 Derived demographic parameters and comparison with other species**

To place our *Pithys albifrons* results in the broader context of bird demography, we compared our estimates of life, senescence rate, and yearly survival rate with estimates for other species, obtained from two sources in the literature. From the first source, the AnAge database (De Magalhães and Costa 2006), we obtained body masses and longevity $(z)$ values in the wild for 749 species deemed to have "acceptable" data quality by the database authors. From the second source (Ricklefs 2000), we obtained $\theta = (\beta_0, \beta_1)$ parameters of a Weibull survival model fit for each of twelve species, also sampled in the wild (Supplemental Materials A). From the Weibull parameters we obtained a hazard-rate mortality function, $\mu(x|\theta)$, and a survival function, $S(x|\theta)$, where $x$ is age. By setting $S(x|\theta) = 0.01$, and solving for $x$, we obtain the age at which 99.9 % of individuals of a given cohort have died. We call this age $z_{99.9}$ and use it as a measure of longevity, both for the species in the Ricklefs (2000) study and for *P. albifrons*. From both the hazard-rate and the survival functions, we can also obtain an estimate of life expectancy $E(x)$, given by:

$$E(x) = \int_x^\infty x\,\mu(x|\theta)S(x|\theta)dx$$

Life expectancy is a convenient metric of the duration of life, because unlike maximum lifespan it does not increase with sample size. Nonetheless, because both the AnAge database and Ricklefs (2000) emphasize longevity, we draw comparisons based on $z$ and $z_{99.9}$. We used the limit of 99.9 because both our dataset and most datasets used in Ricklefs' (2000) paper had a few hundred individuals per species. Besides longevity and life expectancy, we obtained senescence rates (ω) from the Weibull parameters using the solution proposed by Ricklefs (1998), expressed in terms of our parameterization of the Weibull model:

$$\omega = \left(\beta_0 \beta_1 \beta_1^{\beta_0}\right)^{1/\beta_0}.$$

In order to compare survival rates across species, we used the parameter $\phi_{10}$, which denotes a probability of surviving the first year after attaining sexual maturity. We draw comparisons between species graphically, by contrasting longevity with body mass, senescence rate with both mass and longevity; and first-year survival probability with both body mass and longevity.

## 3. Results

Our sample of 33965 net*hours over seven years and 6.25 square kilometers returned 548 captures of 317 individual *P. albifrons*. The mean number of captures per individual was 1.73 (±1.32 sd), with 36% of individuals being captured between 2 and 10 times. Seventy two percent of the individuals where first captured at age seven months or older, with WRP cycle code 'FAJ'. The remaining 28% where younger than seven months at first capture, with cycle codes 'FPJ', 'FCJ', 'FPF', 'FCU', or 'FPU'—where 'U' stands for 'unknown' plumage.

MCMC chains converged to Gelman-Rubin values lower than 1.005 for all survival models that we fitted to data: Gompertz, Weibul, and Exponential. Even though sampling effort varied considerably between years, estimates of recapture probability ($p$) varied only

between 0.21 and 0.31, consistent with the variation in effort (Table 2). Parameter estimates of the Weibull ($\beta_0$ = 0.07±0.009) and Gompertz ($\beta_1$ = 0.02±0.008) models are consistent with extremely low actuarial senescence; nonetheless, DIC ranks the exponential model clearly above the others, with a constant survival probability (at age 10 months or older) of 0.46±0.021 per year (Table 3; Fig. 1). There is substantial overlap in the posterior probability distributions for demographic parameters of the Exponential and Weibull models, with survival probability at age 10 months ($\phi_{x=10}$), life expectancy at age 10 months ($E(x = 10)$), and longevity ($z_{99.9}$) virtually undistinguishable between the two models. The Gompertz model results in estimates of survival probability and life expectancy slightly above and longevity slightly below the estimates for the other two models (Table 3). Differences aside, all models agree with a yearly survival probability between 0.4 and 0.6, life expectancy under 2.5 years, and longevity under 12 years.

