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BIOLOGIA REPRODUTIVA DE PASSERIFORMES SUBTROPICAIS DO SUL DO BRASIL: testando a teoria de convergência latitudinal das fenologias reprodutivas

Dissertação apresentada ao Setor de Ciências Biológicas da Universidade Federal do Paraná, como parte dos requisitos para a obtenção do grau de mestre em Ecologia e Conservação.

Orientador: Dr. James Joseph Roper

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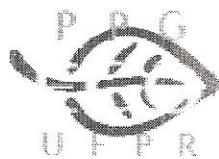
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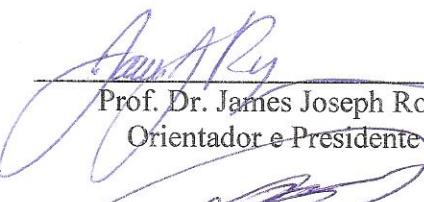
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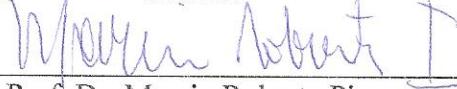
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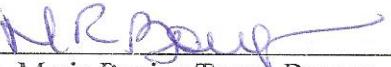
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"Every now and then I break free from the office, the computer, the telephone, the piles of manuscripts, and take up an invitation to visit a field site somewhere. I stumble over logs, get ripped by thorns, bitten by horseflies, stuck in mud, sunburned, and bruised. I sweat, groan, spit, curse, and generally have a wonderful time. I fight back tears when I see old, long-forgotten friends---the wildflowers, ferns, trees, salamanders, fungi, and beetles I once knew so well but whose names now elude me as often as not. I begin to wonder what we, as conservation biologists, lose when we spend our time in conference centers rather than mountains, in airplanes instead of canoes, or peering into computer screens instead of down tortoise burrows."

-Reed F. Noss

"The Naturalists Are Dying Off", Conservation Biology, Vol. 10, No. 01

RESUMO

A biologia reprodutiva das aves no hemisfério norte é estudada há mais tempo que no hemisfério sul. O acúmulo dessa informação permitiu o desenvolvimento da teoria de história de vida de aves que possui enfoque no tamanho de ninhada e de gradientes latitudinais. Outros parâmetros reprodutivos, como duração do ciclo reprodutivo ou número de tentativas reprodutivas, permaneceram por muito tempo negligenciados apesar de sua importância, e ainda não foram incorporados na teoria vigente. A América do Sul temperada oferece uma boa oportunidade de comparação com o Neártico, mas nenhuma síntese senão sobre tamanhos de ninhada foi realizada para qualquer parâmetro reprodutivo no hemisfério sul. Aqui, primeiro reportamos vários parâmetros reprodutivos para 43 espécies de passeriformes em uma região subtropical da Mata Atlântica. Em seguida, compilamos informações publicadas sobre fenologias reprodutivas em todas as Américas, e contextualizamos esses parâmetros da América do Sul temperada e dos trópicos em relação ao Neártico. Na Mata Atlântica, há grande variação nos parâmetros reprodutivos, com algumas características tropicais e outras temperadas. A razão para tal variação não é clara, mas também foi observada em mesma latitude na Argentina. As fenologias reprodutivas nos trópicos e regiões temperadas da América do Sul não possuem qualquer padrão latitudinal, ao contrário das temperadas do Norte. O clima explica boa parte da variação na duração do ciclo reprodutivo entre locais nos trópicos, e ainda para a subordem Passeri no temperado norte. Na região temperada sul, espécies em locais com regimes climáticos diferentes possuem ciclos reprodutivos semelhantes. Sugerimos que variação interanual imprevisível do clima oculte qualquer padrão local dependente de características intrínsecas das espécies (como status migratório).

ABSTRACT

The knowledge of avian breeding biology is older in the northern hemisphere than in southern hemisphere. These accumulating studies resulted in the life history theory of birds, which focus in clutch size evolution and latitudinal gradients. Other breeding parameters like breeding season length and renesting ability are still neglected despite their importance, and still have not been incorporated properly in theory. The avian breeding parameters of temperate South America provides good comparative data to the Nearctic, but no synthesis has been made yet for breeding parameters (except for clutch sizes) in the southern hemisphere. Here, we report several breeding parameters for 43 species in subtropical Atlantic Forest in Brazil. Next, we gathered breeding phenology information from the literature for the Americas, and put temperate south and the tropics in the context with the Nearctic region. In the Atlantic Forest, we found high variation in breeding parameters, with some tropical and some temperate characteristics. It is unclear why this variation exists, but also was seen in Argentina at similar latitude. The breeding phenologies in the tropics and temperate South America have no latitudinal pattern, contrary to the north. Climate partially explains the breeding season length in the tropics and for Passeri in the temperate northern hemisphere. In temperate South America, species in different climate regimes have similar breeding phenologies. We suggest that interannual and unpredictable variation in climate might mask any underlying pattern in breeding phenologies dependent on intrinsic characteristics of species (like migratory status) in temperate South America.

SUMÁRIO

1 INTRODUÇÃO GERAL

1.1 As histórias de vida são fundamentais para o entendimento da evolução

Só perduram na terra seres vivos que alcançam a maturidade e deixam descendentes. Essa ideia, óbvia e elementar a princípio, mostra que a seleção natural poderia ser vista didaticamente em termos de adaptações da sobrevivência e reprodução de forma a maximizar o número de descendentes ao longo das gerações. Mudanças evolutivas que otimizem a captação de recursos, ou para tolerar o ambiente físico e a fuga de predadores, permitem que o organismo continue vivo. Por outro lado, arranjar parceiros reprodutivos, copular e cuidar da prole de forma eficiente contribuem diretamente ao número de descendentes.

A relação entre sobrevivência e reprodução é complexa, porém pode ser facilmente entendida como um dilema evolutivo na alocação de recurso, tempo e risco. Deveria um canário produzir um número ilimitado de filhotes caso o alimento seja virtualmente infinito no verão? Tal canário precisa cuidar dos filhotes e ainda continuar saudável para os anos posteriores. Por outro lado, uma andorinha migratória deve ser inclinada a produzir mais filhotes por temporada, uma vez que o risco de morrer em viagem é grande. A solução a essas dificuldades ambientais para otimizar o número de descendentes é a história de vida do organismo (Ricklefs 2000). A teoria de história de vida tenta entender por que e como as estratégias reprodutivas funcionam em diferentes contextos ambientais (Stearns 1976).

1.2 As aves são modelos tradicionais na teoria de história de vida

Talvez porque as aves são tão universais e seus ninhos tão conspícuos, a teoria de história de vida foi fundada tentando entender a variação no tamanho de ninhada das aves (Lack 1947, Moreau 1944). O padrão mais intrigante era a que o tamanho de ninhada aumentava dos trópicos para as regiões temperadas no Velho Mundo em várias ordens de aves. Décadas mais tarde, ainda estamos tentando explicar o fenômeno, através das diferenças inerentes das espécies, como a filogenia, ou as adaptações de acordo com características ecológicas e climáticas (Jetz et al. 2008). Os mecanismos responsáveis pela variação no tamanho de ninhada incluem principalmente as taxas de sobrevivência dos adultos, taxa predação de ninhos (devido às características do ninho ou diversidade de predadores, Martin 2004) e sazonalidade de recursos condicionada ao clima (Griebeler et al. 2010). A teoria que

tenta explicar o tamanho de ninhada gerou inúmeras novas hipóteses relacionadas às outras características das espécies, e em geral, pode-se notar um contraste entre extremos de história de vida de aves de regiões temperadas e tropicais (TAB. 1). No extremo "rápido", a probabilidade de morrer é alta durante os invernos rigorosos, então essas aves devem investir mais em reprodução. No extremo "lento", a sobrevivência dos adultos é alta, e então pais devem investir menos por unidade de tempo em reprodução (Martin 2004).

TABELA 1. Dois extremos (rápido e lento) na variação de história de vida em aves que refletem também diferenças entre hemisfério norte temperado versus trópicos e hemisfério sul. Adaptado de Martin (2004).

Característica	Rápido	Lento
Tamanho de ninhada	Grande	Pequeno
Massa do ovo	Menor	Maior
Maturação	Cedo	Tardia
Ninhos consecutivos no mesmo ano (por casal)	Variável	Variável
Mortalidade dos adultos	Alta	Baixa
Desenvolvimento	Rápido	Lento
Cuidado parental	Curto	Longo

1.3 A sazonalidade do clima restringe as histórias de vida das aves

A sazonalidade varia latitudinalmente. Em latitudes altas (temperadas) a variação do fotoperíodo e regime de chuva é grande, suficientemente para a existência de estações marcadas (Goetz et al. 2000). A produção de frutas, sementes e insetos são então condicionadas à época do ano. Assim, é natural observar que aves de regiões temperadas reproduzem sazonalmente, com início na primavera, quando o alimento torna-se mais disponível, estendendo até parte do verão, quando os filhotes já estão grandes e prontos para enfrentar o outono e inverno. Em locais muito sazonais e com climas previsíveis, os passeriformes devem reproduzir imediatamente após o início da primavera (extremo rápido no *continuum* das histórias de vida). Um bom exemplo é a migratória Mariquita-de-rabo-

vermelho (*Setophaga ruticilla*) em Michigan. Lá, os casais devem alcançar ao local reprodutivo o mais rápido possível, e, geralmente, tem apenas uma chance de reproduzir (Smith and Moore 2004). Se chegam tardiamente ao local, ou se perdem o primeiro ninho (e. g., por predação), dificilmente possuem tempo suficiente para uma nova tentativa. Já em locais um pouco menos sazonais e com climas menos previsíveis, como no caso do residente gaio pinhoreiro no Arizona (tradução livre, *Gymnorhinus cyanocephalus*), existe uma variação na data de início reprodutivo, dependendo do clima, e no final, dependendo do número de tentativas fracassadas do casal. Devido à imprevisibilidade, em alguns casos as fêmeas são surpreendidas pela neve do fim do inverno enquanto incubam os ovos (Marzluff and Balda 1992). No outro extremo (lento), nas florestas tropicais em Trinidad, a choca barrada (*Thamnophilus doliatus*) reproduz a qualquer momento do ano (Snow and Snow 1964). Nessa espécie, e provavelmente em vários outros passeriformes tropicais, os indivíduos vivem em casal com calendário reprodutivo próprio, mesmo que em resolução populacional a espécie reproduza o ano todo (Roper 2005, Snow and Snow 1964).

1.4 A corrida do ouro: as estratégias reprodutivas das aves temperadas da América do Sul

Uma vez que as latitudes temperadas sul, ao contrário do trópicos, oferecem dados comparativos sob similar fotoperíodo que as regiões amplamente estudadas no hemisfério norte, seria desejável uma quantidade razoável de trabalhos nessa região. No entanto, são raros os estudos que lidaram com história de vida de aves no temperado sul, apesar da existência de resultados intrigantes. Na Austrália (tropical e temperada), o ciclo reprodutivo é relativamente longo em relação a outras regiões de mesma latitude no hemisfério norte, o que foi atribuído a reprodução oportunista em climas imprevisíveis (Wyndham 1986). Por outro lado, na África do Sul, também em região de clima seco (latitude S 29°), os ciclos são curtos (setembro a dezembro) e as aves possuem plasticidade no tamanho de ninhada de acordo com a chuva (Lloyd 1999).

Novos modelos indicam que em regiões temperadas, ninhadas grandes devem ser favorecidas se os períodos propícios para reprodução são curtos e a taxa de predação de ninhos é baixa (Roper et al. 2010). Em uma região de floresta montana na Argentina (S 26°), os ciclos reprodutivos são relativamente curtos e predação de ninhos é baixa, porém, as ninhadas são pequenas. (Auer et al. 2007). De fato, na América do Sul, a média do tamanho

de ninhada é relativamente constante e pequeno ao longo das latitudes (2 a 3 ovos, Jetz et al. 2008, Yom-Tov et al. 1994). No entanto, estudos abrangentes (com várias espécies) que reportam parâmetros reprodutivos não existem para a região subtropical ou temperada no Brasil, portanto este será o objetivo do Capítulo 2 desta dissertação.

1.5 Os ciclos reprodutivos das aves no Neotrópico necessitam de um novo paradigma

Indo de acordo com a ideia de que deve existir um gradiente latitudinal nas fenologias reprodutivas, o trabalho de Snow e Snow (1964) em Trinidad (N 10°) mostrava que os passeriformes poderiam reproduzir quase o ano todo. Naquela época, só existia mais um levantamento extenso dos ciclos reprodutivos em região tropical, no Equador (S 2°), e este estudo parecia ser uma exceção à ideia de gradiente latitudinal (Marchant 1959). Lá no Equador, em vez de iniciar na primavera, as espécies começam a reproduzir no meio do verão até o inverno do hemisfério sul, enquanto os ciclos são curtos (< 5 meses). Isso foi atribuído ao clima semiárido com regime de chuva incomum para outras regiões de mesma latitude. Mais tarde, uma sequência de estudos feitos em Manaus indicava que os passeriformes de clima tropical úmido também poderiam possuir ciclos sazonais (Oniki and Willis 1982a, b, 1983a, b), apesar de que os ciclos não eram congruentes entre espécies. Algumas poderiam começar a reproduzir no fim do período seco, enquanto outras, no fim do período úmido.

A falta de sincronia entre espécies relacionadas e simpátricas em regiões tropicais resultou na hipótese de que as espécies poderiam particionar o ano reprodutivo para evitar competição interespecífica (Ricklefs 1966). Isso seria interessante nos trópicos uma vez que a diversidade é alta e populações estão sempre próximas à capacidade suporte do ambiente (Martin 1987), então, a competição também seria maior. No entanto, essa hipótese foi refutada (Ricklefs 1966), pois o particionamento do tempo entre espécies é independente de latitude, ao menos entre os trópicos e regiões temperadas do hemisfério norte.

O ciclos reprodutivos sazonais na Amazônia poderiam ser atribuídos à existência de duas estações definidas, uma seca e outra úmida. Em linha com essa ideia, na savana da Venezuela (N 9°), os ciclos são curtos em relação ao que se esperava para regiões tropicais (Cruz and Andrews 1989). No entanto, a sazonalidade dos ciclos reprodutivos não é exclusiva de regiões com climas sazonais. No Panamá, por exemplo, alguns passeriformes possuem variações hormonais e gonadais que indicam que essas populações não reproduzem por uma parte do ano, mesmo sem perceptível mudança climática (Wikelski et al. 2000, 2003).

Em resumo, o paradigma latitudinal falha em prever a duração dos ciclos reprodutivos nos trópicos. Adicionalmente, as regiões temperadas do sul permanecem incógnitas a esse respeito. A latitude por si só pouco informa sobre os mecanismos que realmente influenciam os ciclos reprodutivos. Investigar esses mecanismos é objeto do Capítulo 3 dessa dissertação. Em última análise, para qualquer região, os períodos reprodutivos devem ser definidos pela 1) fenologia dos recursos alimentares, que devem ter importância local, uma vez que insetos são mais rapidamente disponíveis na primavera do que frutos e gramíneas (Davis 1933). Infelizmente, a literatura é permeada de incongruências em relação à dieta das aves neotropicais, e inferências utilizando dieta podem não ser satisfatórias. 2) As características intrínsecas das aves, como filogenia e características ecológicas, também devem influenciar as fenologias reprodutivas. Por exemplo, espécies migratórias são restringidas pelo calendário de migração, e podem ter ciclos reprodutivos curtos (Repenning and Fontana 2011). 3) O Clima deve determinar o padrão geral das fenologias alimentares entre locais ou latitudes diferentes. Em altas latitudes, o clima deve ser mais importante que as características intrínsecas, uma vez que espécies diferentes devem convergir os ciclos reprodutivos em um mesmo período de abundância de alimento na primavera. No capítulo 3, utilizamos o 2) e 3) para tentar entender, comparativamente, a variação das fenologias reprodutivas nas regiões tropicais, temperadas da América do Norte e da América do Sul, incluindo nossos dados do capítulo 2 para a Mata Atlântica subtropical.

