UNIVERSIDADE FEDERAL DO PARANÁ

SETOR DE CIÊNCIAS BIOLÓGICAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO

ANDRÉ MAGNANI XAVIER DE LIMA

CARACTERÍSTICAS POPULACIONAIS DE PASSERIFORMES NA REGIÃO SUBTROPICAL DO BRASIL EM RELAÇÃO AO PARADIGMA LATITUDINAL DO RITMO DE VIDA

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, da Universidade Federal do Paraná, como requisito parcial à obtenção do grau de Doutor em Ecologia e Conservação.

Orientador: Dr. James J. Roper

CURITIBA
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Ministério da Educação
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PARECER

Os abaixo-assinados, membros da banca examinadora da defesa da tese, a que se submeteu **André Magnani Xavier de Lima** para fins de adquirir o título de Doutor em Ecologia e Conservação, são de parecer favorável à **APROVAÇÃO** do trabalho de conclusão do candidato.

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O atrativo do conhecimento seria pequeno se,

no caminho que a ele conduz, não houvesse que vencer tanto pudor.

(Friedrich Nietzsche)

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SUMÁRIO

RESUMO

Teorias sobre a evolução de estratégias de vidas em aves classificam as espécies em dois grupos em relação ao balanceamento entre fecundidade e sobrevivência: entre ter estratégias de vida com maior investimento na reprodução (ritmo rápido), comum em zonas temperadas, ou na própria sobrevivência (ritmo lento), mais comuns na zona tropical. Entretanto, não há muitos estudos sobre a variabilidade de estratégias em regiões intermediárias, principalmente no hemisfério sul, como por exemplo, a região subtropical do Brasil. Neste estudo, a biologia reprodutiva de diversas espécies de Passeriformes desta região foi investigada por meio de três abordagens distintas para melhor entender a variabilidade das estratégias de reprodução e suas potenciais consequências para as taxas vitais de cada população. No primeiro capítulo, foram estudadas as características reprodutivas de uma espécie com origem e hábitos tropicais, baseado em três anos de marcação-recaptura e monitoramento de nidificações. No segundo foi explorada a relação entre os parâmetros reprodutivos e a influência destes na fecundidade entre diversas espécies, comparando-os com espécies de uma localidade na Argentina na mesma latitude. No terceiro, indivíduos de quatro espécies com estratégias de vida distintas foram monitorados por três anos, para investigar se a sobrevivência anual é de fato correlacionada à fecundidade. Como resultado, foi apresentado que uma espécie filogeneticamente tropical, quando habitando uma região subtropical, pode ter alguns componentes reprodutivos que remetem a uma estratégia de ritmo rápido, talvez motivados pela necessidade de se reproduzir mais rapidamente que seus parentes tropicais. Em uma escala mais ampla, variadas espécies em duas localidades subtropicais possuem padrões reprodutivos também variados, incluindo ambas estratégias, mesmo com uma clara limitação regional no período reprodutivo e consequentemente no potencial de fecundidade anual. Nestas condições, o tamanho da ninhada é o principal componente relativo à fecundidade na maioria das espécies de Passeriformes nesta região. Como consequência, a sobrevivência de adultos é inversamente relacionada ao tamanho da ninhada, evidenciando que as espécies nesta região enfrentam limitações energéticas, as quais podem ser também as responsáveis por favorecer diferentes adaptações locais em componentes biológicos importantes para o balanceamento das taxas de fecundidade e sobrevivência. Entretanto, outros fatores podem ser tão ou mais importantes que o tamanho da ninhada conforme cada grupo filogenético, aumentando a chance de ocorrência de vários padrões específicos de adaptação, definidos pela interação entre suas limitações filogenéticas e as interações com o ambiente em escala regional e local. Esta grande variabilidade no padrão de adaptação em escala local/regional é um fator importante a ser considerado para a entender evolução das diferentes estratégias de vida das aves.

Palavras-chave: aves, ecologia, Floresta Atlântica, reprodução, sobrevivência, subtropical.

ABSTRACT

Life history theory has classifying species into two groups according to the trade-off among fecundity and survival: those that invest more in reproduction (fast-paced), common in temperate areas, and those that invest more in their own survival (slow-paced), more common in tropical areas. However, few studies were done in intermediary zones, especially in southern hemisphere, like the subtropical area in Brazil. Herein, breeding biology of several passerines in this region was studied in three different approaches to understand variability of breeding strategies and the consequences for population vital rates. In the first chapter, breeding traits of a tropical-origin bird were investigated by mark-resighting and nesting monitoring during three years. In the second, sources of variation in breeding components and consequences for fecundity of several species were explored, while comparing it with species in the same latitude in Argentina. In the third, adult survival of four contrasting and unrelated species was estimated to test whether survival would be inversely correlated with fecundity. The tropical-origin species when inhabiting subtropics had some breeding traits that resemble to fast-paced strategy, perhaps due to time constraints when comparing with their tropical relatives. In comparisons among subtropical locations, several species had a wide variety of breeding patterns, which includes a variety of fast-slow components, despite a clear regional limitation of breeding season length in Argentina. In this context, the clutch size is the most important fecundity component for most passerines, independent of location. Hence, adult survival is inversely related with fecundity, indicating that species in this region are under energetic constraints, which may favor the best local adjustments for the fecundity-survival trade-off of each species. However, other factors might be as well as or even more important, depending upon the *taxa*, and each species may have a unique sort of adaptation, according to their phylogenetic inertia and the local variation in the environmental interaction. This pattern is important and should be more incisively included in the life history theory.

Key words: Atlantic forest, birds, breeding, ecology, survival, subtropical.

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Floresta Atlântica em um dos locais estudados, Morretes, Paraná.

PREFÁCIO

O tamanho e as características de uma população variam em função do tempo, o que tem intrigado pesquisadores desde os primórdios da biologia. Darwin, em sua obra-prima "A origem das espécies" (1859), declaradamente influenciado pelas teorias populacionais de Thomas Malthus (originalmente publicadas em 1798), é enfático sobre a potencial progressão geométrica na produção de novos indivíduos em qualquer população. Darwin também já sugeria que a elevada capacidade de reprodução deveria estar relacionada à taxa de perda de indivíduos em cada população. Desta forma, os dois principais componentes que determinam como uma população varia ao longo do tempo foram por ele explicitamente apontados: fecundidade e sobrevivência.

Analogamente, o conhecimento teórico sobre as propriedades de cada componente populacional e o conhecimento prático sobre a melhor forma de analisá-las evoluiu exponencialmente, com um acúmulo de estudos em variadas áreas da biologia e ecologia. Entre aqueles que podem ser considerados primordiais para a ecologia populacional moderna (Real e Brown 1991), destacam-se os estudos de Volterra (1926), Leslie (1945) e Cole (1954), sobre os fundamentos matemáticos das dinâmicas populacionais.

Desde então, as aves, em conjunto com insetos, têm sido um dos principais organismos utilizados como modelo para o desenvolvimento de teorias sobre a evolução das diferentes estratégias de vida. Na metade do século 20, muitos componentes da ecologia populacional de aves já haviam sido estudados e foram reunidos e analisados por Lack (1954, 1966), os quais contribuíram de modo singular para o embasar diversos estudos sobre mecanismo de regulação em populações em geral (Ricklefs 2000). Outro exemplo, MacArthur (1958) estudou espécies de Parulidae para sugerir que a partilha de recursos entre populações de espécies de um mesmo gênero era necessária para que estas espécies pudessem coexistir, conceito que se estende a praticamente todas as comunidades biológicas.

Mais recentemente, devido ao maior conhecimento teórico e aos avanços tecnológicos, padrões populacionais têm sido investigados de modo mais preciso e abrangente. Já é possível rastrear o deslocamento de indivíduos, em todas as escalas possíveis (Bouten et al. 2013), estimar parâmetros populacionais controlando por efeitos intrínsecos ou extrínsecos (White e Burhnam 1999) ou monitorar condições fisiológicas em larga escala com precisão (Londoño et al. 2014). Como consequência, novos conhecimentos empíricos a respeito da história de vida em aves surgem com maior frequência a cada ano, fomentando e melhor organizando previsões advindas das teorias de evolução das estratégias de vida.

Atualmente, os principais padrões de variação destas estratégias têm sido correlacionados à variação do ritmo metabólico dos organismos, e que também possui tendências latitudinais de variação (Sæther e Bakke 2000, Ricklefs e Wikelski 2002). Em resumo, espécies em áreas tropicais tendem a possuir um metabolismo de ritmo mais lento quando comparadas às espécies que habitam as zonas temperadas (Wiersma et al. 2007, Londoño et al. 2014), e por consequência, durante sua vida também tendem a investir proporcionalmente menos em reprodução do que na própria sobrevivência (Ghalambor and Martin 2001, Ghalambor et al. 2013), por exemplo, gerando proles menores mas com maior potencial de longevidade nos trópicos (Gill and Haggerty 2012).

Entretanto, estudos (populacionais e sobre a biologia de espécies em geral) no hemisfério sul são mais escassos que no hemisfério norte, e os que estão disponíveis indicam que muitas previsões não seriam aplicáveis para ambos os hemisférios (Martin 1996, 2004, Lloyd et al. 2014). A América do Sul inclui-se nesta situação e é possível que muitos padrões biológicos sejam explicados de modo único neste continente devido a seu singular histórico geológico e biogeográfico (Ricklefs 2002). Por exemplo, muitos passeriformes sul-americanos possuem uma distribuição geográfica que abrange mais de um tipo de ambiente ou condição climática em escala regional, por exemplo, comumente habitando desde áreas tropicais até áreas em zonas temperadas (Ridgely e Tudor 1994a, 1994b). Nestas condições, os principais fatores que influenciam na estratégia de cada espécie devem estar associados à sua plasticidade fenotípica. Ou seja, a adaptação de cada *taxa* deve ser resultado da influência conjunta da filogenia (Pienaar et al. 2013), histórico biogeográfico (Carnaval et al. 2014), padrão metabólico (Ricklefs and Wikelski 2002) e plasticidade frente variações locais (Ghalambor and Martin 2001, Pienaar et al. 2013).

Neste estudo, foram levantados dados inéditos sobre os principais componentes populacionais de várias espécies de passeriformes que habitam o leste do Estado do Paraná, cuja área é situada na região subtropical da América do Sul. Em três diferentes abordagens, foram investigados se caracteres populacionais apresentariam um padrão teoricamente esperado, e quais poderiam ser ocasionados devido às singularidades regionais de áreas de transição entre o típico clima tropical e o temperado. *A priori*, a previsão era de que cada espécie revelaria uma estratégia de vida específica, conforme as combinações de suas variáveis populacionais, e que, portanto, não poderiam ser classificadas por uma simplificada dicotomia entre ritmos lento e rápido. No primeiro capítulo, foram estudadas as características reprodutivas individuais de uma espécie florestal de uma família tipicamente tropical, baseado em três anos de marcação-recaptura e monitoramento de nidificações. No segundo, são apresentados dados reprodutivos de diversas espécies, em mais de 1200 ninhos monitorados. Com estes dados foi explorada a relação entre os caracteres reprodutivos e a influência destes na fecundidade e respectivas estratégias entre os vários *taxa*, comparando-os com espécies de uma localidade na mesma latitude na Argentina (Auer et al. 2007). Por fim, o terceiro capítulo busca apresentar estimativas de sobrevivência para quatro espécies com estratégias de vida distintas, para as quais indivíduos foram monitorados por três anos para investigar se a sobrevivência anual estaria de fato correlacionada a componentes da fecundidade.

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CAPÍTULO 1

As características reprodutivas de uma população subtropical da Choquinha-de-garganta-pintada (*Rhopias gularis*: Thamnophilidae) podem ser associadas a um ritmo de vida lento?

Momento da eclosão em um ninho da Choquinha-de-garganta-pintada (*Rhopias gularis*).

Running head: Reproduction in subtropical Star-throated Antwrens

Are the breeding traits in a subtropical population of the Star-throated Antwren (*Rhopias gularis*: Thamnophilidae) slow-paced?

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ABSTRACT

The large family Thamnophilidae (antbirds, suboscines) comprises mostly tropical American species that seems to have a slow-paced life-history. We monitored reproduction of individual pairs of the Star-throated Antwren (*Rhopias gularis*) in subtropical Brazil during three breeding seasons to investigate whether breeding components of this population are adjusted for a more temperate climate and the implications of such adjustments for life-history theory. The antwren is socially monogamous, year-round territorial and incubation (18 d) lasts longer than the nestling stage (13 d), typical of tropical species. More similar to birds of temperate latitudes, the breeding season was relatively short (< 120 d), while nesting success was high (≤ 41%). Particularly, only males were recorded building nests, and reusing nests and nest-sites was not uncommon, both of which resembled energy and time-saving behaviors. Nest survival during incubation within each year declined over time in the season and was low as usual for tropical birds. Instead, nestling survival varied among years, but was constant and higher than incubation. As a consequence, early nests tended to be more successful than late nests, and once eggs hatched, likelihood of success was high. Also, once a pair successfully fledged young, no further nests were attempted within any reproductive season by that pair, even though other pairs can have successful nests later in the season, resulting in averaged annual fecundity of 1.3 fledglings pair^{-1} year^{-1}. We argue that this population of Star-throated Antwren seems to do facultative energy investments for a single brood per year resulting in a combination of uncommon breeding characteristics, which would not be the expected local adaptation of a slow pace species in response the subtropics constraints. We suggest that patterns of local adjustment of life-history traits may be quite variable among South American birds due to their widespread geographical distributions within unique regional climates.

INTRODUCTION

Tropical forest birds share a syndrome of reproductive patterns, including longer breeding seasons (Baker 1939, Griebeler et al 2010), longer nesting cycles (Ricklefs and Brawn 2013), smaller clutch sizes (Skutch 1985) and lower nesting success (Ricklefs 1969) when compared to birds at high latitudes (Roper 2005, Griebeler et al 2010, Roper et al. 2010, Hill and Cooper 2015). These and several other traits are referred to as the "slow" strategy in the slow–fast gradient of life history traits (Sæther and Bakke 2000, Ricklefs and Wikelski 2002, Wiersma et al. 2007, Wiersma et al. 2012), in which variation of life-history traits is correlated with latitude and altitude (Martin 1996, Martin 2004, Hille and Cooper 2015). However, evidence of a latitudinal correlation in life history strategies has a northern hemisphere bias, because fewer species and families have been studied in the south than in the north (Martin 1996, Stutchbury and Morton 2001, 2008, Martin 2004). Furthermore, this latitudinal pattern in life history traits is still controversial (Gill and Haggerty 2012, Lloyd et al. 2014, Martin 2014) and does not seem to be generalizable to much of South America (Martin et al. 2000a, Ghalambor and Martin 2001, Auer et al. 2007, Jetz et al. 2008, Lima and Roper 2009a).

South America has a wide variety of climatic regimes and vegetation zones that also encompass a wide latitudinal variation, resulting in distinctive regional bird communities (Ricklefs 2002). Several species of birds in South America have geographic ranges that include tropical and subtropical (and even southern temperate) latitudes (Ridgely and Tudor 1994a, 1994b), while reproductive ecology of most of these species is unknown or poorly studied (Marini and Garcia 2005). For example, Thamnophilidae (Suboscines) is a large and strictly American family of mostly tropical understory forest insectivorous, permanently territorial and socially monogamous birds that mostly use open cup nests (Ridgely and Tudor 1994b, Morton and Stutchbury 2000, Zimmer and Isler 2003, Reinert et al. 2012). Thus, these life history traits along with long breeding seasons (Roper and Goldstein 1997, Roper 2005, Roper et al. 2010, Reinert et al. 2012) and high adult longevity (Bornschein et al. 2015) place these species in the slow-paced end of the spectrum. However, the reproductive ecology of most species in Thamnophilidae are still unstudied and many are widely distributed geographically (Zimmer and Isler 2003). Considering the wide potential variation in the combination of life-history traits in South America (Ricklefs 2000, 2002), the extent to which the slow-fast continuum is constrained by responses to local conditions remains poorly known (Ricklefs and Wikelski 2002, Pienaar et al. 2013).

The Star-throated Antwren (*Rhopias gularis* Spix 1825) is a Brazilian and Atlantic Forest endemic and monotypic thamnophilid that has a mostly tropical distribution extending partially into the subtropics (Ridgely and Tudor 1994b). This antwren is relatively common in montane and coastal Brazilian Atlantic Forest, from southern Bahia (14ºS) in the north, to Santa Catarina (27ºS) in the south (Ridgely and Tudor 1994b, Zimmer and Isler 2003, Belmonte-Lopes et al. 2012). This antwren forages low in the understory and on the forest floor (Willis 1984) and seems to be resident and territorial (Zimmer and Isler 2003). The nest is an open cup of rootlets in the fork of a low branch in dense vegetation near streams (Zimmer and Isler 2003). Aside from these details, the reproductive ecology of this species remains nearly unknown.

Here we describe breeding traits (mate and site fidelity, nesting cycle, clutch size, breeding season) and estimate daily nest survival rate and overall annual reproductive success (annual fecundity) of the Star-throated Antwren in subtropical Brazil. We used an individual-based approach (Martin 1986, Clutton-Brock and Sheldon 2010) to test if their breeding traits would be representative of a slow pace or if more typical fast paced traits could be recognized, comparing with related species. We predicted that breeding patterns of subtropical populations of this thamnophilid may comprise a mix of slow and fast strategies because they are in the subtropical extreme of the species geographic distribution, where tropical climate is not as stable as in tropical zones. So, if all breeding traits resemble a slow pace strategy, the Star-throated Antwren would not have reproductive adaptation to subtropical climate conditions, and subtropical populations should return very low annual fecundity rates. However, if one or more breeding traits have plasticity and are adjusted for subtropical climate constraints, the antwren should have similar or an even greater fecundity rate comparing to more tropical species.

Specifically, we investigated (1) if the antwren is a typical socially monogamous and long-term territorial or if any sort of plasticity in mate and site fidelity could be recognized (Morton et al. 2000, Lima and Roper 2009a, Chalfoun and Martin 2010), (2) whether the nesting cycle would be as long as or shorter than related species (Ricklefs and Brawn 2013), (3) whether clutch size would be fixed like most known species, or variable like in Variable Antshrike – *Thamnophilus caerulescens* (Uejima et al 2004), (4) whether breeding season would be as long as other related species (Lima and Roper 2009a, Griebeler et al. 2010), (5) whether daily nest survival rates would be as low as in related tropical species (Roper 2005, Roper et al. 2010), and (6) whether number of annual nesting attempts and annual fecundity would be similar or lower than related tropical species (Roper et al. 2010). Thus, we expected to find out at least one breeding trait that could represent a breeding plasticity concerning the slow-fast paradigm, like temporary monogamy, short nesting cycle, short breeding season, a variable clutch size larger than two eggs and high reproductive success, in order to balance potential low annual fecundity.

METHODS

Study site

We studied breeding of the Star-throated Antwren in subtropical Brazilian Atlantic Forest, in the state of Paraná (25.36ºS, 48.48ºW, 450 – 600 m elevation, Figure 1). The study site comprises ~80 ha plot in continuous and well-preserved montane forest on private property in Morretes county. During the summer (January – March) climate in the forest resembles typical humid tropical forest climates, with maximum daily temperature reaching up to 41°C in a monthly average of 30°C and precipitation of 250 mm. However, due to occasional cold fronts, minimum temperature may decrease to 15^{o}C in February, the hottest month, or near 10^{o}C during the months of equinox (summer minimum monthly average = 20^{o}C). In the winter (June – August) cold fronts are more frequent and longer, and average maximum temperature is lower (23^{o}C) than summer, however, maximum temperature may occasionally reach ~35^{o}C. Minimum temperature may decrease under zero (-1^{o}C, average = 13^{o}C month^{-1}) and monthly average of precipitation decrease as well (120 mm). Thus, overall amplitude in annual temperature is 42ºC (-1ºC – 41ºC) and mean annual rainfall is ~2000 mm without a dry season (Maack 2002, IAPAR 2015). Climate according to updated Köppen-Geiger classification is warm temperate (C), fully humid (f) in the transition between hot summer (a) – Cfa, and warm summer (b) – Cfb (Kottek et al. 2006).

Data collecting

Field work was conducted during approximately 22 days per month during breeding seasons (August – March) and seven days per month during the rest of the year, from June 2011 to March 2014. We searched for pairs and nests while walking in the study area, finding individuals by sight and vocalization and using standard methods for finding and monitoring nests (Martin and Guepel 1993). The approximate location of each potential breeding territory was based on finding adult and noting their locations using GPS (Garmin GPSMAP 60). During searches, if adults were not quickly found (< 60 min) in a potential or known territory, we then used playback of vocalizations to attract birds, at most three times, to minimize potential behavioral interference due to playback (Lima and Roper 2009b). Once nesting behaviors were observed (*e.g.* building, feeding, flushing, single mate response to playback*),* we searched more intensively or followed the birds until nests were found. Once the active nest was found, we captured birds near their nests using mist-nets. Captured birds were banded with metal and unique combinations of color bands following standards of the Brazilian bird banding agency (CEMAVE/ICMBio). We searched for each banded pair in their expected territories until finding them at least once weekly through the breeding season.

Data analysis

Monogamy and territoriality.- Patterns of monogamy and territoriality (*i.e.* mate and site fidelity) were determined by following pairs over time (Martin and Guepel 1993). Birds were considered socially monogamous if they remained with the same pair until one member of that pair disappeared (*i.e.* the individual was no longer found within the study area) and permanently monogamous if there is no mate changes through the years. We considered the birds territorial if within any given season sightings of pairs were recorded within exclusive areas (*i.e.* no overllaped sighting records). We considered them as permanently territorial if in subsequent years they were found within the same area (*i.e.* <30 m from previous nests), except in the event of losing a mate. We georeferenced all locations of banded birds and nests using GPS (Garmin GPSMAP 60) and we plotted spatial data in MapSource (version 6.16.3, Garmin Ltd.). For pairs with more than one nesting attempt we calculated the distance between nest locations within pairs (within a season and between years) and between adjacent pairs. The study area has mainly a steep relief and the vertical dimension must be important for estimating territoriality of antwrens. Because we were unable to get very accurate location coordinates, thus, we did not attempt to estimate territory size.

Nesting cycle.- To describe the length of nesting cycle stages (*i.e.* construction, laying, incubation, hatching and nestling stages), we noted the exact dates of events as often as possible. Nests found during construction were observed for one hour intervals, once a day, at which time we noted if the pair was already banded and how many times and which individual carried material and actively built the nest. Nests were considered complete once the inside of the cup was lined and construction was no longer observed. Once the nest was complete, daily visits determined when eggs were laid. After egg laying, nests were visited every 2 – 3 days, except for daily visits to determine exact dates of hatching and fledging. Nestlings were color banded at 10 – 11 days after hatching. Successful nests were those that fledged at least one young, confirmed by subsequently observing parents feeding fledglings soon thereafter.

Breeding season.- Breeding season length (hereafter BSL) was the time interval (in days) between the date of the first egg being laid in the season and that of the first egg being laid in the last nest found during each season. For comparison, we estimated breeding season intensity (Ricklefs and Bloom 1977, hereafter RB), which controls the BSL for synchronicity among pairs. We also estimated breeding season intervalby excluding 5% of first and last nests (Auer et al. 2007, hereafter AU), which may inform on extreme data distribution. We noted daily minimum and maximum temperatures during the years of the study from the nearest climatic station (~15 km, Morretes Station – SIMEPAR), to illustrate the climatic variation during the breeding season.

Reproductive success.- To estimate daily nest survival rate (DSR) we fit six models (in addition to the constant model) that we felt *a priori* were most likely to explain nesting success: 1) time (survival probability varies over the breeding season), 2) year of study (survival probably varies between years for any reason), 3) nest age (day since eggs laid may influence survival; Skutch 1985, Roper and Goldstein 1997, Grant et al. 2005), 4) nest attempt (first *versus* renests, Segura and Reboreda 2012), 5) interaction between nest age and time in the season (Grant et al. 2005, Segura and Reboreda 2012, Du et al. 2014), and 6) additive effect of nest age with year (Styrsky and Brawn 2011). The variables of the model that best fit our data (considering the entire nest cycle interval) were again used to test for differences in factors influencing each nesting stage (*i.e.* model selection for incubation and nestling separately). We estimated nest age when nest was found with eggs by egg opacity (Enemar and Arheimer 1980) and, when possible, age was confirmed by backdating from hatching dates. When a nest was found with nestlings, nestling age was estimated by size and weight in comparison to known-age nestlings (Segura and Reboreda 2012). DSR for all models was estimated with the logit-link function in the nest survival model of the program MARK (White and Burnham 1999), using the RMark interface (Laake 2013) in the program R (R Core Team 2013). We used Akaike Information Criterion for small samples (AIC_c) to compare models, using log-likelihood values and model weighted probability (w_i) for inferences on best models (Burnham et al. 2011). Annual fecundity is the sum of fledglings produced each year by each pair.

Results presentation.- We refer to each breeding season by the year in which it started because the breeding season overlaps the transition between years. Mean ± SD are shown for normally distributed data, otherwise we provide the total range and median. We reported real or beta parameter estimates of best models depending upon the type of covariate (*i.e.,* categorical or continuous) and 95% confidence intervals.

RESULTS

Monogamy and territoriality

We captured and color banded 27 males and 29 females, which comprised 39 breeding pairs during the study. From this total, in 2011, 16 pairs were banded (all individuals but one female) and 34 nest attempts monitored. Another four males and eight females were banded in 2012, with 12 males and 8 females from the preceding year still in the study area, for a total of 16 pairs and 38 nests being monitored. In 2013, another seven males and six females were banded and 12 males and 12 females remained from the previous years (for 19 pairs and 36 nests being followed). We found a grand total of 108 nest attempts during the whole study.

