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A migração de aves na América do Sul: fatores ecológicos que determinam a distribuição e a reprodução de tiranídeos migratórios na região

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Tese apresentada à Comissão Examinadora de Doutorado do Programa de Pós-graduação em Ecologia da Universidade de Brasília para a obtenção do título de Doutora em Ecologia.

Orientador: Prof. Dr. Miguel Ângelo Marini

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Quando não souberes para onde ir,

Olha para trás e saiba pelo menos

De onde vens

(provérbio africano em *Um Defeito de Cor*,
de Ana Maria Gonçalves)

à minha mãe, Emaculada, ao meu pai, Aluísio,

ao meu irmão, Nityan, às minhas irmãs, Rammana e Elana,

aos meus sobrinhos, João Lucas e Ravi,

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RESUMO

A migração de aves é um fenômeno que há muitas décadas tem sido objeto de grande interesse da comunidade científica. A maioria das pesquisas foi por muito tempo focada em um conjunto limitado de sistemas migratórios e de espécies, com ênfase nos sistemas de climas temperados do Hemisfério Norte. Somente no final do século XX, a grande diversidade de padrões e comportamentos migratórios entre aves que migram e que se reproduzem na região Neotropical foi evidenciada. Porém, lacunas de conhecimento importante sobre a ecologia da migração dessas espécies continuam em aberto. A comparação de estratégias migratórias entre espécies derivadas de um mesmo ancestral comum tem se mostrado uma oportunidade única para se avaliar o valor adaptativo da migração. A família Tyrannidae mostra-se como um modelo bastante adequado para estudos comparativos, pois possui espécies de ampla distribuição e abundância no Novo Mundo e representam a família com maior diversidade de espécies migratórias na região Neotropical, além de apresentar comportamento migratório variado e complexo. Nesse contexto, esta Tese de Doutorado visa aprofundar o conhecimento científico sobre os fatores que determinam a migração de aves na região Neotropical, com foco na família Tyrannidae e nas espécies que se reproduzem na América do Sul. Discutirei a tese de que a migração de tiranídeos na América do Sul é determinada pela variação sazonal na competição, e não pela variação sazonal do clima, e que as espécies estudadas se beneficiam do adicional de recursos disponíveis nos sítios reprodutivos, mesmo quando investem mais na migração (i.e., distância de migração). Para tanto, esta Tese está dividida nos seguintes capítulos: 1) Variação sazonal na competição e não produtividade ecológica determinam a migração austral de tiranídeos (*Seasonal variation in competition and not ecological productivity drives the austral migration of tyrant flycatchers*); 2) Tamanho de ninhada associa-se com distância de migração em aves terrestres na América do Sul (*Clutch size associates with migration distance in South American land birds*); e 3) Variação sazonal na competição afeta o tamanho da ninhada e do ovo em aves migratórias terrestre da América do Sul (*Seasonal variation in competition affects clutch and egg size in migratory South American land birds*).

Palavras-chave: competição interespecífica, competição intraespecífica, *green wave hypothesis*, história de vida, migração austral, migração sazonal, tamanho de ninhada, tamanho de ovo, Tyrannidae.

ABSTRACT

Bird migrations are a phenomenon that has long been subject of great interest in the scientific community. Mostly, research has been focused on a limited set of migratory systems and species, with an emphasis on migratory systems in the Northern Hemisphere. Only at the end of the 20th century did the diversity of migratory patterns and behaviors among species that breed and migrate in the Neotropical region begin to be appreciated. However, significant knowledge gaps about the migration ecology of these species still remain. The comparison of migratory strategies among species derived from the same common ancestor holds a unique opportunity to assess the adaptive value of migrations. The Tyrannidae family is an ideal model for studies on migration ecology because it is widely distributed and abundant across most of the New World, represents the family with the greatest diversity of migratory species in the Neotropical region, and exhibits varied and complex migratory patterns. In this context, this thesis aims to deepen the scientific knowledge about the factors that determine the migration of birds in the Neotropical region, focusing on the Tyrannidae family and on species that breed in South America. The thesis defended here is that the migration of tyrant flycatchers in South America is primary driven by seasonality in competition, not by seasonality in climate, and that species benefit from the surplus in the resources available at the breeding grounds, even when they invest more in migration (i.e., migratory distance). In this context, this thesis is based on the following chapters: 1) *Seasonal variation in competition and not ecological productivity drives the austral migration of tyrant flycatchers;* 2) *Clutch size associates with migration distance in South American land birds*; e 3) *Seasonal variation in competition affects clutch and egg size in migratory South American land birds*.

Keywords: austral migration, clutch size, egg size, green wave hypothesis, inter-specific competition, intra-specific competition, life history, seasonal bird migration, Tyrannidae.

SUMÁRIO

INTRODUÇÃO GERAL

O que é a migração animal

A migração animal é um fenômeno comum e diverso, que envolve movimentos de indivíduos entre diferentes áreas geográficas (Berthold, 1993; Dingle & Drake, 2007). É comumente, e primariamente, definida como movimentos populacionais regulares de ida e volta em períodos do ano específicos e, em geral, para destinos que se repetem ano após ano (Berthold, 1993). Porém, essa definição não abrange toda a complexidade da migração, pois a migração não consiste em um padrão único de movimentação e não está restrita a processos ecológicos de populações específicas, podendo abranger também uma escala comportamental individual (Dingle, 2006). Nesse sentido, a migração pode ser entendida como sendo uma adaptação, individual ou populacional, ao uso de recursos que variam no tempo e no espaço, de forma previsível (i.e., sazonal) ou não (Dingle & Drake, 2007). Salvo essas variações, a migração é uma síndrome que possui diversos aspectos em comum entre os diferentes táxons (Dingle, 2006). Isso porque, a migração influencia de forma significativa a dinâmica espacial das populações (Somveille *et al.*, 2013) e possibilita que os organismos otimizem seu balanço energético, valendo-se das variações desses recursos ao mesmo tempo que leva em conta os custos impostos pela jornada migratória (Somveille *et al.*, 2018, 2019).