**Table 2.** Sampling effort per year, measured in net*hours, and corresponding recapture probability ($p$ ± sd) estimated under the exponential model.

| | net*hours | $p$ ±sd |
|---|---|---|
| 2009 | 8,704 | 0.27 ±0.023 |
| 2011 | 2,593 | 0.23 ±0.018 |
| 2013 | 4,279 | 0.21 ±0.023 |
| 2014 | 10,057 | 0.30 ±0.024 |
| 2015 | 8,340 | 0.31 ±0.031 |

Note: We did not sample during 2010 and 2012; those years are not shown in the table but appear in the analyses with recapture probability fixed at 0.

**Table 3.** Model-specific estimates of $\beta_0$, $\beta_1$, yearly survival probability at age 10 months ($\phi_{x=10}$), life expectancy in years at age 10 months, $E(x = 10)$, and life span ($z_{99}$) measured as the age in years at which 99.9% of a cohort is dead. DIC is the Deviance Information Criterion, used for model selection.

| | $\beta_0$ | $\beta_1$ | $\phi_{x=10}$ | $E(x = 10)$ | $z_{99.9}$ | DIC |
|---|---|---|---|---|---|---|
| Exponential | 0.06±0.007 | − | 0.46±0.021 | 2.12±0.131 | 9.87±1.002 | 4211.01 |
| Weibull | 0.99±0.108 | 0.07±0.009 | 0.44±0.058 | 2.08±0.134 | 9.97±1.872 | 4239.84 |
| Gompertz | -3.14±0.174 | 0.02±0.008 | 0.58±0.029 | 2.23±0.114 | 6.85±0.927 | 4280.01 |

Note: The value of $x$ in the column labels is given in months, the temporal unit of the model, but for convenience of interpretation, the table shows survival rates per year, as well as life expectancy and life span in years.