2 SUBTROPICAL SURPRISES: VARIABLE BREEDING PATTERNS IN SOUTHERN BRAZILIAN ATLANTIC FOREST

Capítulo submetido ao periódico The Wilson Journal of Ornithology

Ninho de pula-pula-assobiador (*Myiothlypis leucoblephara*) com filhotes de 11 dias. Essa espécie forrageia nos sub-bosques da Mata Atlântica e produz 3 ovos por ninho. No Sul do Brasil, o ciclo reprodutivo (período de posturas) dura apenas um mês.

SUBTROPICAL SURPRISES: VARIABLE BREEDING PATTERNS IN SOUTHERN

BRAZILIAN ATLANTIC FOREST

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ABSTRACT.---Information on breeding biology of birds is fundamental for the understanding of life history evolution and conservation. While this information is only beginning to accumulate for neotropical birds, the southern subtropics are still neglected. Here we describe breeding dates, nests, and clutches during 2012-2013 breeding season, with 265 nests of 43 species of passerines in subtropical Brazilian Atlantic Forest. Breeding began in September, but some species started as late as December. Average breeding season length was of 57 days, but varied broadly across species (11-149 days). Clutch sizes of two and three were common (species modal range: 2-5). Species renested often, and this was quite frequent in the Saffron Finch (*Sicalis flaveola*). This finch also had the longest breeding season (146 days), high nest success (56%) and large clutch sizes (3-4 eggs). The House Wren (*Troglodytes aedon*) had larger clutch size than reported elsewhere at the same latitude, but breeding season length and nest survival were similar as elsewhere. Incubation, nestling periods and egg measurements are included for some species. In general, breeding season length is similar to that of higher latitudes of northern hemisphere. The wide variation in breeding strategies found at this subtropical latitude suggests that the northern tropical-temperate paradigm of life history theory needs revision.

Key words: breeding phenology, timing of breeding, clutch size, egg sizes, nesting attempts, *Sicalis flaveola*, *Troglodytes aedon*.

Breeding phenologies of many species of birds in North and Central America are reasonably well known (Davis 1933, Johnston 1964, Skutch 1950, Snow and Snow 1964), while in South America, most but few is concentrated in the tropics (Marchant 1959, Marini et al. 2012, Oniki and Willis 1983, Sanaiotti and Cintra 2010) followed by southern temperate latitudes (Mason 1985, Mezquida 2002, 2003). The subtropics comprise a geographically varied region, yet the breeding phenology of southern subtropical passerines were studied only in the Argentinian montane forest (Auer et al. 2007), while the subtropical Atlantic Forest remains unstudied.

New details about breeding biology are now accumulating and they suggest life history of birds in the southern hemisphere is much more complex than expected based on traditional life history paradigms (Auer et al. 2007, Lima and Roper 2009, Marchant 1959, Marini et al. 2012, Martin 1996, Roper et al. 2010, Yom-Tov 1987). The birds of southern subtropics, for example, appear to have shorter breeding seasons and smaller clutches than expected (Auer et al. 2007). Thus, understanding the breeding biology of birds within the subtropics will better inform life history theory.

Additionally, understanding breeding biology of birds is fundamental for conservation (Marini et al. 2012). In South America, deforestation is proceeding faster than research, especially in the Atlantic Forest, which today is ca. 14% of its original size (Ribeiro et al. 2009). Also, the potential for climate change to disrupt breeding patterns implies that we must quickly gather data on basic breeding biology and seasonal patterns in reproduction, thus anticipating and understanding these changes as they occur (Forschhammer et al. 1998, Marini et al. 2009).

Here, we studied the breeding biology of several species of passerine birds in the Atlantic Forest in subtropical Brazil. We describe nest types, breeding phenologies, season

length, incubation and nestling periods, clutch and egg sizes, number of nesting attempts, nest survival probabilities and nest heights.

METHODS

Study Sites.---We studied breeding birds in four locations near the city of Piraquara, state of Paraná, southern Brazil. The Mananciais da Serra (25º 29' S, 48º 59' W, 938-1,016 m asl) is transitional Araucaria Forest and Montane Atlantic Rainforest (Reginato and Goldenberg 2007), with primary and successional vegetation and some open areas. Two sites are near reservoirs (25º 30' S, 49º 01' W, 925 m asl and 25º 30' S, 49º 04' W, 900 m asl), comprising open areas that are regularly mown, orchards and marshes. Another rural area is mostly forested and connects through riparian corridors to other fragments (25º 31' S, 49º 05' W, 915 m asl). Annual rainfall is 1,427 mm, and monthly minimum and maximum temperature range from 9-20 ºC in July to 17-27 ºC in February (Fig. 1).

Data Collection.---We searched for signs of nesting on a daily basis from June 2012 to April 2013. To aid in finding nests and renesting, some birds were captured by mist-netting and in nest-boxes (with trap doors). Captured birds were uniquely color-banded. Adult birds and most nestlings were also banded with numbered metal bands (CEMAVE, National Center of Research for Bird Conservation). Nest-boxes, near the reservoirs, are commonly used by three species: White-rumped Swallow (*Tachycineta leucorrhoa*), House Wren (*Troglodytes aedon*) and Saffron Finch (*Sicalis flaveola*).

To find nests, we followed adult birds (carrying nest material or food) and searched in appropriate places in the understory vegetation. Nests were monitored until no longer in use. The time interval between checks was variable due to logistics (median: 2 days, 90% of checks in < 5 day intervals). Near the dates of egg laying and hatching, we attempted to check nests daily for better precision of nesting phenology. A nest was considered successful if at

least one young fledged. We rechecked nests from as far as possible to minimize disturbance. We recorded fledging dates from unknown nests if we found any young bird unable to fly, with fleshy gape flanges and juvenile plumage.

We calculate breeding season length for each species in two ways, using information of clutch initiations (dates of first eggs): first, the interval in days between the first and last clutch initations (hereafter, BSL) and II) the period in months (and converted to days) estimated using the concept of equally good months for breeding (hereafter $BSL_{adjusted}$) following Ricklefs and Bloom (1977). In calculation of $BSL_{adjusted}$, we used 30 days as a month starting on the date of clutch initiation of the first nest. To compare with one literature study (Auer et al. 2007), we used 28 days as a month and the vernal equinox as day zero. Across species, we report the average date of first clutch initation, BSL and $BSL_{adjusted}$ as mean ± standard error.

The clutch initiation date of nests with incomplete records was inferred by backdating laying dates of subsequent eggs or the average number of days for each nesting period based on nests with complete information. When nesting periods were unavailable, we used the literature to infer clutch initiation dates and clearly noted it in results. For calculating the timing of the nesting cycle, we define the incubation period as the interval in days between the first egg laid and first egg hatched. The nestling period is reported as the number of days from hatching to fledging. When nest checks did not coincide with hatching or fledging events, we used mid-point dates to estimate these transitions, and then, these less accurate dates were used only to estimate the breeding seasons, and some nesting periods when clearly stated. Daily survival rates of nests were estimated when sample size permitted using the program MARK (White and Burnham 1999).

We recorded clutch sizes only for nests that survived through the laying period. Clutch sizes are reported as mean ± standard error and mode. For clutch size comparisons with

literature, two tailed *t* tests were used. We weighed eggs on a digital scale (0.01 g precision) and measured eggs by taking photographs with a ruler for scale and then measuring using the software ImageJ (Schneider et al. 2012).

We measured nest height (to 0.1 m precision) when < 6 m, above which we simply estimated height visually. Nest-boxes or rooftops were not measured. Nests were classified as open-cup (superior entrance), enclosed (pendular or globular with side entrance), and cavity (built inside natural tree holes, nest-boxes and below rooftops) following Auer et al. (2007).

RESULTS

Breeding Phenologies.---A total of 265 nests of 38 species were found, and 22 observations of fledglings provided approximate breeding dates for another 5 species (Table 1). The earliest breeding activity was a nest construction on 13 September by the Southern Beardless Tyrannulet (*Camptostoma obsoletum*). Signs of breeding were observed in nine species in between 7 days prior to the vernal equinox (22 Sep.). The mean date of first clutch initation for 15 species (with n ≥ 3) was 40 days after the equinox (30 Oct., ± 5.41 days, range 29 Sep. − 16 Dec.). For these species, BSL averaged 57 days (± 8.7, range: 11-149 days) and BSL$_{adjusted}$ averaged 66 days (± 8.0, range: 30-146 days, Figs. 2, Table 2)

Nesting Periods.---Incubation periods ranged from the minimum of 13 days in the Rufous Bellied Thrush (*Turdus rufiventris*) to a maximum of 19 days in the White-rumped Swallow. Nestling periods ranged from a minimum of 9.5 days in Rufous-collared Sparrow (*Zonotrichia capensis*) to a maximum of 24 days in White Rumped Swallow (Table 3).

Clutch Sizes and Egg Sizes.---The most common clutch size in 25 species were two and three eggs (both *n* = 10 species, range: 2-5). In the species with one nest, the Variable Antshrike (*Thamnophilus caerulescens*) and Lesser Woodcreeper (*Xiphorhynchus fuscus*) had three, and the Planalto Woodcreeper (*Dendrocolaptes platyrostris*) had four eggs. The Small-

billed Elaenia (*Elaenia parvirostris*), Highland Elaenia (*Elaenia mesoleuca*), Tropical

Kingbird (*Tyrannus melancholicus*), and Ruby-crowned Tanager (*Tachyphonus coronatus*)

each had two eggs. One nest of Southern Rough-winged Swallow (*Pygochelidon cyanoleuca*)

contained five eggs. Clutch sizes for species with $n \geq 2$ are summarized in Table 4. Clutch

sizes in open-cup nests ranged from one to three eggs (2.5 ± 0.1, mode = 3, n = 42 nests, 13

species). Enclosed nests had two or three eggs (2.7 ± 0.1, mode = 3, n = 13 nests, four

species). Cavity nests had two to six eggs (4.0 ± 0.08, mode = 5, n = 110 nests, eight species).

Egg weight for open-cup nests ranged from 1.2-7.2 g (n = 58 eggs). Eggs from enclosed nests

ranged from 1.2-2.9 g (n = 32 eggs). Eggs from cavity nests ranged from 1.5-3.3 g (n = 438

eggs, Table 5).

    Egg Laying Frequencies.---Only the Variable Antshrike (one nest observed), Scalloped

Woodcreeper (*Lepidocolaptes falcinellus*, one nest) and the Mottle-cheeked Tyrannulet

(*Phylloscartes* ventralis, two nests) laid eggs every other day. The Bran-colored Flycatcher

(*Myiophobus fasciatus*, two nests), Swainson's Flycatcher (*Myiarchus swainsoni*, one nest),

White-rumped Swallow (16 nests), House Wren (six nests), Saffron Finch (eight nests),

Rufous-collared Sparrow (*Zonotrichia capensis*, three nests), White-browed Warbler

(*Myiothlypis leucoblephara*, two nests) and Golden-crowned Warbler (*Basileuterus

culicivorus*, two nests) all laid eggs on consecutive days.

    Number of Nesting Attempts.---A pair of Scalloped Woodcreepers initiated a second

clutch on 16 October, after losing a nest with three eggs observed 10 days earlier. A Mottle-

cheeked Tyrannulet first attempt was preyed on during laying (10 Oct. 2012), followed by the

construction of a second nest 93 m from the first, two weeks later (24 Oct.). That three-egg

clutch also failed due to predation (3-6 Nov.). This pair then resumed the construction on an

incomplete nest (8 Nov.) that we found a month earlier (when it was laying in the first nest).

This two-egg nest was preyed on during the nestling stage (11-14 Dec.). On 4 December, a

Bran-colored Flycatcher began laying 9 days after fledging its first three-egg nest, both of which were successful with two young. A Swainson's Flycatcher was seen incubating in 21 December, 12 days after tending an unsuccessful nest with four nestlings. Three pairs of White-rumped Swallow renested after abandonment (possibly due to handling), two of which successfully fledged (6 and 17 Jan.). One pair of House Wren abandoned a nest in incubation (15 Nov., probably due to banding) and then laid in another box 7 days later, with success. Saffron Finches often renested (62% with two and 19% with three nest attempts, Table 6). Three pairs of Saffron Finch had two successes in three attempts each. Another three pairs had two successes in two nest attempts. One pair succeeded in one attempt, three were unsuccessful with one and another with two nest attempts. Two pairs of White-browed Warbler had two unsuccessful attempts (Table 6). Daily nests survival rate calculated for species with 13 nests or more varied from 90-99% and were apparently always high in nest boxes (Table 7).

DISCUSSION

Although it is clear that the breeding season is more or less subsequent to the onset of Spring (vernal equinox), initiation of breeding (first clutch initiation of each species) was spread over almost 3 months after the vernal equinox. BSL was also quite variable, from 1-5 months. No clear patterns in these breeding parameters seemed associated with diet or phylogeny. For example, it is often claimed that flycatchers (Tyrannidae) and other insectivores begin breeding well before the seedeaters (Emberizidae, Davis 1933, Skutch 1950) but here, this was not the case. The Saffron Finch began at the same time as the first flycatchers (Mottle-cheeked Tyrannulet and the Great Kiskadee *Pitangus sulphuratus*) and well before the Blue-and-white Swallow (*Pygochelidon cyanoleuca*).

BSL and initiation of breeding appears to be independent of migration status. The residents House Wren, Gray-throated Warbling finch (*Poospiza cabanisi*), White-browed and Golden-crowned warblers had surprisingly short breeding seasons that were similar to the migrant White-rumped Swallow (FMS unpubl. data of migrant statuses). Migrants also varied broadly with respect to breeding season initiation, with the Southern Beardless Tyrannulet being the earliest to build, before the vernal equinox, whereas the Red-eyed Vireo was the last, beginning in mid-December.

In Argentina at the same latitude, mean initiation date of breeding for 17 species was 22 October (Auer et al. 2007). In that study, initiation dates were corrected by averaging the first 10% of nests to decrease overestimation by pooling three years of sampling and their mean initiation date was similar to this study ($t_{30} = 1.24$, $P = 0.22$). However, if we compare our dates with their true initation dates estimated from figure 1 in Auer et al. 2007, here, birds begin breeding 3 weeks later on average (mean number of weeks after the equinox, Argentina = 1.9 weeks, this study = 4.9 weeks, $t_{30} = 3.46$, $P = 0.001$). BSL was, on average, 57 days (15 species in this study), which is about the same as the 50 days average in Argentina (authors eliminated the first and last 5% of nest initiation dates, $t_{30} = 0.81$, $P = 0.42$). Breeding season length ($BSL_{adjusted}$) in this study was also similar to Argentina (this study = 62 days, Argentina = 78 days, mo. = 28 days, $t_{30} = 1.95$, $P = 0.06$, power: 47%, fig. 1,). Thus, in subtropical South America, breeding seasons are also shorter than expected by the traditional life history theory (Auer et al. 2007) and are more comparable to temperate latitudes (Davis 1933, Ricklefs and Bloom 1977).

Here, clutch size in cup (2.5 ± 0.1, $n = 42$) and enclosed nests (2.7 ± 0.1, $n = 13$) were similar to Argentina (2.4 ± 0.1, $n = 140$ and 2.7 ± 0.1, $n = 122$, respectively), while in cavity species, it was greater here (4.0 ± 0.1, $n = 110$ versus Argentina, 3.5 ± 0.0, $n = 14$), probably due to the White-rumped Swallow (4.8 ± 0.1, $n = 31$). For species that are shared between this

study and Argentina, the House Wren had larger clutch size here (this study: 4.6, $n = 17$, Argentina: 3.5, $n = 8$, $t_{23} = 3.10$, $P = 0.004$), whereas clutch size of the Rufous-bellied Thrush (*Turdus rufiventris*) was similar (this study: 2.5, $n = 12$, Argentina: 2.7, $n = 28$, $t_{38} = 1.1$, $P = 0.27$).

In our study the combination of breeding parameters in the House Wren is surprising because clutch size is larger than in Argentina, yet, $BSL_{adjusted}$ (this study: 67 days, Argentina: 70 days, mo. = 28 days) and nest success are similar (Auer et al. 2007). Also, the Saffron Finch has a long breeding season (146 days, more similar to tropical birds), relatively high nest success and large clutches (similar to temperate birds). Renesting was common, as expected for tropical birds (Roper et al. 2010), even after successful nests and 37% of pairs had two successful nests.