Esta Tese tem o intuito de abordar a *migração* segundo esse conceito, mas me limitarei àqueles movimentos que resultam em mudanças sazonais na área de distribuição dos organismos, geralmente entre um sítio reprodutivo e um não-reprodutivo (ou de invernagem). Esse conceito se diferencia de outros movimentos populacionais, como a *dispersão*, *irrupção* e o *nomadismo* e *vagância*, sobre os quais darei uma visão geral, em razão da diversidade de conceitos relacionados ao tema. A *dispersão* se dá em indivíduos que tenham alcançado a maturidade e envolve mudança ativa de sua localização. É mais comum entre indivíduos jovens e possui distâncias variáveis. Movimentos dispersivos são diferenciados entre *dispersão natal* - quando por fatores endógenos um indivíduo dispersa de seu local de nascimento algumas semanas ou meses após a independência dos pais, geralmente para área não muito distante; e *dispersão na fase adulta* (ou "*spacing*") –

controlada por fatores externos, principalmente como resultado da competição por territórios, fator dependente da densidade populacional da espécie. A *irrupção* é caracterizada quando grande número de indivíduos, jovens e adultos, de uma população deixa seus locais de reprodução em determinados anos, de maneira imprevisível, para outras áreas. As irrupções coincidem com a baixa disponibilidade de alimento na área de reprodução e com altas densidades populacionais e, muitas vezes, ocorrem em populações que se reproduzem em locais cuja disponibilidade de recursos é imprevisível entre anos e estações. Já o *nomadismo* consiste em movimentos extensos e usuais, ocorrendo entre espécies que não possuem área de reprodução claramente definida e não necessariamente retornam para as áreas que ocuparam anteriormente. Os nômades, em geral, habitam locais cujas condições ambientais são erráticas, como regiões áridas, ou os recursos são imprevisíveis, e deslocam-se apenas uma vez ao ano em busca de um ambiente adequado ou recurso específico, ao contrário de espécies irruptivas. Os indivíduos *vagantes* são um visitante exótico, em geral migratório, que normalmente não se reproduz, inverna ou passa por ali (Newton, 2010b). A vagância pode resultar de fenômenos naturais ou de deficiências nos mecanismos fisiológicos de controle, tais como dispersão, expansão populacional, deriva causada por ventos, migração para além do local usual, ou desvios direcionais (Newton, 2010b).

A migração das aves e fatores que a determinam

A migração evoluiu repetidamente em diversos táxons, incluindo invertebrados (Dingle, 2006; Newton, 2010a), mas em nenhum deles é tão diversa e difundida como nas aves. As aves são o grupo de vertebrados de maior mobilidade (Newton, 2010a) e possuem ampla distribuição ao redor do globo (Billerman *et al.*, 2022). Por essa razão, o grupo possui alta diversidade de espécies migratórias, bem como de comportamentos e padrões migratórios (Berthold, 1993; Rappole, 2013). Essas características fazem com que as aves sejam excelentes modelos para se compreender a ecologia da migração, ao mesmo tempo que evidenciam a limitação de se estabelecer uma compreensão geral e única sobre esse tema (Faaborg *et al.*, 2010a).

A migração das aves se diferencia quanto ao deslocamento no tempo e no espaço e quanto à resposta dos indivíduos às variações na disponibilidade de recursos, resultando em inúmeros padrões conhecidos (Dingle & Drake, 2007; Chapman *et al.*, 2011; Newton, 2012; Rappole, 2013). Os migrantes podem ser, por exemplo, *obrigatórios* ou *facultativos*, a depender da previsibilidade de recursos no tempo e no espaço; de *curta* ou *longa* distância; *parciais* onde parte da população permanece no sítio reprodutivo ou no sítio não-reprodutivo, enquanto a outra migra para outros locais (Dingle & Drake, 2007; Chapman *et al.*, 2011; Newton, 2012; Rappole, 2013; Watts *et al.*, 2018). Na prática, há um contínuo entre esses extremos e a distinção entre padrões nem sempre é clara, especialmente quando não há sazonalidade ou previsibilidade na disponibilidade de recursos muito evidentes (Dingle & Drake 2007). A variação latitudinal determina grande parte da diversidade desses padrões, assim como aspectos geográficos, como a topografia, e aspectos climáticos (Jahn *et al.*, 2004, 2012). Tais características são de certa forma responsáveis pela diversidade e complexidade da migração entre continentes e hemisférios (Jahn *et al.*, 2004; Dingle, 2008; Faaborg *et al.*, 2010a).

Com a migração, as aves podem aproveitar o "melhor dos dois mundos" (Greenberg & Marra, 2005), beneficiando-se de recursos excedentes em determinado local e evitando regiões onde os recursos estão se deteriorando ou com disponibilidade limitada (Dingle, 2014), em função de flutuações sazonais e da competição (Somveille *et al.*, 2015). Sob essas circunstâncias, um indivíduo sujeito a uma maior regularidade na oferta de recursos pode ampliar suas chances de sobrevivência e de sucesso reprodutivo do que se ele permanecesse no mesmo local e competisse com as aves residentes (Newton, 2010b). Nesse sentido, a principal vantagem da migração é a possibilidade de aumento do valor adaptativo (*fitness*) frente à limitação de recursos (Winger *et al.*, 2019), que podem ser expressos tanto em termos de aumento das chances de sobrevivência do adulto, quanto do sucesso reprodutivo (Lack, 1954; Winger & Pegan, 2021). Porém, esses benefícios precisam ser balanceados com os custos associados à migração para que essa continue sendo vantajosa (Alerstam *et al.*, 2003).

A migração possui diversos custos intrínsecos e extrínsecos, que são expressos, por exemplo, em termos de tempo, gasto energético e risco de mortalidade (Alerstam & Lindström, 1990). Os custos de migração estão relacionados às distâncias percorridas, à alta exposição à predação e às adversidades ambientais enfrentadas durante a jornada (Wikelski *et al.*, 2003; Newton, 2010b; Lok *et al.*, 2015). Tais custos são elevados, pois podem gerar consequências negativas para o valor adaptativo dos migrantes, como a redução da sobrevivência dos adultos (Alerstam *et al.*, 2003; Alves *et al.*, 2013), que em geral é compensada com o aumento no esforço reprodutivo (Martin, 1987). Por essa razão, as espécies migratórias são normalmente associadas a histórias de vida em que indivíduos adultos possuem baixa sobrevivência e investem mais no tamanho das ninhadas (Jetz *et al.*, 2008a; Sibly *et al.*, 2012; Soriano-Redondo *et al.*, 2020). Por outro lado, acessar ambientes com maior e melhor disponibilidade de recursos pode compensar esses custos (Møller, 2007; Conklin *et al.*, 2017; Winger & Pegan, 2021), favorecendo a sobrevivência de adultos e estratégias reprodutivas mais lentas (Buechley *et al.*, 2021; Winger & Pegan, 2021). Assim, as diversas estratégias de migração entre as aves são resultado desse balanço energético entre custos e benefícios (Somveille *et al.*, 2018), que por sua vez está intrinsicamente ligado ao balanço entre sobrevivência e reprodução (Winger & Pegan, 2021).