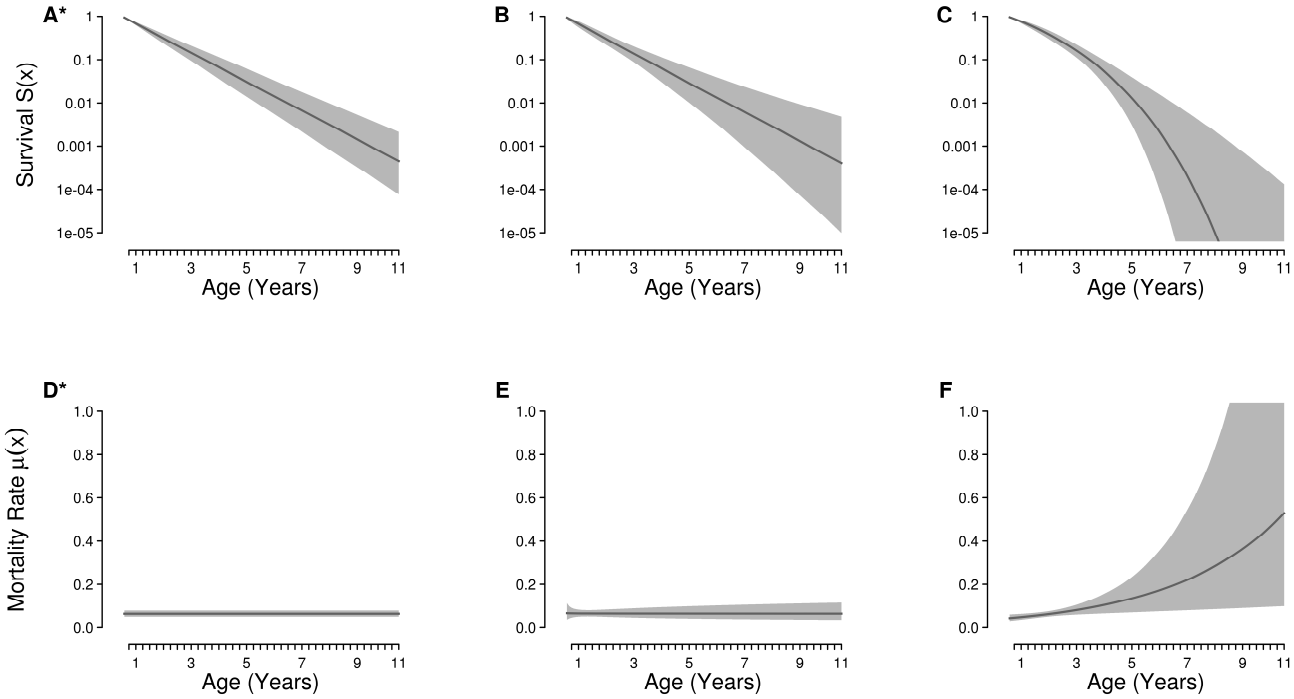


**Figure 1.** Age-specific monthly survival probability, $S$(x), and mortality rate, $\mu$(x), respectively, for the Exponential (A, D), Weibull (B, E), and Gompertz (C, F) survival models. Asterisks highlight the Exponential model, which had the lowest DIC value. All plots start at the age of ten months because we only analyzed individuals from that age on. Shaded areas around the curves show 95% credible intervals.

In accordance with $\beta_0$ and $\beta_1$ estimates for the Weibull model—the best fitting model with senescence—*Pithys albifrons* has a $z_{99.9}$ longevity of 9.97±1.872 years and senescence rate (ω) of 0.06 ± 0.007 year$^{-1}$. The longevity value is well within the range of values reported in the literature for similar-sized bird species (Fig. 2A). The senescence rate, however, is extraordinarily low when compared with published estimates for birds of similar size (Fig. 2B) and longevity (Fig. 2C). The yearly survival rate of *P. albifrons* at 10 months, which is

statistically indistinguishable between the Exponential and Weibull models, is lower than all initial survival rates reported by Ricklefs (2010) for birds of similar size (Fig. 3A) and longevity (Fig. 3B).

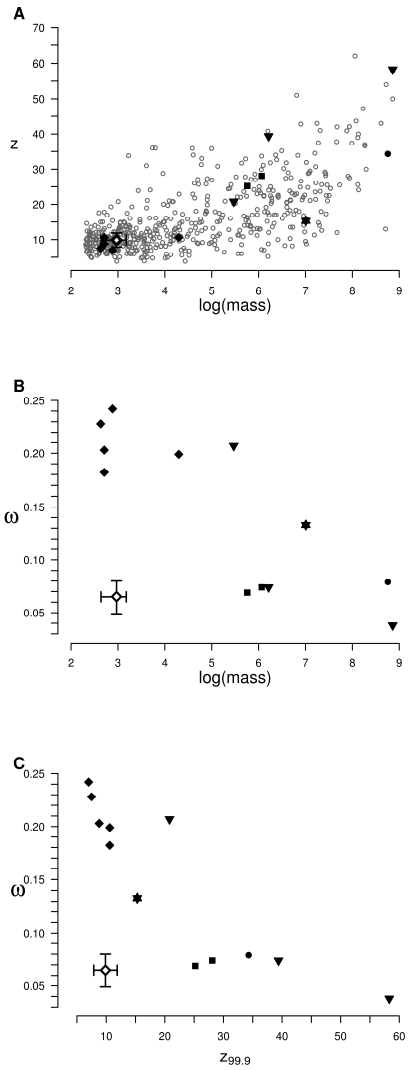


**Figure 2.** *P. albifrons* demographic parameters in contrast with literature-based parameters for other bird species studied in the wild. Open-circle points (in panel A only) obtained from the AnAge database (De Magalhães et al 2000) and filled symbols obtained from Ricklefs (2010); the empty diamond with 95% credibility bars depicts estimates for *P. albifrons* obtained in this study. Different-shaped filled symbols identify bird orders Anseriformes (square), Charadriiformes (circle), Accipitriformes (inverted triangle), Sphenicifomes (star), Procellariformes (triangle), and Passeriformes (diamond). The three panels represent: A) longevity in years ($z$) against the natural logarithm of body mass measured in grams ; B) senescence rate ($\omega$) in units of year$^{-1}$ against log body mass; and C) senescence rate against longevity ($z_{99.9}$). Longevity metrics $z$ and $z_{99.9}$ are, respectively, maximum lifespan observed in the wild, and time for loosing 99.9 % of a model cohort to mortality. Longevity for *P. albifrons* is represented as $z_{99.9}$ in both panels A and C.