Here we describe breeding phenologies for various passerine birds in the subtropical Brazilian Atlantic Forest for the first time and show how they vary from those found at the same latitude in the mountains of Argentina. In Argentina, breeding patterns were concluded to be more similar to tropical patterns (Auer et al. 2007), while the combinations of patterns that we found in southern Brazil are not so easily classified into tropical or temperate. Nest predation was also an important cause of nest failure here, but despite that, variation in life history traits across species suggests both tropical (slow) and temperate (fast) life history strategies (Martin 1996). The surprising clutch sizes, breeding season lengths and number of renesting attempts of the southern House Wren and Saffron Finch suggests that life histories in the subtropics do not easily fit the dogma of tropical-temperate life-history patterns.

ACKNOWLEDGEMENTS

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TABLE 1. Nests (and additional fledging events in parenthesis) found in the Atlantic Forest of subtropical southern Brazil. Nest classification according to Auer et al. (2007): Open-cup (O), Enclosed (E) and Cavity (C). Success is indicated as successful nests/nests with known fate. Individual nest heights (NH) provided, unless $n > 2$, which are indicated as min-max (n, if < total number of nests).

Family and species	Type	Nests	Success	NH (m)
Antbirds (Thamnophilidae)				
Giant Antshrike (*Batara cinerea*)		(1)		
Variable Antshrike (*Thamnophilus caerulescens*)	O	1	1/1	0.4
Tapaculos (Rhynocryptidae)				
White-breasted Tapaculo (*Eleoscytalopus indigoticus*)		(1)		
Ovenbirds and Woodcreepers (Furnariidae)				
Planalto Woodcreeper (*Dendrocolaptes platyrostris*)	C	3		
Lesser Woodcreeper (*Xiphorhynchus fuscus*)	C	2	1/1	
Scalloped Woodcreeper (*Lepidocolaptes falcinellus*)	C	5	1/2	
Olive Spinetail (*Cranioleuca obsoleta*)	E	1 (1)		
Pallid Spinetail (*Cranioleuca pallida*)	E	1 (2)		4.0
Rufous-capped Spinetail (*Synallaxis ruficapilla*)	E	2	0/1	1.0

Family and species	Type	Nests	Success	NH (m)
Spix's Spinetail (*Synallaxis spixi*)		(1)		
Tyrant flycatchers (Tyrannidae)				
Small-billed Elaenia (*Elaenia parvirostris*)	O	3	0/1	
Olivaceous Elaenia (*Elaenia mesoleuca*)	O	2	0/2	2.7, 5.0
Highland Elaenia (*Elaenia obscura*)	O	2	1/1	2.2, 3.4
Southern Beardless Tyrannulet (*Camptostoma obsoletum*)	E	1		
Mottle-cheeked Tyrannulet (*Phylloscartes ventralis*)	E	4 (3)	0/4	1.0- 3.3
Bran-colored Flycatcher (*Myiophobus fasciatus*)	O	4	3/4	1
Euler's Flycatcher (*Lathrotriccus euleri*)	O	1	0/1	2.5
Great Kiskadee (*Pitangus sulphuratus*)	E	4	2/2	4.5, 5.7
Tropical Kingbird (*Tyrannus melancholicus*)	O	1 (1)	0/1	2.4
Fork-tailed Flycatcher (*Tyrannus savana*)	O	1	1/1	4.2
Swainson's Flycatcher (*Myiarchus swainsoni*)	C	3 (1)	0/3	2.0-3.5
Tityras (Tityridae)				
Black-capped Becard (*Pachyramphus marginatus*)	E	1	1/1	4
Crested Becard (*Pachyramphus validus*)	E	6		2.5-19.0 (4)

Family and species	Type	Nests	Success	NH (m)
Vireos (Vireonidae)				
Rufous-browed Peppershrike (*Cyclarhis gujanensis*)		(1)		
Red-eyed Vireo (*Vireo olivaceus*)	O	4 (1)	1/4	0.5-4.0
Rufous-crowned Greenlet (*Hylophilus poicilotis*)	O	1 (1)		5
Swallows (Hirundinidae)				
Blue-and-white Swallow (*Pygochelidon cyanoleuca*)	C	7	5/5	
Southern Rough-winged Swallow (*Stelgidopteryx ruficollis*)	C	1	1/1	
Gray-breasted Martin (*Progne chalybea*)		(1)		
White-rumped Swallow (*Tachycineta leucorrhoa*)	C	38	26/38	
Wrens (Troglodytidae)				
House Wren (*Troglodytes aedon*)	C	22	11/16	
Thrushes (Turdidae)				
Rufous-bellied Thrush (*Turdus rufiventris*)	O	19	0/8	1.0-4.0 (4)
Creamy-bellied Thrush (*Turdus amaurochalinus*)	O	9	3/6	1.2-4.2 (5)
Tanagers (Thraupidae)				
Ruby-crowned Tanager (*Tachyphonus coronatus*)	O	2	1/2	0.3

Family and species	Type	Nests	Success	NH (m)
Sayaca Tanager (*Thraupis sayaca*)	O	4	2/2	4.0, 5.9 (2)
Chestnut-backed Tanager (*Tangara preciosa*)	O	1		
Sparrows (Emberizidae)				
Gray-throated Warbling-Finch (*Poospiza cabanisi*)	O	3 (2)	1/3	1.2-3.0
Saffron Finch (*Sicalis flaveola*)	C	66	35/62	
Double-collared Seedeater (*Sporophila caerulescens*)	O	6 (2)	2/6	0.4-4.1
Rufous-collared Sparrow (*Zonotrichia capensis*)	O	18 (2)	3/16	0.0-15 (16)
Wood-warblers (Parulidae)				
Tropical Parula (*Setophaga pitiayumi*)	E	2 (1)		12
White-browed Warbler (*Myiothlypis leucoblephara*)	E	8	1/8	0.0-0.0 (7)
Golden-crowned Warbler (*Basileuterus culicivorus*)	E	6	1/5	0.0-1.0[1]

[1] Ground nests often built in gullies. Nest heights to the bottom ground.

TABLE 2. Breeding season start and length (BSL) in days for 15 most sampled species in the Atlantic Forest of subtropical southern Brazil. Sample sizes refer to number of clutch initiations. $BSL_{adjusted}$ calculated with and converted using 30 days, following Ricklefs and Bloom (1977).

Species (*n* clutches)	Start	BSL	$BSL_{adjusted}$
Mottle-cheeked Tyrannulet (7)	9 Oct.	65	88
Bran-colored Flycatcher (4)	19 Oct.	47	60
Great Kiskadee (3)	16 Oct.	61	57
Red-eyed Vireo (3)	16 Dec.	11	30
Blue-and-white Swallow (5)	9 Nov.	51	49
White-rumped Swallow (36)	23 Oct.	43	43
House Wren (18)	13 Oct.	65	69
Rufous-bellied Thrush (6)	29 Sep.	99	113
Creamy-bellied Thrush (6)	19 Oct.	46	57
Gray-throated Warbling-Finch (4)	9 Nov.	39	60

Saffron Finch (58)	16 Oct.	149	146
Double-collared Seedeater (7)	3 Dec.	78	82
Rufous-collared Sparrow (13)	14 Nov.	47	60
White-browed Warbler (5)	4 Nov.	15	30
Golden-crowned Warbler (5)	28 Oct.	43	49

TABLE 3. Length of the nesting periods of 13 passerine species in the Atlantic Forest of subtropical southern Brazil. Incubation period is from laying of the first egg until hatching. Nestling period ranges from hatching to fledging. Values are presented as mean and standard error (SE) in parenthesis.

Species	Nest period in days			
	Incubation (SE)	*n*	Nestling (SE)	*n*
Mottle-cheeked Tyrannulet	18	1		
Bran-colored Flycatcher	18 (0.0)	2	13	1
Red-eyed Vireo	15	1	10	1
Southern Rough-winged Swallow			19	1
White-rumped Swallow[1]	19.1 (0.2)	29	24.0 (0.9)[1]	8
House Wren	18.5 (0.3)	6	14.5 (1.9)[2]	5
Rufous-bellied Thrush	13	1		
Sayaca Tanager	15	1	18	1
Saffron Finch	15.4 (0.3)	11	16.3 (0.4)[2]	34
Double-collared Seedeater			11	1
Rufous-collared Sparrow	17	1	9.5[2]	1
White-browed Warbler	17	1		

| Golden-crowned Warbler | 16 | 1 |

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[1] Nestling stages excluding nests with experimental brood manipulation (UW unpubl. data). [2] Estimated using mean dates between visits.

TABLE 4. Clutch sizes of 16 passerine species (n ≥ 2) in the Atlantic Forest of subtropical southern Brazil. Each row indicates the number of nests of the corresponding clutch size by species.

Species	Clutch size					
	1	2	3	4	5	6
Scalloped Woodcreeper			3	1		
Mottle-cheeked Tyrannulet		2	1			
Swainson's Flycatcher			1	2		
Bran-colored Flycatcher		2	2			
Red-eyed Vireo		2	1			
White-rumped Swallow			2	4	23	2
House Wren			2	4	10	1
Rufous-bellied Thrush		6	6			
Creamy-bellied Thrush		1	4			
Sayaca Tanager		1	1			
Rufous-collared Sparrow			5			
Gray-throated Warbling-Finch		1	1			
Saffron Finch			4	24	22	2
Double-collared Seedeater	1	3				
White-browed Warbler			5			
Golden-crowned Warbler		1	3			

TABLE 5. Egg measurements of 20 passerine species in the Atlantic Forest of subtropical southern Brazil. Values are presented as mean (standard error).

Species (*n*)	Egg Measurements (SE for *n* > 2)		
	Weight (g)	Length (mm)	Width (mm)
Variable Antshrike (3)	2.93 (0.19)	21.0 (0.5)	15.4 (0.3)
Mottle-cheeked Tyrannulet (7)	1.60 (0.12)	17.8 (0.3)	13.4 (0.2)
Swainson's Flycatcher (7)	3.04 (0.12)	21.2 (0.3)	16.9 (0.2)
Tropical Kingbird (2)	4.56, 4.32	26.9. 26.2	17.3, 17.4
Bran-colored Flycatcher (2)	1.55, 1.59	17.9, 18.1	12.7, 12.9
Red-eyed Vireo (5)	2.26 (0.14)	20.4 (0.4)	14.7 (0.2)
Blue-and-white Swallow (1)		17.2	13.1
White-rumped Swallow (170)	2.06 (0.02)	19.7 (0.1)	13.9 (0.0)
House Wren (67)	1.75 (0.04)	17.7 (0.1)	13.5 (0.1)
Rufous-bellied Thrush (6)	6.58 (0.13)	31.7 (0.4)	21.2 (0.2)
Creamy-bellied Thrush (5)	5.94 (0.14)	27.4 (0.4)	20.6 (0.2)
Ruby-crowned Tanager (2)	3.60, 3.85	22.0, 23.2	17.0, 17.1
Sayaca Tanager (3)	2.98 (0.19)	22.5 (0.5)	16.3 (0.3)

Rufous-collared Sparrow (18)	2.40 (0.08)	19.0 (0.2)	14.7 (0.1)
Gray-throated Warbling-Finch (5)	2.52 (0.14)	19.8 (0.4)	15.0 (0.2)
Saffron Finch (190)	2.15 (0.02)	19.6 (0.1)	14.4 (0.0)
Double-collared Seedeater (7)	1.43 (0.12)	16.6 (0.3)	12.7 (0.2)
White-browed Warbler (15)	2.62 (0.08)	20.0 (0.2)	15.3 (0.1)
Golden-crowned Warbler (10)	1.74 (0.10)	17.2 (0.3)	13.5 (0.2)
Shiny Cowbird[1] (3)	3.76 (0.19)	21.1 (0.5)	16.8 (0.3)

[1] Three nests of Rufous-collared Sparrow contained one egg of Shiny Cowbird (*Molothrus bonariensis*).

TABLE 6. Number of pairs by nest attempts during the 2012-2013 breeding season in the Atlantic Forest of subtropical southern Brazil. Each row indicates the *n* of banded pairs with the corresponding number of nesting attempts in columns. Number of known pairs with at least one success is in parenthesis.

Species	Nest attempts		
	One	Two	Three
Scalloped Woodcreeper		1 (1)	
Mottle-cheeked Tyrannulet	2 (0)		1 (0)
Bran-colored Flycatcher	2 (1)	1 (1)	
Swainson's Flycatcher	1 (0)	2 (0)	
White-rumped Swallow	31 (24)	3 (2)	
House Wren	8 (5)	1 (1)	
Rufous-bellied Thrush	2 (0)	2 (0)	
Saffron Finch	3 (1)	10 (8)	3 (3)
Double-collared Seedeater	1 (1)	1 (0)	
Rufous-collared Sparrow	3 (0)	3 (1)	
White-browed Warbler	4 (1)	2 (0)	
Golden-crowned Warbler	6 (1)		

TABLE 7. Daily nest survival rates (DSR) for several species with ≥ 13 nests each in the Atlantic Forest of subtropical southern Brazil. Nest survival probability is the daily survival rate (DSR) raised to estimated nesting period (Table 3). Range of nest survival probability (in parenthesis) is based on cumulative standard errors.

Species	DSR (SE)	Sample size	Nest survival probability
White-rumped Swallow	0.990 (0.003)	37	0.65 (0.56-0.74)
House Wren	0.988 (0.005)	16	0.67 (0.55-0.81)
Saffron Finch	0.981 (0.004)	59	0.54 (0.47-0.63)
Rufous-collared Sparrow	0.901 (0.027)	13	0.06 (0.03-0.14)

Figure legends

FIG. 1. Monthly mean temperature and precipitation (1961-2013) in Curitiba, around 20 km from study areas (INMET 2013).