A variação sazonal na disponibilidade de recursos no ambiente é um dos principais fatores que determinam a migração das aves (Alerstam & Lindström, 1990; Somveille *et al.*, 2015, 2018). A distribuição de aves migratórias ao longo do ciclo anual é comumente relacionada com fatores ambientais associados com a disponibilidade de recursos e com a produtividade ecológica (Jahn et al., 2010b; van Wijk et al., 2012; La Sorte et al., 2014; Thorup et al., 2017; MacPherson et al., 2018). Fatores como a temperatura, precipitação e o vigor da vegetação (do termo em inglês *vegetation greenness*; está relacionado à variação na cobertura verde da vegetação) têm sido utilizados em diversos estudos como preditores da abundância sazonal de recursos alimentares essenciais para as espécies migratórias (van Wijk et al., 2012; La Sorte et al., 2014; MacPherson et al., 2018). A variação sazonal da temperatura está correlacionada com a duração do dia e prediz, principalmente, a migração de aves em altas latitudes, onde a sazonalidade da temperatura é mais intensa e os invernos mais severos (Lack, 1960; van Wijk *et al.*, 2012). Nessas regiões, os insetos, importante recurso alimentar para muitas aves migratórias, emergem com o aumento da temperatura, durante a primavera (Both *et al.*, 2006; van Asch & Visser, 2007). Em regiões de climas mais amenos e com menor amplitude térmica anual, fatores como ciclos de seca e chuva podem ter mais influência sobre a migração (Dingle, 2008; Faaborg *et* *al.*, 2010a), tendo em vista que a emergência de determinadas ordens de insetos está associada ao aumento da precipitação e umidade (Janzen & Schoener, 1968; Pinheiro *et al.*, 2002). A fenologia da vegetação também é um fator responsável pela distribuição das aves migratórias ao longo do ciclo anual (La Sorte et al., 2014). A hipótese da onda verde (*green wave hypothesis*) sugere que espécies migratórias seguem a dinâmica da cobertura verde da vegetação ao longo de um gradiente latitudinal ou altitudinal (Drent *et al.*, 1978; Owen, 1980). Essa hipótese foi elaborada a partir de estudos com aves herbívoras, que durante a primavera seguem o fluxo de crescimento da vegetação e beneficiam-se dos ricos nutrientes associados à vegetação jovem (Drent *et al.*, 1978; Owen, 1980). Porém, aplica-se também a aves insetívoras (La Sorte et al., 2014; Thorup et al., 2017; La Sorte & Graham, 2021), pois a fenologia dos insetos coincide também com a fenologia da vegetação durante a primavera (van Asch & Visser, 2007; Forrest & Thomson, 2011). É importante ressaltar, no entanto, que a importância de cada um desses fatores para cada espécie migratória é contexto dependente, variando geograficamente (Jahn *et al.*, 2004; Faaborg *et al.*, 2010a) e de espécie para espécie de acordo com sua sensibilidade a determinado parâmetro (Youngflesh *et al.*, 2021).

Outros fatores determinantes para a migração das aves, mas que não têm sido amplamente abordados em estudos sobre a ecologia da migração, são a competição intraespecífica e interespecífica. Esses fatores são relevantes para a compreensão da migração das aves ao redor do globo porque os recursos energéticos estão disponíveis não apenas em termos de quantidade e qualidade no ambiente, mas também considerando a intensidade da competição por esses recursos (Somveille *et al.*, 2018). São diversos os estudos que sugerem que as aves migratórias sofrem limitação de recursos nos sítios não-reprodutivos e competem por hábitat e alimento (Greenberg, 1986; Perez-Tris & Telleria, 2002; Brown & Sherry, 2006; Powell *et al.*, 2021). A competição interespecífica, por exemplo, influencia a estrutura de comunidades de aves como um todo durante o período não-reprodutivo, pois afeta negativamente a condição corporal e a taxa anual de retorno de indivíduos de espécies migratórias menos competitivas por meio da competição por territórios (Powell *et al.*, 2021). Da mesma maneira, a competição intraespecífica nos sítios não-reprodutivos pode afetar a dinâmica anual das populações, por exemplo, por meio da segregação de habitats mediada pela dominância social (Marra & Holmes, 2001; Perez-Tris &

Telleria, 2002). Tais evidências corroboram com a hipótese de que a competição nos sítios não-reprodutivos é um dos fatores determinantes para a origem do comportamento migratório em aves (Cox, 1968; Rappole & Jones, 2002; Winger *et al.*, 2019), no qual indivíduos jovens saem de ambientes altamente competitivos em busca de novas áreas para se reproduzirem e aumentarem suas chances de sobrevivência (Rappole & Jones, 2002; Winger *et al.*, 2019). Além disso, a competição e outras interações bióticas são especialmente relevantes para definirem os limites da distribuição de espécies migratórias nos sítios reprodutivos e não-reprodutivos principalmente quando o clima não é um fator de estresse extremo para as espécies (Louthan *et al.*, 2015). Assim, a competição poderia exercer uma influência maior em sistemas migratórios de climas menos variáveis e extremos.

À medida que os recursos são esgotados localmente, migrar para regiões menos competitivas pode, portanto, ser altamente vantajoso, uma vez que esses locais são capazes de fornecer um adicional de recursos não disponíveis nos sítios não-reprodutivos, tanto para os adultos quanto para a prole (Somveille *et al.*, 2018; Winger *et al.*, 2019). Aves reproduzindo-se em ambientes com menor competição apresentam maiores tamanhos de ninhada, maior quantidade de recrutas e menores taxas de predação (Gustafsson, 1987; Arcese & Smith, 1988; Martin & Martin, 2001; Holmes, 2007). Isso porque há uma maior e melhor disponibilidade de recursos indispensáveis para a reprodução, como locais de nidificação e recursos alimentares, favorecendo o aumento nas taxas de entrega de alimento no ninho, a melhoria na condição corporal dos ninhegos e o aumento no número de tentativas reprodutivas numa mesma estação (Gustafsson, 1987; Martin & Martin, 2001; Perez-Tris & Telleria, 2002; Holmes, 2007). Adicionalmente, a competição a que as aves migratórias estão sujeitas durante o período não-reprodutivo pode ter efeitos negativos sobre o período reprodutivo (Akresh *et al.*, 2019; Powell *et al.*, 2021). Indivíduos sujeitos a uma intensa competição em seus sítios não-reprodutivos e ocupando territórios de baixa qualidade podem ter chances reduzidas de sucesso reprodutivo em função de sua baixa condição corporal e de atraso na chegada ao sítio de reprodução (Marra *et al.*, 1998; Norris *et al.*, 2004; Akresh *et al.*, 2019; Powell *et al.*, 2021). Por outro lado, indivíduos em maior vantagem competitiva nos sítios não-reprodutivos são capazes de chegar mais cedo nos sítios reprodutivos, garantindo acesso a territórios de melhor qualidade e mais tempo e energia para reproduzirem-se (Tonra *et al.*, 2011; Bejarano & Jahn, 2018).