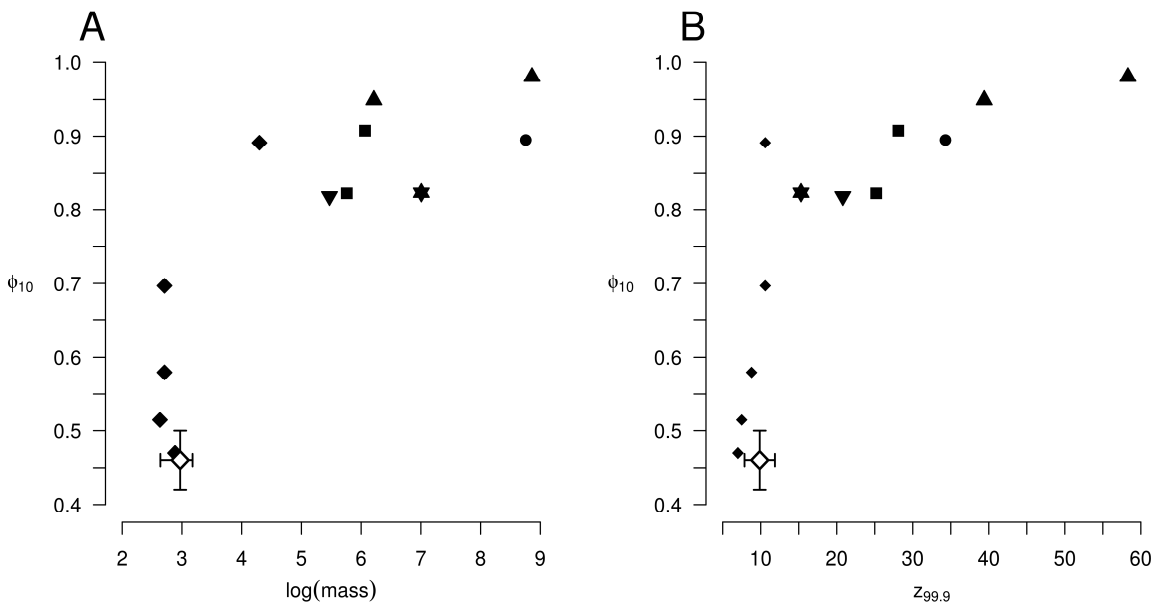


**Figure 3.** Survival probability of *P. albifrons* and twelve other bird species in contrast with longevity ($z_{99.9}$; A) and with the logarithm of body mass in grams (log(mass); B). The filled symbols represent data from wild bird populations published by Ricklefs (2010); the empty diamond represents *P. albifrons* parameter estimates obtained in this study, with 95% credibility intervals. Different-shaped filled symbols identify bird orders Anseriformes (square), Charadriiformes (circle), Accipitriformes (inverted triangle), Sphenicifomes (star), Procellariformes (triangle), and Passeriformes (diamond).

## 4. Discussion

Our results demonstrate that the studied population of *Pithys albifrons* does not show signs of actuarial senescence. The models with higher DIC values also corroborate with this results once the value of the estimated parameters represents null or negligible effects of age in survival. Comparisons with other bird species demonstrate that this may be an exceptional case. Although Weibull model did not have the lowest DIC value, the similarity of the results for this model with the ones for the exponential model permit us to use the estimated Weibull parameters for comparisons with other species. Senescence rate estimated for *P. albifrons* is the lowest ever registered for passerines (Ricklefs 2000). The senescence rate for the white-plumed-antbird is not related to its size or longevity and his exceptionally low rate of aging may be due to the fact that this is a very peculiar species.

The white-plummed-antbird is a species with an exceptionally slow pace of live and its peculiar life style may lead to very low metabolic expenses. The protracted and frequently suspended molt of this species leads to a very slow energy expenditure that can easily be supplied by the food intakes (Johnson and Wolfe 2012). *Pithys albifrons* also show no signs of territoriality or intra-specific competition (Willis 1981), avoiding metabolic expenses in defending territory or food sources. Although *Pithys albifrons* food resource is errant, this species has high mobility and can visit more than one ant swarm each day, looking for the best place to forage and inhibiting food shortage (Willis 1981). These behaviors may lead to a lower senescence rate in comparison with other passerines that does not have such slow pace of life. The senescence rate estimated for *P. albifrons* does not guarantee a high longevity for this species, though, and the longevity of this species is probably more related to the risky life strategies it takes.