FIG. 2. Breeding timeline of 43 passerines (by family) in the Atlantic Forest of subtropical southern Brazil. Abscissa: days since vernal equinox (22 Sep., dotted vertical line). Diamonds indicate the first nest construction recorded for each species. Vertical lines indicate dates of clutch initiation (observed or inferred). Horizontal bars show the range of the nestling and fledgling stages together. To estimate some laying dates we followed Auer et al. (2007) as follows: Small-billed Elaenia and Olivaceous Elaenia had similar nesting periods as their Small Billed Elaenia; Rufous-bellied and Creamy-bellied thrushes as their Rufous-bellied Thrush. Dates for the Blue-and-white Swallow were inferred from the nesting periods of the White-rumped Swallow.
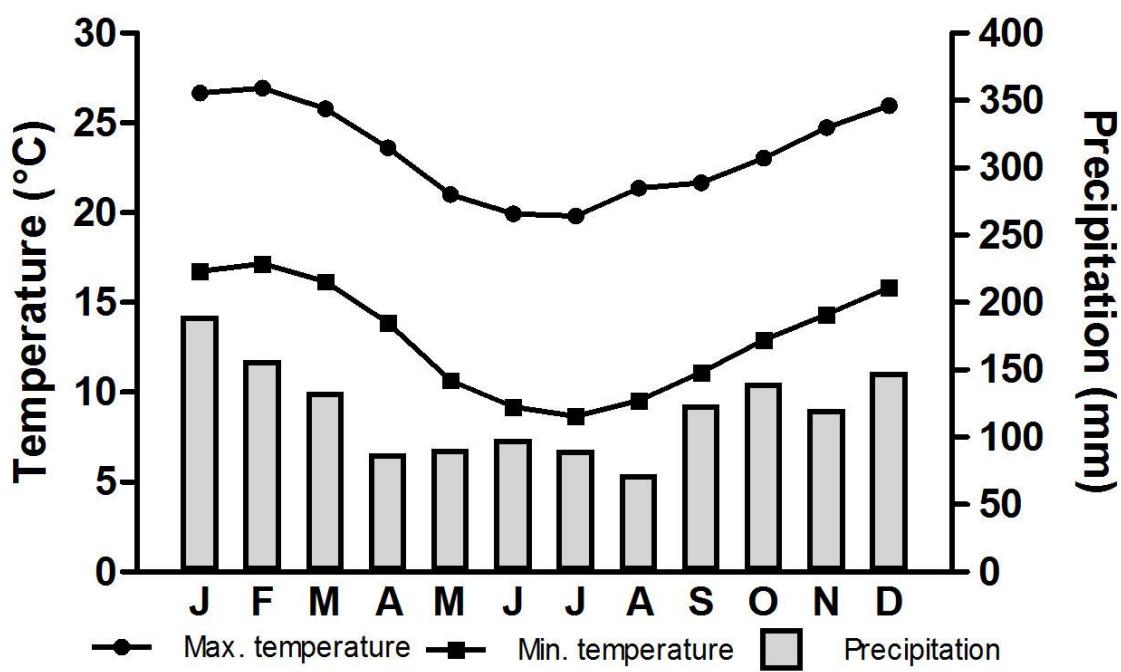
FIG. 1.
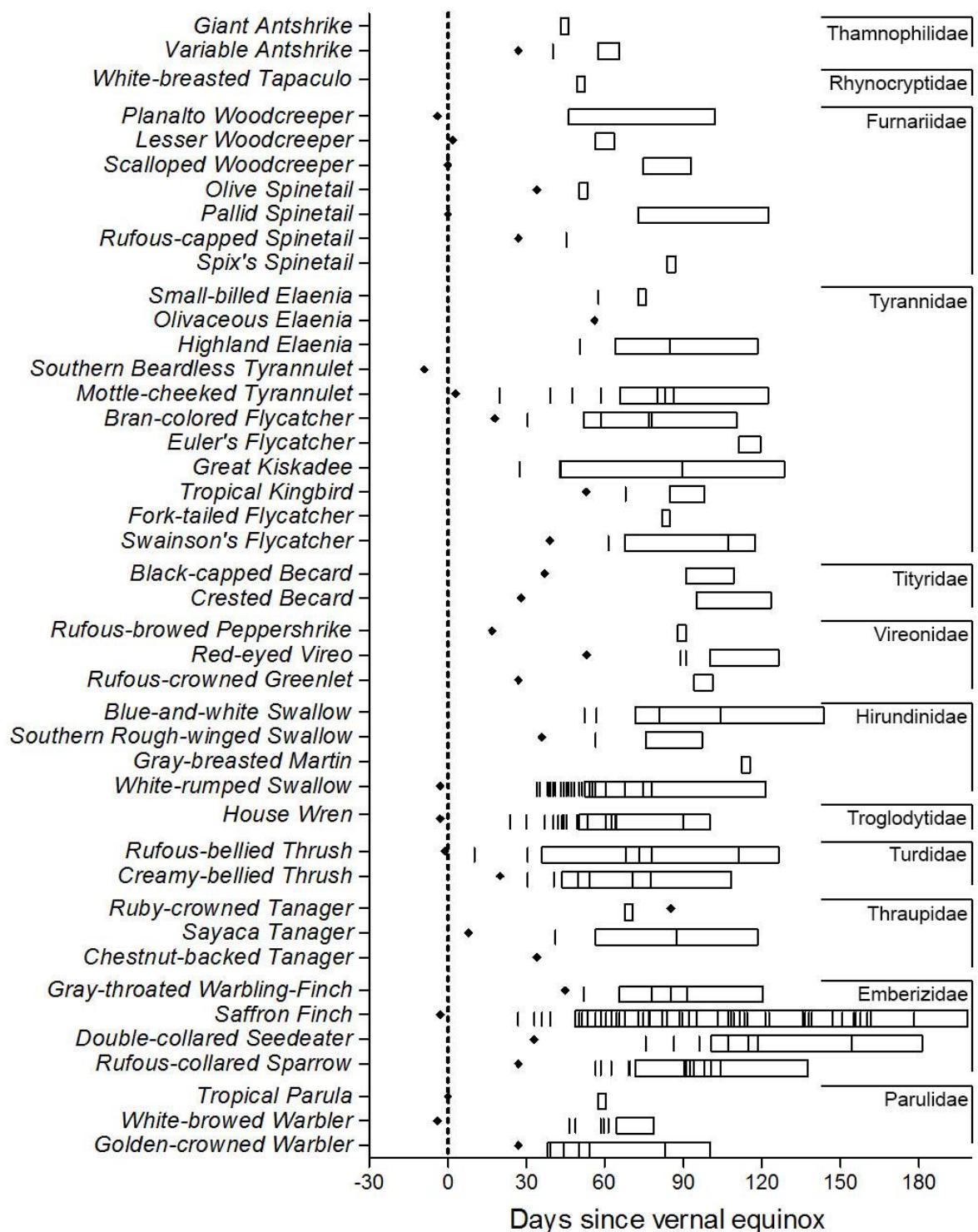
FIG. 2.

3 BREEDING SEASONS FOR PASSERINES IN THE NEW WORLD: WHAT ARE THE PATTERNS?

Capítulo elaborado de acordo com as normas do periódico The Auk.
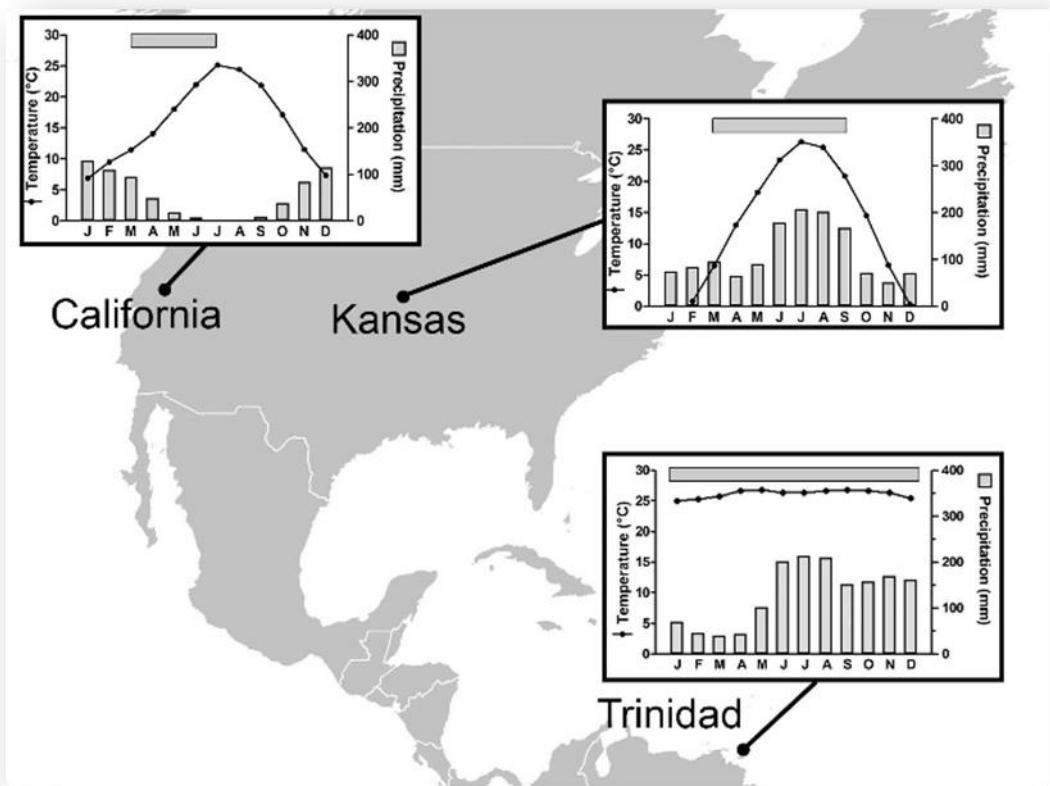
As fenologias reprodutivas são influenciadas indiretamente pela sazonalidade de temperatura e chuva. Barra horizontal: conjunto dos ciclos reprodutivos de passeriformes. Em Trinidad, espécies podem reproduzir o ano todo. No Kansas, os ciclos reprodutivos são congruentes com o aumento de temperatura e chuva. Na Califórnia, as espécies reproduzem com o aumento da temperatura, mesmo que isso signifique um período mais seco.

Breeding season patterns in the Americas

RESEARCH ARTICLE

Breeding seasons for passerines in the New World: what are the patterns?

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ABSTRACT

Breeding phenologies of birds have fundamental influence in their breeding strategies. Avian life history theory suggests that high latitudes have shorter and synchronous, and low latitudes, longer and less synchronous breeding seasons. This latitudinal paradigm makes unrealistic assumptions and hides many processes involved in determining breeding phenologies and their evolution. A synthesis of breeding phenology in South American birds does not exist and accumulating information indicates that breeding patterns disagree with the prevailing paradigm. Here we attempt to explain variation in breeding phenologies of passerines in the Americas based on climate models, and to put the southern temperate birds in the context of the current life history theory. Climate models agree with observed breeding phenologies of the northern and tropical birds, but do not explain any major pattern in temperate South America, where phenologies can be constant in different climates, and breeding patterns can vary greatly within locations. We suggest that continentality far south, and unpredictable climate due to high inter-annual variation might mask any discernible pattern in breeding phenology in temperate South America.

RESUMO

Fenologia reprodutiva dos passeriformes no Novo Mundo: quais são os padrões?

A fenologia reprodutiva das aves influencia fundamentalmente as suas estratégias reprodutivas. A teoria de história de vida das aves postula que em altas latitudes, os ciclo reprodutivos devem ser curtos e síncronos, enquanto que nos trópicos, longos e espalhados no tempo. No entanto, esse paradigma latitudinal esconde muito dos processos envolvidos na evolução dos ciclos reprodutivos. Para a América do Sul, não existe uma síntese sobre fenologias reprodutivas, mesmo que estudos acumulados tenham demonstrado que os padrões reprodutivos nessa região desafiam o paradigma vigente. Nesse trabalho, nós tentamos explicar a variação na fenologia reprodutiva de passeriformes nas Américas através de modelos climáticos, e, em seguida, colocamos as aves temperadas da América do Sul no contexto do paradigma de história de vida. Nossos modelos climáticos funcionam bem para o Neártico e para os trópicos, mas falham em descrever qualquer padrão na América do Sul temperada. No temperado sul, as fenologias são constantes em diferentes regimes climáticos, enquanto que parâmetros reprodutivos variam grandemente nos mesmos locais. É possível que continentalidade reduzida mais ao sul e alta variação interanual no clima podem contribuir para mascarar os padrões intrínsecos nas fenologias reprodutivas das aves da América do Sul temperada.

INTRODUCTION

Life history theory in passerine birds has focused on evolution and latitudinal variation of clutch size, while ignoring many possible alternatives (Martin 2004). The current paradigm in life history theory states that birds in higher latitudes have larger clutches than birds in lower latitudes (Lack 1947, Moreau 1944). Explanations other than latitude for the evolution of clutch size have been suggested, such as breeding season length, resource seasonality and nest predation (Griebeler et al. 2010, Roper et al. 2010). These alternatives have received less attention than latitudinal trends, in which the traditional view is temperate and tropical birds as extremes in a life history continuum (fast and slow, Tieleman et al. 2004).

We may ask ourselves whether the latitudinal gradient is a robust idea. First, the current life history theory for birds remains strongly biased towards the northern hemisphere (Martin 2004). Second, it implies convergent evolution to similar climate regimes at similar latitudes in both hemispheres. However, there are interesting differences in reproductive patterns in the southern hemisphere in relation to Africa and Australia, where breeding season length for many species is longer than those in the northern hemisphere at the same latitudes (Wyndham 1986). In South America, clutch sizes are smaller and more constant over a variety of latitudes, whereas can vary widely both latitudinally and seasonally in North America (Jetz et al. 2008, Yom-Tov et al. 1994).

Breeding season length is often overlooked despite its important role in life histories of birds (e. g., Heming et al. 2013). For instance, observational and simulation studies suggest that, when breeding seasons are longer (as in tropical latitudes), the ability to renest is more important than variation in clutch size in their contribution to annual reproductive success (Farnsworth and Simons 2001, Griebeler et al. 2010, Roper 2005, Roper et al. 2010). In the Neotropics, a confounding pattern is that geographic distribution of many lower taxa extends

from the tropics to southern temperate latitudes, therefore life history characteristics are expected to be similar in all latitudes because of phylogeny (Martin 2004). Some breeding phenology synthesis exists for other parts of the world (Ricklefs 1966, Wyndham 1986), but are still lacking in the South America. For the northern hemisphere in the New World, evidence indicates a relationship between latitude and breeding season lengths (Ricklefs and Bloom 1977). We suggest that the emphasis on latitude is insufficient to explain life history patterns in the New World, in part for neglecting zoogeographic differences in different regions between Americas (Ortega and Arita 1998).

Here, we describe latitudinal variation in breeding phenology in passerine birds in the New World, and contrast the southern hemisphere with the northern hemisphere breeding phenologies. We used published breeding season information for birds of the New World along with information we gathered in the field in south Brazil. Next, we attempt to determine what broad-scale factors (latitude, climate) explain variation in breeding season length for temperate and tropical regions using model selection. We predict climate, phylogeny and ecology (migratory status) will better explain breeding season length variables than latitude. Breeding seasons should be longer where temperature and precipitation (thus, primary productivity) is greatest and most constant, as climate does not act as a time constraint (Martin 1987, Wikelski et al. 2000, 2003). Resident passerines should also have longer seasons as they are not constrained by migration schedules (Smith and Moore 2004). Different clades have distinct evolutionary adaptations, and so clades should respond in breeding season length in particular ways to environment constraints. If temperate South America follows latitudinal patterns similar to those in North America, then these predictions should be mirror images in latitudes in both hemispheres, and the breeding seasons should be shorter and more synchronous at higher latitudes, as observed in North America (Ricklefs and Bloom 1977).

METHODS

Published Breeding Records

We compiled data from the literature and ours (Atlantic Forest, S 25° W 48°) for breeding passerines in the New World that report geographic coordinates and breeding parameters of one or preferably of assemblages of species (Supplementary Table S1). The lack of consensus on how to report breeding season length (BSL) for a given species makes gathering this information difficult. Ideally, one should report the first and last date of the same nest event in the season (e.g., first egg laid of the first nest and first egg laid of the last nest), or the distribution of nesting events across time. In records used here, nesting events are reported as nest construction, first egg, end of laying, beginning of incubation, fresh eggs, and cloacal protuberances. Because we are looking for broad patterns, small differences in the nest events should be unimportant, and so we simply refer to them as clutch initiations.

Unfortunately, it is common to include the development of the last nest of the season in BSL, and for example, report it from the first nest construction until the last nestling had fledged. Other examples include the ending of breeding season as the last egg laying date (irrespective of development), fledging date, last active nest and absence of brood patches. Thus, estimating the last date of a breeding season can be difficult as well. In these cases, we retrieved incubation and nestling periods from the same papers when available (otherwise, the average for the available species: 14 days of incubation, 15 days of nestling), and then, subtracted these from the last active nest date to obtain the clutch initiation. With this approach, we assume that a theoretical clutch initiation of the last successful nest is good enough approximation to perform the analyses, although this neglects the existence of unsuccessful clutch initiations at the end of breeding seasons.

Here, duration of the breeding season is calculated in two ways, depending of the available data. The first method is the time interval in months from first and last clutch initiation of each species (hereafter, breeding interval, BI). To generate dates for imprecise reporting (e.g., late July) we used simple rules. If the nest was reported early or late in a month, we used the first and last day of the month, respectively. If reported mid month, we used day 15 of that month. If first or last half of a month was reported, we used days 7 and 21 respectively. These estimates should never have more than a week difference from the true date. Dates were then allocated to weeks and converted to fraction of month of 30 days. The second method (here, BSL) follows Ricklefs and Bloom (1977), using the monthly proportion of clutch initations for each breeding season as follows:

$$(1)\ BSL = e^{-\sum p_i \ln p_i}$$

Where p_i = proportion of clutch initiations in month i. BI and BSL estimate breeding season length in terms of number of months, but BSL it is not affected by bimodality and intermittence in nest events across months. BSL is more conservative than BI because it de-emphasizes extreme nest dates. For papers that report the distribution of nest events for several years individually, we pooled nests per month among years to estimation of both BI and BSL.