Every year, at least one mate of each pair was found every week through the breeding season. When neither one mate nor the pair was found within a two-week interval, they were no longer found in the study area. All pairs remained together within each season, five pairs banded during 2011 (31%) were together in 2012, and seven pairs in 2012 (40%) remained together in 2013. Two of these pairs were found in the same area from the previous year during all three breeding seasons (pairs D and L, Figure 2). Six males and four females were seen at the beginning of a breeding season with a new mate, after the disappearance of their previous mate, in the same territory of the previous year. Only one clear divorce occurred of a pair that successfully bred in 2011 and 2012 (once each year), when in 2013 both individuals had new mates and nested in adjacent territories.

All renesting attempts of 20 pairs were within 76 m from any previous attempt (mean = 39.2 ± 19.5 m). The minimum distance between active nests in adjacent territories was 84.7 ± 51.2 m (min = 26 m, in 24 pairs with active nests in adjacent territories). Another 19 pairs attempted only one nest during the study and disappeared or changed mates (Figure 2).

Nesting cycle

Nests found in early construction and checked daily (n = 16) were completed in 3 – 8 days (median = 4 d). Fourteen banded males were found during nest construction, 13 of which were observed during two days (n = 27 h of total observation time). Only males were observed building in a total of 83 events. Females were nearby in 37 events, but they did not participate in nest construction. Nests were always found low in the understory (25 – 130 cm) and 88% were in streams margins (< 2 m, n = 95), while all nests were always less than 14 m from streams, usually in steep margins. We did not identify plant species used as nest substrates, however, apparently any species with horizontal and forked branches or sufficiently strong leaves at low height may be used for nesting. Nests sites (*i.e.* the particular plant in which nests were found) were reused five times, by five pairs, for subsequent nest attempts. Birds can also reuse nests: two pairs reused their own nests in subsequent breeding attempts and one pair laid eggs in a nest built by a different pair in the previous year. Males may feed females prior to nesting, what we observed once in two pairs.

Egg-laying occurred 2 – 9 d (median = 5 d, n = 26) after nest construction ended, except in two nests, in which the first egg was laid 32 and 36 d later. Second eggs were laid 1 – 3 d after the first (17 after 1 d, 4 after 2 d, and 1 after 3 d). There was no variation in clutch size, which had always two eggs in 80 nests. Due to imperfect observations, we could not ascertain whether two nests that had only one egg were indeed one-egg clutches or the consequence of predation.

Both parents incubate eggs but only females were seen incubating at dusk or dawn (14 nests observed once each). Incubation on- and off- bouts may last more than two hours (personal observations during capturing). The interval from laying the first egg to hatching was 17 – 19 days (median = 18 d, n = 19). Hatching was asynchronous, with one (n = 9) or two days (n = 5) between hatching. We could not determine if hatching followed the laying sequence. The nestling stage lasted 12 – 15 days (median = 13 d, n = 16, Table 1). After fledging, all fledglings were found with adults in their natal territory (mean of first observed day = 1.4 ± 1.2 d, in 28 successful nests of 23 pairs), and they were subsequently found for a variable number of days (mean of last observed day = 16.6 ± 14.5 d, min = 5 d, max = 75 d). Also, seven of these pairs were seen apparently out of their territory boundaries (distance range = 108 – 193 m, median = 144 m), and three of them were never found again.

Of those 23 successful pairs, we found a total of 16 pairs foraging together without their offspring 65.6 ± 14.9 d after the fledging date, similar to typical non-breeding season behavior (after 21 successful nests, 5 pairs were seen after successful nests in more than one year). None of those 16 successful pairs showed any signs suggesting they were attempting another nest within the same breeding season, after their successes. This includes seven pairs whose young fledged prior to the end of December, while other nests were initiated after that time (n = 17) and as late as January 12. Renesting occurred after 39 nesting failures, which began 1 – 31 d after failure (median = 8 d). The average of nesting attempts was 2 attempts pair^{-1} year^{-1} (range = 1 – 5) in 78 attempts of 28 pairs.

Breeding season

The first signs of nest construction were in September 14. In each year, the earliest egg was laid on September 18 in 2011, September 19 in 2012 and October 1 in 2013. The last egg was laid on January 7 in 2012, January 12 in 2013 and January 4 in 2014. Thus, BSL was 110 d in 2011, 116 d in 2012 and 96 d in 2013 (three year average = 107 d, total range = 117 d). Egg laying peaked in October when 47% of the eggs were laid (n = 74 eggs of 37 nesting attempts with known fate, see below). All first nest attempts of all pairs begun prior to 15 November (n = 39), no longer than 58 d after the beginning of the breeding season (Figure 3). Breeding season intensity estimated by RB resulted in 96 d of breeding activity in 2011, 77 d in 2012 and 99 d in 2013 (three year average = 91 d). Breeding season interval by AU was 95 d in 2011, 102 d in 2012, and 88 d in 2013 (three year average = 98 d).

Reproductive success

Of the 108 nests, 28 of 78 nesting attempts of known fate were successful (36%), in which 12 of 39 first nest attempts were successful (31%). Seventeen nests were never completely built, eggs were never laid in nine nests, and four nests had uncertain fates due to incomplete observations, all of which was not included in further analysis. The apparent annual success was 21% in 2011 (6 of 28 attempts in total), 52% in 2012 (12 of 23), and 37% in 2013 (10 of 27). In most (86%) failed nests eggs or young simply disappeared and was considered predation (43 of 50 failures). One nest failed due to a falling branch and six nests were abandoned during incubation. Pairs of three of these abandoned nests were never seen again but the other three pairs remained in their territory and renested. Eight partial predation events resulted in three later failures and five successes.

In modeling DSR, two single factor models (year and nest age) and their additive model had the lowest AIC_c values and together had w_i = 0.70 among all models (Table 2). In separating the nest age into incubation and nestling stages, and then modelling constant, time, year, and the additive effect of time with year, time was the most important factor during incubation (w_i = 0.58, β = -0.012 ± 0.006) and year was the most important factor during the nestling stage (w_i = 0.63, Table 3). Thus, during incubation, probability of successfully hatching varied from 46% early in the season (DSR = 0.958 ± 0.015) to 4% late in the season (DSR = 0.841 ± 0.061). And, during the nestling stage, probability to fledge varied between 40 – 90% because DSR was lower in 2011 (0.936 ± 0.025 day^{-1}) in comparison with 2012 and 2013 (DSR = 0.991 ± 0.007, Table 4, Figure 4).

A total of 51 fledglings of 23 pairs were produced during the three-year interval, of which 10 were in 2011 (0.36 fledglings $nest^{-1}$), 21 in 2012 (0.91 fledglings $nest^{-1}$) and 20 in 2013 (0.74 fledglings $nest^{-1}$). Annual fecundity over all nests with known fate was 1.30 ± 0.45 fledglings $pair^{-1}$ (0.71 ± 0.51 in 2011, 1.31 ± 0.29 in 2012, and 1.42 ± 0.43 in 2013). Annual success varied among pairs such that, in ten pairs that were together at least during two years, two were successful once each year in their first (and only) nest attempt each year (pairs J and V, Figure 2). One pair was successful each year with their second nest attempt (pair E). Five pairs were successful with one attempt in one year, and two in another (pairs B, G, O, R, U). One pair attempted three nests unsuccessfully in their first year, and were succeeded in their first attempts in the next years (pair L). Other (pair D) failed in all four attempts in the first year and in one attempt (plus two nesting attempts in which eggs were not laid) in the second year, and was successful only in the single attempt of the third year.

DISCUSSION

Breeding ecology in this subtropical population of the Star-throated Antwren comprises a mix of slow and fast life-history traits, thus suggesting that some traits may be in response to variable conditions in subtropics. Slow traits included social monogamy, permanent territoriality, small and fixed clutch size and slow development rate during nesting cycle. On the other hand, the short breeding season with few breeding attempts each year, great nestling success, and single success per year are similar to temperate, and usually fast-paced, birds. These reproductive patterns suggest that this antwren, despite the tropical origin, respond to variation in environmental conditions by increasing investment for a single annual reproduction. This behavior is in an opposite direction to the typical low investment of slow-paced and tropical birds with long breeding seasons.

Monogamy and territoriality

Evidence suggests that the Star-throated Antwren is socially monogamous and year-round territorial, as are Thamnophilids in general (Zimmer and Isler 2003). All but one changes in pairs occurred following disappearance of the mate. In the single example of divorce, both new pairs went on to attempt new nests, suggesting disappearances could be more related with mortality and independent of nest fate and sex. Apparently, in other thamnophilids, lower rates of mate-switching also occur (*Myrmotherula fulviventris*, Greenberg and Gradwohl 1997, *Thamnophilus atrinucha*, Roper 2005, *Formicivora acutirostris* – Reinert 2008, *Myrmeciza exsul* – Woltmann and Sherry 2011, but see Morton et al. 2000). Thus, general patterns of mate and site fidelity in the Star-throated Antwren are those expected by phylogeny.

Nesting cycle

The fixed clutch size of two eggs is typical of thamnophilids (but see Skutch 1969, Zimmer and Isler 2003) and seems also constrained by phylogeny in the Star-throated Antwren (Pienaar et al. 2013). Thus, clutch size is not free to vary as in other temperate birds, limiting their breeding traits to other means in which they might vary to fit local conditions. Small clutches are a slow-pace breeding component because they require less energetic demand than larger clutches and the difference favors individual survival (Ricklefs and Wikelsi 2002).

Incubation lasts longer (18 d) in the Star-throated Antwren than in most thamnophilids (< 16 d), whereas the nestling stage is similar (~13 days; Skutch 1969, Oniki 1975, Roper and Goldstein 1997, Zimmer and Isler 2003, Reinert 2008, Roper et al. 2010, Bernardon et al. 2014). This may indicate reduced attentiveness during the incubation in comparison with the nestling stage, such that adults avoid risking their own survival at a time when the risk is relatively high (Ghalambor and Martin 2001, Fontaine and Martin 2006, Ghalambor et al. 2013) and the reduced attentiveness results in longer incubation intervals. Then, as the probability of nesting success increases as the nest gets closer to fledging, attentiveness may increase because the future reproductive value of the young is also rapidly increasing.

Two nesting traits of the Star-throated Antwren may also suggest an adjustment to allocate energy in a limitant environment, although it is not possible to categorize such adjustment like adaptation or plasticity due to the absence of data from northern populations. 1) Apparently only males build nests and 2) nests and nest-sites may be reused, including nests that were built by other male. In the family Thamnophilidae, studies that address nest construction showed that both sexes build nests (Reinert 2008, Lara et al. 2012), and in some species females may build at a slower rate than males (Skutch 1969, Zimmer and Isler 2003, Reinert 2008, Zyskowski et al 2008). We suggest that with male-only (or male-mostly) nest construction, the male would allow the female to conserve energy, thereby permitting more rapid nesting or renesting.

Reusing nests and nest-sites is uncommon in passerines (Bergin 1997, Cavitt et al. 1999, Aitken et al. 2002) but is not unknown in thamnophilids (*Hylophylax naevioides* – Styrsky 2005, *Formicivora acutirostris* – Reinert 2008). However, using nests built by others was not previously reported in the Thamnophilidae. Reducing construction time by using already-built nests allows more rapid nesting and renesting (Cavitt et al. 1999). Nest-site limitation (Redmond et al. 2007) could explain nest-site reuse, although appropriate nest-sites near creeks seem to be unlimited, but would not explain nest re-use. Thus, we suggest that the combination of male-only nest construction and nest reuse are both time-saving behaviors that may effectively speed up the nesting process (Lens et al. 1994, Moreno et al. 2011). These behaviors may increase the potential fecundity by increasing the odds for a successful nesting due to reduced exposure (Styrsky and Brawn 2011, Robertson and Olsen 2015) or by allowing more attempts within each season (Roper 2005, Roper et al. 2010).

The period of post-fledging parental care in the Star-throated Antwren seems to last almost two months, as in other thamnophilids (Willis 1972, Reinert 2008) which may also be longer, from 3 to nearly 6 months in the tropical Western Slaty Antshrike (Roper et al. 2010). Extended post-fledgling parental care is a slow-paced trait that must increase juvenile survival probability (Russell 2000, Grüebler and Naef-Daenzer 2010, Tarwater and Brawn 2010), which may outweigh the benefits of repeated nesting (Roper 2005, Roper et al 2010).

Breeding season

The breeding season is relatively short in the Star-throated Antwren. In the same region, other thamnophilids have longer breeding seasons (the Marsh Antwren *Formicivora acutirostris*, ~175 d, Reinert 2008, Reinert et al. 2012, the Variable Antshrike *Thamnophilus caerulescens*, ~150 d, Uejima 2004). In central Brazil, where seasonality includes a dry season, BSL of the Band-tailed Antbird (*Hypocnemoides maculicauda*) is similar to the Star-throated Antwren, but the timing of breeding is different and clearly not associated with similar climatic conditions (Pinho et al. 2009). Other species of tropical thamnophilids in Panama had much longer seasons, from 170 d to full-year breeding (Roper and Goldstein 1997, Roper 2005, Roper et al., 2010, JJR unpublished data). Thus, BSL in the Star-throated Antwren was shorter than most typical tropical thamnophilids and seems to be locally adjusted, in contrast to the fixed clutch size.

The beginning of the breeding season of the Star-throated Antwren began more or less at the same time as other sympatric forest passerines (Zimmer and Isler 2003, Lima and Roper 2009a, Repenning and Fontana 2011). All first nest attempts began within the first 60 days (almost half) of their entire breeding season interval ($\leq$ 116 d). Breeding synchrony within populations in birds tends to increase with seasonality (Griebeler et al. 2010, Rose and Lyon 2013), especially if photoperiod is a cue for timing of breeding (Wikelski et al. 2000), and must contribute for this early peak in nesting attempts. Nesting initiation seems correlated with rising temperatures (greater than 30^{o}C, Figure 3), that might be associated with increased food abundance in the subtropics

(Wyndham 1986, Oppel et al. 2013). In addition, because of the increasing rate of nest failure over time, early nesting should be also favored due to greater nest success. Thus, beginning of breeding season may result from complex and correlated physiological and environmental factors, which require further study for understanding each factor independently.

While the earliest successful nests finished with time remaining in the breeding season to attempt another nest, after success pairs never renested within the same breeding season. Yet, even with nest failure, time remaining for a successful nest was often available for pairs that no longer attempted additional nests. Limitations in individual productivity may be caused by variation in general predation risk (Ghalambor and Martin 2001, Fontaine and Martin 2006) and by decline in food abundance (Lepage et al. 1998, Ricklefs 2010, Borgmann et al. 2013). We suggest that the breeding season interval in this population of the Star-throated Antwren is a response to both. BSL in other bird families in South America, including populations from both subtropical and tropical latitudes, may be similar (< 120 d, Lima and Roper 2009a, Marini et al. 2009, 2012b), longer (120 – 180 d, Piratelli et al. 2000, Marini and Durães 2001, Repenning and Fontana 2011, Marini et al. 2012a) or much shorter (< 60 d, Auer et al. 2007) than in the Star-throated Antwren. Thus, we suggest that such large variation in BSL across bird species in South America may reflect not only the responses to latitudinal and regional variation in climate, but it is also a result of the local plasticity of each species' breeding strategy.

Reproductive success

Nest predation was the main cause of nest failure in the Star-throated Antwren as in many other birds and average DSR (0.960 day^{-1}) was within the range of other comprehensive studies (0.931 – 0.991 day^{-1}, Yanes and Suárez 1997, Robinson et al. 2000, Mezquida and Marone 2001, Auer et al. 2007, Brawn et al. 2011, Remeš et al. 2012). DSR, however, in the Star-throated Antwren decreased over time during incubation and was lower during the incubation than the nestling stage. While constant during the nestling stage, the end result was that later nests were less likely to survive. Such temporal decline of DSR in incubation (from 0.958 day^{-1} in first day to 0.841 day^{-1}, 115 days later) should favor early nesting. Temperature may play a main role in predation risk (Robinson et al. 2000, Reichert et al. 2012), and so would likely cause such time-dependence in DSR (Grant et al. 2005). For instance, predatory activity of local snakes depends on temperature (Marques et al 2014), and may explain why early nests (colder climate, fewer snakes) are more successful than later nests. The Red-crested Cardinal (*Paroaria coronata*) in more temperate Argentina had similar pattern of decreasing nest survival through the breeding season, and increased with nest age (Segura and Reboreda 2012).

Activity at nests was clearly not associated with an increase in predation risk (Skutch 1985, Roper and Goldstein 1997) because DSR during the nestling stage was greater than during incubation (Table 4). Thus, perhaps here, increased parental activity and attentiveness increases the chance for nest defense (Segura and Reboreda 2012) and thus survival to fledging (Figure 4). Increasing probability of success through the nesting cycle interval was found in subtropical and temperate Argentina (Auer et al. 2007, Segura and Reboreda 2012) and in North America (Grant et al. 2005). Also, a similar pattern was suggested for the neotropical Wire-tailed Manakin (*Pipra filicauda*) in Ecuador (Ryder et al. 2008), but these authors warned on the uncertainty of confidence intervals. Thus, this breeding trait in the Star-throated Antwren is more temperate-like and fast-paced, because it seems to favor fecundity over adult survival (Ghalambor and Martin 2001). As consequence of a more fast-paced breeding strategy, this antwren had an overall probability of nest success of 36% while in other tropical antbirds the probability may be less than 10% (*Cercomacra tyrannina* – Morton and Stutchbury 2000, *Thamnophilus atrinucha* – Roper 2005).

Fewer (2 – 3) nesting attempts each year in comparison to other antbirds (Morton and Stutchbury 2000, Roper 2005, Reinert 2008, Roper et al. 2010, Styrsky and Brawn 2011) seems like consequence of a short breeding season. *A priori*, few renesting attempts were expected because the breeding season should be shorter than for tropical antbirds, assuming that renesting rate is constant everywhere (Griebeler et al. 2010, Roper et al. 2010). However, the end of breeding season was in the early summer, before the occurrence of subtropical influence in climate conditions, which begin in fall. In this context, this antwrens stopped breeding much sooner than apparently possible, considering the time remaining before increased seasonal climate constraints. This suggests that the antwren may avoid to breed while chances of nest predation increase over the breeding season (Ghalambor and Martin 2001, Fontaine and Martin 2006), rather than exclusively in response to food or other seasonal resource limitation.

For pairs which were already successful in any year, considering the trade-off between allowing young to remain in the natal territory consuming resources and attempting for a second-brood, apparently young are of greater future reproductive value. In the same region, both the Marsh Antwren and the Variable Antshrike can have more than one success per pair per year (Reinert 2008, Uejima 2004). Also, several thamnophilids in Panama may attempt additional nests after success (Morton and Stutchbury 2000, Roper and Goldstein 1997, Roper 2005, Roper et al., 2010), including the related Checker-throated Antwren (*Epinecrophylla fulviventris* – JJR, unpublished data). Nonetheless, annual success per pair in Star-throated Antwrens (1.3 fledgeling pair^{-1} year^{-1}) was within the range of values found in other antbirds (0.5 – 1.6 fledgeling pair^{-1} year^{-1}, Morton and Stutchbury 2000, Roper 2005, Reinert 2008, Styrsky and Brawn 2011), and this population seems to be stable with a single success and few attempts. Thus, the increased rate of reproductive success of the Star-throated Antwren, with short BSL and lack of post-success attempts, have returned a reproductive rate similar or greater than tropical birds, but in a short period, and those traits together more closely resemble a fast-paced strategy.

At the individual level, the large variability in annual fecundity among pairs may reflect variation in reproductive experience (Goodburn 1991, Roper 2005, Desprez et al. 2011, Zabala and Zuberogoitia 2014). Perhaps, those atypical behaviors that we interpreted like time and energy saving to permit rapid nesting may in fact depend only on the individual experience (Winkler and Allen 1996, Ardia 2005, Roper 2005, Fontaine and Martin 2006, Ghalambor et al. 2013, Shizuka and Lyon 2013), since these behaviors were found in some but not most pairs. In long-lived species, experience can be very important for breeding success (Sasvári and Hegy 2011, Zabala and Zuberogoitia 2014), and seems to be important for the Star-throated Antwren, but testing this will require long-term monitoring of marked pairs.

In summary, the subtropical population of the Star-throated Antwren has slow-paced traits, similar to other thamnophilids, but at the same time, the species has some traits that resemble fast-paced (and temperate) species. The seasonality in subtropics reduces the potential timing of breeding, but also reduces the nest predation risk early in the season, thereby resembling a pattern more typical in higher latitudes. Thus, the Star-throated Antwren combines the benefits of low costs of slow-paced traits with specific benefits of fast-paced traits, likely to speed up and increase the likelihood of annual success (Du et al. 2014). Nesting early in the season, nest reuse (allowing rapid renesting) and greater nestling survival together favor a greater reproductive success than what is usually observed in the tropics. Due to the increasing rate of nest failure over time, adults apparently invest more time and energy in rearing the fledglings rather than attempting a double-brood. Then, young may have high odds of first-year survival, while minimizing reproductive costs for their parents (Böhning-Gaese 2000, Morton and Stutchbury 2000, Johannessen et al. 2009, Gill and Haggerty 2012, Santos and Nakagawa 2012). We hypothesize that tropical populations of the Star-throated Antwren would show only slow-paced traits, especially long breeding seasons, low nesting success, great number of annual nesting attempt, including multiple-brood, but without nests nor nest-sites reusing. Similar hypotheses on the pace of life-history traits could also be tested in other widely distributed species in South America, studying at the latitudinal or climatic extremes of each species geographic range (Moore et al. 2005, Bears et al. 2009, Rose and Lyon 2013). Considering the great variation of climate regimes within the geographic distribution of many species in South America (Behling 1998, Ricklefs 2002, Carnaval et al. 2014), investigation on their plasticity will uncover information that is essential for understanding the evolution of life history in birds.

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Table 1. Length (in days) of stages of the nesting cycle in the Star-throated Antwren in southern Brazil.

Nest Stage	Median	Min-max	N
Nest construction	4	3 – 8	16
First egg lay	5	2 – 9	26
Second egg lay	1	1 – 3	22
Incubation	18	17 – 19	19
Nestling	13	12 – 15	16
Total	35	33 – 40	13

Table 2. Summary of model selection results evaluating the effects of year, time in the year, nest age and renesting on the daily nest survival rates of the Star-throated Antwren in southern Brazil, based on 78 known-fate nest attempts during 2011 – 2013 breedin seasons. K = number of estimated parameters, and w_i = AIC_c weight. Full is the model containing all single factors. Minimum AIC_c = 294.3.

Model	ΔAIC_c	w_i	K	Deviance
Year + Nest Age	0.00	0.35	4	286.2
Year	1.21	0.19	3	289.5
Nest Age	1.63	0.16	2	291.9
Constant	1.79	0.11	1	294.1
Full	2.82	0.08	6	285.0
Nest Attempt	3.57	0.05	2	293.8
Nest Age x Time	3.80	0.03	3	293.2
Time	174.71	0.00	109	227.0

Table 3. Summary of model selection results evaluating the effects of the time in the season and year on daily survival rates of incubation and nestling stages of the Star-throated Antwren in southern Brazil. *K* = number of estimated parameters, w_i = AIC_c weight, Minimum AIC_c during incubation = 150.5, and during the nestling stage = 51.3.

Nest Stage	Model	ΔAIC_c	w_i	K	Deviance
Incubation	Time	0.00	0.58	2	146.4
	Constant	1.52	0.27	1	150.0
	Time + Year	3.61	0.09	4	146.0
	Year	4.77	0.05	3	149.2
Nestling	Year	0.00	0.63	3	45.2
	Time + Year	2.02	0.23	4	45.2
	Constant	3.84	0.09	1	53.1
	Time	5.50	0.04	2	52.7

Table 4. Effects of most important factors, time in the season and year, for daily nest survival of each nesting stage and the reproductive success of the Star-throated Antwren in southern Brazil. Parameters are the estimated daily survival rate (DSR) and 95% confidence interval (CI) obtained from the partial nest cycle models (Table 3) and derived estimates.