Apesar das inúmeras evidências da influência da competição, tanto nos sítios reprodutivos quanto nos sítios não-reprodutivos, sobre a distribuição e a reprodução das aves migratórias, são raros os estudos de larga escala que abordem as consequências da competição sobre as comunidades de aves (mas veja Elsen *et al.*, 2017; Somveille *et al.*, 2018). A maior parte dos estudos existentes são em nível local e focam em comunidades isoladas e populações (Gustafsson, 1987; Marra & Holmes, 2001; Martin & Martin, 2001; Norris et al., 2004; Powell et al., 2021). Por essa razão, há lacunas de conhecimento importantes que devem ser preenchidas para ampliar sobre os padrões de larga escala que determinam a migração sazonal de aves.

A migração de aves na região Neotropical

A migração das aves é amplamente distribuída ao redor do planeta (Somveille *et al.*, 2013) e possui alta diversidade de padrões, que variam entre espécies, populações e regiões geográficas (Jahn *et al.*, 2004, 2012; Lehikoinen & Sparks, 2010). Apesar disso, por muitos anos, a ideia que prevaleceu sobre a migração de aves foi a de que ela consiste em movimentos regulares de longa distância entre os sítios de reprodução, localizados em regiões temperadas de clima altamente sazonal e com alta abundância de recursos em determinada época do ano, e os sítios não-reprodutivos, localizados em climas mais amenos localizados em baixas latitudes (Hayes, 1995). Essa visão, no entanto, baseou-se em um conjunto limitado de sistemas de migração localizados no Hemisfério Norte, onde está concentrada a maioria dos pesquisadores e recursos financeiros para pesquisa (Hayes, 1995; Jahn *et al.*, 2004; Faaborg *et al.*, 2010a).

Nos últimos anos, diversos autores têm feito esforços para chamar a atenção para a necessidade de se ampliar estudos de migração para outros sistemas de migração, como os da região Neotropical (e.g., Dingle, 2008; Faaborg *et al.*, 2010a; Jahn *et al.*, 2017a, 2020). A migração na região Neotropical é mais comum e diversa do que se pensava anteriormente (Jahn *et al.*, 2020). Assim como em outros sistemas de migração do

Hemisfério Sul, a migração de aves que se reproduzem na região Neotropical difere em diversos aspectos da migração de aves que se reproduzem em latitudes temperadas do Hemisfério Norte (Faaborg *et al.*, 2010a). As migrações aqui observadas ocorrem a partir de movimentos, em geral curtos, em variadas direções, que podem ser latitudinais, longitudinais e altitudinais. Isso se dá principalmente em razão da ausência de grandes barreiras geográficas (Chesser, 1994; Jahn et al., 2020). Nesse sentido, a migração de aves que se reproduzem na região Neotropical se dá principalmente em quatro sistemas principais: Austral, Intratropical, Altitudinal e Longitudinal, cujos principais padrões de movimentação estão esquematizados na figura 1. As definições, as quais descreverei a seguir, baseiam-se principalmente em Jahn et al. (2020) e Faaborg et al. (2010b).

O sistema Austral é formado por espécies que se reproduzem na porção sul da América do Sul (temperada) e migram durante o período não-reprodutivo para sítios localizados ao norte, nas regiões tropical ou sub-tropical (Chesser, 1994; Faaborg *et al.*, 2010a; Jahn *et al.*, 2020). Esse sistema é composto majoritariamente por espécies da família Tyrannidae (ca. 30%) e é o que possui o maior número de espécies documentadas (220 espécies) (Chesser, 1994; Stotz *et al.*, 1996), com alta predominância de espécies migratórias em altas latitudes (Faaborg *et al.*, 2010a). O sistema Intratropical é formado por espécies que realizam migrações de modo restrito à região tropical, compreendida entre os trópicos de câncer e de capricórnio (Faaborg *et al.*, 2010a; Jahn *et al.*, 2020). Esse sistema é altamente complexo, pois abrange inclusive movimentos altitudinais e longitudinais (Jahn *et al.*, 2020). A migração longitudinal, i.e., aquela que ocorre no sentido leste-oeste, tem sido mais bem documentada somente nos últimos anos (e.g., Areta & Bodrati, 2010; Guaraldo, 2014; Lees, 2016; Pinho *et al.*, 2017). Possivelmente por essa razão, Faaborg et al. (2010b) não incorporou o conceito de migração longitudinal em suas definições. Por outro lado, recentemente, Jahn et al. (2020) o amplia e o considera um sistema migratório em separado. Por fim, o sistema Altitudinal possui espécies que realizam deslocamentos ao longo de um gradiente altitudinal. Esses movimentos são comuns e estendem-se por toda a região Neotropical, sendo observados, principalmente, em regiões montanhosas do México, da América Central, do norte da América do Sul e da Mata Atlântica, bem como nos Andes (Jahn *et al.*, 2020).