Some studies only report dates for first and last clutch initations, and so only BI can be estimated. In a large subset of the data with five or more clutch initiations, we were able to estimate both BI and BSL for each breeding cycle. Thus, by using regression to relate both estimates (BSL = 1.07 + 0.67* BI, $r^2 = 0.77$, $F_{1,131} = 441.8$, $P < 0.001$), we could then substitute BI and estimate BSL for all species.

To compare the breeding phenology of a set of five or more species between locations, we estimated joint BSL in two ways: the first method is the average BSL, which is the mean calculated by pooling studies ($n \geq 5$ nests per species) in 1°x1° coordinate grids. The second

method, total BSL is the number of species (rather than clutches initiated) breeding each

month, calculated with equation 1. That is, *p* in equation 1 is substituted for the proportion of

species nesting that month, rather than the proportion of clutches initiated that month. Total

BSL account for asynchrony in breeding among species. The initiation of breeding date (IOB)

is the date of the first clutch initiation by species. To make both hemispheres comparable, we

adjusted dates such that the relative to the vernal equinox was day 0. We use mean and

standard deviation of IOB of each local set of species as a measure of local breeding

phenology variation. We present these variables graphically on the context of latitude and

habitats following the respective phenology literature.

For model selection, temperatures and rainfall in 0.5° cells were obtained from the

Climatic Research Unit, University of East Anglia, for years 1901-2002 (Mitchell and Jones

2005). We use the mean monthly annual temperature [T(mean)] and temperature seasonality

[$(T$(season)], which is the absolute difference between summer and winter temperatures (three

mo average) averaged in 1°x1° coordinate grids. We also included total annual precipitation

[P(annual)], and the number of rainy months [P(month)], which is an index based on the

average monthly precipitation in 1°x1° coordinate grids. This index is calculated for each grid

using equation 1 (using mm month^{-1} rather than nest month^{-1}). Analogous to BSL, *P*(month)

estimates in number of months, and the seasonality is inversely related to *P(month)*.

To control, in part, for phylogeny, we separate the analysis by suborder (Tyranni and

Passeri). Species were classified as migrant (if any migratory activity) or resident. Nest type

carries a strong phylogenetic signal (Simon and Pacheco 2005), and might also influence BSL

via nest predation (Griebeler et al. 2010, Martin and Li 1992). Thus, to control for phylogeny

and ecology, we only used non-cavity nests in model selection. Nest types were obtained from

the same papers or another reliable source (Supplementary Table S1). Non-cavity nests are

open nests (cup shaped with superior entrance) or enclosed nests (pendular or globular nests

with side entrances). Cavity nests are built in secondary tree holes, nest-boxes, or beneath the roof of buildings.

Data analysis

To illustrate the latitudinal paradigm, we first test the influence of the latitudinal gradient alone on BSL in each hemisphere. Then, also for latitude, we contrast similar temperate latitudes across North and South America, and treat the tropics as a unit (-23° to 23° of latitude). We used simple linear models and visually examined residuals for normality, and $\log_e$ transformed BSL for tropical analyses to fulfill this requirement. Next, we built models for non-cavity nesters for each suborder (Tyranni and Passeri) that combine hemisphere, climate and migratory status (hereafter, climate models) to explain BSL for temperate North America ($\geq 23°$ latitude) and temperate South America together ($\leq -23°$ latitude). We excluded the breeding season of species that the number of clutch initation dates were omitted in the original work. The main predictors are T(mean), T(season), P(annual), P(month), hemisphere and migratory status (resident or migratory). We used the corrected Akaike information criterion (AICc) to choose the best models (Burnham and Anderson 2002). We calculated all possible models that include the main predictors and second order effects with migratory status and hemisphere. Relationship between climate predictors were tested using cross correlations by restricted maximum likelihood method, and if a model included two strongly correlated predictors for both hemispheres ($r \geq 60$ and $P < 0.05$), the model was disregarded. Separately, we built models for tropical latitudes in the same layout, but without the predictor hemisphere and its interactions. If more than one model had ΔAICc < 2, we averaged the parameters across these models (Richards et al. 2010), and evaluated the explanatory weight of variables by relative importance (Burnham and Anderson 2002). We evaluated simple (no averaging required) models by partial r^2. For comparison with climate

models, we built simple latitudinal models for temperate regions together (BSL = absolute

latitude + hemisphere + absolute latitude x hemisphere), and for the tropics (BSL = absolute

latitude).

RESULTS

Latitudinal Gradients

We gathered information of 355 breeding cycles for 263 species in one or more locations

from Patagonia (S 42°) through Washington, USA (N 46°), near the border with Canada

(Figure 1). Both hemispheres have a latitudinal trend in BSL (Figure. 2 A, B), but in the

southern hemisphere, the fit is poor. Excluding the tropics from both hemispheres, the

latitudinal trend only persists weakly in temperate North America, where the BSL decreases

from 2.6 to 1.5 months from N 25° to N 40° of latitude (Figure 2C, Table 1). The latitudinal

trend disappears in temperate South America after excluding the tropics. Controlling for

latitude, the temperate North America has shorter BSL (2.0 mo) than South America (2.4 mo

Table 1.).

Breeding Phenology Patterns

The proportion between total BSL and average BSL in each location does not vary in any

consistent way latitudinally (hereafter, both referred as BSL, Figure 3). Low tropical latitudes

(S 10° to N 10°) have longer BSL and IOB is quite variable. Patterns change abruptly in mid

and high latitudes, when BSL and variation in IOB are more or less constant. This leap in

BSL and variation in IOB is less marked in the northern hemisphere, where subtropical

Florida (N 29°) and tropical Jamaica (N 18°) have more variable IOB and longer BSL than

the roughly same latitudes in Brazilian subtropical forest (S 25°) and tropical savannas (S 15°,

S 19°). These southern tropical savannas have roughly similar IOB variation and BSL as

subtropical Atlantic forest (S 25°) and northwestern Argentinian montane forest (S 26°). The set of species in wetlands and semi-arid regions in Argentina at the same latitude have similar BSL (S 34°). Venezuelan savannas (N 7°) and Ecuadorian semi-arid shrublands (S 2°) starts breeding latter than other humid locations at same range of latitude. In temperate South America, however, wetlands and semi-arid Argentina starts breeding at the same time (S 34°), and in North America, the birds in semi-arid scrub in California start earlier than the grassland and woodland birds in Kansas (both N 39°). Dry places in temperate regions in north and south have short IOB variation (California, Texas and Argentina).

Models for predicting BSL

We used a subset of 180 non-cavity nesting species and 225 breeding cycles in the New World to predict BSL, for which all predictor variables were available. In the temperate North America, we used 12 Tyranni and 38 Passeri breeding cycles. In the temperate South America, 25 Tyranni and 30 Passeri. In the tropics, 53 Tyranni and 67 Passeri breeding cycles.

Correlations between latitude and T(mean) are negative and strong in temperate regions where both suborders occur in our dataset (Figure 4). Latitude has stronger positive correlation with T(season) in the temperate South America and tropics. In regions occupied by southern Tyranni, P(month) increases in high latitudes, and those occupied by southern Passeri, P(annual) decreases in high latitudes. No strong correlations ($r > 60$) between climate factors were congruent for both hemispheres in either suborder. Thus, we tested models with all combinations of climate variables for temperate regions. In the tropics, P(annual) is strongly positively correlated with P(month) where Tyranni occurs. Also for tropical Tyranni, T(season) is strongly and negatively correlated with P(annual), and T(season) is strongly and negatively correlated with P(month). Therefore, in the tropics, if eligible models include

strong correlated climate variables simultaneously, these models were disregarded in the analysis with the respective suborder.

In temperate birds, the best climate model (lowest AICc) performed better than the latitudinal model only for Passeri, while climate and latitude models were equivalent for Tyranni (Table 2). Averaged models in temperate regions for both suborders include the hemisphere predictor with the greatest relative importance (Table 3). Interaction terms between climate variables and hemisphere would indicate that climate affects BSL differently in the temperate North and South America for both suborders (Table 3). However, the interactions between hemisphere, T(mean) and P(annual) were unimportant for Tyranni. Also for Tyranni, P(annual) has negligible effect in BSL. Migratory Tyranni might have shorter BSL than residents, but migratory status is the least important factor.

For temperate Passeri, in contrast, T(season), P(month) and their interactions with hemisphere are very important (Table 3). An increase in T(season) causes a decrease in BSL, but the interaction with hemisphere shows that this is true only in North. In temperate South America, BSL is independent of, or negatively correlated with T(season). An increase in P(month) increases BSL in the north, but in the temperate South America P(month) is associated with a decrease in BSL. Migratory Passeri and places with lower P(annual) should have shorter BSL, but these effects have the lowest importance.

In the tropics, latitudinal models are unimportant, and all climate models performed better (Table 2). In Tyranni, only one model with two predictors was selected. T(mean) accounts for 36% of variation in BSL, and P(month) for another 14% (Table 4). Any increase in either or both variables results in longer BSL. BSL is independent of migratory status in tropical Tyranni. In tropical Passeri, P(month) is the best predictor of BSL and the two are positively related. Moreover, both T(season) and migratory status have low importance in BSL. Migratory behavior in Passeri and increase in T(season) might decrease BSL.

The fits from the best climate models in temperate South America for both suborders were poor (Figure 5A and 5B). There, the observed BSL varies by 2.1 months for Tyranni and 3.5 for Passeri, while a variation of 0.3 and 0.7 months was predicted, respectively. On the other hand, in the northern hemisphere the climate model provided a good fit for both suborders. In the tropics, the simpler model for Tyranni ($R^2 = 0.41$) yielded better predictions than the model for Passeri ($R^2 = 0.30$) (Figure 5C and 5D).

DISCUSSION

If latitude were of primary importance in the evolution of clutch size, we would expect that reproductive patterns over latitude would be more or less mirror images in the northern and southern hemispheres due to convergent evolution. Here, with breeding phenologies, we show that this is not the case. The continents are not geographical mirrored images and so, life history patterns are not expected to be equal either.

In addition, the latitudinal paradigm is simplistic because it expects a linear trend in BSL between temperate regions and tropics in each hemisphere. However, the tropics and north temperate regions have phylogenetically distinct avifaunas (Ortega and Arita 1998). For example, Mexico has more bird species with South American origins than from North America (Escalante et al. 1988), thus, part of Mexico, Central America and northern South America should not be included in the latitudinal gradient of the northern hemisphere like previously done (e. g., Ricklefs 1966, 1977). If the tropics are excluded from each hemisphere in analysis (Figure 2C), the latitudinal trend decreases notably for temperate North America, and becomes invalid in the temperate South America, indicating that something more must be responsible for BSL variation.

Surprisingly, climate is more correlated with latitude in south temperate birds, and less in northern birds (Figure 4). Yet, breeding phenologies in temperate South America are

completely independent of latitude. Indeed, the BSL and IOB are relatively constant from temperate to tropical mid latitudes (S 34°to S 15°, Figure 3), and from humid and dry regions. Drier climates in low latitude tropics and in temperate North America, on the other hand, have shorter BSL than elsewhere. In contrast, in arid Australia and Ethiopia, breeding seasons are longer than more humid places at similar latitudes, which was attributed to unpredictable climates causing opportunistic breeding (Wyndham 1986).

Climate models are better alternatives than the latitudinal model in the tropics and for temperate Passeri. Nevertheless, increasing seasonality in temperature and rainfall is associated with increasing, rather than decreasing (as expected) BSL for Passeri from southern hemisphere. If so, perhaps other factors like unpredictable seasonality results in longer BSL, as in for Australia and Ethiopia (Wyndham 1986). In the tropics, migration appears to have little influence in explaining this variation, contrary to expectations. Much of the literature examines or comments on the influence of migratory behavior determining IOB, in comparison to resident species, and assumes that migratory birds are constrained by time to arrive in the breeding grounds, thus should have shorter BSL (Jahn and Cueto 2012, but see Repenning and Fontana 2011).

The low explanatory power of climate models in temperate South America is surprising. Temperate latitudes have more seasonal climates, and so seasonality should play an important role in determination of BSL through temporal constraint of good months for breeding (Martin 1987). As expected, in the northern Passeri, seasonality of temperature and precipitation are strongly associated with BSL. On the other hand, when climate seasonality is not a constraint in BSL (like in the tropics) one should expect less convergence in breeding parameters, and phylogenetic and autecology factors might matter more. However, climate is also very important in tropics in BSL determination. This suggests a simple, but often overlooked explanation; that climate is very diverse within the tropics. This becomes clear as

one looks from seasonal Venezuelan savannas (Cruz and Andrews 1989, Figure 2) and semi-arid Ecuador (Marchant 1959, 1960) to humid forests in Amazonia (Oniki and Willis 1982a, b, 1983a, b) and Costa Rica (Wolfe et al. 2009).

Temperate South American birds have longer BSL than temperate North America birds, but climate should still be seasonal in relation to the tropics. Therefore, we would expect that southern temperate latitudes should have characteristics that lie between these two extremes. Both northern and tropical latitudes have BSL in part explained by climate, and so, why is BSL in temperate South American birds so hard to explain? From the simple latitudinal and continental perspective, from mid to high latitudes in South America, the width of the continent decreases along with continental influence on climate, and marine influences increase, thereby increasing humidity (Jahn and Cueto 2012). Greater humidity towards the south might dampen any clear latitudinal or climate trend in BSL (Jahn and Cueto 2012). An increase in humidity towards higher latitudes is clear in North America if one considers the more arid North American southwest. However, information about timing of breeding in this region is hard to find (in part, due to lack of reporting when describing other aspects of reproduction), and as a consequence, probably inflating the latitudinal trend due to more information from eastern humid mid latitudes, such as Florida and Jamaica (Figure 2).

In temperate South America, constancy in BSL and IOB across latitudes and biomes are combined with local variation in ways that have no clear connection with phylogeny or ecology. For example, breeding parameters in southern Brazilian Atlantic forest birds are quite variable among sympatric species (F. Marques-Santos personal communication). Also, within-latitude combinations of breeding parameters, such as high nest survival, large clutch sizes and long breeding seasons (such as the Saffron finch *Sicalis flaveola*, F. Marques-Santos personal communication), or short breeding seasons and small clutch sizes (Auer et al. 2007) indicate that life histories in these regions are not yet explained.

In temperate western semi-arid and woodlands in Argentina, a study of four years showed that breeding phenologies varied widely between two sympatric Warbling finches and between years. The Ringed Warbling-Finch (*Poospiza torquata*) IOB can vary by 1 month and BSL varied from 0.8 to 3.1 months, while the Cinnamon Warbling-Finch (*Poospiza ornata*) only bred substantially in one year. This was attributed to unpredictable, variable food availability between years (Mezquida and Marone 2003). Great dependence on food availability in breeding seasons is also seen in two bamboo specialists (*Sporophila*) in subtropical Brazil, where they breed upon bamboo flowering, irrespective of time of year (Areta et al. 2013). This pattern could appear to generate a long BSL if records were collated over years, but in fact, within any year, BSL would be short. Higher latitudes in South America have greater inter-annual and intra-seasonal variation in net primary productivity in comparison with temperate North America (due to the El Niño Southern Oscillation (Goetz et al. 2000, Nobre et al. 2006). If this phenomenon often determines timing of breeding by food limitation through climate variation in temperate South America (Jahn and Cueto 2012, Martin 1996), it is quite possible that the El Niño overwhelms any intrinsic ecological of phylogenetic influences on breeding phenologies, and so, small differences in autecology of each species may take each breeding season unique.

In conclusion, latitudinal gradients as explanations for life histories of birds has become outdated and hides much of the existing variation driven by different climates, especially in the extremely variable South American continent. Breeding season length should be better studied as a promising variable for better understanding the evolution of life histories (and reports standardized, a good starting example: Mezquida and Marone 2003). Thus, the extreme species diversity and variable life histories of South American birds are ripe for the picking in future studies. We recommend that detailed within and among season

variation in breeding patterns be examined in the context of local climate variation, to help better understand the evolution of South American life histories of passerine birds.