*P. albifrons* is the distinctest bird of the also distinct ant-followers guild. Being considered a subordinate bird in this guild, *P. albifrons* individuals are expected to wait in the marginal areas for its food resource. This is not what happens and individuals from these species are frequently observed foraging between larger ant-followers and in the middle of the ant swarms (Willis 1981). This foraging strategy lead to frequent antagonistic encounters with larger birds and ants and increases age-independent mortality risk. The high mobility found for this species should also facilitate encounter with predators and, once again, increase the mortality risk.Longevity records are influenced by the population size and by the duration of the study that recorded the maximum lifespan. Although these bias can be accounted in models that compare longevity records, the fact that *P. albifrons* longevity is lower than what would be expected for its senescence rate leads us to discourage the use of longevity as proxy for senescence. Senescence comparisons are more reliable when senescence rate is used, since this value is calculated by the rate of survival variation with age for the whole population and not a record of only one long lived individual.

The small amount of evidences on actuarial senescence prevents us on making stronger assumptions about *P. albifrons* age-constant survival. Only the increase on the number of empirical evidences for actuarial senescence (or for the lack of it) would make easier to understand if *P. albifrons* is a real exception or if this pattern of aging is more widespread than what is expected. Posterior studies should focus on accumulating empirical evidences on senescence rates for other passerines. The model proposed by Colchero and Clark (2012) is a good way of using the huge amount capture-mark-recapture data available for investigating actuarial senescence. More investigation should be done in *P. albifrons* to understand if the lack of actuarial senescence is a rule for this species or if the other populations with different annual survival will show different patterns of aging. Other aspects

of senescence should also be investigated, such as reproductive senescence, to look for possible trade-offs that guarantee the age-constant survival in the white-plummed-antbird.

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## 4. Conclusão

Neste trabalho apresentamos evidências empíricas de ausência de senescência atuarial em uma espécie de passeriforme, *Pithys albifrons.* Apesar da taxa de sobrevivência desta ave não variar com a idade, esta espécie possui longevidade menor do que outras espécies com o mesmo peso. Este fato pode ser explicado pela baixa taxa de sobrevivência anual, a menor quando comparada com outras aves. Concluímos, então, que a falta de senescência atuarial nesta espécie é compensada por uma baixa taxa de sobrevivência.

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# AULA DE QUALIFICAÇÃO

## PARECER

Aluno(a): PEDRO VITOR RIBEIRO MARTINS
Curso: ECOLOGIA
Nível: Mestrado
Orientadora: Dra. Gonçalo Ferraz (UFRGS)

**Título**

**"Variação da sobrevivência com a idade no Papa-formigas-de-topete, Pithys albifrons (Aves: Linnaeus, 1766)."**

**BANCA JULGADORA**

| TITULARES: | SUPLENTES: |
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**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA – PPG ECO**

ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 07 dias do mês de Abril do ano de 2016, às 09h00min, no Auditório dos PPG's ATU/CFT/ECO – Campus III – INPA/V3, Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Jansen Alfredo Sampaio Zuanon**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o(a) Prof(a). Dr(a). **Luiza Magalli Pinto Henriques**, do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a). **Cintia Cornélius Frische**, da Universidade Federal do Amazonas - UFAM, tendo como suplentes o(a) Prof(a). Dr(a). Tânia Margarete Sanaiotti, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a). Albertina Pimentel Lima, do instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **PEDRO VÍTOR RIBEIRO MARTINS**, intitulado: "**EVIDÊNCIA DE SENESCÊNCIA EM UM PASSERIFORME TROPICAL: VARIAÇÃO DA PROBABILIDADE DE SOBREVIVÊNCIA COM A IDADE EM *PITHYS ALBIFRONS* (PASSERIFORME: SWAINSON, 1824)**", orientado pelo(a) Prof(a). Dr(a). Gonçalo Nuno Côrte-Real Ferraz de Oliveira Universidade Federal do Rio Grande do Sul – UFRGS. Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

- [x] APROVADO(A)
- [ ] REPROVADO(A)
- [x] POR UNANIMIDADE
- [ ] POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Jansen Alfredo Sampaio Zuanon _____

Prof(a).Dr(a). Luiza Magalli Pinto Henriques _____

Prof(a).Dr(a). Cintia Cornélius Frische _____

Prof(a).Dr(a). Tânia Margarete Sanaiotti _____

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