<table>
<tr><th>Nest Stage (d)</th><th>Parameter</th><th colspan="12">Covariate</th></tr>
<tr><td rowspan="6">Incubation (18)</td><td></td><td colspan="12">Time in the Season</td></tr>
<tr><td></td><td colspan="6">Early (Day 1)</td><td colspan="6">Late (Day 115)</td></tr>
<tr><td>DSR (SE)</td><td colspan="6">0.958 (0.015)</td><td colspan="6">0.841 (0.061)</td></tr>
<tr><td>95% CI</td><td colspan="6">0.914 – 0.980</td><td colspan="6">0.681 – 0.929</td></tr>
<tr><td>Hatch Probability</td><td colspan="6">0.46</td><td colspan="6">0.04</td></tr>
<tr><td>N</td><td colspan="12">64</td></tr>
<tr><td rowspan="6">Nestling (13)</td><td></td><td colspan="12">Year</td></tr>
<tr><td></td><td colspan="4">2011</td><td colspan="4">2012</td><td colspan="4">2013</td></tr>
<tr><td>DSR (SE)</td><td colspan="4">0.936 (0.025)</td><td colspan="4">0.992 (0.007)</td><td colspan="4">0.991 (0.008)</td></tr>
<tr><td>95% CI</td><td colspan="4">0.865 – 0.971</td><td colspan="4">0.946 – 0.998</td><td colspan="4">0.943 – 0.998</td></tr>
<tr><td>Fledging Probability</td><td colspan="4">0.42</td><td colspan="4">0.90</td><td colspan="4">0.89</td></tr>
<tr><td>N</td><td colspan="4">12</td><td colspan="4">13</td><td colspan="4">11</td></tr>
<tr><td rowspan="4">Total (31)</td><td></td><td colspan="12">Time + Year</td></tr>
<tr><td></td><td colspan="3">Early 2011</td><td colspan="3">Late 2011</td><td colspan="3">Early 2012/13</td><td colspan="3">Late 2012/13</td></tr>
<tr><td>Success Probability</td><td colspan="3">0.19</td><td colspan="3">0.02</td><td colspan="3">0.41</td><td colspan="3">0.04</td></tr>
<tr><td>N</td><td colspan="6">28</td><td colspan="6">50</td></tr>
</table>

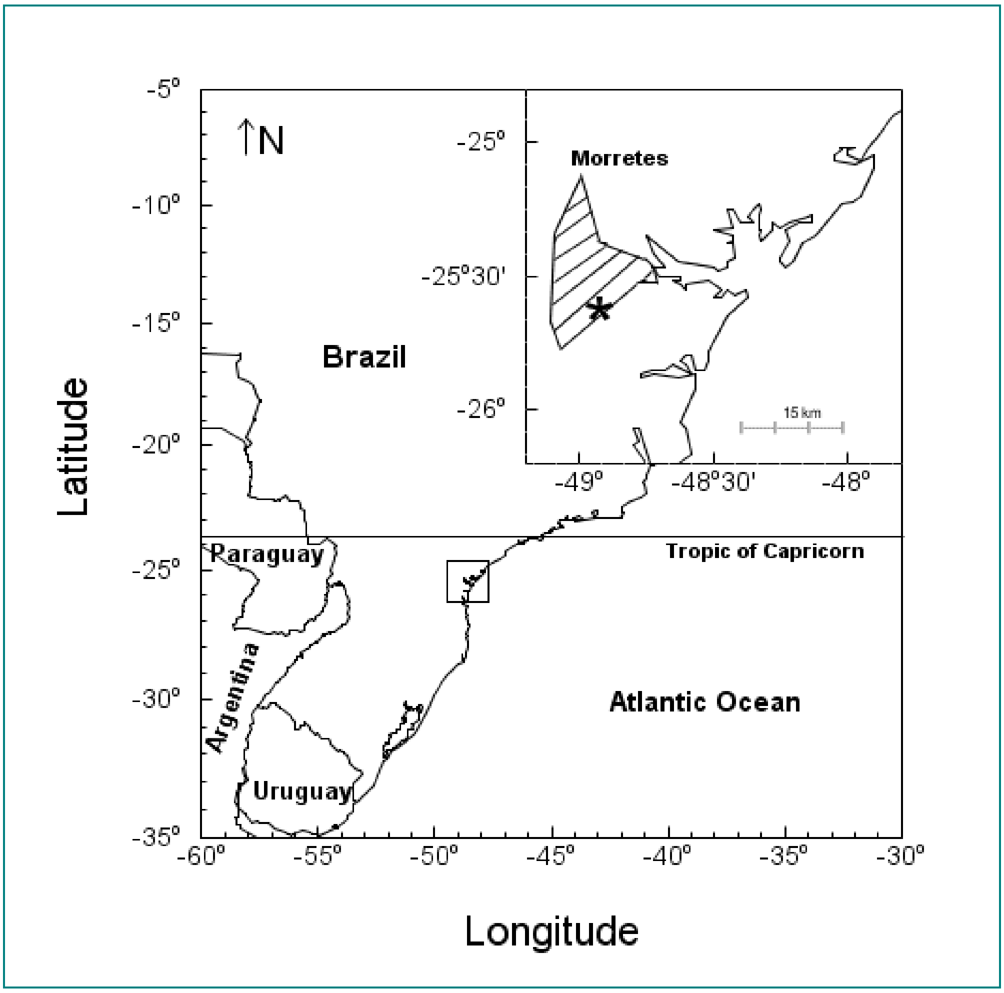

Figure 1. Study area in southern Brazil. The inset map shows the location of the study site in Morretes (lined area), in the state of Paraná.

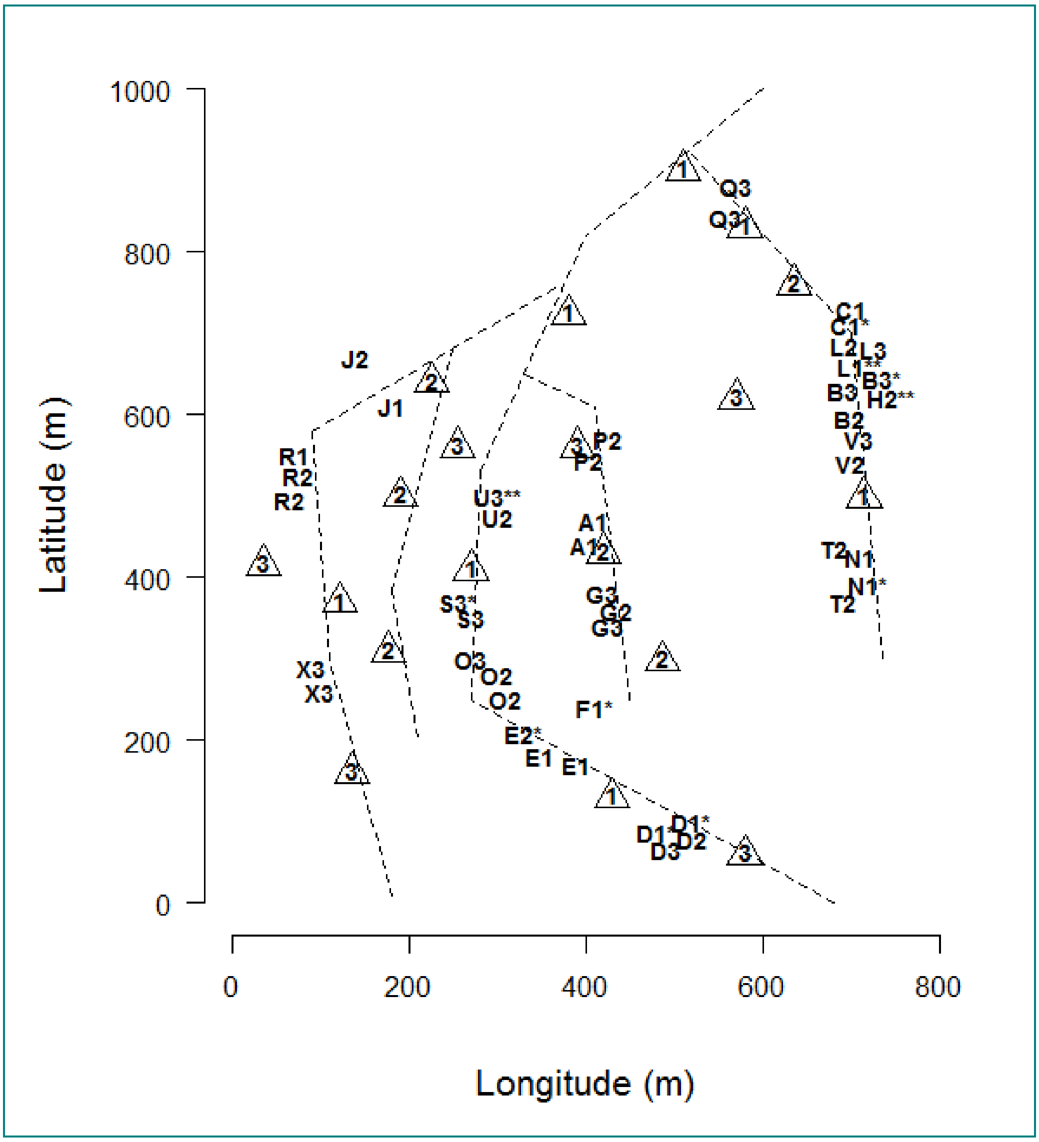

Figure 2. Map of nests with known fate of the Star-throated Antwren (N = 78) in the study site. Each letter designates a pair and year is coded sequentially where 1 = 2011, 2 = 2012 and 3 = 2013. Each nest-site of the same pair closer than 20 m from other previous nest-site were indicated by one asterisk (*). Triangles are nests of pairs with only one nesting attempt during all study. Dashed lines represents the spatial position and link between streams. Coordinates of the origin (0,0) are 25.6160°S and 48.8051°W.

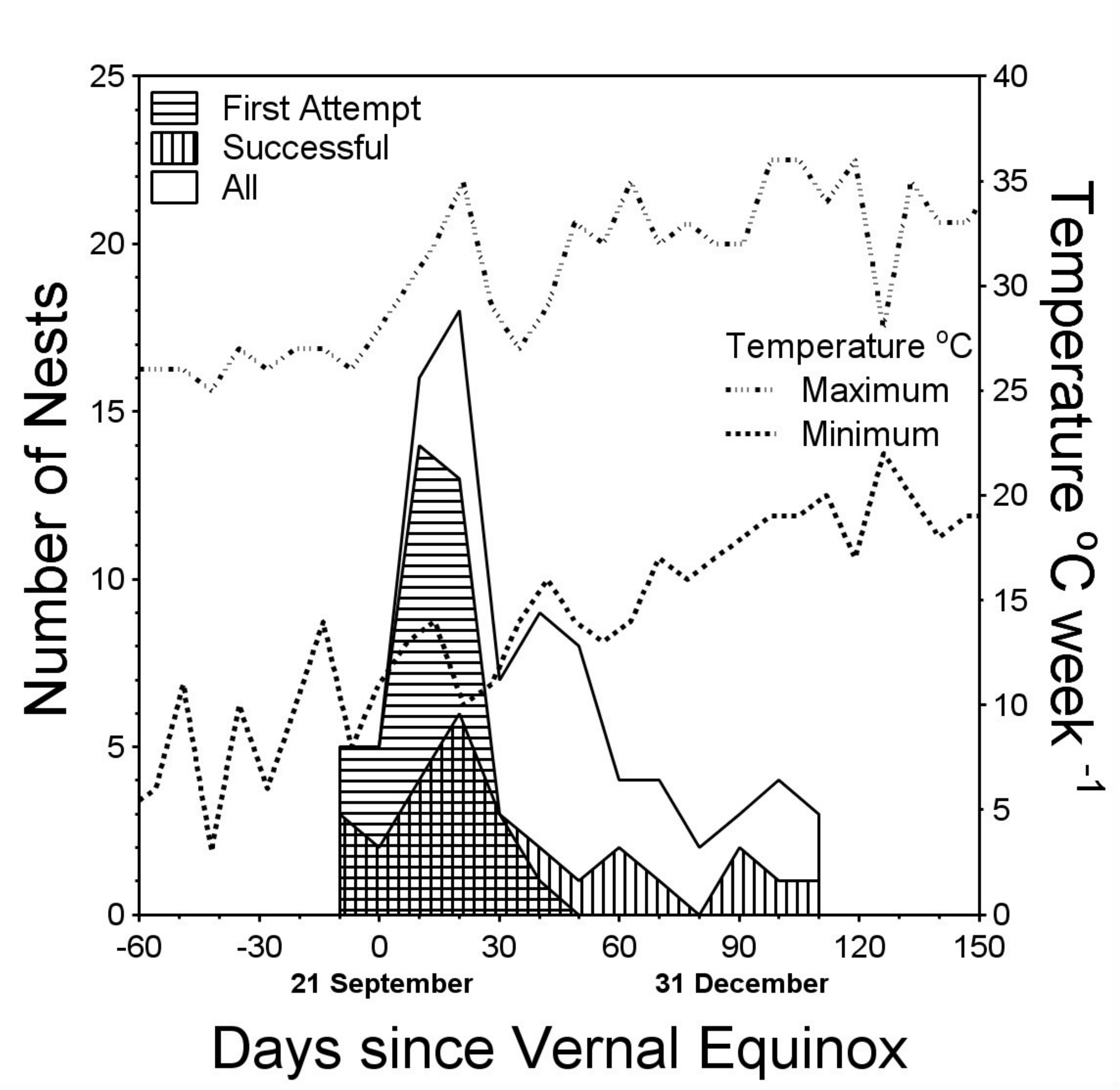

Figure 3. Temporal sequence of nesting of the Star-throated Antwren in relation to the date of vernal equinox during the breeding seasons of 2011 – 2013 and the amplitude of weekly minimum and maximum temperatures during same interval. Nests (N = 78) were grouped by first and renest nesting attempts and by fate. Nesting initiation dates were grouped at each 10 days interval.

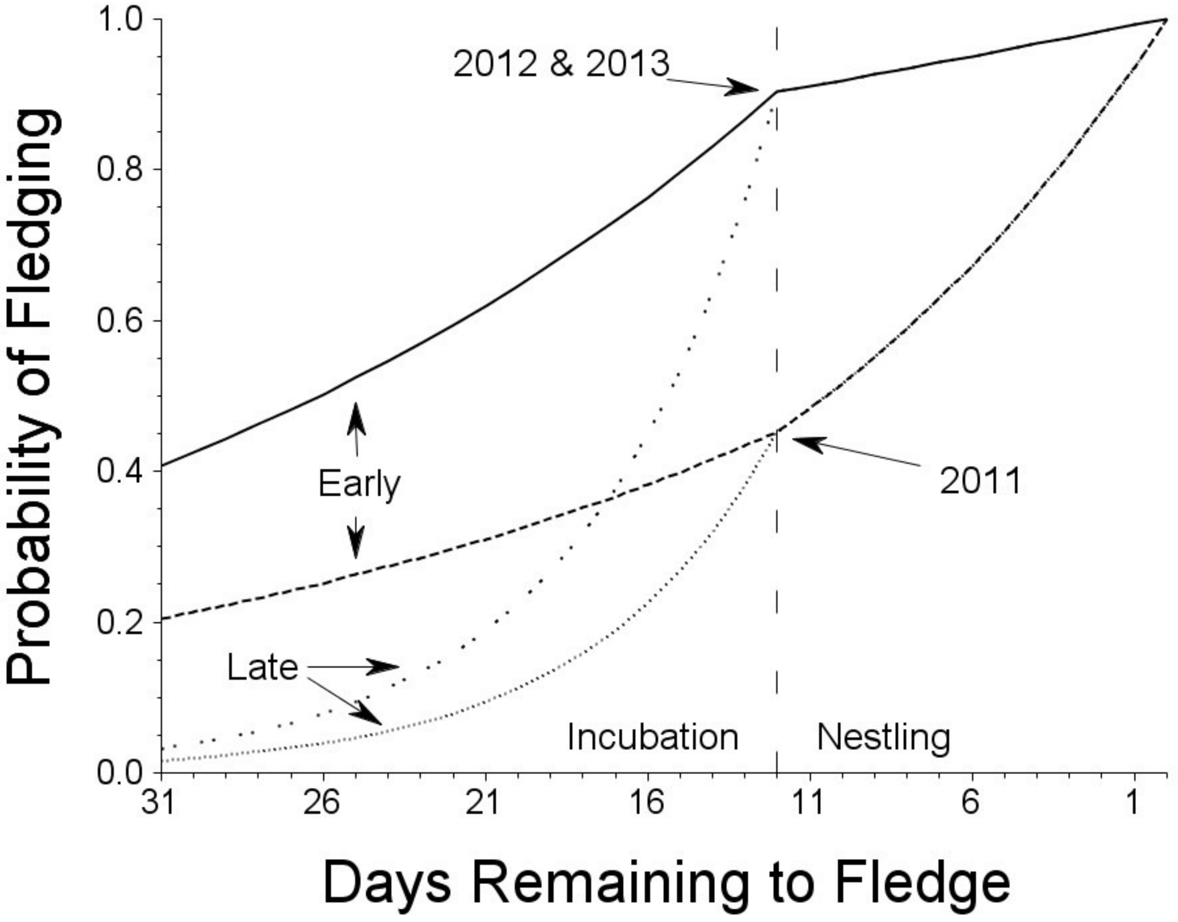

Figure 4. Probability of fledging by days remaining to fledge in the Star-throated Antwren during the three breeding seasons in southern Brazil, using rates calculated from the parameters estimates of best inferred models (Table 4). During incubation, early nests are estimated at the first day of the nesting cycle (DSR = 0.958 day^{-1} for all years) and late nests at the last day (0.841 day^{-1}). During nestling, survival rates were constant within each year, but the rate in 2011 (0. 936 day^{-1}) was lower than those in 2012/2013 (0.991 day^{-1}), so estimates are different.

CAPÍTULO 2

Variabilidade dos caracteres reprodutivos de Passeriformes entre duas localidades na região subtropical da América do Sul e consequências para a fecundidade anual.

Ninhos (em sentido horário) de Limpa-folha-coroado (*Philydor atricapillus*), Choquinha-de-garganta-pintada (*Rhopias gularis*), Borboletinha-do-mato (*Phylloscartes ventralis*) e caixa-ninho de Andorinha-de-sobre-branco (*Tachycineta leucorrhoa*).

Running head: Reproductive patterns and fecundity in subtropical birds

Variability of breeding traits among passerines in two subtropical locations of South America and implications for annual fecundity.

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ABSTRACT

Annual fecundity is a measure of fitness in which regional environmental variation as well as phylogenetic inertia must be important influences. We compare variation in breeding traits among several species and two subtropical locations in South America to better understand how reproductive strategies vary locally, whether variation is convergent among species and how that variation influences annual fecundity. Nesting (N = 1230 attempts) of 91 passerine species from 25 families was studied in subtropical Brazil (25^{o}S) during 2000 – 2014. Breeding traits were described and compared with data from northern Argentina at same latitude using bootstrap (for breeding season, clutch size, nesting cycle), logistic regression (for nest survival) and Monte Carlo simulations (to estimate annual fecundity). In Brazil, breeding occurred over a 213 d interval, but no individual species bred over the entire interval. Breeding began at different times and season length varied among species, from 64 – 185 d. Clutch sizes tended towards 2 – 3 eggs, with two species laying up to 7 eggs. Nesting cycle (egg laying to fledging) varied from 25 – 43 d. Probability of nesting success varied from low to high (16 – 59% probability of nest success) and fecundity varied between 1.4 – 6.3 fledglings pair^{-1} year^{-1}. In paired comparisons controlling for phylogeny, breeding seasons were shorter in Argentina than in Brazil, while timing of breeding and other breeding components varied both among locations. In Brazil, fecundity tended to be greater (due to double-brooding) in most families, but in Parulidae this pattern was reversed. At this subtropical latitude, breeding season length limits double-brooding, therefore fitness may be influenced by three main components: breeding season length, clutch size or nest survival rate. While species may have a variety of combinations of life-history traits explaining their fecundity, the largest differences in fitness among species are due to limitations in number of successful nests each year. We comment on how these results inform the slow-fast paradigm.

Key-words: birds, breeding season, fast-slow gradient, local adaptation, productivity.

INTRODUCTION

Annual fecundity is one measure of fitness that reflects how organisms integrate evolutionary constraints with local conditions during reproduction (Skutch 1949, Sæther and Bakke 2000, Ricklefs and Wikelski 2002, Etterson et al. 2011). Evolutionary constraints in the plasticity of breeding traits may determine how fecundity is limited by a variety of environmental factors, especially those factors related to climate that may influence the food abundance, nest success and fledgling survival (Ricklefs 2000, Roper et al. 2010, Styrsky and Brawn 2011, Oppel et al. 2013, Streby et al. 2014). Each species has a more or less unique evolutionary history (Sæther et al. 2013), yet, convergence on particular strategies may occur under similar environmental conditions. While convergence is known in some specific traits, such the latitudinal variation in clutch size (Moreau 1944, Lack 1954, Cody 1966, Cardillo 2002, Jetz et al. 2008), how optimal breeding strategies are locally determined seems to vary among species (Moore et al. 2005, Bears et al. 2009, Gill and Haggerty 2012, Rose and Lyon 2013, Hille and Cooper 2015), and is not well understood yet (Martin 2014). To better understand plasticity in reproductive strategies, breeding traits in birds must be analyzed in the context of local environmental variability (Moore et al. 2005, Griebler et al. 2010, Roper et al. 2010, Ricklefs 2010, Hille and Cooper 2015).

The slow–fast paradigm of life history traits classifies species within a continuum with respect to life history traits and their plasticity to variable conditions. Tropical conditions (constant and high temperatures, long breeding seasons) generate slow-paced traits (small clutch size, low success, greater adult survival), while temperate conditions (seasonal climate, short breeding seasons) generate fast-paced traits (large clutch size, high success, lower adult survival – Martin 1996, Sæther and Bakke 2000, Ricklefs and Wikelski 2002, Oli 2004, Ricklefs and Wikelski 2002, Wiersma et al. 2007, Griebeler et al. 2010). Yet, this continuum refers to extremes and may not pertain to breeding patterns in intermediate conditions, or explain how widespread species respond to locally unique and variable conditions. There are many potential combinations of breeding traits that may optimize annual fecundity and that may be independent of the latitude (Ghalambor and Martin 2001, Ricklefs and Wikelski 2002, Bears et al. 2009, Tieleman 2009, Du et al. 2014).

In South America, different climate regimes and vegetation formations (ecoregions) can occur within the same latitude, and many bird species may be found in more than one ecoregion, both within and across latitudes (Ridgely and Tudor 1994a,1994b). Species that evolved in tropical America, potentially slow-paced (*e.g.* Thamnophilidae, Conopophagidae, Pipridae, and other New World suboscine), and that evolved elsewhere, potentially fast-paced (Hirundinidae, Turdidae, Troglodytidae and other oscine), may all be found breeding at the same location (Ridgely and Tudor 1994a, 1994b). Especially in subtropical South America, slow-paced species would confront shorter breeding seasons but longer daylength, while fast-paced species would have longer breeding seasons but shorter daylength (Lima and Roper 2009, Griebeler et al. 2010, Roper et al. 2010, Rose and Lyon 2013), comparing with each species origin zone (Ricklefs 2006). Thus, during breeding season at intermediary latitudes, time for foraging will increase for tropical birds and decrease for temperate birds in a daily basis, while the opposite would be expected with time for breeding in an annual basis. Such large variation in environmental conditions must influence breeding traits (*e.g.* clutch size, breeding season, renesting and daily provisioning rates) and nesting predation risk, all of which directly influence on annual fecundity. However, if food abundance and predation rates may locally vary, independent of the latitude, thus, flexible reproductive traits would be adjusted towards an optimal local breeding strategy.

How breeding traits of birds vary across latitudes and ecoregions remains poorly known in South America because the breeding biology and ecology of most species are still unstudied (Ricklefs 2002, Martin 2004, Marini and Garcia 2005). Here, to examine local variation in breeding strategies among passerine from subtropical South America, we describe their breeding traits in southern Brazil and compare with traits of related species at the same latitude in northern Argentina (Auer et al. 2007). Specifically, we compare variation in breeding season length, clutch size, nest cycle interval duration, nest survival, and estimates of potential annual fecundity. If latitudinal constraints in breeding patterns are much greater than environmental constraints, species should have similar patterns in both locations, likely in an intermediate position in the slow–fast continuum. However, if environmental variation within subtropical areas may influence breeding strategies, two mutually exclusive hypotheses may be set: species may show convergence in variation (adjustments) of breeding traits, or each *taxa* may have unique local variation of traits. We predict that environmental variation is important and that unique variation of reproductive traits may be found in each *taxa*, what would reinforce the importance of plasticity in life-history strategies (Ghalambor and Martin 2001, Fontaine and Martin 2006, Bears et al. 2009, Ghalambor et al. 2013, Pienaar et a. 2013, Du et al. 2014).

METHODS

Study area

The nesting cycle of several passerine birds was studied in subtropical Brazil (25^{o}S) between the years 2000 – 2014 in six forested locations within the Atlantic Forest biome, longitudinally distributed along ~200 km and varying between 50 – 1000 m a.s.l. (Figure 1). Birds were studied at different locations, often during different years, and descriptions include unpublished data (see Table 1 and Acknowledgments). In this region there are four well-defined seasons. Summers (January – March) resemble typical tropical rainforests, with maximum daily temperatures to 41^{o}C, with a monthly average of 30^{o}C and monthly average rainfall of 250 mm. Winters (June – August) are cool, with an average monthly maximum of 23^{o}C while minimum monthly average temperatures are 12^{o}C (rarely to -5^{o}C and more rarely to 35^{o}C), and monthly average rainfall is 120 mm. Thus, the yearly temperature range is 46ºC (-5ºC – 41ºC), with no clear dry season and mean annual rainfall varying between 1500 – 2400 mm (Maack 2002, IAPAR 2014). Regional climate based on the updated Köppen-Geiger classification is humid and warm temperate (Cf – Kottek et al.

2006). More details on the regional climate variation during the breeding season were provided in the first chapter.

Nest search and monitoring

In the field, we observed birds to identify breeding or nesting behaviors as we searched for nests in potential nest-sites, following Martin and Geupel (1993). Each year, nest searches and observations began prior to the onset of breeding (July) and continued until well after the last active nests were finished (March). Once found, nests were checked every three days on average, but more often at transitions (egg-laying, hatching, fledging). We noted species, location, nest stage (construction, egg-laying, incubation, hatching, nestling, fledging) and contents (eggs or nestlings) at all nests. We defined the interval (in days) from the first egg laid to the first egg to hatch as the incubation period, the first egg hatched to fledging as the nestling period and the sum of both stages was defined as the entire nest cycle interval duration (NC). We reported for each species the mode, minimum and maximum clutch size, and the mode of observed intervals or maximum estimated interval of each nest stage (incubation and nestling).