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Figure 1. Number and location of species samples with breeding season length (BSL) reported in literature in the New World used in this study. Each circle is the number of breeding cycles inside a 1°x 1° coordinate square. Each breeding cycle is calculated using the dates of nests in the breeding season. Each location has one breeding cycle per species in one or more years, in which case the date of nests were lumped across years.

Figure 2. Linear regressions of breeding season length (BSL) across absolute latitudes in northern and southern hemisphere with and without tropical influence in latitudinal gradient. Dots are species. Upper models, A) and B), including all latitudes, with BSL converted to $\log_e$. Vertical aggregation of points is result of multi-species studies at given latitude. C) The latitudinal model is no longer significant in the Southern hemisphere when analyzing temperate regions only.

Figure 3. Breeding phenology of passerines in various locations in the Americas. Circles are average initiation dates of breeding across species (with standard deviation). Light gray bars are the total duration of the breeding season length (*total* BSL) of a local set of species. Dark gray bars are the *average* BSL of individual species (without temporal reference in X-axis). Some locations were nudged by 1° of latitude to prevent overlap.

Figure 4. Significant ($P < 0.05$) and strong ($r > 60$) correlations among latitude and climate variables in locations where non-cavity passerines breed. In temperate regions, A) North: $n = 12$ Tyranni and $n = 38$ Passeri breeding cycles, South: $n = 25$ Tyranni and $n = 30$ Passeri. Tropics B), $n = 53$ Tyranni and $n = 67$ Passeri breeding cycles. Latitude: absolute degrees, T(mean): mean temperature, T(season): temperature seasonality, P(annual): mean annual precipitation, P(month): number of rainy months. For each suborder, if occurred

simultaneously high correlations ($r > 0.6$) in both hemispheres between pairs of climate

variables, these two variables were not used together in the same model.

Figure 5. Climate model fits for prediction of breeding season length (BSL) for non-cavity

passerine nesters in A) temperate Tyranni, B) temperate Passeri in North and South America,

C) tropical Tyranni and D) tropical Passeri. Each graph has a different climate model detailed

in Tables 3 and 4. R^2 values in bold type are from the model to all dataset, and normal type to

temperate North or South America separately.
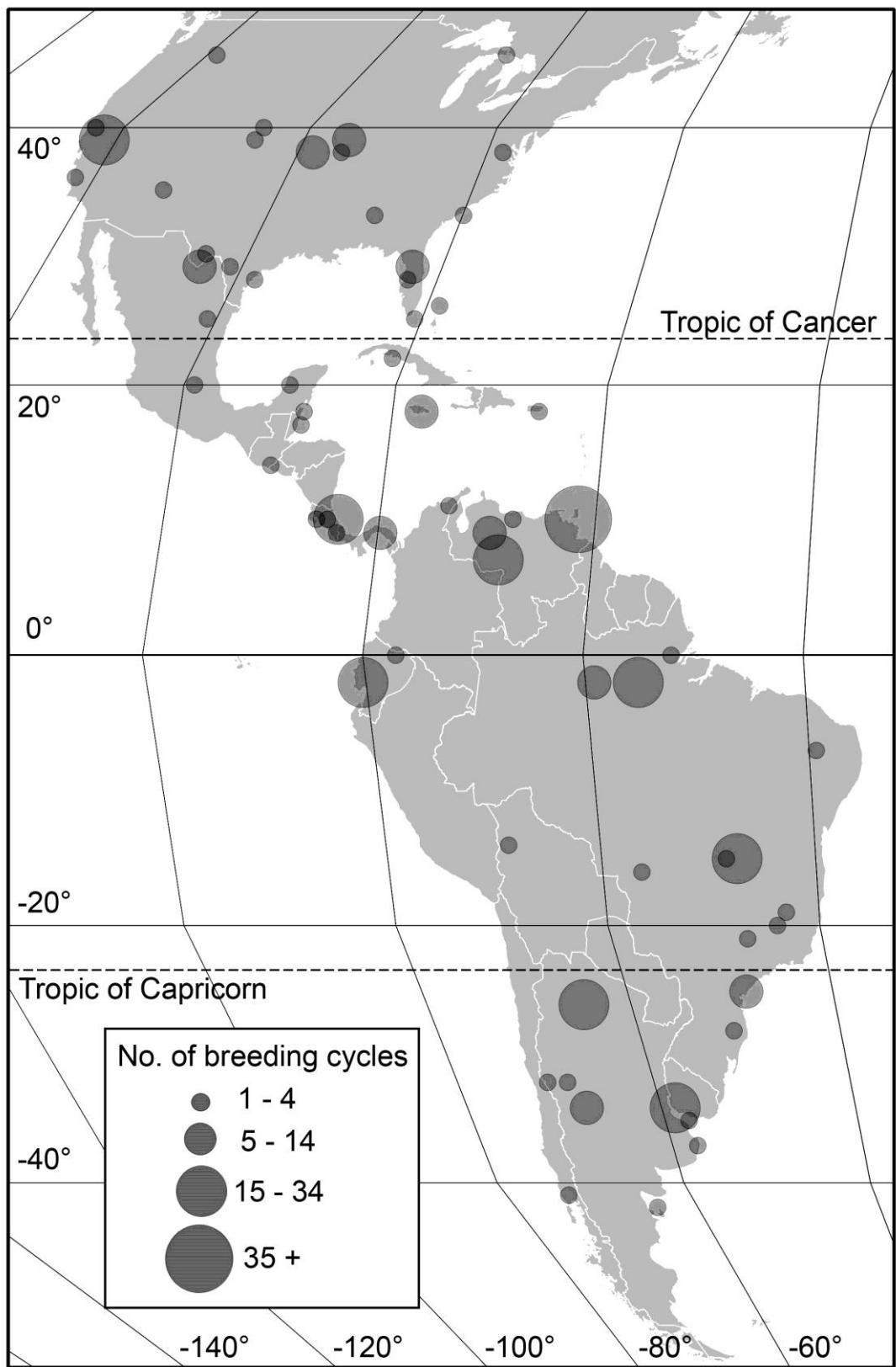
Figure 1.
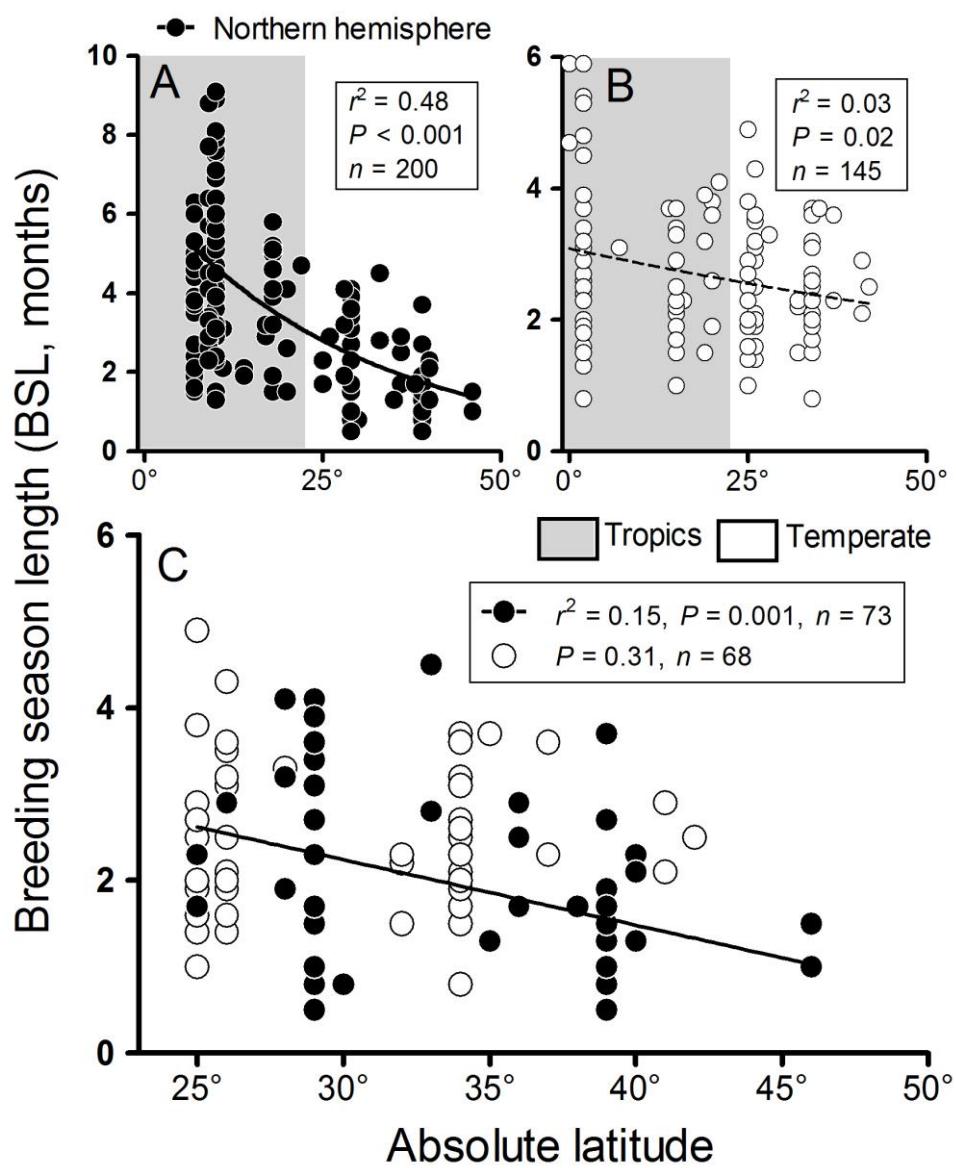
Figure 2.
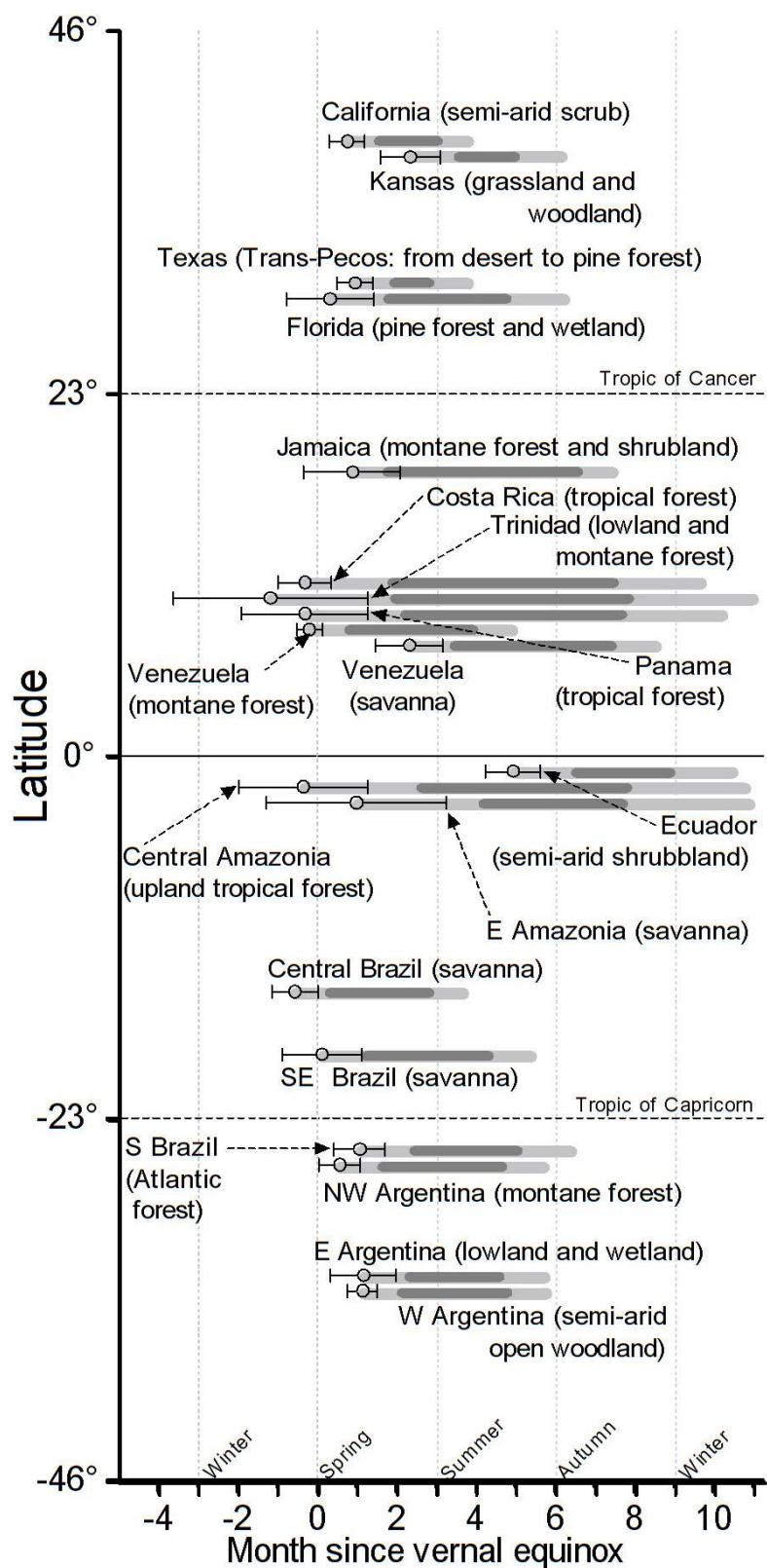
Figure 3.
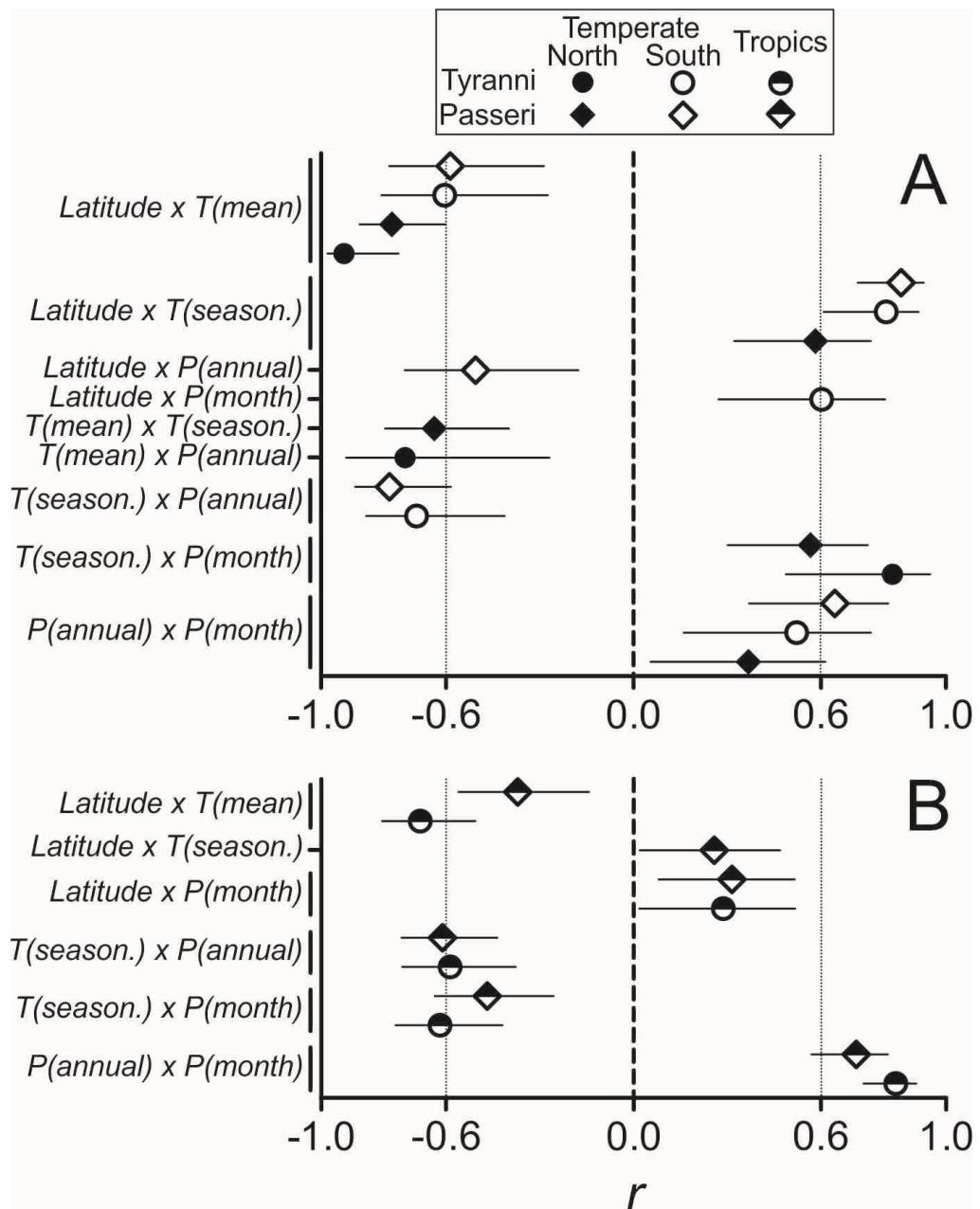
Figure 4.
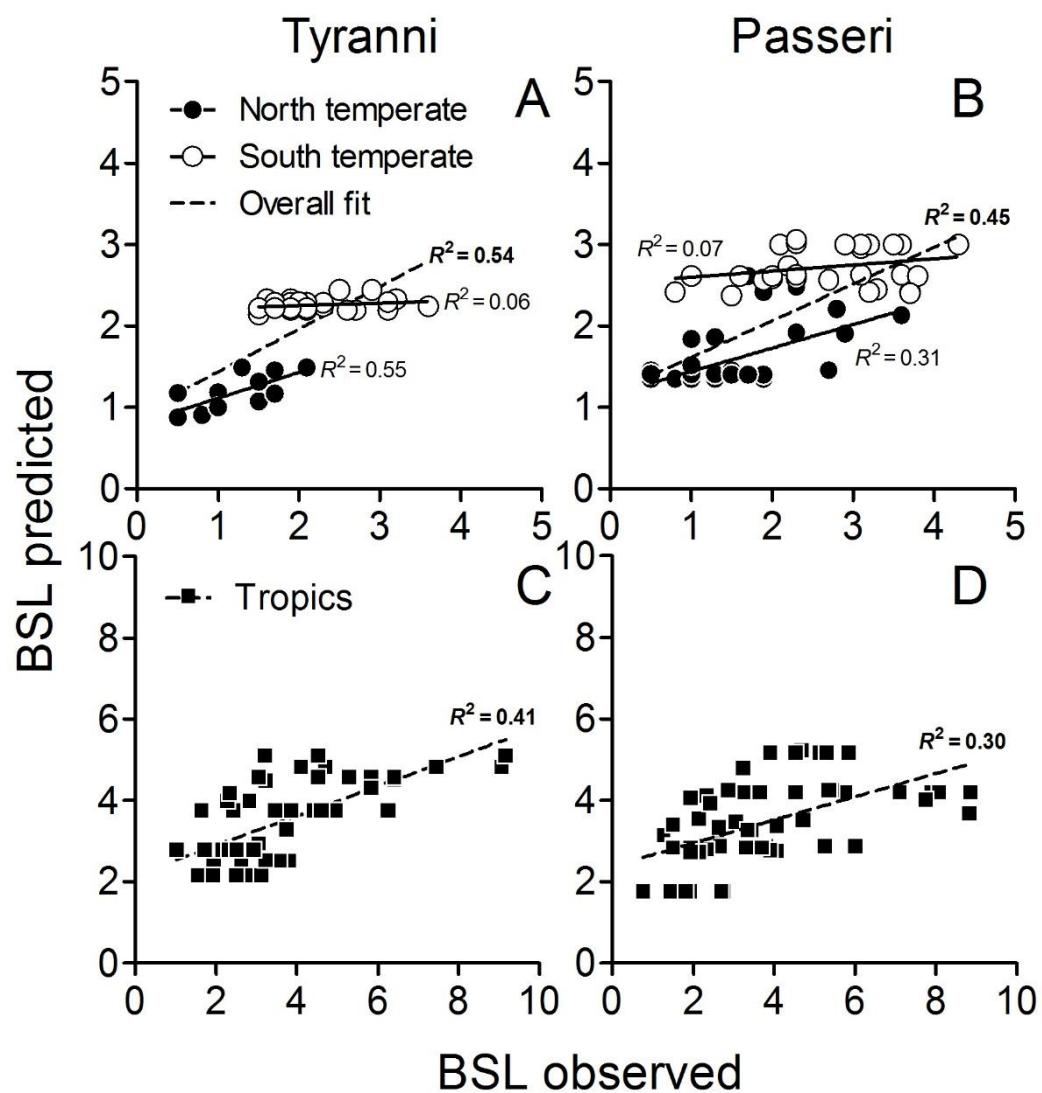
Figure 5.