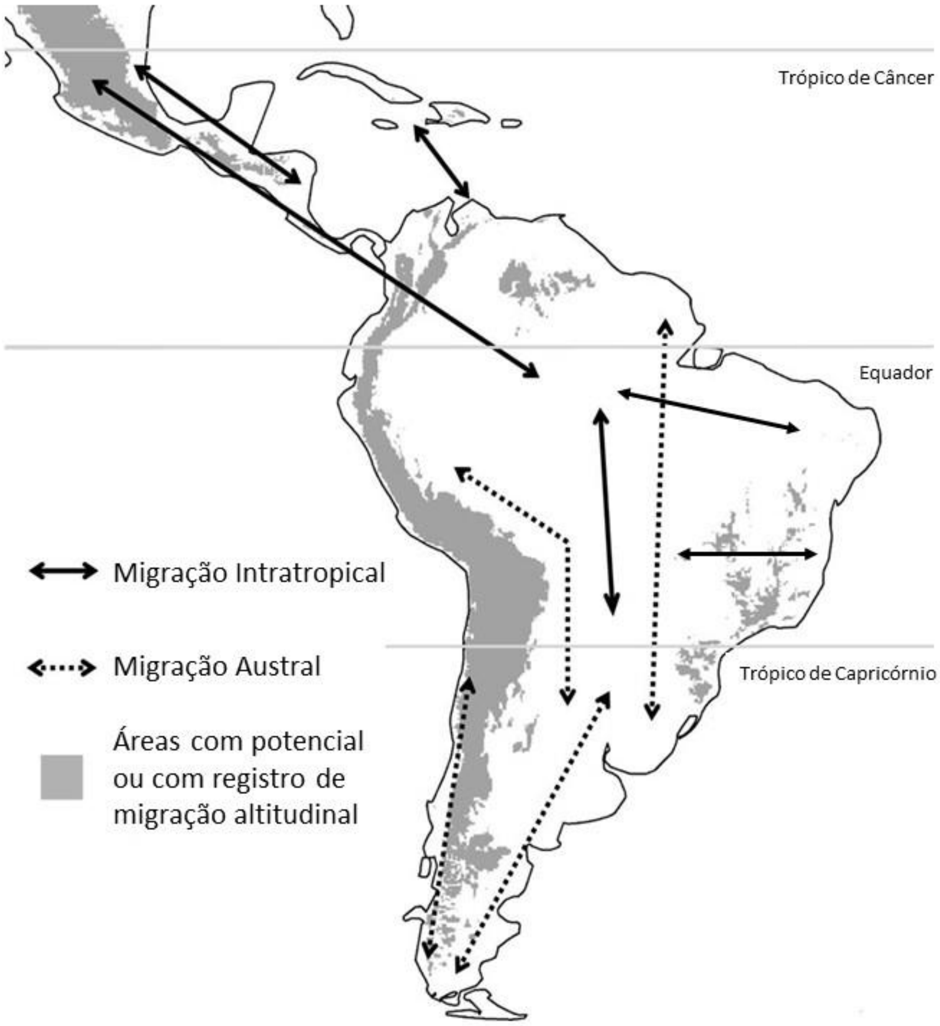


Figura 1. Padrões gerais dos movimentos migratórios dentro da região Neotropical. Os migrantes altitudinais presumidamente realizam movimentos de curta distância dentro das áreas sombreadas ou adjacentes a áreas não sombreadas. Modificada de (Faaborg *et al.*, 2010a).

Além disso, a migração na região Neotropical é caracterizada por temperaturas mais amenas e menos sazonais, quando comparada a outros sistemas de clima temperado do Hemisfério Norte (Dingle, 2008). Essa distinção se dá em parte devido à geografia da América do Sul, que influencia de sobremaneira o clima do continente (Dingle, 2008; Faaborg *et al.*, 2010a). Além da maior parte do continente estar localizada em latitudes médias e baixas, a diminuição na disponibilidade de áreas terrestres em direção ao sul e seu formato triangular faz com que a porção continental sofra mais influência das águas costeiras, que agem como tampões e amenizam o clima na região (Faaborg *et al.*, 2010a). Nesse caso, a região Neotropical tem climas mais marcados por ciclos sazonais de seca e chuva, os quais têm demonstrado exercer forte influência sobre as estratégias das espécies que aqui migram (Lees, 2016; MacPherson *et al.*, 2018).

Por fim, o clima ameno somado à maior disponibilidade de terras em latitudes mais baixas influencia as distâncias de migração e a ocorrência de migrações parciais (Jahn *et al.*, 2004). Esses fatores permitem que as espécies vindas de regiões temperadas não necessitem viajar distâncias muito longas para encontrarem hábitats propícios para passarem o período não-reprodutivo (Chesser, 1994). Uma consequência das curtas distâncias de migração é que é relativamente comum observar que os sítios não-reprodutivos sejam próximos ou mesmo sobrepostos aos sítios reprodutivos, favorecendo a ocorrência da migração parcial (Chesser, 1994; Chan, 2001; Jahn *et al.*, 2012). A ocorrência de migração parcial é alta em regiões de climas mais amenos e menos previsíveis (Jahn *et al.*, 2012). Cerca de 70% das espécies que se reproduzem e migram na região Neotropical são migrantes parciais (Stotz *et al.*, 1996). As migrações parciais, bem como as de curtas distâncias, climas amenos, e variedade de padrões e rotas, são características comuns à migração observada em outros continentes do Hemisfério Sul, como a África e Oceania (Chan, 2001; Dingle, 2008). Isso sugere que a ecologia da migração e as pressões seletivas atuando sobre as aves migratórias no Hemisfério Sul são comuns entre si e distintas do Hemisfério Norte. Por essa razão, o conhecimento sobre a migração na região Neotropical não deve ser depreendido somente a partir de estudos feitos em sistemas temperados do Hemisfério Norte.

Por que e como estudar a migração na região Neotropical

Apesar da alta diversidade de padrões e de comportamentos observados entre as espécies migratórias que se reproduzem na região Neotropical (Chesser, 1994; Jahn *et al.*, 2004; Faaborg *et al.*, 2010a), ainda há importantes lacunas de conhecimento sobre a ecologia e hábitos migratórios da vasta maioria de suas espécies (Dingle, 2008; Faaborg *et al.*, 2010b; Jahn *et al.*, 2020). Essa carência de conhecimento se dá em parte devido à difícil documentação da extensão dos movimentos migratórios realizados na região, uma vez que a maioria das espécies que ali se reproduzem migram para áreas ocupadas por populações residentes co-específicas (Stotz *et al.*, 1996; Jahn *et al.*, 2012; Lees, 2016). A visão limitada sobre os migrantes dessa região e a falta de conhecimento sobre o comportamento dessas aves levou muito autores a chamarem atenção por mais estudos na região desde meados dos anos 90 (Levey, 1994; Hayes, 1995; Jahn *et al.*, 2004). Porém, ainda que tenha havido avanços no conhecimento da migração na região desde então (revisão em Jahn *et al.*, 2020), há aspectos ecológicos e evolutivos importantes por serem explorados (Jahn & Cueto, 2012; Jahn *et al.*, 2017a).