Breeding season

We defined breeding season length (BSL) as the interval between the very first egg laid and the last egg laid in any season, by species. When a nest was found with eggs or nestlings, we estimated their initiation date by back-dating based on egg translucency (Enemar and Arheimer 1980), hatching date or nestling size as compared to known nests (Auer et al. 2007, Segura and Reboreda 2012). We reported for each species the breeding starting date, the distribution of starting dates and the maximum BSL.

Nesting success

A nest was successful if one or more young fledged, otherwise nests were unsuccessful. The proportion of successful nesting attempts and daily nest survival rate (DSR) were calculated for each species. DSR was estimated using the logit-link function in a constant nest survival model, S(.), in the program MARK (version 7.1, White and Burnham 1999), using the RMark interface (Laake 2013).

Annual fecundity

Fecundity was defined as the number of fledglings produced per pair per year (Etterson et al. 2011), assuming that all species are monogamous and that there was no mortality among fledglings. Based on breeding parameters estimated from our data and Auer et al. (2007), we used simulations to generate and compare probabilities of annual reproductive success among species. Monte Carlo simulations were used to model fecundity following Roper et al. (2010) as a consequence of the interaction among the breeding parameters: DSR, NC, BSL, and renesting intervals: after success (PS) and after failure (PF). Annual fecundity of each simulated pair was estimated as the product of the sum of the estimated number of successful nests for that pair and the mode of clutch size (CS) for that species. Fecundity was estimated by simulating 600 pairs for each combination within a range of two sorts of renesting intervals, which reasonably simulates DSR without being too computer intensive (Appendix A). Renesting intervals are unavailable for most species, and so we used the same range of parameter values for all species (in days): PS (15, 30, 45, 60, 75, 90) and PF (0, 5, 10, 15, 20, 25, 30). Thus, annual fecundity was simulated for a total of 25200 pairs for each species. For properly comparing fecundity estimates among locations, we measured BSL following Auer et al. (2007). Source code for fecundity simulations (Suplementary Material 1) was developed in the Program R (Version 3.1.0, R Core Team 2014).

Data analysis

We pooled data from all years and locations due to sample size and to include all possible variation in breeding traits at this subtropical latitude in Brazil. We compared each breeding trait of species, families and suborders studied in Brazil with those from related *taxa* in Argentina at similar latitude (~25^{o}S) and partially overllaped elevation range, 700 – 2000 m (Auer et al. 2007, more details in Blake and Rougés 1997). For comparisons of nest initiation dates, CS and NC, we generated 10,000 bootstrap replicates using the package boot (version 1.3-9) in the program R. To examine convergence among these traits, we compared the distribution probabilities of each parameter, and when distribution was not available, we measured the difference between the mean of our bootstrapped data and those reported by Auer et al. (2007) using bias-corrected and accelerated (BCa) 95% confidence interval (Efron 1987, Manly 1991). Nest initiation dates in Argentina were reported in 7-day intervals, and so we grouped data in the same interval for these comparisons. We also estimated and compared nesting success probabilities among species by exponentially raising the DSR estimates and 95% confidence intervals to the power relative to number of days in the nest cycle. We followed the taxonomic classification of Ohlson et al. (2013) for data description and paired comparisons, excepting for comparisons including species within Tyrannoidea, which were all considered as Tyrannidae.

To examine whether breeding traits (BSL, CS, NC and DSR) vary together in patterns that may be considered fast or slow, we used correlation analysis controlling for phylogenetic interactions, by using phylogenetic independent contrasts (Felsenstein 1985). The phylogeny tree used for estimating contrasts was the posterior distribution of 10,000 trees obtained in Jetz et al. (2012, www.birdtree.org). Fecundity estimates were fit in multiple regression as the independent variable in function of all breeding traits. We calculated the partial coefficient of determination (r^2) to evaluate how much influence each trait has among locations in each *taxa*. We used Phylogenetic Generalized Least Square (package caper – Orme et al. 2013) to compare the variation of traits contribution for fecundity controlling for the phylogenetic relationships among species. All analyses were carried out in Program R.

We classified breeding strategies into three categories in the context of the slow-fast variation in life history traits, to understand if variation in fecundity can be related with the relative pace of specific traits. 1) Modal clutch size (< 3 slow, otherwise fast). 2) Development rate during the nesting cycle, measured as adult weight (from our field data, or from del Hoyo et al. 2014) divided by the interval duration of the nest cycle. This is similar to growth rate, but includes the entire time interval during which eggs or nestlings remain in the nest and are exposed to potential failure. Three categories were more or less equally distributed according to our sample (slow: < 0.5, mid: 0.5 – 1.0, fast: > 1.0 g day^{-1}). 3) All combinations between clutch size and developmental rate, respectively – SS (slow + slow), SM (slow + mid), SF (slow + fast), FS (fast + slow), FM (fast + mid) and FF (fast + fast). We then plotted annual fecundity rates grouped by either phylogeny, location (Brazil, Argentina) and breeding strategy.

RESULTS

Breeding parameters from 1230 nests of 91 species in 25 families were used in these analyses (Table 1), in addition to those taken from the literature. Four species were found in both Brazil and Argentina: *Phylloscartes ventralis* (Rhynchocyclidae)*, Troglodytes musculus* (Troglodytidae), *Turdus rufiventris* (Turdidae) and *Zonotrichia capensis* (Emberizidae). A total of five families were also common in both locations: Rhynchocyclidae (with 5 species), Tyrannidae (14 spp.), Turdidae (4 spp.), Parulidae (6 spp.) and Emberizidae (5 spp.).

Breeding season

All breeding (N = 1151 nests, 88 spp.) occurred within a 213 d interval, beginning on August 15 (*Camptostoma obsoletum,* 38 d prior to the vernal equinox). Because this early nest was found already during incubation, we estimated that nest construction started up to two weeks before the first record. Very first sign of construction was seen in July 30 in 2012, from an individual of *Pitangus sulphuratus* nearby to one study location (~20 km), in coastal altered-habitat. The last egg laid was on March 16 (176 d after the vernal equinox, *Sporophila caerulescens*). Overall breeding activity was greater in October (63 spp. with active nests) and November (62 spp.) comparing to other months (Figure 2A). First nests of the breeding season by species (with 7+ nests) began from late August to late October, except for the *S. caerulescens*, which began in December (Table 2). The shortest BSL (species with 10+ nests) was 64 days in *Basileuterus culicivorus* (Parulidae) and the longest, of 185 d, in *Sicalis flaveola* (Emberizidae, also the longest BSL by family, Figure 2B). The shortest BSL by family (76 species in 13 families, 15+ nests per family) was 97 d in Conopophagidae (2 spp.). Average BSL was 142 d (SD = 26) and breeding began before the vernal equinox in the Tyranni (Dendrocolaptidae, Furnariidae, Thamnophilidae and Tyrannidae) and always after in Passeri (*e.g.* Thraupidae and Emberizidae, Figure 2C).

In comparing Brazil with Argentina, breeding began on similar dates in two of the four species that bred in both locations: *T. musculus* (Brazil: day 55, adjusted to the equinox, 95% CI = days 47 – 60; Argentina: day 52, 95% CI = days 47 – 58, p = 0.79) and *Z. capensis* (Brazil: day 77, 95% CI = days 64 – 90; Argentina: day 69, 95% CI = days 61 – 78, p = 0.46). Breeding onset in *P. ventralis* was later in Brazil (Brazil: day 72, 95% CI = days 50 – 96; Argentina: day 45, 95% CI = days 41 – 50, p = 0.01) while in *T. rufiventris* was earlier in Brazil (day 47, 95% CI = days 40 – 53) than in Argentina (day 77, 95% CI = days 73 – 81, p < 0.01, Figure 3). The range of observed BSL of the four species in Brazil was ~100 – 140 d (Figure 2B) and in Argentina was ~30 – 70 d (Auer et al. 2007), and thus, the BSL in simulated data was longer for species in Brazil than in Argentina (Figure 3).

Breeding began in two families on similar dates: Tyrannidae (Brazil: day 54, 95% CI = days 48 – 60, 19 spp.; Argentina: day 55, 95% CI = days 52 – 58, 5 spp., p = 0.68) and Parulidae (Brazil: day 52, 95% CI = days 45 – 60, 7 spp.; Argentina: day 55, 95% CI = days 52 – 58, 4 spp., p = 0.43).

Turdidae began earlier in Brazil (day 45, 95% CI = days 40 – 50, 4 spp.) than in Argentina (day 73, 95% CI = days 70 – 77, 3 spp., $p < 0.01$), while Emberizidae began later in Brazil (day 87, 95% CI = days 82 – 93, 5 spp.) than in Argentina (day 64, 95% CI = days 61 – 68, 3 spp., $p < 0.01$). In most families and suborders in Brazil, BSL was longer than in Argentina, while timing of breeding was independent among locations (Figure 3).

Clutch size

Clutch size was observed in 710 nesting attempts of 67 species (21 families). Clutch size was 2 – 3 eggs in Tyranni and 2 – 5 eggs in Passeri (Table 3, Appendix B). The probability that data on clutch size in Argentina is coming from the same distribution of species in Brazil was 0.41 in *P. ventralis* (Brazil: mean = 2.5 eggs, 95% CI = 1.8 – 3.3 eggs, Argentina: mean = 2.6 eggs) and 0.08 in *T. rufiventris* (Brazil: 2.5 eggs, 95% CI = 2.3 – 2.8 eggs, Argentina: 2.7 eggs), and thus, estimates are similar. On the other hand, *T. musculus* had a larger clutch size in Brazil (4.0 eggs, 95% CI = 3.7 – 4.3 eggs) than Argentina (3.5 eggs, $p < 0.01$), while *Z. capensis* showed the reverse, with a smaller clutch size in Brazil (2.3 eggs, 95% CI = 2.1 – 2.5 eggs) than Argentina (2.6 eggs, $p = 0.03$, Figure 4).

Clutch size by family was independent of location, while suborders differed. Clutch size in Passeri was independent of location (Brazil: 2.7 eggs in 31 spp., Argentina: 2.6 eggs in 12 spp.), while the probability that clutch size among Tyranni in Argentina (mean = 2.8 eggs, 6 spp.) was within the expected range found in Brazil (mean = 2.5 eggs, 95% CI = 2.3 – 2.7 eggs, 37 spp.) was 0.01 (Figure 4).

Nest cycle interval

In Brazil, incubation interval varied from 12 d (*Thamnophilus caerulescens*) to 20 d (*Conopophaga melanops* and *Tachycineta leucorrhoa*) and was similar in Tyranni (bootstrapped mean = 16.4 d, 95% CI = 14.7 – 17.7 d, 9 spp.) and Passeri (bootstrapped mean = 16.2 d, 95% CI = 14.9 – 17.3 d, 9 spp., p = 0.78). Nestling stage varied from 12 d (*S. caerulescens*) to 25 d (*Pygochelidon cyanoleuca*) and was also similar between Tyranni (bootstrapped mean = 16.4 d, 95% CI = 14.6 – 18.4 d, 9 spp.) and Passeri (15.8 d, 95% CI = 14.0 – 19.0 d, 12 spp., p = 0.70). The total nesting cycle (from egg laying to fledging) varied from 25 d (*T. caerulescens*) to 43 d (*T. leucorrhoa* and *P. cyanoleuca*) and was also similar in Tyranni (32.3 d, 95% CI = 30.1 – 35.4 d, 9 spp.) and Passeri (32 d, 95% CI = 29.3 – 36.2 d, 12 spp., p = 0.72). Total nesting interval was noted for 21 species in 10 families (Table 4).

For comparinsons among species between locations we only had single observations. Incubation interval was similar among locations in *P. ventralis* (Brazil = 18.0 d, Argentina = 17.8 d), in *T. rufiventris*. (Brazil = 13.0 d, Argentina 13.1 d) and in *T. musculus* (Brazil = 16.0 d, Argentina = 15.8 d). The probability that the mean of nestling interval duration in Argentina was within the expected range in Brazil was: 0.45 in *P. ventralis* (16.0 d, 95% CI = 15.0 – 17.5; Argentina: 17.1 d), 0.21 in *T. rufiventris* (13.6 d, 95% CI = 12.7 – 14.6 d; Argentina: 14.4 d), 0.24 in *T. musculus* (15.8 d, 95% CI = 14.5 – 16.6 d; Argentina =14.8 d).

Incubation intervals were similar across locations in Tyranni (bootstrapped mean in Brazil = 16.4 d, 95% CI = 15.2 – 17.4 d, 9 spp.; Argentina = 17.3 d, 95% CI = 16.1 – 18.5 d, 6 spp., p = 0.48) and in Passeri (bootstrapped mean in Brazil = 15.9 d, 95% CI = 14.4 – 17.7 d, 12 spp.; Argentina = 14.8 d, 95% CI = 14.0 – 15.6 d, 11 spp., p = 0.12). Nestling intervals were also similar across locations within Tyranni (Brazil = 16.4 d, 95% CI = 14.7 – 18.4 d, 9 spp.; Argentina = 17.8 d, 95% CI = 16.2 – 19.2 d, 5 spp., p = 0.58) and Passeri (Brazil = 15.4 d, 95% CI =13.3 – 18.1 d, 12 spp.; Argentina = 13.4 d, 95% CI = 12.3 – 14.8 d, 12 spp., p = 0.10).

Body weight varied between 9 – 75 g among species in Brazil, and between 6 – 75 g among species in Argentina. Development ratio varied between 0.30 – 2.68 g d^{-1} in Brazil and between 0.16 – 2.68 g d^{-1} in Argentina (Appendix C).

Nesting success

In 832 nests of 80 species, 49% of nests were successful (N = 412). The percentage of observed nests that were successful varied from 19% in *B. culicivorus* (DSR = 0.941 d^{-1}, SE = 0.015, N = 16 nests) to 86% in *P. cyanoleuca* (DSR = 0.988 d^{-1}, SE = 0.006, N = 16 nests) among 21 species (with 7+ nests). Percentage of expected nest success (based on DSR carried to the exponent of the nest cycle interval) varied from 16 – 59% (Table 4).

DSR was lower in *T. musculus* in Brazil (0.975 d^{-1}, SE = 0.004, N = 57 nests, 95% CI = 33 – 55%) than Argentina (0.988 d^{-1}, SE = 0.005, success probability = 69%). DSR was similar across locations in *P. ventralis* (Brazil: 0.962 d^{-1}, SE = 0.019, N = 10 nests, 95% CI = 5 – 61%; Argentina: 0.974 d^{-1}, SE = 0.006, success probability = 42%), *Z. capensis* (Brazil: 0.947 d^{-1}, SE = 0.013, N = 22 nests, 95% CI 9 – 41%; Argentina: 0.950 d^{-1}, SE = 0.012, success probability = 25%) and *T. rufiventris* (Brazil: 0.960 d^{-1}, SE = 0.007, N = 46 nests, 95% CI = 19 – 44%; Argentina: 0.948 d^{-1}, SE = 0.006, success probability = 22%, Figure 5).

DSR, among families, was similar in Tyrannidae (Brazil- 0.976 d^{-1}, SD = 0.008, 5 spp., 59 nests, range = 27 – 54%, Argentina: 0.967 d^{-1}, SD = 0.012, 5 spp., range = 19 – 57%) and Emberizidae (Brazil: 0.963 d^{-1}, SD = 0.015, 3 spp., 133 nests, range = 27 – 54%, Argentina: 0.960 d^{-1}, SD = 0.012, 3 spp., range = 19 – 48%). DSR in Turdidae was greater in Brazil (mean = 0.960 d^{-1}, SD = 0.007, 3 spp., 73 nests, range = 32 – 47%) than Argentina (mean = 0.949 d^{-1}, SD = 0.006, 3 spp., range = 22 – 27%). DSR in Parulidae was lower in Brazil (mean = 0.949 d^{-1}, SD = 0.011, 2 spp., 24 nests, range = 18 – 26%) than Argentina (mean = 0.975 d^{-1}, SD = 0.008, 4 spp., range = 40 – 51%, Figure 5).

The range of DSR and probability of nesting success was independent of location in Tyranni (Brazil: 0.968 d^{-1}, SD = 0.012, 9 spp., range = 22 – 55%; Argentina: 0.971 d^{-1}, SD = 0.015, 6 spp., range = 19 – 71%) and Passeri (Brazil: 0.965 d^{-1}, SD = 0.014, 12 spp., range = 18 – 59%;

Argentina: 0.965 d^{-1}, SD = 0.015, 11 spp., range = 19 – 69%). Overall DSR was equal in both locations (Brazil: 0.967 d^{-1}, SD = 0.012, 21 spp., Argentina: 0.967 d^{-1}, SD = 0.015, 17 spp.).

Annual fecundity

In Brazil, the simulated annual fecundity varied from 1.4 (*Z. capensis*) to 6.3 fledglings $pair^{-1}$ (*T. musculus*) in 21 species (mean = 3.0 fledglings $pair^{-1}$, SD = 0.8). Average annual fecundity was similar in Tyranni (2.9 fledglings $pair^{-1}$, SD = 0.5) and Passeri (3.1 fledglings $pair^{-1}$, SD = 0.4). Nineteen percent of all pairs of all species were unsuccessful (2% in *P. cyanoleuca* to 54% in *B. culicivorus*). Single-success pairs comprised 56% of all breeding pairs (40% in *Mionectes rufiventris* to 80% in *T. leucorrhoa*), while the remaining 25% had success twice (1% in *M. leucoblephara* to 64% in *P. cyanoleuca*).

Annual fecundity in Argentina varied from 0.7 (*Elaenia parvirostris*) to 3.3 fledglings $pair^{-1}$ (*T. musculus*), and was similar in Tyranni (2.0 fledglings $pair^{-1}$, SD = 0.4, 7 spp.) and Passeri (2.3 fledglings $pair^{-1}$, SD = 0.4, 10 spp.). Thus, overall annual fecundity was lower in Argentina (2.1 fledglings $pair^{-1}$, SD = 0.8) than in Brazil (3.0, Figure 6A). In Argentina, a greater proportion of pairs was unsuccessful (33%) and successful once (63%), but a smaller proportion had two successes (4%) than in Brazil (19, 56 and 25%, Figure 6B).

The four species occuring in both locations had greater fecundity in Brazil: *P. ventralis* (Brazil: 2.8 fledglings $pair^{-1}$, 23% unsuccessful and 16% double-brooded; Argentina: 2.2 fledglings $pair^{-1}$, 30% unsuccessful and 3% double-brooded), *T. musculus* (Brazil: 6.3 fledglings $pair^{-1}$, 11% unsuccessful and 31% double-brooded; Argentina: 3.3 fledglings $pair^{-1}$, 16% unsuccessful with no double-brooding), *T. rufiventris* (Brazil: 2.6 fledglings $pair^{-1}$, 23% unsuccessful and 10% double-brooding; Argentina: 1.8 fledglings $pair^{-1}$, 27% unsuccessful and 11% double-brooded) and *Z. capensis* (Brazil: 1.4 fledglings $pair^{-1}$, 37% unsuccessful and 10% double-brooded; Argentina: 1.2 fledglings $pair^{-1}$, 60% unsuccessful and 1% double-brooded).

Among families, species of Parulidae were exceptions, in which fecundity in Brazil (1.5 fledglings pair^{-1}, SD = 0.1, 2 spp.) was lower than in Argentina (2.6 fledglings pair^{-1}, SD = 0.4, 4 spp., Figure 7A), as well the proportion of unsuccessful pairs (49 – 56% in Brazil vs. 13 – 26% in Argentina) and double-brooded pairs (1 – 2% vs. 5 – 13%).

Phylogenetic independent contrasts of breeding traits (BSL, CS, NC and DSR) were unrelated among species in Brazil and in Argentina as well (Pearson correlation coefficient < 0.4 and $p > 0.05$ in all paired correlations). Coefficients in multiple regression of all traits but NC had important effect in fecundity rates, with largest effect of DSR in both locations (Table 5). Similar results were found with PGLS (Table 5).

In comparing families, we included PS and PF as covariates in the multiple regression, and results were variable among families and locations. PS ($r^2 = 0.32$) and BSL ($r^2 = 0.25$) most strongly influenced variation of fecundity among Tyrannidae in Brazil, while CS ($r^2 = 0.82$) explained most variation of fecundity in Argentina. In Turdidae, PS ($r^2 = 0.49$) and PF ($r^2 = 0.48$) were the most important breeding traits in Brazil, while PF ($r^2 = 0.56$) and BSL ($r^2 = 0.33$) were the most important in Argentina. Fecundity of Parulidae in Brazil was influenced by PF ($r^2 = 0.95$), while in Argentina the variation was shared among four variables: BSL, incubation interval, PS and PF ($r^2 = 0.20 – 0.29$). Within Emberizidae, in Brazil CS ($r^2 = 0.82$) was the most important variable, while in Argentina it was the BSL ($r^2 = 0.70$, Table 6).

Annual fecundity tended to increase from slow to fast trait combinations, but it was greater in species classified with large clutch size (fast pace) and slow nesting development rate (FS, Figure 7B, Appendix C). Comparing within each class of breeding strategy and among locations, species from Argentina tended to have lower fecundity rates in all classes. Among the four paired species, *Z. capensis* was the only one that were classified with different strategies over each location, due to reduced clutch size in Brazil (2 eggs, slow) than in Argentina (3 eggs, fast).

DISCUSSION

Local variation in breeding traits within and across locations shows that breeding plasticity of passerines includes a sort of distinctive responses to variation in environmental conditions at local scale, according to our predictions. Breeding traits vary widely and characteristics that resemble slow- and fast-paced traits are found together in both locations, suggesting that there are several ways for breeding adjustment among species within this subtropical latitude. The most important differences in breeding traits with consequences for fecundity were related to the variation in the breeding season length, clutch size and nest survival rate. For instance, only a single nesting success per year was possible in Argentina due to the short breeding season, thus only clutch size may increase annual fecundity of species over there. On the other hand, several species in Brazil can successfully raise two broods within one season, depending upon the combination of nest survival rate and breeding season lenght. Maximizing annual fecundity by increasing the number of nesting successes or increasing clutch size are distinctive ways to allocate energy for reproduction each year at each location.

The annual and spatial variation in our data does not seem important in the context/scale of this research. For example, the breeding activity of the Star-throated Antwren was intensively studied during three seasons and there was no important variation in breeding season interval, although some variation in nest survival was found (first chapter). However, most nests of most species were randomly searched through the years of study, thus our data must be representative of a more long-term and averaged trend concerning the variability of breeding traits.

Breeding season

Breeding begins at different times for different species and peaked for most species soon after the vernal equinox in Brazil. At high-latitudes, such as North America, breeding almost never begins prior to the equinox, and usually begins more synchronously about two months after the equinox

(Baker 1939, Ricklefs and Bloom 1977). Across locations, environmental conditions seems to constrain BSL independent of phylogeny, since almost all species in Brazil had longer seasons and were less synchronous than species in Argentina. Thus, species in Argentina must be alike in their response to local conditions, suggesting convergence among species. So, with respect to initiation of breeding, species in Brazil tend towards the slow-paced traits, while species in Argentina tend towards fast-paced traits. Yet, these trends are not always consistent. For instance, the four species found in both locations varied in their timing of breeding: in Argentina *P. ventralis* began earlier while *T. rufiventris* began later than in Brazil, and other species did not vary. In addition, *Z. capensis* already had local adaptation in BSL reported in more tropical location, in respect to altitude (Moore et al. 2005), but here in subtropics any variation was found among locations in this species.

Thus, local variation in environmental conditions may influence BSL and reproductive synchrony similar to the way latitudinal variation influences breeding patterns (Cooper et al. 2005, Rose and Lyon 2013). Species may respond to subtle differences in unique ways, perhaps due to different seasonality in some resources availability (McNamara et al. 2008, Borgmann et al. 2013) or because of specific physiological constraints (Ricklefs and Wikelsi 2002) that may also depend on the species geographical range (Cardillo 2002, Busch et al. 2011). Breeding season seems to increase towards lower latitudes (Marini and Durães 2001, Maia-Gouvêa et al. 2005, Marini et al. 2007, 2012), with exceptions (Anciães et al. 2012). However, breeding seasons in other locations at temperate latitudes in South America may be up to two months longer than those reported by Auer et al. (2007), including a variety of species (Mezquida and Marone 2001, Bugoni et al. 2002, Moreno et al. 2005, Reppening and Fontana 2011, Pretelli and Isacch 2013, Carro et al 2014, Hayes 2014). Thus, variation in BSL may vary more longitudinally than latitudinally in subtropical South America. This pattern could be generated by a combination of influences from both oceans (Atlantic and Pacific) on this relatively narrow region in South America, likely because the high aridity levels (and rain shadow) caused by the Pacific ocean (Lepage and Lloyd 2004) in comparison with the Atlantic coast. The causes of variation in BSL are likely to also include, in addition to intrinsic phylogenetic constraints (Pienaar et al 2013), variation at the level of the individual, such as experience, territory quality and perhaps ability to avoid nest predation (Ghalambor and Martin 2001, Roper 2005, Fontaine and Martin 2006, Reichert et al. 2012).

Clutch size

Clutches in most species were smaller than those of birds farther south (Yom-Tov et al. 1994, Mezquida and Marone 2001, Moreno et al. 2005) and from North America (Ricklefs and Bloom 1977, Martin et al. 2000). In both locations, small clutch size (*i.e.* 2 – 3 eggs) was common, especially in Tyranni, and suggest a slow-pace of life in this large group. This pattern corroborate with the hypothesis that seasonality effects in the southern hemisphere would be less determinant than in the north for selecting clutch size among birds (Evans et al. 2005, Samaš et al. 2013).