Table 1. Statistic results for linear models of absolute latitude predicting breeding season length (BSL) across temperate regions in the light of the northern hemisphere paradigm of life histories. Df are numerator and denominator degrees of freedom, respectively. Corresponding graphs in Figure 2C.

Continent (predictor)	R^2 / partial r^2	b	df	F	P
North America (latitude, $\geq 23°$)	0.15	-0.08	1, 71	13.4	0.001
South America (latitude, $\leq -23°$)	0.02	-0.02	1, 66	1.1	0.31
Temperate New World	0.20		3, 137	11.43	< 0.001
(absolute latitude)	0.06	-0.05		11.3	0.001
(hemisphere) N-S	0.04	0.42		6.7	0.01
(absolute latitude x hemisphere)	0.02	0.05		3.4	0.07

Table 2. Model selection results for Tyranni and Passeri in temperate and tropical regions of the Americas. The climate models have averaged parameters and resulting R^2 if more than one model is used (more details in Figure 5). The number of parameters excludes the intercept. Range of ΔAICc for models used in averaging is presented. For more details about the climate models, see Table 3.

Model	Tyranni			Passeri		
	R^2	ΔAICc range	n models (n parameters)	R^2	ΔAICc range	n models (n parameters)
Temperate						
Climate	0.54	0-1.99[a]	9 (8)	0.45	0-1.74[b]	5 (7)
Latitudinal	0.52	1.60	1 (2)	0.39	3.12	1 (2)
Tropics						
Climate	0.41	0[c]	1 (2)	0.30	0-1.94[d]	3 (3)
Latitudinal	0.04	23.47	1 (1)	0.00	30.71	1 (1)

Lowest AICc values: [a] 67.2, [b] 161.62, [c] 47.07, [d] 78.48.

Table 3. Model averaged parameters between climate models to explain the variation in breeding season length (BSL) in temperate North and South America together. *T*(mean): mean annual temperature, *T*(season): temperature seasonality, *P*(annual): mean annual precipitation, *P*(month): months of precipitation, hemisphere: temperate north or south. Migratory status: migratory or resident. Relative importance calculated with Akaike weights (Burnham and Anderson 2002). More details about the models in the text and Table 2.

Tyranni	Relative importance	*b*	SE	*Z*	*P*
Intercept		1.82	0.97	1.9	0.06
Hemisphere (N-S)	1.00	0.37	1.14	0.3	0.75
T(mean)	0.31	-0.09	0.04	2.1	0.03
T(season)	0.41	-0.04	0.03	1.3	0.20
P(annual)	0.28	0.00	0.00	1.4	0.17
Migratory status (M-R)	0.09	0.23	0.76	0.3	0.76
Hemisphere x T(mean)	0.31	0.13	0.06	2.2	0.03
Hemisphere x P(annual)	0.11	0.00	0.00	1.4	0.17
T(season) x Migratory status	0.27	-0.11	0.06	1.8	0.08
Passeri	**Relative importance**	***b***	**SE**	***Z***	***P***
Intercept		0.60	0.79	0.7	0.46
Hemisphere (N-S)	1.00	3.70	1.28	2.8	0.005
T(season)	1.00	-0.09	0.03	2.7	0.008
P(annual)	0.17	0.00	0.00	1.1	0.26
P(month)	1.00	0.26	0.10	2.6	0.01
Migratory status (M-R)	0.26	0.18	0.20	0.9	0.37
Hemisphere x *T*(season)	0.40	0.11	0.08	1.5	0.14
Hemisphere x *P*(month)	1.00	-0.38	0.13	2.9	0.003

Table 4. Model averaged parameters between climate models to explain the variation in breeding season length (BSL) in the tropical America. More details about the models and parameters in the text, Table 2 and 3.

Tyranni	Partial r^2	b	SE	t	P
Intercept		-1.42	0.57	-2.5	0.02
T(mean.)	0.36	0.14	0.03	5.3	0.005
P(month)	0.14	0.06	0.02	2.9	< 0.001

Passeri	Relative importance	b	SE	Z	P
Intercept		-0.31	0.29	1.0	0.30
T(season)	0.23	-0.04	0.06	0.7	0.51
P(month)	1.00	0.17	0.03	5.8	< 0.001
Migratory status (M-R)	0.21	0.09	0.16	0.5	0.59

SUPPLEMENTARY MATERIAL

Table S1. Species and references cited in this study. P. ref.: bibliography with breeding cycle information (if boldface, used in model selection). N. ref.: bibliography for nest type (if **P**, the citation was the same from P. ref.). MS ref.: bibliography from migratory status.

Taxa (and species common name)	P. ref.	N. ref.	MS ref.
Tyranni			
Thamnophilidae			
Gymnopithys leucaspis (Bicolored Antbird)	93		
Gymnopithys rufigula (Rufous-throated Antbird)	**63**	**P**	d
Hylophylax naevius (Spot-backed Antbird)	93		
Myrmeciza exsul (Chestnut-backed Antbird)	**94**	v	v
Percnostola rufifrons (Black-headed Antbird)	**65**	s	d
Sakesphorus bernardi (Collared Antshrike)	**41**	q	d
Taraba major (Great Antshrike)	**36**	**P**	v
Thamnophilus atrinucha (Black-crowned Antshrike)	**74, 94**	v	v
Thamnophilus doliatus (Barred Antshrike)	**86, 94**	v	v
Willisornis poecilinotus (Scale-backed Antbird)	**65**	v	v
Conopophagidae			
Conopophaga lineata (Rufous Gnateater)	**42**	l	v
Conopophaga melanops (Black-cheeked Gnateater)	**38**	**P**	**P**
Grallariidae			
Grallaricula ferrugineipectus (Rusty-breasted Antpitta)	**61**	**P**	v
Dendrocolaptidae			
Dendrocincla fuliginosa (Plain-brown Woodcreeper)	**64, 86**	g	v
Dendrocolaptes sanctithomae (Northern Barred-Woodcreeper)	**94**	v	v
Lepidocolaptes angustirostris (Narrow-billed Woodcreeper)	**43**	l	v
Lepidocolaptes souleyetii (Streak-headed Woodcreeper)	94		
Xiphorhynchus guttatus (Buff-throated Woodcreeper)	**86**	g	v
Furnariidae			
Anumbius annumbi (Firewood-gatherer)	**50**	v	v
Aphrastura spinicauda (Thorn-tailed Rayadito)	**57**	**P**	v
Certhiaxis cinnamomeus (Yellow-chinned Spinetail)	**17**	v	v
Furnarius rufus (Rufous Hornero)	**50**	l	l
Hylocryptus rectirostris (Chestnut-capped Foliage-gleaner)	**23**	g	d
Phacellodomus striaticollis (Freckle-breasted Thornbird)	**50**	v	v
Phleocryptes melanops (Wren-like Rushbird)	**50**	g	g
Spartonoica maluroides (Bay-capped Wren-Spinetail)	**14**	**P**	**P**
Synallaxis albescens (Pale-breasted Spinetail)	**17, 45**	v	d
Syndactyla rufosuperciliata (Buff-browed Foliage-gleaner)	**8**	**P**	d

Rhynchocyclidae

Hemitriccus striaticollis (Stripe-necked Tody-Tyrant)	78		
Leptopogon superciliaris (Slaty-capped Flycatcher)	86		
Mionectes macconnelli (McConnell's Flycatcher)	**66**	s	d
Mionectes oleagineus (Ochre-bellied Flycatcher)	**86, 94**	g	d
Mionectes rufiventris (Gray-hooded Flycatcher)	**2**	**P**	d
Phylloscartes ventralis (Mottle-cheeked Tyrannulet)	**8, 46**	l	l
Tolmomyias flaviventris (Yellow-breasted Flycatcher)	86		
Tolmomyias sulphurescens (Yellow-olive Flycatcher)	**5**, 86	g	v

Tyrannidae

Arundinicola leucocephala (White-headed Marsh-Tyrant)	**17**, 86	g	v
Camptostoma obsoletum (Southern Beardless-Tyrannulet)	**41, 43**, 86	q	v
Contopus cinereus (Tropical Pewee)	86		
Elaenia chiriquensis (Lesser Elaenia)	**51**, 78	51	51
Elaenia cristata (Plain-crested Elaenia)	78		
Elaenia flavogaster (Yellow-bellied Elaenia)	78		
Elaenia parvirostris (Small-billed Elaenia)	**8**	l	z
Elaenia strepera (Slaty Elaenia)	**8**	**P**	v
Empidonax difficilis (Western Flycatcher)	**19, 76**	t	t
Empidonax hammondii (Hammond's Flycatcher)	**76**	t	t
Empidonax traillii (Willow Flycatcher)	**35**	t	t
Empidonomus aurantioatrocristatus (Crowned Slaty Flycatcher)	**43, 52**	v	v
Empidonomus varius (Variegated Flycatcher)	78		
Euscarthmus meloryphus (Tawny-crowned Pygmy-Tyrant)	**41**	q	v
Fluvicola pica (Pied Water-Tyrant)	86, **17**	i	v
Hymenops perspicillatus (Spectacled Tyrant)	**70**	**P**	d
Lathrotriccus euleri (Euler's Flycatcher)	**1, 8**, 86	l	z
Machetornis rixosa (Cattle Tyrant)	**17**	g	v
Megarynchus pitangua (Boat-billed Flycatcher)	78, 86		
Muscigralla brevicauda (Short-tailed Field Tyrant)	**41**	v	v
Myiarchus ferox (Short-crested Flycatcher)	78		
Myiarchus swainsoni (Swainson's Flycatcher)	**43**	**P**	l
Myiarchus tyrannulus (Brown-crested Flycatcher)	78		
Myiodynastes maculatus (Streaked Flycatcher)	86		
Myiopagis gaimardii (Forest Elaenia)	86		
Myiophobus fasciatus (Bran-colored Flycatcher)	86		
Myiozetetes cayanensis (Rusty-margined Flycatcher)	**17**, 78	g	v
Phaeomyias murina (Mouse-colored Tyrannulet)	**41**	q	q
Pitangus lictor (Lesser Kiskadee)	**17**	v	d
Pitangus sulphuratus (Great Kiskadee)	**17, 50**, 78	k	l
Platyrinchus mystaceus (White-throated Spadebill)	86		
Poecilotriccus plumbeiceps (Ochre-faced Tody-Flycatcher)	**8**	**P**	d
Polystictus superciliaris (Gray-backed Tachuri)	**32**	**P**	d