A comparação entre diferentes estratégias migratórias a partir de espécies derivadas de um mesmo ancestral comum é uma oportunidade única para se compreender e avaliar o valor adaptativo que cada estratégia apresenta (Dingle, 2008; Jahn & Cueto, 2012). Espécies de parentesco próximo compartilham uma mesma origem evolutiva e características de história de vida e, por isso, são modelos interessantes para se estudar as causas e consequências da migração (Jahn & Cueto, 2012). Porém, esse tipo de pesquisa é ainda raro e está quase que exclusivamente limitado ao porquê da migração (Jahn *et al.*, 2012; Guaraldo *et al.*, 2016; MacPherson *et al.*, 2018). Ainda há um vasto campo de conhecimento sobre as bases ecológicas e evolutivas da migração de aves a ser explorado por estudos comparativos (Bennett & Owens, 2002) como, por exemplo, sobre a diversidade de histórias de vida observada entre espécies migratórias (Yom-Tov et al., 1994). Estudos comparativos têm o potencial de esclarecer essas relações e são fundamentais, por exemplo, para ampliar o conhecimento sobre aves neotropicais, que lidam com uma grande diversidade de desafios ambientais e têm uma grande variedade de estratégias de histórias de vida (Dingle, 2008; Jahn & Cueto, 2012).

Estudos comparativos e de larga escala na região Neotropical necessitariam de um esforço grande e contínuo de coleta de dados. Uma alternativa mais rápida e viável seria a de utilizar dados já coletados. Museus, literatura e ciência cidadã têm sido importantes fontes de dados para estudos comparativos de longo prazo e de larga-escala (Chesser, 1998; Heming et al., 2013; Lees, 2016; La Sorte & Somveille, 2020), principalmente onde não há coleta sistematizada de dados (Remsen Jr., 2001). Essa tem sido a alternativa que melhor disponibiliza registros para uma extensa área geográfica, pouco amostrada, como a região Neotropical, e com relativa facilidade de acesso aos registros (Remsen Jr., 2001; Lees, 2016). A síntese de dados provenientes de museus é bastante promissora para o estudo de aves migratórias, apesar de pouco explorada (Remsen Jr., 2001; Jahn et al., 2004; Marini et al., 2020). Isso porque os museus possuem diferentes tipos de espécimes (e.g., peles, esqueletos, ovos, ninhos) e, portanto, possibilitam responder perguntas nos mais variados campos de estudo (Webster, 2017). As coleções oológicas, por exemplo, representam um potencial inexplorado para estudos de biologia das aves, podendo contemplar desde estudos de história de vida até perguntas mais complexas sobre os impactos antropogênicos sobre a reprodução das aves (Marini *et al.*, 2020). Além disso, dados de ciência cidadã, como os dados de avistamento de aves compartilhados por meio de plataformas como o eBird (www.ebird.org; Sullivan et al. 2009) e Wikiaves (www.wikiaves.com.br; Wikiaves 2022), têm sido cada vez mais utilizados em estudos de distribuição e de migração de aves (e.g., La Sorte et al., 2014; Schubert et al., 2019). Cabe ressaltar, no entanto, que é necessário considerar que, ao utilizar esse tipo de dado, possíveis vieses de amostragem sejam considerados, tais como vieses espaciais, temporais e de esforço de coleta, assim como possíveis problemas de identificação (Johnston *et al.*, 2020).

A migração na família Tyrannidae

Tyrannidae está entre as famílias de aves do Novo Mundo que mais migram e é de longe o grupo mais móvel entre os Passeriformes suboscines (Sick, 1997; Fitzpatrick, 2019). É a maior família do Novo Mundo, com 449 espécies, divididas em 101 gêneros (Fitzpatrick, 2019), e apresenta pico de riqueza na região Neotropical. É um grupo amplamente estudado (Heming *et al.*, 2013) e, também, bastante amostrado em coleções científicas, acumulando milhares de registros (peles, ninhos e ovos) depositados em museus pelo mundo (Marini *et al.*, 2020). Apesar disso, possui lacunas de conhecimento quanto à migração. Não se sabe ao certo quantas espécies da família pertencem a cada um dos sistemas migratórios da região Neotropical.

No sistema Austral, Tyrannidae apresenta um domínio taxonômico nunca visto em outros sistemas; é a família com o maior número de migrantes (ca. de 76 espécies), o que equivale a um terço das espécies migratórias neste sistema (Chesser, 1994). Os outros sistemas Neotropicais não possuem números consolidados e nunca foram objeto de estudos específicos. Mas, ainda assim, é notável o avanço do estado de conhecimento sobre a família nos últimos anos, incluindo a descrição de movimentos e de áreas de distribuição sazonais e a identificação de fatores ecológicos que determinam a migração (e.g., Jahn *et al.*, 2009, 2013b; Marini *et al.*, 2013; Paiva & Marini, 2013; Guaraldo *et al.*, 2016; Lees, 2016; Bravo *et al.*, 2017; MacPherson *et al.*, 2018; Dias *et al.*, 2021; Gorleri *et al.*, 2021). Além da riqueza de espécies, Tyrannidae possui uma incomum diversidade de funções ecológicas, comportamentais e morfológicas quanto à migração, normalmente irradiada em diferentes famílias (Chesser 1994). Com essas características, não é surpresa que seja um grupo atrativo para estudos de migração e que seja considerado o melhor modelo para se compreender a migração na região Neotropical (Faaborg *et al.*, 2010a; Jahn & Cueto, 2012).

Objetivos

Nesse contexto, esta Tese propõe-se a aprofundar o conhecimento científico sobre os fatores que determinam a migração de aves na região Neotropical, com foco na família Tyrannidae e nas espécies que se reproduzem na América do Sul. Está dividida nos seguintes capítulos:

***Capítulo 1**:* Variação sazonal na competição e não produtividade ecológica determinam a migração austral de tiranídeos

Seasonal variation in competition and not ecological productivity drives the austral migration of tyrant flycatchers

***Capítulo 2**:* Tamanho de ninhada associa-se com distância de migração em aves terrestres na América do Sul

Clutch size associates with migration distance in South American land birds

***Capítulo 3**:* Variação sazonal na competição afeta o tamanho da ninhada e do ovo em aves migratórias terrestre da América do Sul

Seasonal variation in competition affects clutch and egg size in migratory South American land birds

No ***Capítulo 1***, investiguei possíveis fatores que determinam a distribuição sazonal de aves na região, utilizando dados de ocorrência de espécies disponibilizados na plataforma de ciência cidadã, eBird. Para tanto, testei duas hipóteses: i) se a variação sazonal na produtividade ecológica (temperatura, precipitação e *vegetation greenneess*) está associada com a distribuição sazonal de aves migratórias; ii) se a competição nos sítios reprodutivo e não-reprodutivos varia sazonalmente. No ***Capítulo 2***, investiguei como a migração interage com parâmetros da história de vida, com o intuito de avaliar como as aves migratórias da região balanceiam os custos e os benefícios da migração. Especificamente, utilizando dados de coleções oológicas avaliei como a reprodução (i.e., tamanho da ninhada e o tamanho de ovo) de aves migratórias correlaciona-se com a distância de migração e comparei se essa se diferencia entre as aves que migram e as aves que não migram. Por fim, no ***Capítulo 3***, investiguei a correlação entre a reprodução (i.e., tamanho da ninhada e o tamanho de ovo) e a variação sazonal na competição intraespecífica e interespecífica entre os sítios reprodutivo e não-reprodutivos, com o intuito de avaliar como as aves migratórias otimizam a migração na região e se a competição é um fator que limita a energia disponível ao longo do ciclo anual.