At species level, breeding traits vary between locations. Of the four species found in both locations, three response types were observed: the House Wren had larger clutches in Brazil than in Argentina, the Rufous-collared Sparrow had larger clutches in Argentina, and clutch size of the remaining species was similar among locations. Thus, the species with variable BSL had fixed CS, and those in which CS was flexible showed fixed BSL. Comparing species traits between locations revealed unique responses to local conditions (Cardillo 2002).

Nest cycle interval

Nest cycle interval was quite variable among species, but no variation was found within species among locations. Thus, interval duration of each stage in the nesting cycle seems to be fixed among the compared species. When comparing the developmental ratio, rates varied widely in both locations, with similar patterns across locations. Thus, both locations have species with slow and fast paced traits with respect to development rate, while plasticity regarding intervals of nesting cycle stages seems unlikely.

Nesting success

Nest success in Brazil encompasses a wide range of rates (16 – 59%) that resembles patterns found in both tropical (<30%) and temperate latitudes (>50%, Ricklefs 1969, Ricklefs and Bloom 1977, Robinson et al. 2000, Roper 2005, Roper et al 2010, Brawn et al. 2011, Remeš et al. 2012). Interestingly, low nest success have been also reported farther south in South America (Mezquida and Marone 2001, Mezquida 2004, Moreno et al. 2005, Pretelli and Isacch 2013) and in South Africa (Martin et al. 2006). It seems clear that, at least in South America, the latitudinal variation in nest predation is not robust as it would be expected in birds from northern continents, suggesting that local factors are very important for reproductive strategies among passerines.

Local variation in nest predation suggests that plasticity in other breeding traits might be important to balance reproductive success. For instance, *T. musculus* had similar BSL in both locations, while nest success was lower and clutch size was larger in Brazil than in Argentina. In contrast, CS was similar in the Turdidae, but they had greater DSR and earlier and longer breeding seasons in Brazil than in Argentina. Thus, plasticity in breeding strategies vary as specific responses to local environmental variability. However, it remains to be analyzed whether each variable response may simply be plasticity, or a complex synergy between phylogeny (and inherent life history traits), limiting resources and individual experience (Moore et al. 2005, Du et al. 2014).

Annual fecundity

The simulated fecundity ranged from less than annual replacement and, especially in Brazil, to greater than annual replacement. Excepting for the NC of species from Argentina, all the other breeding traits have an important positive effect in fecundity rates of species from both locations, in which nest survival was the component that explained most variation in models. Thus, fecundity rates are the outcome of the combination of DSR and the other breeding traits. The short breeding season in Argentina is an important factor because limits timing of breeding in species at that location, in which double-brooding was unlikely for most species, following predicted latitudinal patterns (Griebeler et al. 2010, Roper et al 2010). In Brazil, however, longer BSL than Argentina allows for higher rates of multiple-brood. Because of this limitation in breeding potential, the clutch size is also an important source of variation in fecundity in both locations, especially when DSR is high, in which an additional egg in a brood could contribute more to annual fecundity than an additional nesting attempt. Fecundity rates were variable among species and within-families, which seems to be better explained by unique combinations of breeding components. If the populations examined are more or less stable, this wide variation in fecundity implies that adult survival rates should also longitudinally vary in this latitude (Wolfe et al. 2014).

Field records of double-brooding of any species requires uniquely marked pairs followed throughout the breeding cycle for monitoring all nesting attempts, and such studies are extremely rare in South America. In our study, we had such field records of double-brood for *T. caerulescens* (Thamnophilidae), *P. cyanoleuca* (Hirundinidae), *T. musculus* (Troglodytidae), *T. rufiventris* (Turdidae) and *S. flaveola* (Emberizidae), all of which had great probability for double-brooding according to our fecundity estimates. On the other hand, species that had mainly estimates of single brood were never observed even attempting another nest within the breeding season after a success (even when time to nest remained, based on other pair nesting records): *C. melanops* (Conopophagidae, Lima and Roper 2009), *Rhopias gularis* (Thamnophilidae, first chapter), *B. culicivorus* (Parulidae) and *T. leucorrhoa* (Hirundinidae).

In Argentina species tend to be limited to one successful nest per year. Maximizing fecundity in this situation can only be accomplished by reducing renesting interval (Cavitt et al. 1999, Roper 2005, Styrsky 2005, Roper et al 2010), because reducing predation risk seems unlikely (Roper

2005) and reducing the nest cycle seems uneffective. Yet, in more temperate locations in South America a similar short breeding season did not limit species annual productivity to a single brood (Moreno et al. 2005, Carro et al 2014). Thus, while latitudinal variation in environmental conditions may constrain annual fecundity on a broad scale, species may respond in singular ways to local conditions to maximize fecundity. This may explain why fecundity was greater in the warblers (Parulidae) in Argentina than in Brazil, in constrast to most species. This also illustrates how a latitudinal dichotomy in the pace of life paradigm may be inappropriate for birds in subtropics.

In subtropical Brazil, contrasting (slow and fast) strategies clearly coexist, which seem to be independent of phylogeny. Thus, a classification between slow-fast pace of life appears to be descriptive of patterns at the extremes of environmental conditions that generate those paces (high versus low latitudes or elevations), and this paradigm seems less suited for explaining strategies in places between those extremes, such as the subtropics. For instance, a latitudinal gradient of the pace of life does not explain well how, at the same latitude, some species can have large clutches while others have small ones, or why some species have double-brood by reducing post-fledgling parental care, while other species extend post-fledgling parental care for a single annual brood (Russell 2000, Russell et al. 2004, Lima and Roper 2009, Tarwater and Brawn 2010, first chapter)**.**

Additionally, estimating the importance of each component for the breeding cycle and annual fecundity are extremely difficult in the field. Thus, modeling (using bootstrap and Monte Carlo methods) offers a powerful tool to estimate and compare these components based on usually small sample sizes (Farnsworth and Simons 2001, Grzybowski and Pease 2005, McNamara et al. 2008). We found that the proportion of successful breeders in the populations can widely vary among species, from < 50% to > 90% in some cases. In another example, DSR was similar in three unrelated species (*Chiroxiphia caudata*, *C. melanops* and *S. caerulescens*), yet they varied from 9% to 30% in unsuccessful pairs, due to the combinations of the other breeding traits. Thus, this ratio might also indicate the likelihood of of individual contribution to population parameters, based on the combined effects of breeding traits. Variation in the proportion of breeders in a population is important for understanding population dynamics (Rees et al. 1991, Jenouvrier et al. 2005, Tryjanowski et al. 2005) and only through modeling we were able to perceive such pattern.

Finally, breeding traits of birds in subtropical South America vary among species and locations and were not well predicted by the slow- and fast-paced paradigm of breeding in birds. Only timing of breeding was similar and independent of phylogeny across locations. Nonetheless, species may vary distinctively within breeding season intervals, which is unexpected under a latitudinal slow-fast continuum and may cause specific consequences for fecundity. Thus, while traits of birds at high and low latitudes may be more clearly predicted by the fast-slow paradigm, in the subtropics unique combinations of traits that would be indicative of both slow and fast concepts may be locally mixed. Thus, there is not a simple continuum of life-history or breeding traits. Life history evolution may be more locally influenced than regularly considered, and thus, each species may have a singular life-history pattern as response to local constraints when not hindered by phylogenetic inertia (Ricklefs 2006, Pienaar et al. 2013).

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Table 1. Summary of localities coordinates, elevation and sampling effort during the study in southern Brazil.

Location (m a.s.l.)	Lat., Long.	Years	N Nests	N Species
Curitiba (930)	25°27S, 49 °14W	2001, 2002, 2005 – 2007, 2012	120	21
Guaraqueçaba (20 – 100)	25 °10S, 49 °17W	2006 – 2007	79	34
Morretes (100 – 600)	25 °36S, 48 °48W	2011 – 2014	284	56
Piraquara (900)	25 °30S, 49 °00W	2003 – 2007, 2009 – 2013	625	65
São João do Triunfo (800)	25 °41S, 50 °10W	2003, 2004	55	36
VilaVelha- Ponta Grossa (920)	25 °14S, 50 °00W	2000 – 2003	103	1

Table 2. Earliest date of nest initiation and breeding season length (BSL) in 25 passerine species in southern Brazil from 2000 – 2014.

Suborder	Family	Species	Earliest Date	BSL	N
Tyranni	Furnariidae	*Lepidocolaptes falcinellus*	20 September	39	8
	Thamnophilidae	*Thamnophilus caerulescens*	7 September	179	142
		Rhopias gularis	14 September	125	84
	Conopophagidae	*Conopophaga melanops*	12 October	97	20
	Rhynchocyclidae	*Mionectes rufiventris*	13 September	141	8
		Phylloscartes ventralis	5 October	111	10
	Tyrannidae	*Myiophobus fasciatus*	21 October	109	15
		Myiarchus ferox	28 October	53	7
		Pitangus sulphuratus	19 August	126	30
		Tyrannus melancholicus	18 October	88	9
	Pipridae	*Chiroxiphia caudata*	20 September	144	29
Passeri	Hirundinidae	*Pygochelidon cyanoleuca*	19 September	146	19
		Tachycineta leucorrhoa	18 October	58	122
	Troglodytidae	*Troglodytes musculus*	19 September	144	103
	Turdidae	*Turdus rufiventris*	19 September	126	74
		Turdus albicollis	4 October	73	11
		Turdus amaurochalinus	13 October	92	23
	Vireonidae	*Vireo olivaceus*	29 September	112	24
	Parulidae	*Myiothlypis leucoblephara*	15 October	31	8
		Basileuterus culicivorus	11 October	89	22
	Thraupidae	*Tachyphonus coronatus*	25 October	103	8
		Thraupis sayaca	11 October	63	7
	Emberizidae	*Sicalis flaveola*	19 September	185	168
		Zonotrichia capensis	30 September	131	31
		Sporophila caerulescens	1 December	113	10

Table 3. Clutch size of 19 passerine families in subtropical Brazil (Appendix B for species).

Suborder	Family	Mode	Min	Max	Mean	N Species	N Nests
Tyranni	Dendrocolaptidae	3	3	4	3.3	2	8
	Furnariidae	2				3	6
	Thamnophilidae	2	1	4	2.1	6	218
	Formicariidae	3				1	1
	Conopophagidae	2	1	2	1.9	1	20
	Grallaridae	2				1	2
	Rhynchocyclidae	3	1	4	2.8	5	20
	Tyrannidae	2	1	4	2.4	11	27
	Tityridae	3				2	2
	Pipridae	2				1	25
Passeri	Hirundinidae	5	2	8	4.4	4	83
	Turdidae	3	1	4	2.5	4	61
	Troglodytidae	5	2	6	4.0	1	42
	Coerebidae	3				1	2
	Thraupidae	2	1	3	2.2	11	30
	Parulidae	3	1	3	2.6	4	25
	Vireonidae	2	1	7	2.5	1	13
	Emberizidae	4	2	5	3.0	5	128
	Fringilidae	4	2	4	2.5	2	2

Table 4. Nesting stages interval estimates (Inc – Incubation, Nes – Nestling), apparent nesting success (AS), constant daily survival rates (DSR) and probability of success (Success) for 21 bird species in southern Brazil.

Taxa	Nesting stage (d)		AS	DSR (SE)	Success	N
	Inc (N)	Nes (N)	%		%	
Tyranni						
Thamnophilus caerulescens	12 (15)	13 (13)	23	0.943 (0.005)	23	134
Rhopias gularis	18 (13)	13 (16)	36	0.962 (0.005)	30	73
Conopophaga melanops	20 (2)	20 (2)	35	0.967 (0.009)	26	20
Mionectes rufiventris	14 (1)	18 (4)	71	0.981 (0.011)	54	7
Phylloscartes ventralis	18 (1)	16 (4)	60	0.962 (0.019)	27	10
Myiophobus fasciatus	18 (1)	15 (5)	83	0.975 (0.011)	43	10
Pitangus sulphuratus	16 (6)	21 (4)	67	0.980 (0.007)	47	24
Tyrannus melancholicus	16 (3)	17 (4)	63	0.981 (0.011)	53	8
Chiroxiphia caudata	17 (4)	17 (8)	58	0.967 (0.009)	32	24
Passeri						
Tachycineta leucorrhoa	19 (25)	24 (16)	64	0.982 (0.003)	46	78
Pygochelidon cyanoleuca	18 (1)	25 (8)	86	0.988 (0.006)	59	16
Troglodytes musculus	16 (8)	16 (13)	70	0.975 (0.004)	44	57
Turdus albicollis	14 (3)	14 (3)	45	0.971 (0.012)	44	11
Turdus rufiventris	13 (1)	14 (12)	57	0.960 (0.007)	33	46
Turdus amaurochalinus	14 (3)	14 (4)	44	0.957 (0.012)	29	16
Vireo olivaceus	15 (1)	13 (6)	33	0.963 (0.010)	35	18
Myiothlypis leucoblephara	17 (2)	15 (2)	25	0.957 (0.017)	25	8
Basileuterus culicivorus	16 (1)	14 (2)	19	0.941 (0.015)	16	16
Sporophila caerulescens	13 (4)	13 (4)	56	0.967 (0.016)	42	9
Sicalis flaveola	15 (15)	15 (28)	57	0.977 (0.003)	50	102
Zonotrichia capensis	16 (1)	11 (6)	36	0.947 (0.013)	23	22

Table 5. Coefficients of general linear model and PGLS analyses in fecundity rates. Values in parenthesis refers to species from northern Argentina (Auer et al. 2007) and values outside parenthesis refers to species from southern Brazil. BSL – breeding season length; CS – clutch size; DSR – daily nest survival rate; NC – nest cycle length.

	Linear Model				PGLS			
Parameter	Estimate	SE	*F*	P	Estimate	SE	*F*	P
Intercept	1.499 (-2.014)	1.220 (1.786)	1.22 (-1.12)	0.237 (0.281)	-59.815 (-34.768)	8.744 (5.884)	-6.84 (-5.90)	<0.001 (<0.001)
BSL	0.722 (0.775)	0.150 (0.148)	4.80 (5.21)	<0.001 (<0.001)	0.025 (0.026)	0.004 (0.005)	5.92 (5.16)	<0.001 (<0.001)
CS	0.800 (1.208)	0.146 (0.340)	5.46 (3.55)	<0.001 (0.003)	1.094 (0.781)	0.150 (0.208)	7.26 (3.74)	<0.001 (0.002)
DSR	23.155 (17.650)	3.128 (3.990)	7.51 (4.42)	<0.001 (<0.001)	62.597 (34.985)	9.639 (6.565)	6.49 (5.32)	<0.001 (<0.001)
NC	-1.112 (-0.255)	0.261 (0.371)	-4.25 (-0.68)	<0.001 (0.504)	-0.106 (-0.010)	0.023 (0.019)	-4.48 (-0.55)	<0.001 (0.59)

Table 6. Percent variation explained (partial r^2) for breeding components when ≥ 10% in multiple-regression of annual fecundity estimates by each breeding component across 21 bird species from southern Brazil and 17 species from northern Argentina. Model R^2 and partial r^2 for species from Argentina are in parentheses. Values lower than 0.05 were omitted. BSL – breeding season length, CS – clutch size, I – incubation, N – nestling, DSR – daily nest survival rate, PS – post-success interval, PF – post-failure interval.

Taxa	Model	Partial r^2						
(N species Bra–Arg)	R^2	BSL	CS	I	N	DSR	PS	PF
Tyrannidae	0.93	0.25	0.12				0.32	0.14
(5 – 6)	(0.95)		(0.82)					
Turdidae	0.83						0.49	0.48
(3 – 3)	(0.90)	(0.33)					(0.11)	(0.56)
Parulidae	0.88							0.95
(2 – 4)	(0.77)	(0.24)		(0.20)			(0.25)	(0.29)
Emberizidae	0.95		0.82					
(3 – 3)	(0.92)	(0.70)	(0.12)					(0.13)
Tyranni	0.92	0.10	0.51			0.11	0.14	0.10
(9 – 7)	(0.95)		(0.82)					
Passeri	0.95	0.34	0.47					
(11 – 10)	(0.90)		(0.31)		(0.30)	(0.10)		(0.18)
All	0.94	0.31	0.45					
(21 – 17)	(0.92)		(0.57)			(0.13)		(0.12)

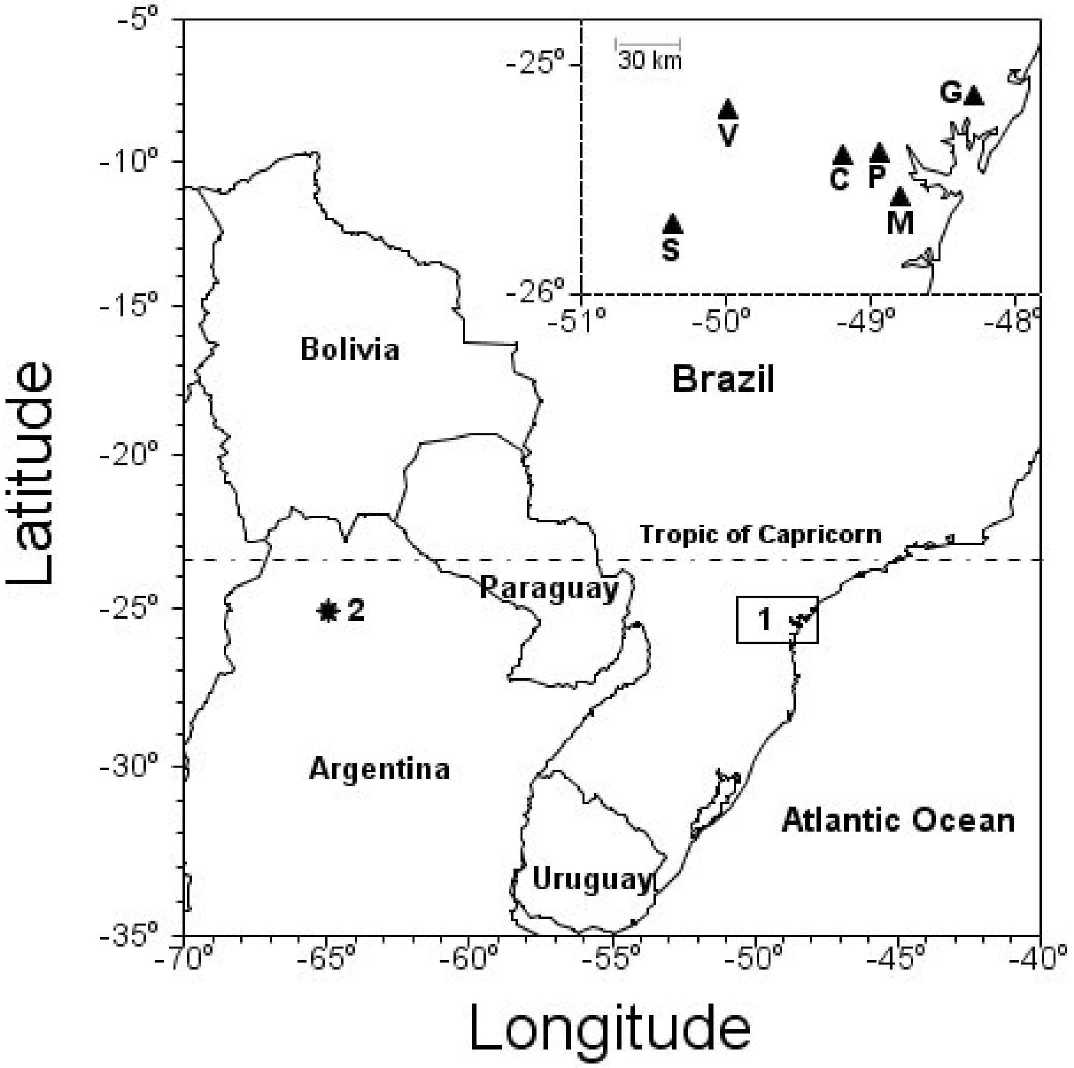


Figure 1. Study sites at same subtropical latitude (~25º) in Brazil and Argentina. 1) Study locations in southern Brazil, represented in small map in the upper right corner. Each triangule is one study site and the letters are the initial letter of each location in Table 1. 2) Study location in northeastern Argentina, in El Rey National Park (Auer et al. 2007).

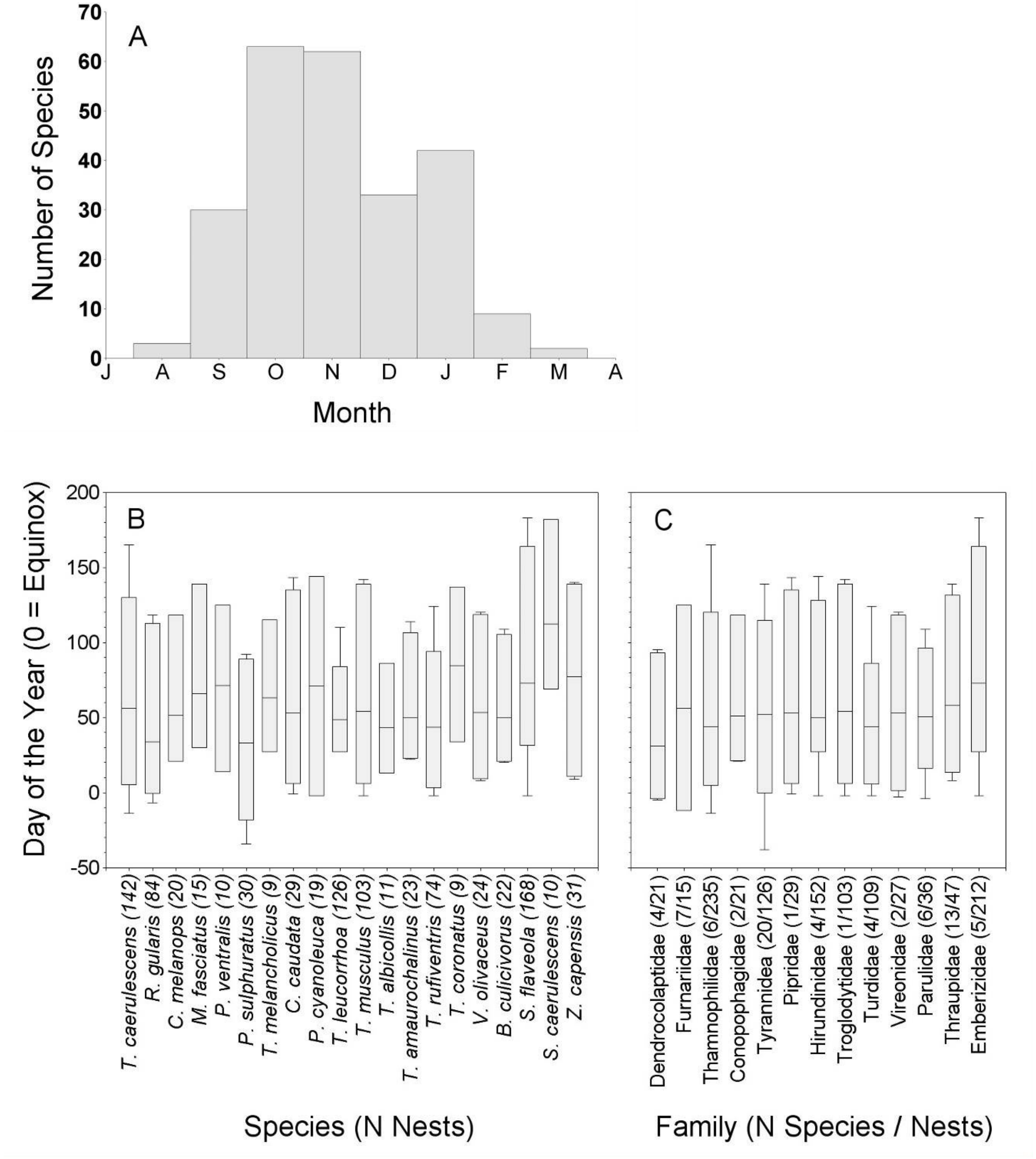


Figure 2. (A) Distribution of nest initiation dates (N = 1151 nests, 88 spp.) in southern Brazil through 2000 – 2014. B) Boxplot of temporal distribution of nesting attempts in the 20 species with largest sample size. C) Nest initiation dates grouped by family. Boxplot error bars indicate the 5% and 95% percentile. Adjusted day of the year uses the vernal equinox (September 21) as day 0.