Pseudelaenia leucospodia (Gray-and-white Tyrannulet)	**41**	q	d
Pyrocephalus rubinus (Vermilion Flycatcher)	**17, 41, 50, 52, 90**	k	z
Satrapa icterophrys (Yellow-browed Tyrant)	**50**	g	v
Sayornis nigricans (Black Phoebe)	**20, 90**	k	t
Sayornis phoebe (Black Phoebe)	**39**	t	t
Sayornis saya (Say's Phoebe)	**62, 90**	t	62
Serpophaga munda (White-bellied Tyrannulet)	**54**	**P**	v
Stigmatura budytoides (Greater Wagtail-Tyrant)	**52**	**P**	v
Sublegatus modestus (Southern Scrub-Flycatcher)	**52**	**P**	z
Suiriri affinis (Campo Suiriri)	**40**	**P**	**P**
Suiriri islerorum (Chapada Flycatcher)	**40**	**P**	**P**
Suiriri suiriri (Suiriri Flycatcher)	**43**, 78	g	d
Todirostrum cinereum (Common Tody-Flycatcher)	**17**	g	v
Tyrannus dominicensis (Gray Kingbird)	**17**	t	t
Tyrannus melancholicus (Tropical Kingbird)	**17**	k	v
Tyrannus niveigularis (Snowy-throated Kingbird)	**41**	q	d
Tyrannus savana (Fork-tailed Flycatcher)	**44, 50, 52, 88**	l	l
Tyrannus tyrannus (Eastern Kingbird)	**60**	t	t
Tyrannus verticalis (Western Kingbird)	**20**	k	**P**
Xolmis coronatus (Black-crowned Monjita)	**52**	**P**	d
Xolmis pyrope (Fire-eyed Diucon)	**37**	v	v
Zimmerius chrysops (Golden-faced Tyrannulet)	**29**	**P**	d
Pipridae			
Antilophia bokermanni (Araripe Manakin)	**28**	g	g
Manacus candei (White-collared Manakin)	**94**	v	v
Manacus manacus (White-bearded Manakin)	78, **86**	v	v
Manacus vitellinus (Golden-collared Manakin)	93		
Pipra erythrocephala (Golden-headed Manakin)	**86**	v	v
Pipra mentalis (Red-capped Manakin)	93, **94**	v	v
Cotingidae			
Phibalura flavirostris (Swallow-tailed Cotinga)	**9**	e	v
Passeri			
Laniidae			
Lanius ludovicianus (Loggerhead Shrike)	10		
Vireonidae			
Cyclarhis gujanensis (Rufous-browed Peppershrike)	**43**, 78, **86**	l	l
Hylophilus decurtatus (Lesser Greenlet)	**94**	v	d
Vireo atricapilla (Black-capped Vireo)	**83**	k	**P**
Vireo griseus (White-eyed Vireo)	10		
Vireo latimeri (Puerto Rican Vireo)	**89**	**P**	d
Vireo modestus (Jamaican Vireo)	21		
Vireo olivaceus (Red-eyed Vireo)	**39, 41, 86**	k	l
Corvidae			
Aphelocoma californica (Scrub Jay)	**20**	t	t
Aphelocoma wollweberi (Mexican Jay)	90		
Corvus brachyrhynchos (American Crow)	**39**	t	t

Corvus caurinus (Northwestern Crow)	**20**	t	t
Cyanocitta cristata (Blue Jay)	**10, 39**	t	t
Cyanocorax cristatellus (Curl-crested Jay)	**43**	**P**	v
Gymnorhinus cyanocephalus (Pinyon Jay)	**49**	k	t
Pica nuttalli (Yellow-billed Magpie)	**20**	k	t
Sittidae			
Sitta pusilla (Brown-headed Nuthatch)	10		
Remizidae			
Auriparus flaviceps (Verdin)	**90**	t	t
Paridae			
Baeolophus bicolor (Tufted Titmouse)	10		
Baeolophus inornatus (Oak Titmouse)	**20**	t	t
Poecile carolinensis (Carolina Chickadee)	10		
Poecile atricapillus (Black-capped Chickadee)	**39**	t	t
Aegithalidae			
Psaltriparus minimus (Bushtit)	**20**	k	v
Hirundinidae			
Hirundo rustica (Barn Swallow)	**20**	t	t
Petrochelidon fulva (Cave Swallow)	**68**	t	t
Progne chalybea (Gray-breasted Martin)	86		
Pygochelidon cyanoleuca (Blue-and-white Swallow)	**46**	l	l
Stelgidopteryx ruficollis (Southern Rough-winged Swallow)	86		
Tachycineta bicolor (Tree Swallow)	**56**	x	**P**
Tachycineta cyaneoviridis (Bahama Swallow)	4		
Tachycineta leucorrhoa (White-rumped Swallow)	**46, 50**	l	l
Troglodytidae			
Campylorhynchus brunneicapillus (Cactus Wren)	**27**	k	t
Campylorhynchus yucatanicus (Yucatan Wren)	**91**	**P**	v
Cantorchilus leucotis (Buff-breasted Wren)	**3**	**P**	v
Cantorchilus nigricapillus (Bay Wren)	**94**	v	v
Catherpes mexicanus (Canyon Wren)	**34**	k	t
Cyphorhinus phaeocephalus (Song Wren)	**71**, 93	v	**P**
Pheugopedius rutilus (Rufous-breasted Wren)	86		
Thryophilus rufalbus (Rufous-and-white Wren)	**3**	**P**	d
Thryothorus ludovicianus (Carolina Wren)	10		
Thryothorus superciliaris (Superciliated Wren)	**41**	q	d
Thryothorus ludovicianus (Carolina Wren)	**39**	t	t
Troglodytes aedon (House Wren)	**8, 33, 41, 46, 50, 86, 95**	l	w
Polioptilidae			
Polioptila melanura (Black-tailed Gnatcatcher)	**90**	t	t
Polioptila plumbea (Tropical Gnatcatcher)	41		
Ramphocaenus melanurus (Long-billed Gnatwren)	86		
Turdidae			
Catharus dryas (Spotted Nightingale-Thrush)	**8**	**P**	v

Catharus occidentalis (Russet Nightingale-Thrush)	**82**	v	v
Hylocichla mustelina (Wood Trush)	**39**	t	t
Myadestes genibarbis (Rufous-throated Solitaire)	21		
Sialia sialis (Eastern Bluebird)	10, **39, 92**	t	t
Turdus albicollis (White-necked Thrush)	**85**	g	d
Turdus amaurochalinus (Creamy-bellied Thrush)	**7, 43, 46**	l	z
Turdus fumigatus (Cocoa Thrush)	**85**	g	d
Turdus grayi (Clay-colored Thrush)	93		
Turdus jamaicensis (White-eyed Thrush)	21		
Turdus leucomelas (Pale-breasted Thrush)	**42, 43**, 78	g	v
Turdus leucops (Pale-eyed Thrush)	**31**	**P**	d
Turdus nigriceps (Slaty Thrush)	**8**	**P**	d
Turdus nudigenis (Spectacled Thrush)	**85**	h	v
Turdus rufiventris (Rufous-bellied Thrush)	**8, 46, 50**	l	l
Turdus migratorius (American Robin)	**39**	t	t
Mimidae			
Melanoptila glabrirostris (Black Catbird)	**58**	**P**	**P**
Melanotis hypoleucus (Blue-and-white Mockingbird)	**82**	v	v
Mimus gilvus (Tropical Mockingbird)	86		
Mimus longicaudatus (Long-tailed Mockingbird)	41		
Mimus polyglottos (Northern Mockingbird)	10		
Mimus saturninus (Chalk-browed Mockingbird)	**50, 72**	g	**P**
Toxostoma curvirostre (Curve-billed Thrasher)	**24**	k	d
Toxostoma longirostre (Long-billed Thrasher)	**24**	k	d
Toxostoma rufum (Brown Trasher)	**39**	t	t
Motacillidae			
Anthus furcatus (Short-billed Pipit)	6		
Thraupidae			
Cypsnagra hirundinacea (White-rumped Tanager)	**79**	n	v
Habia fuscicauda (Red-throated Ant-Tanager)	**94**	n	v
Habia rubica (Red-crowned Ant-Tanager)	86		
Neothraupis fasciata (White-banded Tanager)	**22**	n	d
Paroaria gularis (Red-capped Cardinal)	78		
Ramphocelus carbo (Silver-beaked Tanager)	**67, 86**	g	v
Ramphocelus passerinii (Passerini's Tanager)	**94**	v	v
Saltator coerulescens (Grayish Saltator)	86		
Saltatricula multicolor (Many-colored Chaco Finch)	**53**	**P**	d
Schistochlamys melanopis (Black-faced Tanager)	78		
Spindalis zena (Western Spindalis)	21		
Tachyphonus rufus (White-lined Tanager)	**86**	v	v
Tangara cayana (Burnished-buff Tanager)	78		
Tangara palmarum (Palm Tanager)	**67, 86**	n	v
Thraupis episcopus (Blue-gray Tanager)	**67**, 78, **86**, 93, **94**	p	v
Cardinalidae			
Cardinalis cardinalis (Northern Cardinal)	10, **39**	t	t
Paroaria coronata (Red-crested Cardinal)	**81**	**P**	v

Passerina cyanea (Indigo Bunting)	**39**	t	t
Spiza americana (Dickcissel)	**39**	t	t
Emberizidae			
Ammodramus aurifrons (Yellow-browed Sparrow)	**17**	g	v
Ammodramus humeralis (Grassland Sparrow)	**17**	g	v
Ammodramus maritimus (Seaside Sparrow)	**12**	k	**P**
Arremon flavirostris (Saffron-billed Sparrow)	**8**	**P**	v
Arremon torquatus (White-browed Brush-Finch)	**8**	**P**	d
Arremonops conirostris (Black-striped Sparrow)	**94**	a	v
Atlapetes semirufus (Ochre-breasted Brush-Finch)	**47**	**P**	v
Chondestes grammacus (Lark Sparrow)	**20**	t	t
Diuca diuca (Common Diuca-Finch)	**37, 53**	53	z
Euneornis campestris (Orangequit)	21		
Loxigilla violacea (Greater Antillean Bullfinch)	21		
Loxipasser anoxanthus (ellow-shouldered Grassquit)	21		
Melozone fusca (Canyon Towhee)	**20**	t	t
Oryzoborus funereus (Thick-billed Seed-Finch)	**94**	v	d
Pipilo erythrophthalmus (Rufous-sided Towhee)	10, 18		
Poospiza hispaniolensis (Collared Warbling-Finch)	**41**	q	d
Poospiza ornata (Cinnamon Warbling-Finch)	**55**	**P**	**P**
Poospiza torquata (Ringed Warbling-Finch)	**55**	**P**	**P**
Rhodospingus cruentus (Crimson-breasted Finch)	**41**	q	d
Sicalis citrina (Stripe-tailed Yellow-Finch)	**30**	**P**	**P**
Sicalis flaveola (Saffron Finch)	**17, 46, 50**	l	l
Spizella wortheni (Worthen's Sparrow)	**13**	c	v
Sporophila caerulescens (Double-collared Seedeater)	**25, 46**	l	l
Sporophila corvina (Variable Seedeater)	94		
Sporophila hypoxantha (Tawny-bellied Seedeater)	**26**	**P**	**P**
Sporophila intermedia (Gray Seedeater)	**17**	u	v
Sporophila peruviana (Parrot-billed Seedeater)	**41**	q	d
Sporophila telasco (Chestnut-throated Seedeater)	**41**	q	v
Volatinia jacarina (Blue-black Grassquit)	**41**, 86	v	z
Zonotrichia capensis (Rufous-collared Sparrow)	**8, 37, 46, 50**	l	l
Coerebidae			
Coereba flaveola (Bananaquit)	**17**, 21, **82, 86**	l	w
Parulidae			
Basileuterus bivittatus (Two-banded Warbler)	**8**	**P**	v
Basileuterus culicivorus (Golden-crowned Warbler)	**46**, 86	l	l
Basileuterus leucoblepharus (White-browed Warbler)	**46**	l	l
Basileuterus signatus (Pale-legged Warbler)	**8**	**P**	d
Basileuterus tristriatus (Three-striped Warbler)	**16**	**P**	**P**
Dendroica petechia (Yellow Warbler)	**77**	j	**P**
Geothlypis aequinoctialis (Masked Yellowthroat)	**8**	**P**	v
Geothlypis poliocephala (Gray-crowned Yellowthroat)	**48**	j	d
Icteria virens (Yellow-breasted Chat)	**39**	t	t
Limnothlypis swainsonii (Swainson's Warbler)	**11**	**P**	**P**

Myioborus brunniceps (Brown-capped Redstart)	**8**	**P**	v
Myioborus miniatus (Slate-throated Redstart)	**15, 59, 75**	v	**P**
Setophaga ruticilla (American Redstart)	**84**	j	**P**
Icteridae			
Agelaioides badius (Bay-winged Cowbird)	**50**	g	o
Agelaius phoeniceus (Red-winged Blackbird)	10, **20**	t	20
Agelaius tricolor (Tricolored Blackbird)	**20**	k	o
Cacicus cela (Yellow-rumped Cacique)	17, 86		
Chrysomus icterocephalus (Yellow-hooded Blackbird)	86		
Euphagus cyanocephalus (Brewer's Blackbird)	**20**	o	t
Gymnomystax mexicanus (Oriole Blackbird)	**17**	y	v
Icterus nigrogularis (Yellow Oriole)	**17**	v	v
Molothrus ater (Brown-headed Cowbird)	20		
Molothrus bonariensis (Shiny Cowbird)	17, 86		
Molothrus oryzivorus (Giant Cowbird)	86		
Psarocolius decumanus (Crested Oropendola)	78, 86		
Psarocolius montezuma (Montezuma Oropendola)	87		
Quiscalus lugubris (Carib Grackle)	**17**, 86	o	d
Quiscalus major (Boat-tailed Grackle)	10		
Sturnella militaris (Red-breasted Blackbird)	**17, 41**	g	d
Sturnella neglecta (Western Meadowlark)	**20**	k	o
Fringillidae			
Carduelis psaltria (Lesser Goldfinch)	**69**	k	**P**
Carduelis tristis (American Goldfinch)	**20**	k	**P**
Carpodacus mexicanus (House Finch)	**20**	k	t
Euphonia jamaica (Jamaican Euphonia)	21		
Sporagra magellanica (Hooded Siskin)	**50, 53**	l	v
Sylviidae			
Polioptila caerulea (Blue-grey Gnatcatcher)	**20, 73**	k	**P**
Passeridae			
Passer domesticus (House Sparrow)	**80**	k	**P**

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4 CONSIDERAÇÕES FINAIS

No capítulo 2, reportamos informações reprodutivas de dezenas de aves de uma região subtropical de Mata Atlântica que podem ser relevantes em vários níveis. No mais básico, os padrões reprodutivos observados nos permitiram apontar algumas espécies que são potencialmente incongruentes com a teoria de história de vida vigente, e, portanto, devem ser melhor investigadas no futuro. Nossas informações permitiram ainda a comparação com parâmetros reprodutivos de uma comunidade em outra região subtropical na Argentina. Ambas regiões apresentam espécies com algumas características reprodutivas tropicais e outras temperadas. Por exemplo, os tamanhos de ninhada, em média, são pequenos em relação aos estudos em latitudes similares no hemisfério norte, enquanto que a duração dos ciclos é relativamente curta. Mesmo assim, pudemos observar grande variação nesses dois parâmetros (ninhadas de 2 a 5 ovos, ciclos de algumas semanas até 5 meses). Finalizamos o capítulo com um série de perguntas, como, por exemplo: por que algumas espécies (e. g., *Sicalis flaveola*) reproduzem tão extensivamente, mesmo com alta sobrevivência de ninhos? Ao mesmo tempo, outras espécies (e.g., *Troglodytes aedon*, gênero *Basileuterus*) possuem ciclos demasiadamente curtos, com apenas uma ou duas tentativas reprodutivas por casal, encerrando qualquer evidência reprodutiva no fim da primavera, mesmo com longa temporada chuvosa e com altas temperaturas de verão pela frente. As informações desse capítulo ainda foram úteis no desenvolvimento do capítulo 3, e tem potencial para serem utilizadas em modelos e simulações para o entendimento dos mecanismos que governam as histórias de vida (como em Roper et al. 2010).

Em vista das incongruências observadas nos parâmetros reprodutivos do capítulo 2, e da existência de uma lacuna na síntese das fenologias reprodutivas no Novo Mundo, o capítulo 3 fornece pontos importantes. O primeiro, que as fenologias no Neotrópico, em qualquer latitude, podem ser sazonais, ao contrário do que previa a teoria. Em segundo lugar, que as regiões temperadas do sul diferem dos trópicos e do Neártico, pois locais com regimes climáticos diferentes possuem fenologias similares. Em qualquer parte do mundo, e ainda mais na região tropical sul, há grande variação local nas fenologias, não facilmente explicada por *status* migratório (capitulo 3), ou outras características ecológicas ou filogenia (discussão, capítulo 2). É possível que variação interanual imprevisível do clima seja responsável pela diversidade de fenologias no temperado sul, que oculte as diferenças intrínsecas entre as espécies.

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