Com base nos resultados encontrados, proponho a tese de que, diferentemente de sistemas de migração boreais, a migração de tiranídeos na América do Sul é determinada pela variação sazonal na competição, e não pela variação sazonal do clima, e que essas espécies se beneficiam do adicional de recursos disponíveis nos sítios reprodutivos, mesmo quando investem mais na migração.

CAPÍTULO 1

Seasonal variation in competition and not ecological productivity drives the austral migration of tyrant flycatchers

Variação sazonal na competição e não produtividade ecológica determinam a migração austral de tiranídeos

Abstract

Evidence suggest that migrants track seasonal variation in ecological productivity, particularly in highly seasonal environments. However, energy is available not only in terms of resource abundance and quality, but also in terms of the degree of competition for these resources. We tested two hypotheses on the factors driving the seasonal movements of migratory birds within South America: (1) seasonal variation in key environmental factors (green wave hypothesis), and (2) seasonal variation in competition. We estimated weekly encounter rates across the annual cycle for 33 bird tyrant flycatcher species using eBird occurrence information, and intersected them with temperature, precipitation, and vegetation greenness estimates to test our green wave predictions. We summarized encounter rate estimates by season and estimated the locations and size of species' breeding and non-breeding ranges. We compared range sizes and tyrant flycatcher species richness estimates between seasons to test our competition predictions. We found evidence that the non-breeding grounds had higher competition than the breeding grounds, with smaller ranges and more tyrant flycatcher species. In contrast, we found little evidence that large-scale environmental variation drove seasonal migration. All regions where the species occurred displayed similar environmental seasonality, indicating that species were not tracking ecological productivity towards a resource surplus on their breeding grounds. Competition is the primary factor driving seasonal bird migration in South America. Despite sharing characteristics of bird migration found in the Northern Hemisphere, large-scale environmental seasonality played a secondary role as a driver of bird migration in South America. Our findings support the hypothesis that bird migration originated as a response by juvenile birds to locate vacant breeding habitat.

Keywords: Austral migration, eBird, ecological productivity, green wave hypothesis, intra-specific competition, inter-specific competition, Neotropical birds, seasonal bird migration.

Introduction

Animals migrate to regions that provide resources necessary for self-maintenance and reproduction, while avoiding regions where resources are deteriorating, or their availability is reduced (Dingle, 2014). It is this relationship with resource quality and availability that is thought to drive seasonal animal migration across the globe (Alerstam & Lindström, 1990; Somveille *et al.*, 2015, 2018). Several studies have linked migratory bird distributions to seasonal changes in key environmental factors that are associated with food availability and ecological productivity across the annual cycle (Jahn et al., 2010b; La Sorte et al., 2014; Thorup et al., 2017; MacPherson et al., 2018). For example, there is evidence supporting the role of seasonality in temperature (van Wijk *et al.*, 2012; Somveille *et al.*, 2015), precipitation (Lees, 2016; MacPherson *et al.*, 2018), and vegetation greenness (Thorup et al., 2017; La Sorte & Graham, 2021) as environmental factors driving seasonal bird migration. Many of these studies also support the “green wave” hypothesis, which posits that migratory herbivores track vegetation green-up along latitudinal or elevational gradients during spring migration (Drent *et al.*, 1978; Owen, 1980). Because of the close ecological relationship between plants and insects, the green wave hypothesis is relevant for both herbivorous and insectivorous bird species (La Sorte & Graham, 2021), but associations vary depending on species’ sensitivity to vegetation green-up (Youngflesh *et al.*, 2021).

An alternative ecological driver of bird migration that has not been broadly tested is the seasonal variation in intra- and inter-specific competition. This driver is relevant because energy is available not only in terms of resource abundance and quality, but also in terms of the degree of competition for these resources within and among species (Somveille *et al.*, 2018). Both intra-specific and inter-specific competition have been suggested as drivers of the evolution of migratory behavior (Cox, 1968; Rappole & Jones, 2002). Natural selection should favor movement out of highly competitive environments in search of new breeding locations, increasing the chances of survival and reproductive success (Cox, 1968; Rappole & Jones, 2002). Several studies have reported that migratory birds are limited by key resources on their non-breeding grounds, such as food and space (Greenberg, 1986; Perez-Tris & Telleria, 2002; Brown & Sherry, 2006; Powell *et al.*, 2021), and associated competition for habitat (Marra, 2000; Perez-Tris & Telleria, 2002). However, the role of intra- and inter-specific competition in driving seasonal migration between the breeding and the non-breeding grounds remains unclear.

Recent global-scale studies suggest that birds respond to common underlying ecological drivers during migration, such as seasonality of resources and winter harshness (Somveille *et al.*, 2015). However, evidence points to asymmetrical patterns in species' geographical distributions (Somveille *et al.*, 2013) and migratory behaviors (Dingle, 2008; Jahn *et al.*, 2020) between the Northern and Southern Hemispheres. This asymmetry presumably is due to the distinct historical and geographical features between these two regions (Dingle, 2008; Faaborg *et al.*, 2010a), and suggests that the factors driving seasonal bird migration in the austral system in the Southern Hemisphere differ from those operating in the boreal system in the Northern Hemisphere. Studies investigating continental-scale patterns of bird migration have focused primarily on the Northern Hemisphere, such as the Nearctic-Neotropical migration system (La Sorte & Fink, 2017; Youngflesh et al., 2021) and the Palearctic-African migration system (Thorup *et al.*, 2017; Briedis *et al.*, 2020). Boreal migration systems are characterized by increasing land mass towards the pole, strong temperature seasonality, and long migration distances (Faaborg *et al.*, 2010a). Austral migration systems in the Southern Hemisphere, in contrast, are characterized by reduced land mass towards the pole, lower temperature seasonality, shorter migration distances, higher diversity of migration routes and strategies, and a larger number of species that undertake partial migrations where only a portion of the population migrates (Chan, 2001; Jahn *et al.*, 2004; Dingle, 2008). Despite the growing number of biogeographical studies of bird migration (e.g., Griffioen & Clarke, 2002; Jahn *et al.*, 2013b; Bravo *et al.*, 2017), significant knowledge gaps remain in our understanding of the large-scale patterns and drivers of seasonal bird migration within austral migration systems (but see Dingle, 2008; Jahn *et al.*, 2020).