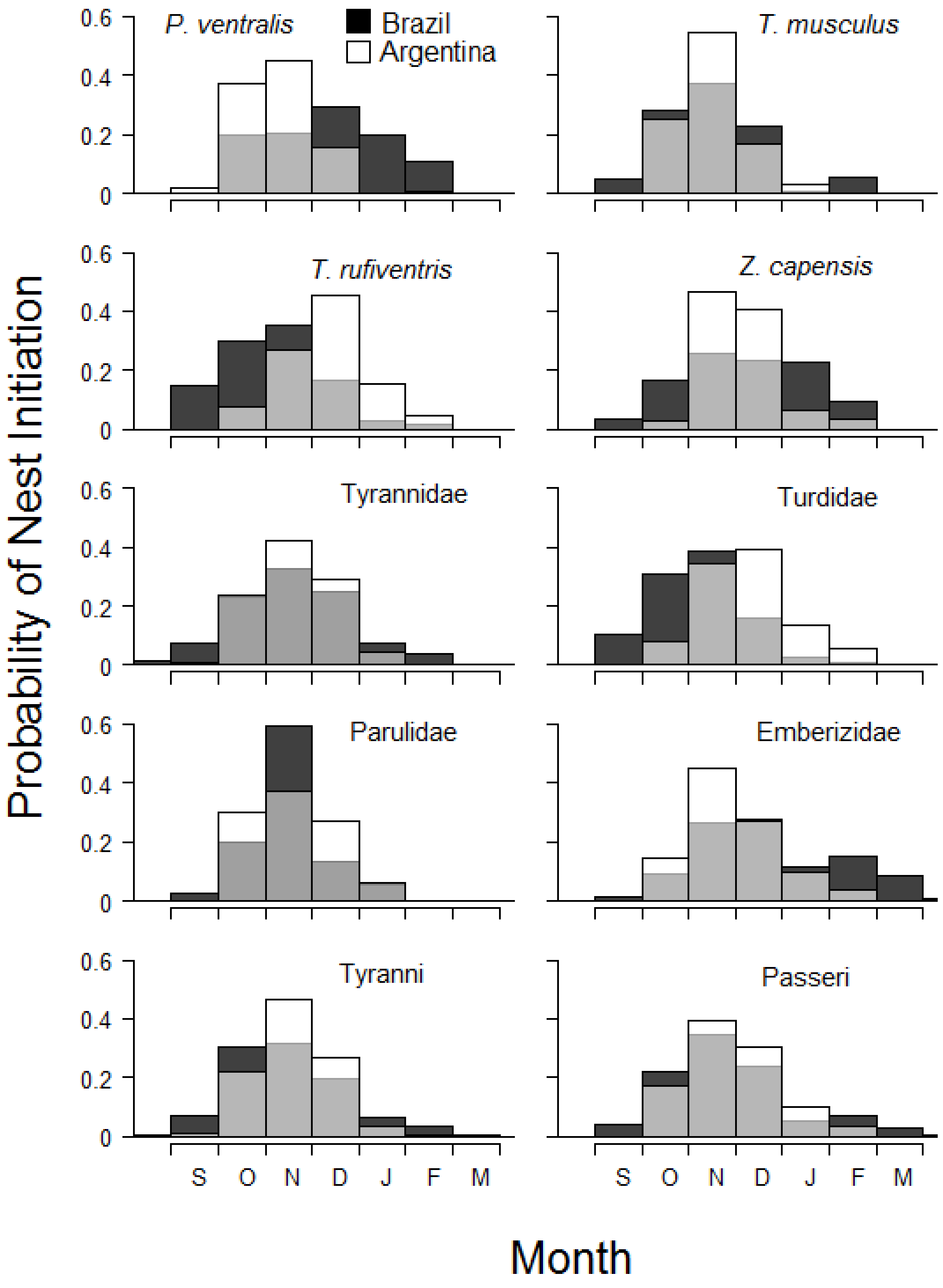


Figure 3. Comparative distributions of nesting initiation dates generated by 10,000 bootstrapped replicates among subtropical populations of passerine species in Brazil and Argentina. Gray areas indicate the amount of overllaped distributions.

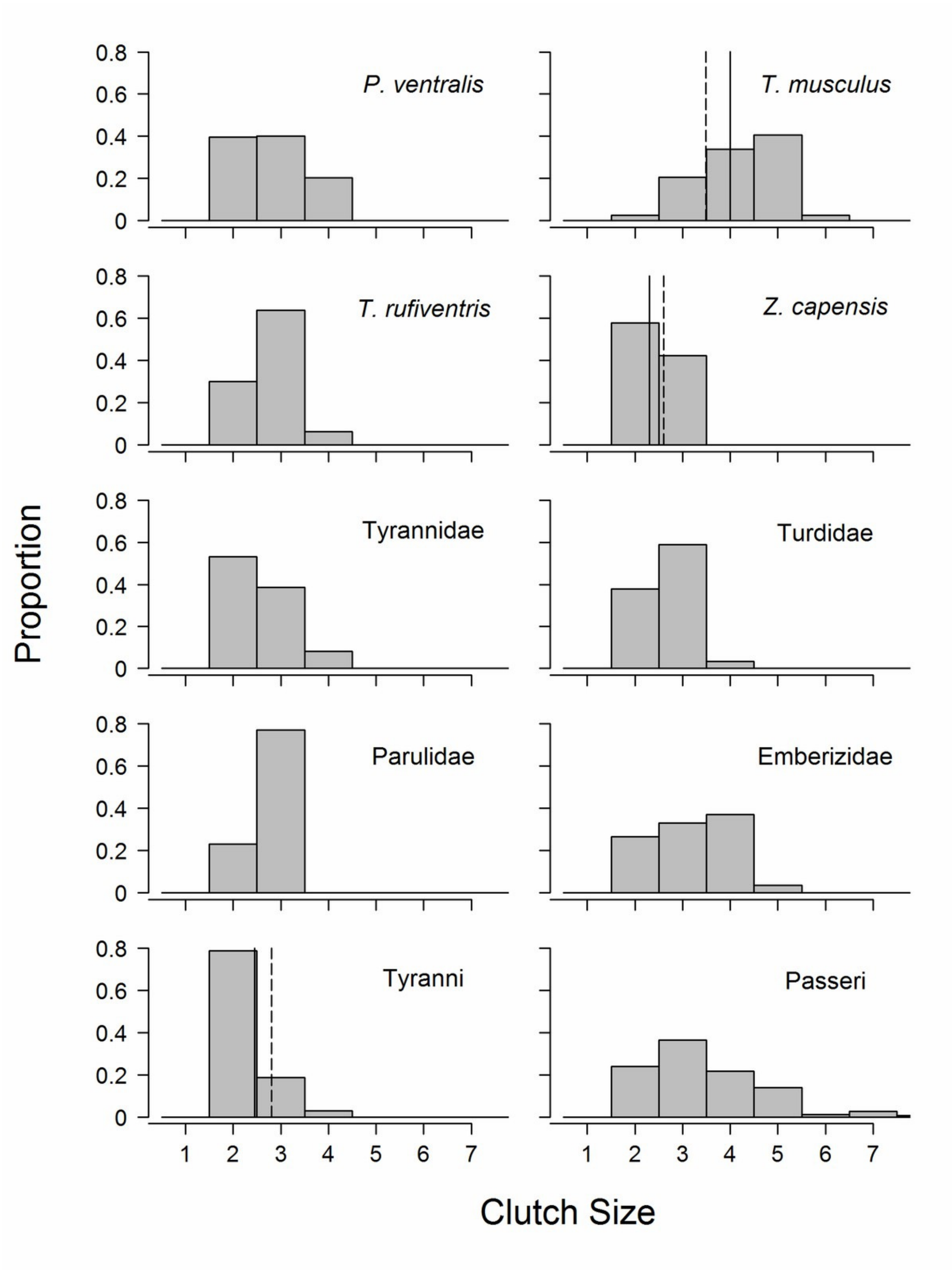


Figure 4. Bootstrapped distributions of clutch size in southern Brazil. Dashed lines indicate the mean clutch size in subtropical Argentina (Auer et al. 2007) when $p < 0.05$, in comparison with clutch size in Brazil (continuous lines).

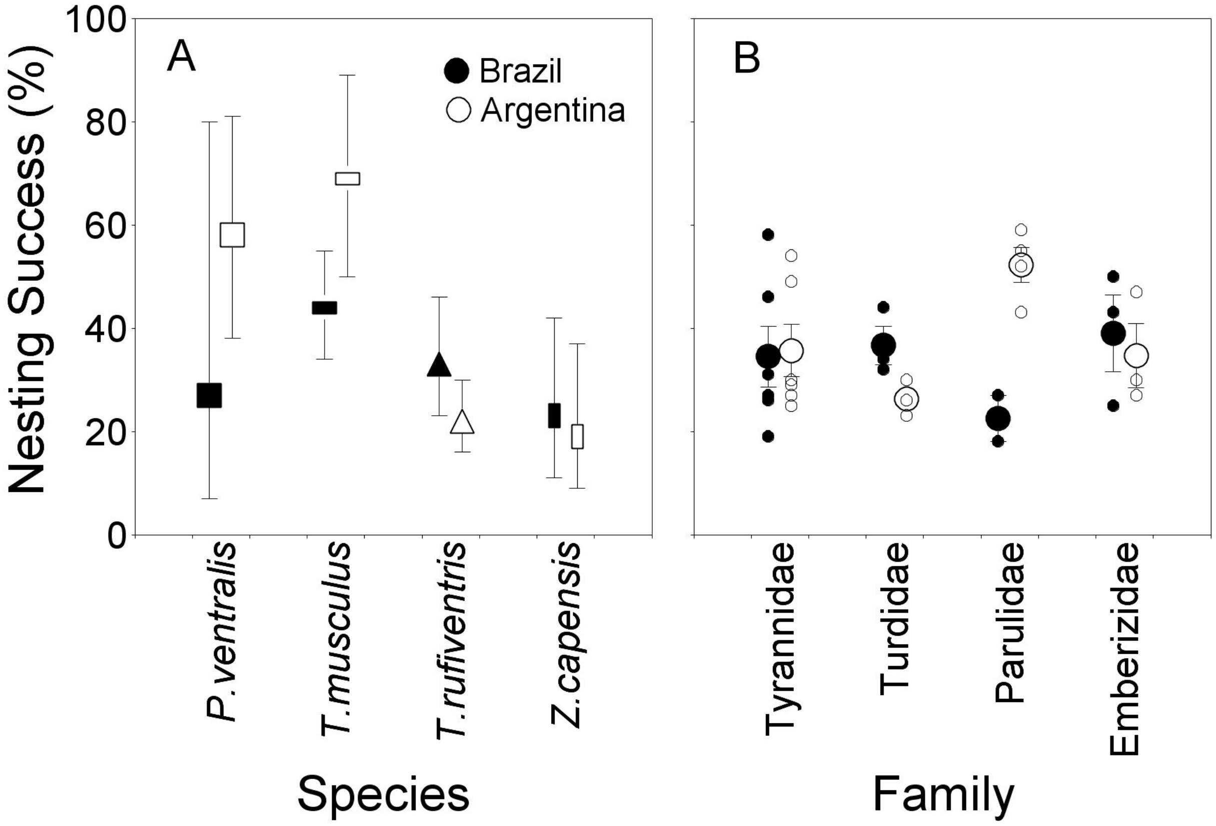


Figure 5. Probability of nesting success compared between Brazil and Argentina populations of four species and four families (see text for sample size). A) Species comparisons, showing probability of survival and the 95% confidence interval. B) Family comparisons, showing the average probability of nest survival among species (large symbols) and the probability for each species (small symbols). Bars indicate standard error.

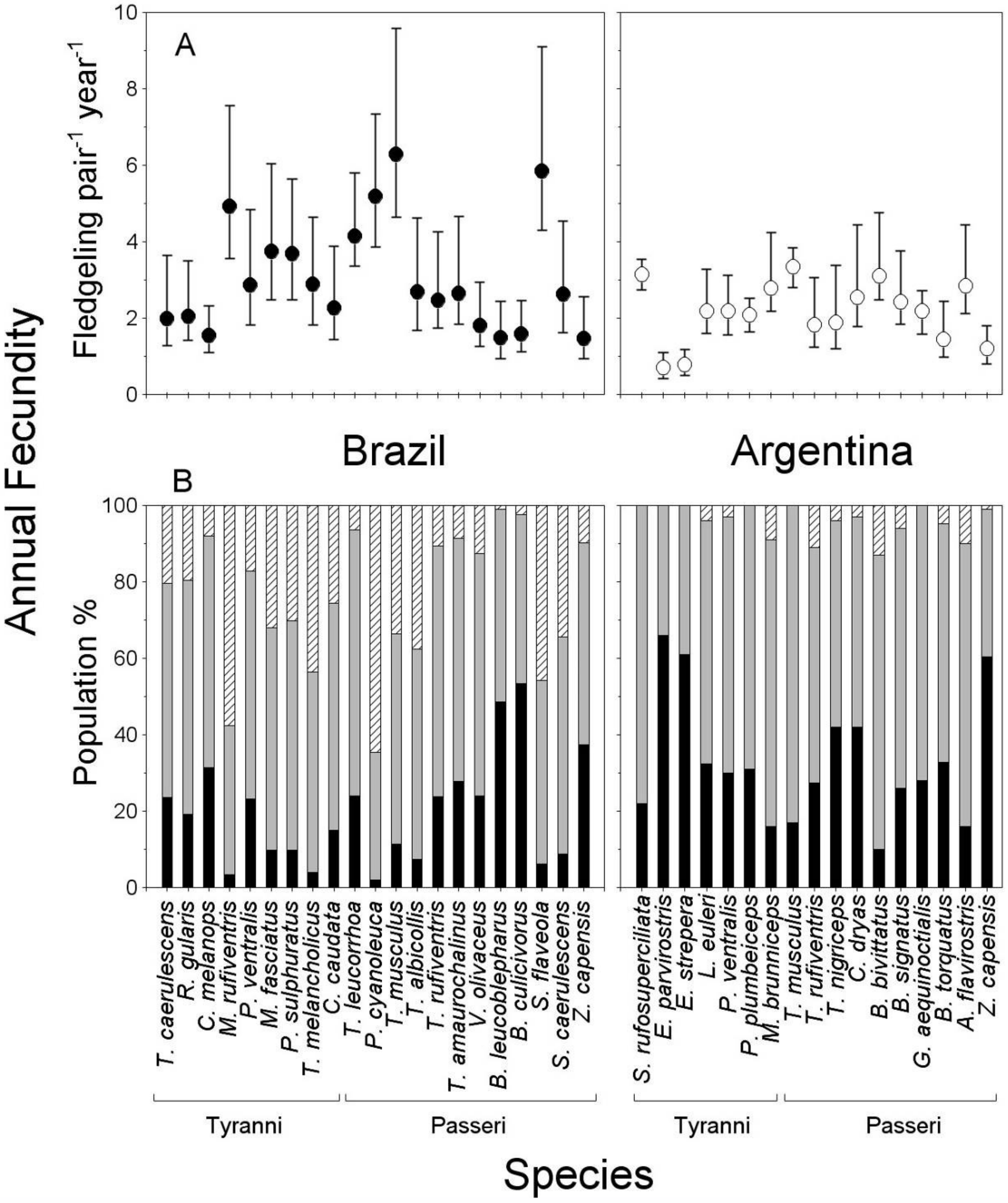


Figure 6. Simulated variation in annual fecundity of birds in subtropical Brazil and Argentina. A) Bars indicate the minimum, mean and maximum annual fecundity of each species, as consequence of variation in the renest intervals (see Methods for details). B) Proportion of pairs by number of successful nests per year – black indicates no success, gray indicates one success, hashed indicates double-brooded pairs.

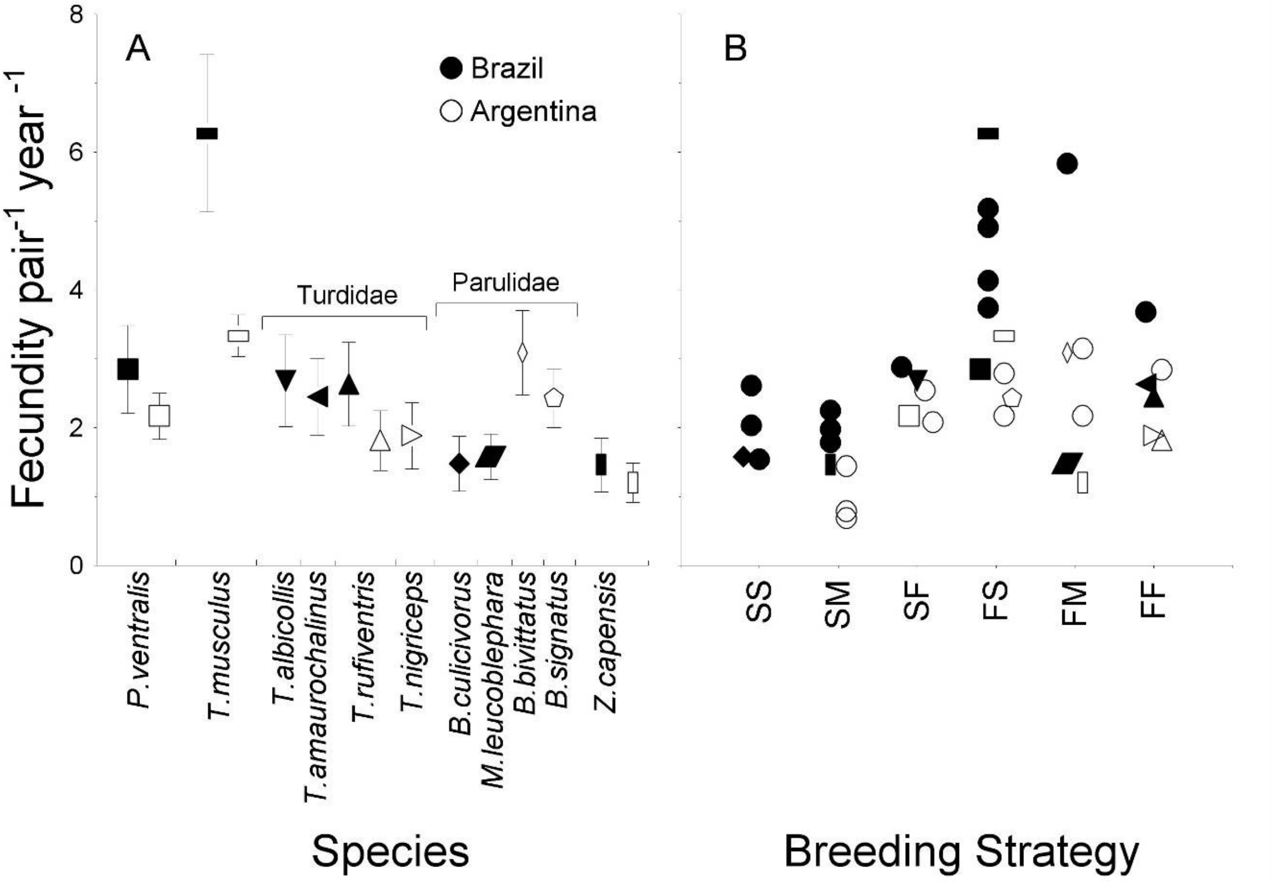
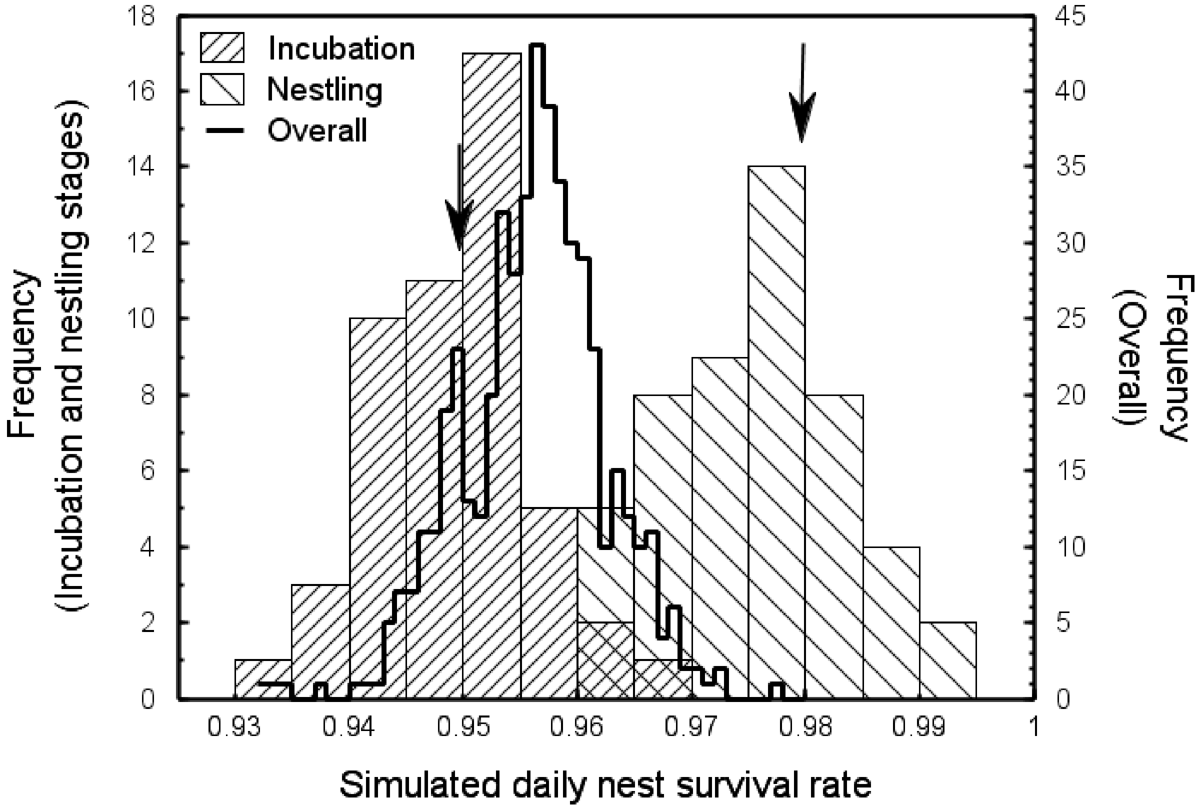


Figure 7. Variation in annual fecundity of birds in subtropical Brazil and Argentina, paired by (A) phylogeny and (B) breeding strategy (see Methods for classes definition). Each point indicates mean fecundity rate and bars indicate the minimum and maximum rates. Each symbol refers to one species and circles refer to species no included in A.

Appendix A. Ranges in values of daily nest survival rate (DSR) for the Star-throated Antwren (*Rhopias gularis*) generated by the simulation of 20 replicates of a population size of 30 pairs (total of 600 pairs) based on empirical DSR (data obtained in first chapter). Arrows show the averaged DSR values obtained from field work for incubation (DSR = 0.949 d^{-1}) and for nestling stage (DSR = 0.978 d^{-1}), indicating that the mean and confidence intervals were equal to those estimated by the program MARK. Thus, the simulation reflects sampling procedures and illustrates patterns expected in nature.



Appendix B. Clutch size in 67 species of passerine birds in subtropical Brazil. When only the mode is shown, only one clutch or clutch size was observed.

Suborder	Family	Species	Mode	Min	Max	Mean (SD)	N
Tyranni	Dendrocolaptidae	*Dendrocolaptes platyrostris*	4	2	4	3.3 (1.2)	3
		Lepidocolaptes falcinellus	3	3	4	3.3 (0.5)	5
	Furnariidae	*Synallaxis spixi*	2				3
		Synallaxis ruficapilla	2				1
		Philydor atricapillus	2				2
	Thamnophilidae	*Drymophila squamata*	2				2
		Dysithamnus mentalis	2				1
		Haplospiza unicolor	2				2
		Myrmeciza squamosa	2				2
		Rhopias gularis	2	1	2	1.9 (0.3)	88
		Thamnophilus caerulescens	2	1	4	2.3 (0.5)	123
	Formicariidae	*Chamaeza campanisona*	3				1
	Grallariidae	*Grallaria varia*	2				2
	Conopophagidae	*Conopophaga melanops*	2	1	2	2.0 (0.2)	20
	Platyrinchidae	*Platyrinchus mystaceus*	2				2
	Rhynchocyclidae	*Mionectes rufiventris*	3	2	3	2.8 (0.4)	6
		Leptopogon amaurocephalus	3				1
		Phylloscartes oustaleti	3	1	3	2.3 (0.8)	6
		Phylloscartes ventralis	3	1	4	2.5 (1.0)	6
		Todirostrum poliocephalum	2				1
	Tyrannidae	*Cnemotriccus fuscatus*	2				3
		Elaenia obscura	2	1	2	1.5 (0.7)	2
		Elaenia parvirostris	2				1
		Lathrotriccus euleri	3				1
		Myiarchus ferox	3				1
		Myiarchus swainsoni	4	3	4	3.8 (0.5)	4
		Myiodynastes maculatus	2				1
		Myiophobus fasciatus	3	2	3	2.5 (0.6)	4
		Myiozetetes similis	2				1
		Pitangus sulphuratus	3	2	3	2.5 (0.7)	2
		Tyrannus melancholicus	2	2	3	2.4 (0.5)	5
		Tyrannus savana	3	1	3	2.0 (1.4)	2

Suborder	Family	Species	Mode	Min	Max	Mean (SD)	N
	Tityridae	*Pachyramphus marginatus*	3				1
		Schiffornis virescens	3				1
	Onychorhynchidae	*Myiobius barbatus*	2				5
	Pipridae	*Chiroxiphia caudata*	2				25
Passeri	Hirundinidae	*Progne chalybea*	2				1
		Pygochelidon cyanoleuca	3	2	4	3.1 (0.5)	13
		Stelgidopteryx ruficollis	3	3	5	3.5 (1.0)	4
		Tachycineta leucorrhoa	5	1	7	4.8 (1.4)	65
	Troglodytidae	*Troglodytes musculus*	5	1	6	4.0 (1.1)	42
	Turdidae	*Turdus albicollis*	2	1	3	2.2 (0.8)	6
		Turdus amaurochalinus	3	2	3	2.6 (0.5)	16
		Turdus flavipes	2				1
		Turdus rufiventris	3	1	4	2.5 (0.8)	38
	Vireonidae	*Vireo olivaceus*	2	1	7	2.5 (1.5)	13
	Parulidae	*Basileuterus culicivorus*	3	1	3	2.5 (0.7)	17
		Myiothlypis leucoblephara	3				6
		Phaeothlypis rivularis	2				1
	Thraupidae	*Habia rubica*	2	2	3	2.2 (0.4)	5
		Ramphocelus bresilius	2				2
		Tachyphonus coronatus	2	1	3	1.8 (0.8)	6
		Tachyphonus rufus	2	2	3	2.3 (0.6)	3
		Thraupis sayaca	2	2	3	2.3 (0.6)	3
		Thraupis cyanoptera	2				1
		Tangara cyanocephala	2				1
		Tangara seledon	2				1
		Tersina viridis	3				1
		Saltator similis	3	1	3	2.5 (1.0)	4
	Coerebidae	*Coereba flaveola*	3				2
	Emberizidae	*Poospiza cabanisi*	2	1	3	2.0 (1.0)	3
		Sicalis flaveola	4	1	5	3.3 (0.9)	98
		Sporophila caerulescens	2	1	3	1.7 (0.7)	9
		Sporophila lineola	3				1
		Zonotrichia capensis	2	1	3	2.3 (0.6)	18
	Fringillidae	*Euphonia cyanocephala*	3				1
		Euphonia pectoralis	4				1

Appendix C. Classification of each species from Brazil and Argentina in a local scale of fast-slow breeding pace according to their clutch size, ratio of body weight per nest cycle interval and the combined breeding strategy. See methods for classification criteria.

Location / Family	Species	Clutch		Weight	Ratio		Breeding
		Size	Class	(g)	(g d^{-1})	Class	Strategy
Brazil							
Thamnophilidae	*Thamnophilus caerulescens*	2	slow	15	0.58	mid	SM
	Rhopias gularis	2	slow	12	0.39	slow	SS
Conopophagidae	*Conopophaga melanops*	2	slow	20	0.50	slow	SS
Rhynchocyclidae	*Myiophobus fasciatus*	3	fast	10	0.33	slow	FS
	Phylloscartes ventralis	3	fast	9	0.30	slow	FS
Tyrannidae	*Mionectes rufiventris*	3	fast	14	0.44	slow	FS
	Pitangus sulphuratus	3	fast	65	1.86	fast	FF
	Tyrannus melancholicus	2	slow	35	1.13	fast	SF
Pipridae	*Chiroxiphia caudata*	2	slow	25	0.78	mid	SM
Hirundinidae	*Tachycineta leucorrhoa*	5	fast	20	0.45	slow	FS
	Pygochelidon cyanoleuca	3	fast	13	0.30	slow	FS
Troglodytidae	*Troglodytes musculus*	4	fast	12	0.40	slow	FS
Turdidae	*Turdus albicollis*	2	slow	65	2.50	fast	SF
	Turdus amaurochalinus	3	fast	68	2.62	fast	FF
	Turdus rufiventris	3	fast	75	2.68	fast	FF
Vireonidae	*Vireo olivaceus*	2	slow	20	0.61	mid	SM
Parulidae	*Basileuterus culicivorus*	2	slow	10	0.36	slow	SS
	Basileuterus leucoblepharus	3	fast	18	0.58	mid	FM
Emberizidae	*Sicalis flaveola*	3	fast	18	0.60	mid	FM
	Sporophila caerulescens	2	slow	9	0.36	slow	SS

Location / Family	Species	Clutch		Weight	Ratio		Breeding
		Size	Class	(g)	(g d^{-1})	Class	Strategy
	Zonotrichia capensis	2	slow	23	0.72	mid	SM
Argentina							
Furnariidae	*Syndactyla rufosuperciliata*	4	fast	27	0.70	mid	FM
Rhynchocyclidae	*Phylloscartes ventralis*	3	fast	9	0.26	slow	FS
	Lathrotriccus euleri	3	fast	11	0.34	slow	FS
Tyrannidae	*Elaenia parvirostris*	2	slow	18	0.53	mid	SM
	Elaenia strepera	2	slow	20	0.59	mid	SM
	Poecilotriccus plumbeiceps	3	fast	6	0.16	slow	FS
Troglodytidae	*Troglodytes musculus*	4	fast	12	0.39	slow	FS
Turdidae	*Catharus dryas*	2	slow	40	1.39	fast	SF
	Turdus nigriceps	3	fast	50	1.96	fast	FF
	Turdus rufiventris	3	fast	75	2.68	fast	FF
Parulidae	*Basileuterus bivittatus*	3	fast	15	0.58	mid	FM
	Basileuterus signatus	3	fast	13	0.45	slow	FS
	Geothlypis aequinoctalis	3	fast	14	0.61	mid	FM
	Myioborus brunniceps	3	fast	10	0.34	slow	FS
Emberizidae	*Arremon flavirostris*	3	fast	26	0.95	fast	FF
	Buarremon torquatus	2	slow	22	0.77	mid	SM
	Zonotrichia capensis	3	fast	23	0.72	mid	FM

MATERIAL SUPLEMENTAR 1 (*SUPLEMENTARY MATERIAL* 1)

FEC {function}

Function to estimate annual fecundity in birds

Description:

The function simulates annual nesting attempts for a population based on their breeding parameters (breeding season and nest cycle length, clutch size, renest intervals and daily nest survival probabilities).

Usage:

FEC(DATA)

FEC(DATA, XX=DATA[,1], name=DATA[,2], NPairs=DATA[,3], CS=DATA[,4], BSL=DATA[,5], I=DATA[,6],N=DATA[,7],PS=DATA[,8],PF=DATA[,9],DSR=DATA[,10],NSR=DATA[,11])

Arguments:

XX - Replicates

NPairs - Number of Pairs

CS - Clutch size (number of eggs)

BSL - Breeding season length (d)

I - Incubation stage length (d)

N - Nestling stage length (d)

PS - Time to next attempt after Success (d)

PF - Time to next attempt after Failure (d)

DSR - Daily survival rate (incubation stage)

NSR - Daily survival rate (nestling stage)

Value:

FEC creates an output.rda object, which contains the raw simulated data (annual nesting attempts for each replicates and Npairs) in a dataframe called “fulltable”. The fulltable data frame has three result columns for each simulated nest attempt, in addition to the entered parameters:

- Nday {the last day within the nest cycle length in which the nest attempt was active}
- Success {if nest attempt was successful (1) or not (0)}
- Fecundity {the product of Clutch size and Success}.

As result, FEC returns estimates of mean (SD) annual fecundity, mean (SD) annual attempt, the rate of attempt per success by model, and the proportion of success within population. The function records the output as an object.

References:

Roper, J. J., K. A. Sullivan, and R. E. Ricklefs (2010). Avoid nest predation when predation rates are low, and other lessons: testing the tropical–temperate nest predation paradigm. Oikos 119:719–729.

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James Joseph Roper

#Example simulating one species:

```
sp1 <- data.frame(XX=10, name="Rhopias gularis", Npairs= 10, CS=2, BSL=94, I=18, N=13, PS=100, PF=2, DSR=0.949, NSR=0.979)
FEC(sp1)
```

#Código da função – Script

```
FEC <- function(DATA, XX=DATA[,1], name=DATA[,2], NPairs=DATA[,3], CS=DATA[,4],
BSL=DATA[,5],
I=DATA[,6],N=DATA[,7],PS=DATA[,8],PF=DATA[,9],DSR=DATA[,10],NSR=DATA[,11]) {

  SPDATA <- data.frame(XX, name, NPairs, CS, BSL, I, N, PS, PF, DSR, NSR)

  Fecundity <- function(XX, name, NPairs, CS, BSL, I, N, PS, PF, DSR, NSR) {
    NC <- I+N
    Pair <- rep(NA,NPairs)
    Fecundity <- rep(NA,NPairs)
    output <- data.frame()

    for (r in 1:XX) {

      for (t in 1:NPairs){

        di <- 0 #day counter during incubation
        dn <- 0 #day counter during nestling period
        j <- 0 #day counter for BSL
        att <- 0 #counter for number of nesting attempts

        repeat{
          x <- runif(1)
          s <- 0


          if(di<=I) {

            j <- j+1

            if (x <= DSR){
              di <- di + 1
              i <- di+dn

            }
            if (x > DSR){
              j <- j+PF-1
              di <- di + 1
              i <- di+dn
              Pair <- t
              Success <- s
              Nday <- i
              att <- att+1
              Attempt <- att
              Fecundity <- CS*s
              result <-
```

```
data.frame(r,name,BSL,CS,I,N,PF,PS,DSR,NSR,Pair,Attempt,Success,Nday,Fecundity,row.names=
NULL)
              output <- rbind(output,result)
              di <- 0
              dn <- 0
              i <- di+dn
              next
            }
          }

          if(di>I) {

            j <- j+1

            if (x <= NSR){
              dn <- dn + 1
              i <- di-1+dn
              if(dn>=N) {
                s <- 1
                Pair <- t
                Success <- s
                Nday <- i
                att <- att+1
                Attempt <- att
                Fecundity <- CS*s
                result <-
data.frame(r,name,BSL,CS,I,N,PF,PS,DSR,NSR,Pair,Attempt,Success,Nday,Fecundity,row.names=
NULL)
                output <- rbind(output,result)
                j <- j+PS-1
                di <- 0
                dn <- 0
                i <- di+dn
              }

            }
            if (x > NSR){
              dn  <-  dn + 1
              i <- di-1+dn
              Pair <- t
              Success <- s
              Nday <- i
              att <- att+1
              Attempt <- att
              Fecundity <- CS*s
              result <-
data.frame(r,name,BSL,CS,I,N,PF,PS,DSR,NSR,Pair,Attempt,Success,Nday,Fecundity,row.names=
NULL)
              output <- rbind(output,result)
              j <- j+PF-1
```

```
          di <- 0
          dn <-  0
          i <- di+dn
          next

         }
       }
       if (j >= BSL && i>=3) {next}
       if (j >= BSL && i<=2) {break}

      }
      #cat("\n", "pair  - ", t,"\n")

     }
     cat("\n", "iter  - ", r,"\n")
     }
   return(output)
  }
 final <- list()
 fulltable <- data.frame()
 fecunditytable<- data.frame()

  for (sp in 1:nrow(DATA)) {
   final[[sp]] <-
Fecundity(SPDATA[sp,1],SPDATA[sp,2],SPDATA[sp,3],SPDATA[sp,4],SPDATA[sp,5],SPDATA[s
p,6],SPDATA[sp,7],SPDATA[sp,8],SPDATA[sp,9],SPDATA[sp,10],SPDATA[sp,11])
   fulltable <- rbind(fulltable,final[[sp]])
   totalatt<-final[[sp]]
   tr<-totalatt$r
   tp<-totalatt$Pair
   ts<-totalatt$Success
   tf<-totalatt$Fecundity
   ta<-totalatt$Attempt
   tt<-data.frame(tr,tp,ts,tf,ta)
   af<-aggregate(tt, by=list(tt$tr, tt$tp), FUN=sum)
   at<-aggregate(tt, by=list(tt$tr, tt$tp), FUN=max)
   mf<-mean(af$tf)
   mat<-mean(at$ta)
   sdf<-sd(af$tf)
   sdat<-sd(at$ta)
   atsum<-sum(at$ta)
   ssum<-sum(tt$ts)
   atts<-(atsum/ssum)
   ttss0=sum(af$ts==0)
   ttss1=sum(af$ts==1)
   ttss2=sum(af$ts==2)
   ttss3=sum(af$ts==3)
   totalpairs=nrow(af)
   pzero<-ttss0/totalpairs
   pum<-ttss1/totalpairs
```

```
   pdois<-ttss2/totalpairs
   ptres<- ttss3/totalpairs
   fecunditytable[sp,1]<-SPDATA[sp,2]
   fecunditytable[sp,2]<-SPDATA[sp,4]
   fecunditytable[sp,3]<-SPDATA[sp,5]
   fecunditytable[sp,4]<-SPDATA[sp,6]
   fecunditytable[sp,5]<-SPDATA[sp,7]
   fecunditytable[sp,6]<-SPDATA[sp,8]
   fecunditytable[sp,7]<-SPDATA[sp,9]
   fecunditytable[sp,8]<-SPDATA[sp,10]
   fecunditytable[sp,9]<-SPDATA[sp,11]
   fecunditytable[sp,10]<-mf
   fecunditytable[sp,11]<-sdf
   fecunditytable[sp,12]<-mat
   fecunditytable[sp,13]<-sdat
   fecunditytable[sp,14]<-atts
   fecunditytable[sp,15]<-pzero
   fecunditytable[sp,16]<-pum
   fecunditytable[sp,17]<-pdois
   fecunditytable[sp,18]<-ptres
   cat("\n", "Model  - ", sp,"\n")
   }
 colnames(fecunditytable) <- c("Model", "CS", "BS", "I", "N","PF","PS","DSR","NSR", "F'", "SD",
"Mean att", "SD", "Attempts/Success", "P0", "P1", "P2", "P3")
 save(fulltable, file=paste(SPDATA[1,2],"output.rda",sep=""))
 write.table(fecunditytable, file=paste(SPDATA[1,2],"fecundity.txt",sep=""))
 return(fecunditytable)
}
```

CAPÍTULO 3

A sobrevivência anual de Passeriformes na região subtropical do Brasil pode ser prevista pelo tamanho da ninhada?

Ninhada com dois ovos de Choquinha-de-garganta-pintada (*Rhopias gularis*), com três no Sabiá-laranjeira (*Turdus rufiventris*) e com cinco na Andorinha-de-sobre-branco (*Tachycineta leucorrhoa*).

Running head: Bird survival rates in southern Brazil

Does clutch size predict annual survival of passerines in subtropical Brazil?

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ABSTRACT

Survival is an important component of population dynamics which is unstudied in most bird species, although the actual knowledge on the minority of birds decisively contributes to life history theory. Tropical birds have often small clutches and high survival rates, while temperate birds tend to have the opposite, as result of the fecundity-survival trade-off. We examine whether survival in passerines breeding in a subtropical latitude would be reasonably predicted by this trade-off. The four species comprise a wide range of pace-of-life, from a small clutch size (2 eggs, Star-throated Antwren) to a large clutch (up to 7 eggs, White-rumped Swallow). Species were monitored with mark-recapture and resights during three breeding seasons for estimates of annual survival. Species had wide variation in survival rates, which were accordingly to predictions. The Star-throated Antwren had the greatest survival, with important annual variation ($\phi = 0.65 - 0.92$), likely due to an occasional extreme climate condition. The other species had lower survival than the antwren, proportionally to their mean clutch size ($R^2 = 0.71$), while body size did not explain that well. We argue that the wide variation found in survival rates encompasses both tropical and temperate patterns and thus, the trade-off between survival and fecundity is occuring even within this single subtropical location. Although some convergence may occur due to occasional climate constraints, each species seems to have a unique life-history strategy constrained by phylogeny. Long-term research on survival of subtropical birds is required for better understanding how different strategies may result from intermediate climate conditions along phylogenetic inertia.

Key-words: apparent survival; fecundity; latitude; life history; slow-fast gradient; trade-off.

INTRODUCTION

Understanding survival is fundamental for population ecology, yet requires long-term population monitoring studies that are lacking for most bird species. Environment and life history traits are, of course, important influences on survival (Lebreton et al. 1992, Brawn et al. 1999, Sandercock et al. 2000, Hagen et al. 2007), and their variability increase complexity on this issue. Sampling bias may also introduce problems in survival studies and model testing provides ways to reduce associated problems (Sandercock 2006). Even though, rough estimates of survival and even simple return rates of birds have been useful for the development of the life history theory and understanding population dynamics (Willis 1974, Karr et al. 1990, Martin et al. 1995, Johnston et al. 1997).

Survival in birds seems to be correlated with latitude and with large variation in altitude (Hille and Cooper 2015). Tropical birds tend to have lower metabolic rates (Wiersma et al 2007, Londoño et al. 2014) and greater adult survival rates (Peach et al. 2001, Parker et al. 2006, Wolfe et al. 2014) when compared to temperate birds (Martin and Li 1992, Johnston et al. 1997, Cilimburg et al. 2002, Hilton-Jr and Miller 2003). Thus, small clutch sizes in tropical birds might be the result of a trade-off between how birds invest in survival and fecundity in the context of local environmental conditions (Murray 1985, Martin 1996, Gill and Haggerty 2012, Martin 2014). However, survival rates may vary within as well as across latitudes (Moore et al. 2005, Tieleman 2009, Boonekamp et al. 2014, Wolfe et al. 2014, Hille and Cooper 2015), especially in the southern hemisphere (Ghalambor and Martin 2001, Covas et al. 2004, Blake and Loiselle 2008, 2013, Lloyd et al. 2014). In southern hemisphere, although survival of birds seems to be greater than expected (Lloyd et al. 2014), empirical evidence is still lacking because survival is unstudied in most species. Therefore, even preliminary survival estimates for southern species are important to contribute for filling this gap (Martin 2004).

Life history patterns among passerine in subtropical South America are quite variable and seem to locally comprise singular combinations of traits (Martin et al. 2000, Ricklefs 2002, Auer et al. 2007, Lima and Roper 2009, first and second chapter). A large variation in adult survival rates was reported in subtropical Argentina (Ghalambor and Martin 2001) and includes intermediary to high estimates, in comparison with studies in more tropical locations (Ryder et al. 2008, Rodrigues et al. 2013, Duca and Marini 2014, Wolfe et al. 2014). However, how the trade-off between survival and fecundity (Nordling et al. 1998, Ghalambor and Martin 2001, Knowles et al. 2009) locally vary in South America remains unknown.

Here, we estimate annual survival of passerine species with distinctive clutch sizes in subtropical Brazil and compare the relationship of clutch size and survival estimates among this species. If there is a trade-off between survival and fecundity, then survival and clutch size should be inversely correlated across species. If, however, resources devoted to reproduction are not limiting, then survival and reproduction may be uncoupled. In addition, survival may be correlated with body size, because in more broad scale, larger animals commonly have greater survival rates than small ones (Zammuto 1986, Sæther 1989). We predicted that both clutch size and body weigth are correlated with survival rates at this subtropical location.

METHODS

Species descriptions

The Star-throated Antwren (*Rhopias gularis*, 12 g, family Thamnophilidae) is an insectivore endemic to the Atlantic forest of Brazil. The antwren is monogamous and year-round territorial, which seems to be the most common social behavior in the family (Zimmer and Isler 2003). The antwren nests in the forest understory and has a fixed clutch size of two eggs (see first chapter). The White-rumped Swallow (*Tachycineta leucorrhoa*, 19 g, family Hirundinidae) is migratory and inhabits open areas near water, lays 4 – 7 eggs and breeds in central and southern South America (Ridgely and Tudor 1994, Turner 2004). The Green-headed Tanager (*Tangara seledon,* 20 g, Thraupidae) is frugivorous and is found in southern and central Atlantic forest. This tanager nests in large epiphytes in forest edges and lays usually 3 eggs per clutch (Sick 1997, Hilty 2011). The Golden-crowned Warbler (*Basileuterus* culicivorus, 12 g, Parulidae) is insectivorous, territorial and common in neotropical forests (Vilaça and Santos 2010). The warbler nests on the ground with a clutch size of 2 – 4 eggs (Curson 2010), but locally, the mean clutch size is 2.5 eggs (see second chapter).

Study area

Field work was conducted in private areas in three municipalities in the state of Paraná, in southern Brazil: in Guaraqueçaba (25^{o}10S, 49^{o}17W) in an area of ~100 ha (50 – 200 m elevation), in Morretes (25^{o}36S, 48^{o}48W) in an area of ~80 ha (100 – 500 m elevation), both of which are lowland montane Atlantic Forest, and, in Piraquara (25^{o}30S, 49^{o}00W) in two, ~50 ha areas (800 – 900 m elevation), in mixed Araucaria forest near reservoirs (Figure 1). At this subtropical latitude, four seasons are evident, independent of the altitude. During the summer (January – March) climate resembles to typical humid tropical forests, with maximum daily temperature reaching up to 41^{o}C, with monthly average of 30^{o}C and precipitation of 250 mm. In the winter (June – August) average maximum temperature is lower (23^{o}C) than in summer, minimum temperature may decrease under zero (-3^{o}C, minimum monthly average = 12^{o}C) and monthly precipitation decrease as well to 120 mm. Thus, overall amplitude of annual temperature is 44ºC (-3ºC – 41ºC), with no clear dry season and mean annual rainfall varying between 1500 – 2400 mm (Maack 2002, IAPAR 2014). Regional climate based on the updated Köppen-Geiger classification is humid and warm temperate (Cf – Kottek et al. 2006).

Species sampling

During breeding seasons (September – February) of 2011 – 2013, individuals of each species were captured and banded with unique combination of colored bands and one numbered metal band.

Periodic censuses of each species were carried out, and were somewhat different for each species because of the differences in nesting and foraging behaviors. Star-throated Antwrens were found especially during the breeding season as part of an ongoing study on their reproduction in Morretes. We systematically searched for breeding birds, at least once each week throughout the breeding season, or when checking nests, on a 2 – 3 days basis. For details on population monitoring and breeding ecology of this antwren, see the first chapter. Golden-crowned warblers were observed similarly, because they were found when searching for nests of the antwren, and were often captured together with the antwren.

The White-rumped Swallow has been studied since 2003 when nest-boxes (a wood nest box fixed in poles or trees) were first placed near a reservoir in Piraquara. Breeding females were captured in the nest-box during incubation and males were often captured while feeding nestlings within the box. Each year birds were recaptured and new birds were banded. Here, we only included individuals captured since 2011.

Green-headed Tanagers were captured, color-banded and then observed at four feeding stations with food *ad libitum* maintained year-round in Morretes and Guaraqueçaba. During eight weeks prior to the breeding season (mid July – mid September), tanagers at feeding stations were observed one day every two weeks from dawn till dusk. During breeding season, we daily monitored tanagers for one whole week in each month.

Data analysis

Annual apparent survival (ϕ) and recapture (p) probabilities were estimated using the Live-Recapture Cormack-Jolly-Seber model in program MARK (version 7.1, White and Burnham 1999). In analyzing survival, recaptures and resightings were treated as the same sort of presence record and were grouped by year. We compared the constant annual survival $\phi(.)$ and time (year) dependent annual survival $\phi(\mathrm{yr})$ among species. We assumed that recapture probability (p) was constant, survival was independent of sex, and only included breeding adults. We used Akaike Information Criterion for small samples (AIC_c) to compare and rank models (Burnham et al. 2011). We checked for overdispersion using the median $\hat{c}$ method available in MARK.

To estimate consequences of variable survival rates in longevity, we derived the median longevity and maximum longevity from parameter estimates of the constant model $\phi(.)$. Maximum longevity was the top 95th percentile assuming survival constant with age, calculated using the function uniroot in R (Version 3.1.0, R Core Team 2014). We fitted linear regression to annual survival against clutch size, body weight and the ratio of clutch size per body weight to determine if there are important differences in how these variables explain variation in survival. We consider the ratio of clutch size and body weight as a measure of reproductive pace (*i.e.* lower ratios suggest slower pace, Wiersma et al. 2012). Mean body weigth was gathered during capturing protocol and clutch size was noted in the field (see second chapter), except for the tanager (Hilty 2011). In these comparisons, we also included the Black-cheeked Gnateater (*Conopophaga melanops*), an understory and Atlantic forest endemic, for which local data are available (Lima and Roper 2009).

RESULTS

A total of 185 birds were captured during the first two years: 44 Star-throated Antwrens (80% recaptured in any season, 36% in both seasons), 67 White-rumped Swallows (28% recaptured in any and 4% in both), 37 Green-headed Tanagers (43% recaptured in any and 11% in both), and 28 Golden-crowned Warblers (35% recaptured in any and 32% in both, Table 1).

Survival was constant over time for all species except the Star-throated Antwren, in which year, $\phi(yr)$, was important for estimates (w_i = 0.85, Table 2). Survival rate in the antwren was greatest of all species in the first year (ϕ = 0.920, SE = 0.060), while the second year (ϕ = 0.653, SE = 0.087) was similar to that of the warbler (ϕ = 0.634, SE = 0.075, Figure 2). Survival was lowest in the White-rumped Swallow (ϕ = 0.285, SE = 0.051), followed by the Green-headed Tanager (ϕ =

0.465, SE = 0.076, Table 3). Recapture probability (*p*) varied between 0.884 – 1.000 among all species (Table 3). Overdispersion was low (< 1.3) for all species and so correction was unnecessary.

The derived longevity was greatest in the Star-throated Antwren (mid = 3.5 yr, max = 15.0 yr) and lowest in the Golden-crowned Warbler (mid = 1.5 yr, max = 6.6 yr). Longevity was intermediate in the Green-headed Tanager (mid = 0.9 yr, max = 3.9 yr) and the White-rumped Swallow (mid = 0.6 yr, max = 2.4 yr, Figure 3).

Annual survival was inversely explained by clutch size ($R^2 = -0.71$, Figure 4A). Body weight had lower percentage explaining survival ($R^2 = -0.42$, Figure 4B) than clutch size. The ratio of clutch size and body weight had the lowest percentage explaining survival among the three variables ($R^2 = -0.10$, Figure 4C).

DISCUSSION

As predicted, survival of the four species at this subtropical location ranged from relatively high (Star-throated Antwren) to low (White-rumped Swallow) rates, which were inversely related to clutch size. This wide variation in survival encompasses rates similar to birds in tropical and temperate latitudes (Johnston et al. 2007, Blake and Loiselle 2013, Covas et al. 2014). Also, a strong relation between survival and clutch size is congruent with the trade-off in investment between reproduction and survival, similarly to studies in subtropical Argentina (Ghalambor and Martin 2001) and South Africa (Collingham et al. 2014). In a local scale, this trade-off parallels the latitudinal clutch size paradigm. That is, the more tropical-like species (*i.e.* the antwren and gnateater, which inhabit tropical forests) have small clutches and similar to greater survival than other tropical related species (Blake and Loiselle 2008, 2013, Wolfe et al. 2014), while the most temperate-like species (*i.e.* the swallow, which migrates before winter) have the largest clutch size and lowest survival. On the other hand, body weight did not contribute for predicting survival, different than in subtropical Africa (Collingham et al. 2014), likely because all species may be considered into the same small size category (Sæther 1989).

For the swallow, as a migratory species, it is not surprising that its survival would be lower than that of residents. However, migration in this species is all within-continent and over relatively short distances, although whether this could increase survival remains unknown. Some swallows (~5%) reared in our nest-boxes returned the next year and nearly the half were found dead in nest boxes at the beginning of the subsequent breeding season (as were some older adults), which suggests that migration have a high cost. Additionally, dispersal is a likely confounding factor for survival rates in all species, which in this study was uncertain. Philopatry for breeding sites in the White-rumped Swallow is unstudied, but the very low survival rates suggest that they may disperse each year.

Resident species had greater survival than the swallow, but rates varied among species according to the clutch size. Some variation perhaps could also be associated to differences in sampling methods, however, recapture estimates were high to near absolute, because of our intensive resighting monitoring approach, suggesting that this specific variance was minimized. For instance, while Green-headed Tanagers are more likely to disperse because they are frugivore (Price et al. 1999), some individuals were found in the same area for at least three years, as the other resident species. Even though, survival estimates for tanagers should be conservative, because we were unable to exclude first year birds, which might be lower than more experienced individuals (Sandercock et al. 2000).

Survival in the antwren was different each year. The low estimate in the second year was still as high as the highest estimate for the other resident species, while the highest year was much greater even when compared with tropical birds (Johnston et al. 2007, Blake and Loiselle 2013, Wolfe et al 2014). We suggest that climate variation may explain this variation in survival estimates because in the winter of 2013 there was an unusual extreme weather event. A rare and extreme cold front reduced temperatures to near or below (depending exactly on where measured) the minimal historical mean for southern Brazil, and this was around two months prior to the third breeding season (which started on July 23, during few days). Extreme climate can influence survival (Salewski et al. 2013) and, considering that the antwren is mostly tropical-like (but see the first chapter), it may have reduced their survival at that year. Indeed, climate conditions may be the limiting factor for the southern distribution of the antwren. Yearly estimates of the other species did not suggest any clear difference, although also the warbler and the tanager both tended to lower survival estimates in the second comparing to the first year. No variation in survival of the White-rumped Swallow would be expected due to this cold front, since every winter the species is at tropical latitudes (Turner 2004). Thus, survival rates differed among species within the same latitude, but the influence of subtropical climate may still be an important but stochastic source of variation in survival of subtropical populations (Wolfe and Ralph 2009, Gill and Haggerty 2012).

For most species, the longevity predicted from parameter estimates was similar to empirical data of related species, suggesting tolerable accuracy for our estimates (Krementz et al. 1989). The maximum longevity estimate of the Star-throated Antwren was similar to that observed in other thamnophilids, such as the Marsh Antwren (~16 yr, *Formicivora acutirostris*) in the same region, or similar to other related species from more tropical locations (see review in Bornschein et al. 2015). Longevity in the Green-headed Tanager was similar to that of other *Tangara* spp. in the neotropics (5 – 7 yr, Snow and Lill 1974, Lentino et al. 2003). Warblers in northern latitudes have been recaptured up to eight years after banding (Faaborg and Arendt 1989, Rodrigues 2002). That is also similar to the maximum longevity here predicted for the Golden-crowned Warbler, although latitudinal variation in breeding components among several species within this family is recognized (Cox and Martin 2009). In the congener of the White-rumped Swallow, the North American and temperate Tree Swallow (*Tachycineta bicolor*), longevity was much greater (8 – 10 yr, Hussel 1982, Robertson et al. 1992) than in our study, suggesting that our survival estimates for the swallow are underestimated.

We found that survival rates of four sympatric passerine species are inversely related to variation in clutch size. Thus, reproduction must have an important cost for survival of these birds, rather than environmental constraints. The slow-fast paradigm has been invoked to explain large-scale differences in life-history traits (Hille and Cooper 2015), however, it may also explain this variation in bird survival in a local-scale. Hence, variation in species´ pace of life is not exclusively found according to latitudinal or altitudinal variation and it can also be found within the same intermediate latitude. Long-term research on breeding and survival of subtropical birds is required for better understanding how much of variation in life-history strategies are related to variation in climate conditions and to phylogenetic inertia.

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Table 1. Number of individuals captured (and banded) and recaptured among four passerine species in southern Brazil during 2011 – 2013 breeding seasons. Total means recaptured in addition to new captures.

Species	Year			
	2011	2012		2013
	Captured	Recaptured	Total	Recaptured
Star-throated Antwren (*Rhopias gularis*)	30	26	40	25
White-rumped Swallow (*Tachycineta leucorrhoa*)	38	10	39	12
Green-headed Tanager (*Tangara seledon*)	11	6	32	14
Golden-crowned Warbler (*Basileuterus culicivorus*)	23	16	18	10

Table 2. Model selection results for annual survival estimates of four passerine species in southern Brazil. ΔAIC_c = relative difference in Akaike Information Criterion for small samples, w_i = AIC_c weight, L = model likelihood, K = number of model parameters.

Species	Model	ΔAIC_c	w_i	K	Deviance
Star-throated Antwren	ϕ(yr)	0.0	0.85	3	0.5
	ϕ(.)	3.5	0.15	2	6.1
White-rumped Swallow	ϕ(.)	0.0	0.73	2	0.2
	ϕ(yr)	2.0	0.27	3	0.1
Green-headed Tanager	ϕ(.)	0.0	0.73	2	1.9
	ϕ(yr)	1.9	0.27	3	1.5
Golden-crowned Warbler	ϕ(.)	0.0	0.67	2	0.9
	ϕ(yr)	1.5	0.32	3	0.1

Table 3. Estimates of probability of survival (ϕ) and probability of recapture (*p*) from CJS models of four passerine species in southern Brazil.

Species	Model parameters	ϕ	*p*
Star-throated Antwren	Constant	0.819 ± 0.086	0.884 ± 0.095
	Year 1	0.920 ± 0.060	0.941 ± 0.056
	Year 2	0.653 ± 0.087	
White-rumped Swallow	Constant	0.285 ± 0.051	1.000
	Year 1	0.263 ± 0.071	1.000
	Year 2	0.307 ± 0.073	
Green-headed Tanager	Constant	0.465 ± 0.076	1.000
	Year 1	0.545 ± 0.150	1.000
	Year 2	0.437 ± 0.087	
Golden-crowned Warbler	Constant	0.634 ± 0.075	1.000
	Year 1	0.695 ± 0.095	1.000
	Year 2	0.555 ± 0.117	

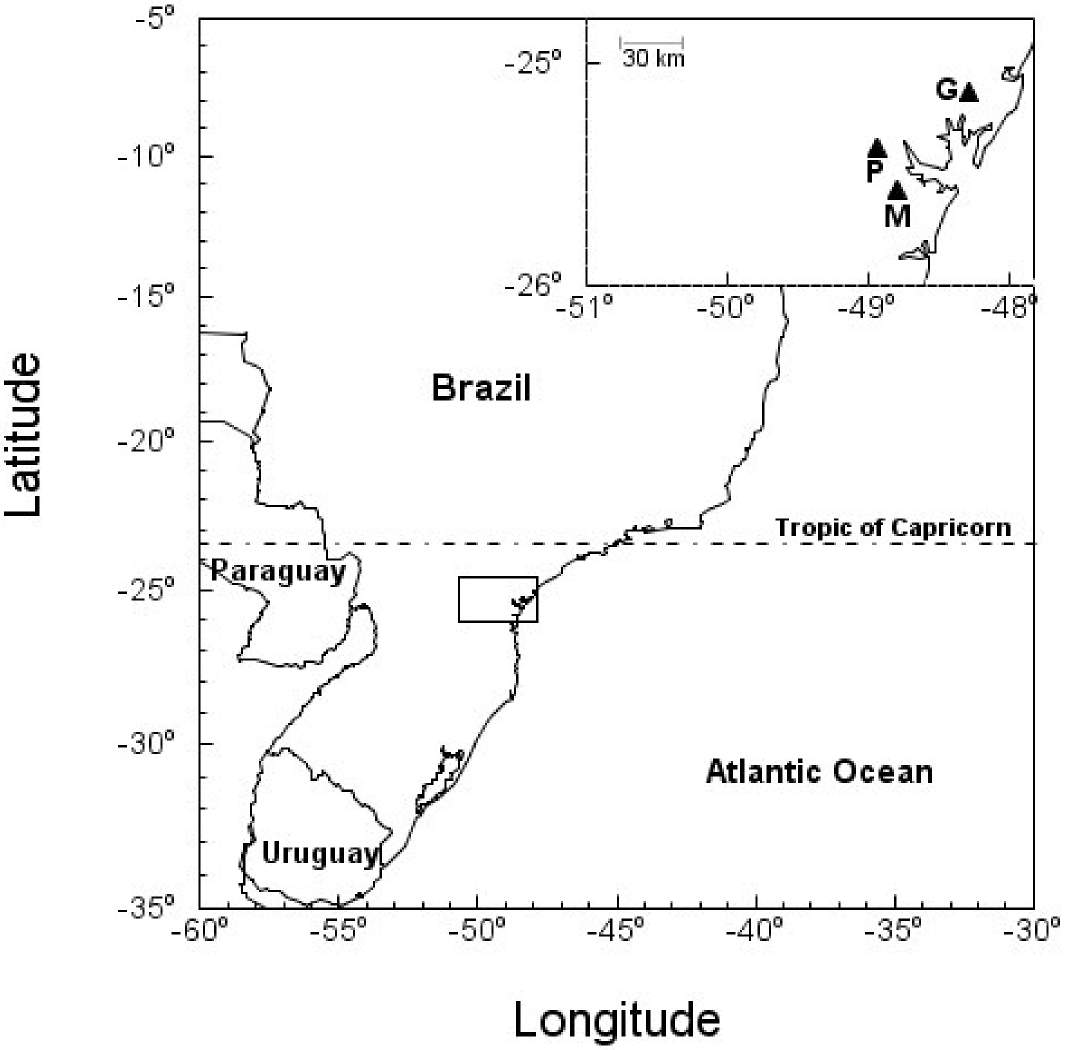


Figure 1. Subtropical location of the study sites in southern Brazil. Each triangle indicates each study site (G – Guaraqueçaba, M – Morretes, P – Piraquara).

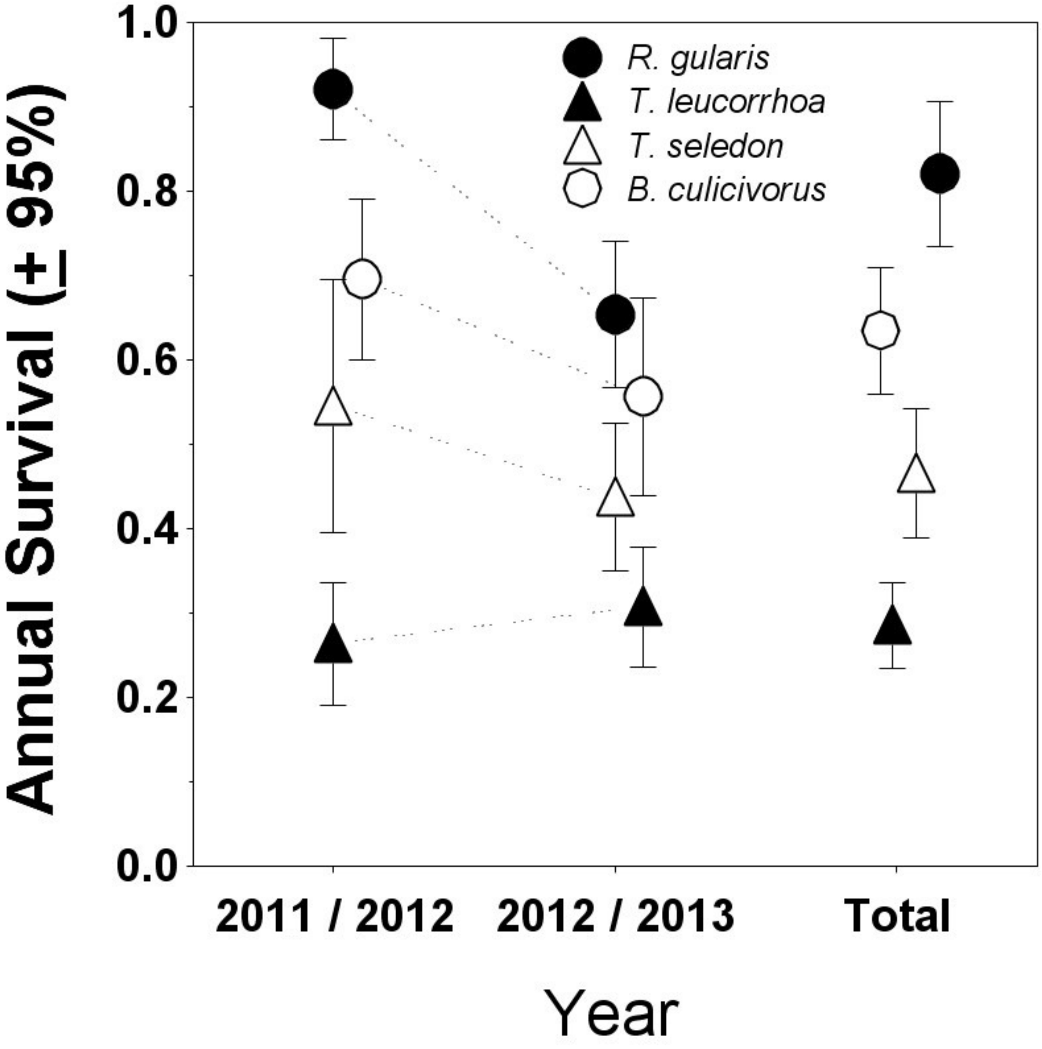


Figure. 2. Annual adult survival estimates for birds in southern Brazil through three breeding seasons, during 2011 – 2013, and total. Bars indicate standard errors.

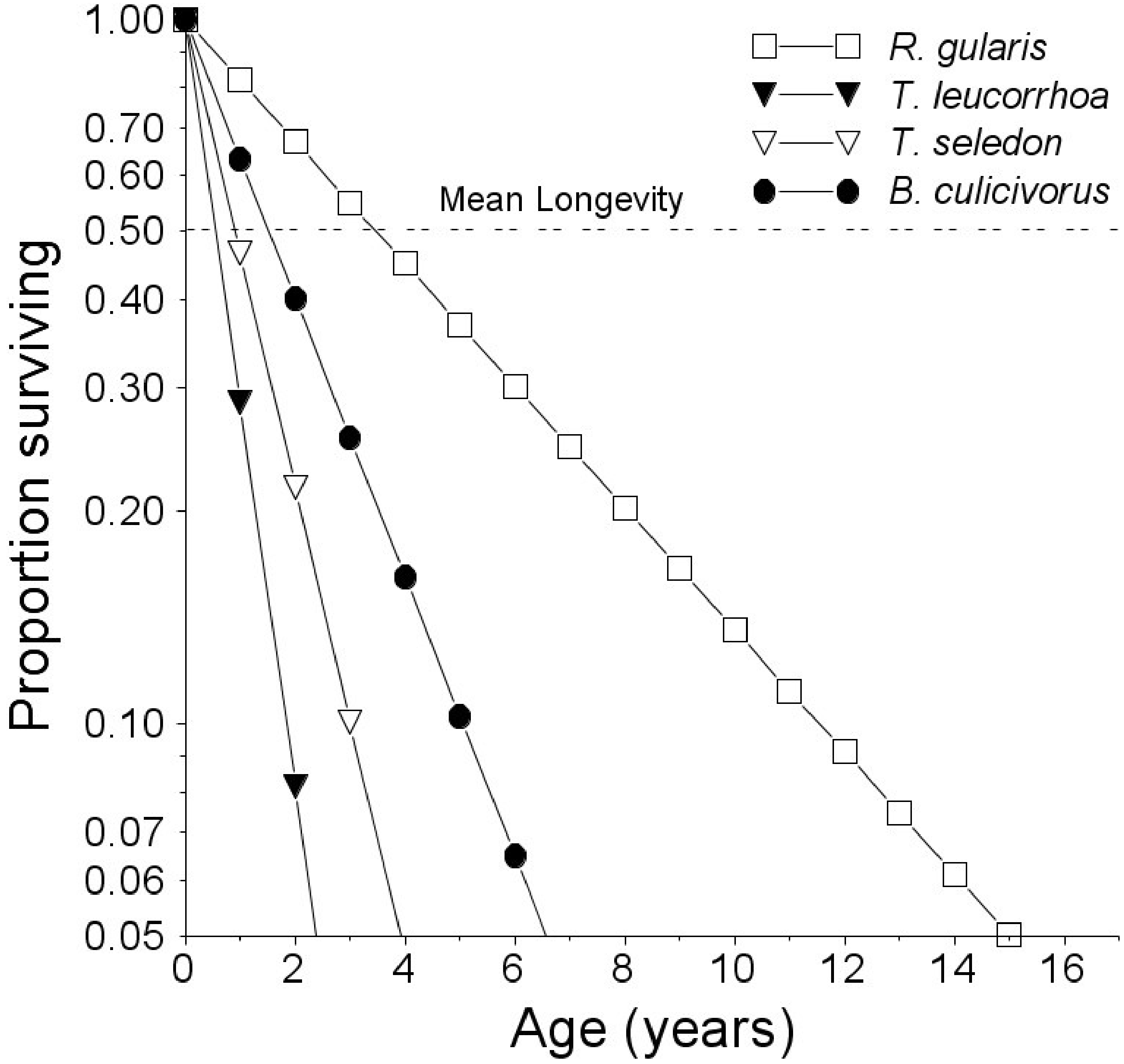


Figure. 3. Constant proportional survival function of four bird species in southern Brazil. Median and maximum likely longevity was calculated as the time (yr) when likelihood of proportional survival would be 50% and 5% respectively.

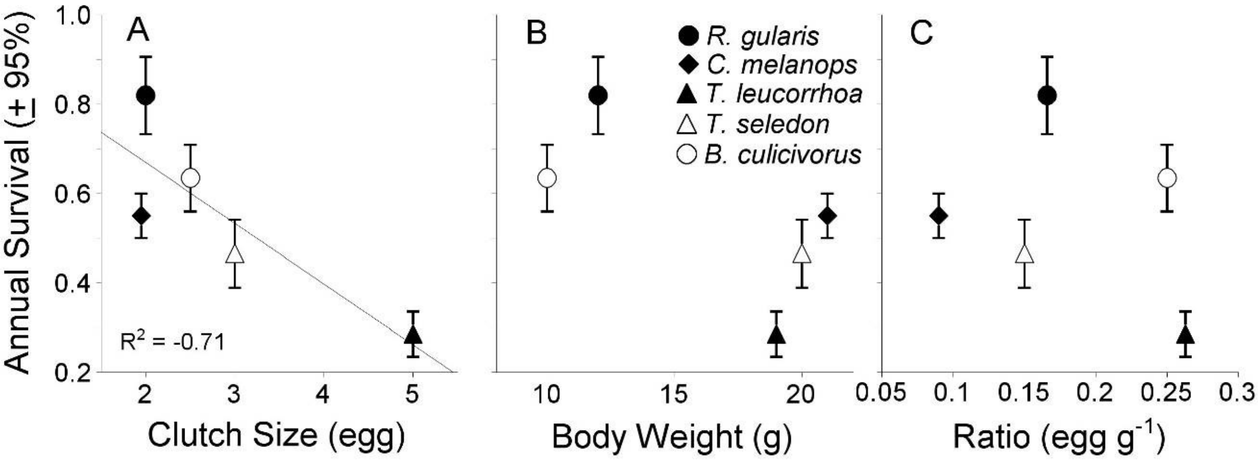
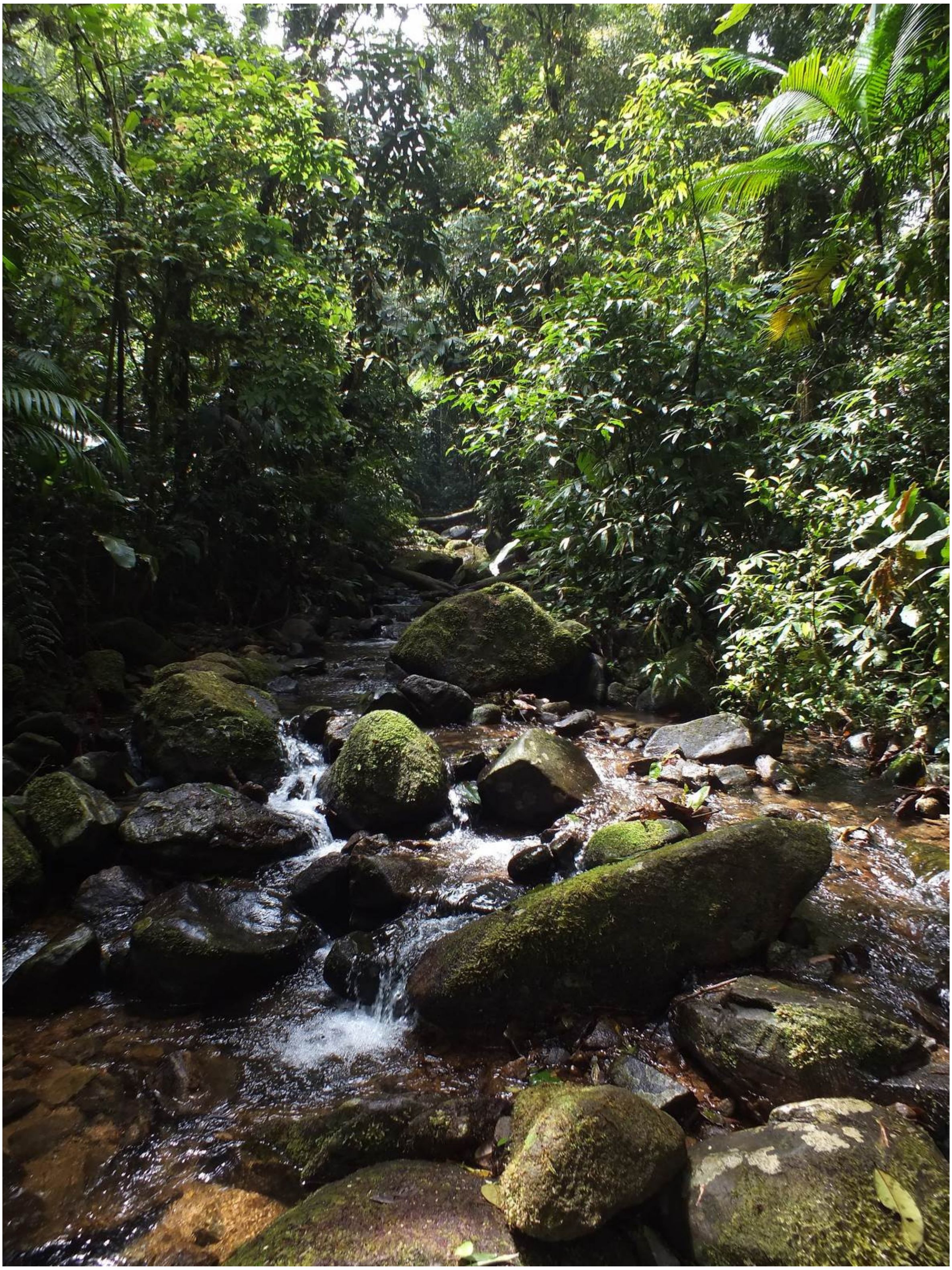


Figure. 4. Scatter plot of apparent annual survival against clutch size, body weight and ratio between both in five bird species in southern Brazil. Each symbol represents one species. Bars indicate standard errors.



Floresta Atlântica em um dos locais de estudo, Morretes, Paraná.

CONCLUSÕES GERAIS

Uma espécie de Passeriforme de uma família com padrões tipicamente associados a ambientes tropicais, quando habitando uma região subtropical, pode apresentar características reprodutivas singulares que remetem a uma estratégia voltada a um maior investimento na reprodução (ou seja, uma estratégia de ritmo mais “rápido”). Em uma escala mais ampla, espécies em duas localidades subtropicais apresentaram padrões reprodutivos variados, incluindo amplo espectro de estratégias (entre maior investimento na reprodução ou na sobrevivência). O período reprodutivo, o tamanho da ninhada e a probabilidade de sucesso de cada ninho são os principais parâmetros que influenciam no potencial de fecundidade das espécies de Passeriformes nesta região. Porém, há convergência na reprodução de espécies relacionada à limitação na época e duração do período reprodutivo, que resulta em distintos potenciais de fecundidade anual em cada localidade. As espécies com ritmo de vida mais lento tendem a ter poucas chances de múltiplas reproduções por ano, reduzindo a fecundidade potencial. Outro importante parâmetro populacional, a sobrevivência de adultos é inversamente relacionada ao tamanho da ninhada, evidenciando que os custos energéticos associadas à reprodução nesta região seriam maiores que potenciais limitações climáticas. Processos biológicos que demandam alto custo energético tendem a gerar processos adaptativos, especialmente naqueles caracteres biológicos que possam influenciar no balanceamento das taxas de fecundidade e sobrevivência. Em geral, a ocorrência de variadas estratégias reprodutivas em uma latitude intermediária indica que na região estudada cada espécie pode apresentar uma plasticidade fenotípica singular, ao invés de ocorrer um padrão subtropical e intermediário comum à maioria das espécies, o que seria esperado se a principal fonte de variação nos caracteres populacionais fosse exclusivamente relacionada à variação latitudinal. Esta plasticidade é expressa de forma singular em cada espécie em função da interação entre limitações filogenéticas e as interações únicas com o ambiente em escala regional e local.