Our study aims to address these knowledge gap by investigating the drivers of austral bird migration in South America. Here, we test two hypotheses on the factors driving the seasonal movements of migratory birds within South America. The first is that seasonal variation in key environmental factors drives bird migration and the second is that seasonal variation in competition on the non-breeding and breeding grounds drives bird migration. To test these hypotheses, we estimated weekly encounter rates across the annual cycle for 33 species of tyrant flycatchers (Tyrannidae) that breed and migrate within South America. To test the first hypothesis, we intersected weekly encounter rate estimates for the 33 species with three environmental variables commonly associated with ecological productivity: temperature, precipitation, and vegetation greenness. Our expectation is that the breeding grounds will display greater seasonality in temperature, precipitation, and vegetation greenness and associations with the highest annual levels will occur during spring migration and the breeding season and associations with the lowest annual levels will occur during the non-breeding season. To test the second hypothesis, we used the weekly encounter rate estimates for the 33 species to estimate species' breeding and non-breeding range sizes and the species richness of tyrant flycatcher species within each species' breeding and non-breeding ranges. Our expectation is that, compared to the non-breeding range, the breeding ranges will be larger and contain fewer tyrant flycatcher species.

Methods

Using observations of tyrant flycatcher (Tyrannidae) species from a citizen science database, we first combined species presence and absence information with habitat covariates (landcover and elevation) to estimate species weekly encounter rate across the annual cycle. We intersected these encounter rate estimates with three environmental variables commonly associated with ecological productivity to test our predictions from the green wave hypothesis. We then estimated the locations and size of species' breeding and non-breeding ranges using the encounter rate estimates summarized by season. Lastly, we compared breeding and non-breeding range sizes and tyrant flycatcher richness between the breeding and non-breeding seasons to test our competition predictions.

Bird occurrence data treatment

We considered 33 species of tyrant flycatchers (Tyrannidae) in our analysis that breed and migrate within South America. Tyrant flycatchers are distributed throughout the Americas and an important migratory bird family within the Neotropical region, representing one third of all Austral migratory species (Chesser, 1994). Species were selected for analysis after a careful review of their distributions and behavior based on information from Birds of the World (Billerman *et al.*, 2020) and Chesser (1995) (Table S1.1). We included species with clear seasonal movements (i.e., full migrants), and partial migrants that mostly displayed migratory behavior throughout their annual range. Species that displayed unclear seasonal movements, were sedentary, irruptive or nomadic were not included in the analysis.

We compiled occurrence data for the 33 species from the eBird Basic Dataset (EBD) (www.ebird.org/science/download-ebird-data-products). eBird is a semi-structured citizen science platform where participants compile their bird observations in checklist format from any time and location using a variety of pre-defined sampling protocols (Sullivan *et al.*, 2009). eBird data allows inferences on species' non-detections and the effort information provided by eBird participants enables the development of species distribution models that account for variation in detectability (Sullivan *et al.*, 2009). Performance of species distribution models improves considerably when addressing non-detection and variation in effort, allowing robust ecological inferences (Johnston *et al.*, 2021), including for data-poor species (Gorleri *et al.*, 2021). We inferred non-detections by using "complete" checklists in our analysis where all species detected by the observer are identified and reported. We filtered checklists collected within the boundaries of South America countries (U.S. Department of State, 2013) from 1 January 2002 to 30 September 2020. We minimized variation in collection procedure and effort by selecting checklists collected under the 'travelling count' and 'stationary count' protocols that were less than 5 hours in duration, less than 5 km in length, and had 10 or fewer observers. We also subsampled detections and non-detections prior to modelling to address temporal bias, spatial bias and class imbalance (Strimas-Mackey *et al.*, 2020). For this, we defined a regular hexagonal grid of 5 km spacing between the hexagon centers within our study area, and randomly sampled one detection and one non-detection checklist from each hexagon cell for each week. To improve model accuracy of rare species, and to reduce the high proportion of non-detections, we did not subsample the detections of species with <300 detections (Robinson *et al.*, 2018).

Modeling encounter rates

We estimated encounter rates for the 33 species by associating species detection/non-detection (response) with two habitat covariates (land cover and elevation). Encounter rate describes the “apparent distribution” of the species and corresponds to the probability of an observer encountering and recording a species at a given site. Land cover data were acquired from the Moderate Resolution Imaging Spectroradiometer (MODIS) (Justice *et al.*, 1998) MCD12Q1 v006 land cover product (Friedl & Sulla-Menashe, 2019). We used 16 land cover types from UMD LC_Type2 classification of MODIS MCD12Q1 v006 (Friedl & Sulla-Menashe, 2019). Elevation data was derived from the 250 m global digital elevation model product GMTED2010 (Danielson & Gesch, 2011), and was acquired at a 1 km spatial resolution from Amatulli et al. (2018).

For each species, we fit balanced random forest models followed by calibration of the model estimates. The balanced random forest approach deals with the imbalanced data classification problem and improves the prediction accuracy of the detections (rare class) by generating trees with an equal number of detections and non-detections (Chen *et al.*, 2004). Calibration realigns the predictions with observations and can be useful to understand the accuracy of model predictions (Vaughan & Ormerod, 2005). For model calibration, we generated prediction probabilities using the random forest described above and modeled the observed encounter rate against the predicted probabilities with a generalized additive model (GAM; Wood, 2011) constrained to be monotonically increasing. The resulting prediction is the combination of the random forest and the calibration GAM. Smooth calibration plots were used as a diagnostic tool to assess model fit and the ability of the model to distinguish sites with high encounter rates from those with low encounter rates. Smooth parameters were set with 15 degrees of freedom and a gamma penalty of 1.4 but were adjusted when necessary to improve the quality of the GAM fit. For model fit and calibration, we followed the guidelines provided by Johnston et al. (2021) and Strimas-Mackey et al. (2020). The balanced random forests models were implemented in the R software for statistical computing and graphics (R Core Team, 2021) using the R package *ranger* (Wright & Ziegler, 2017). The GAM analysis was implemented using the R package *scam* (Pya, 2021).

We validated the models using a semi-independent dataset containing an equal number of detections and non-detections for each month. We derived the validation dataset from the whole dataset before fitting the random forests. First, we randomly selected 20% of the detections and 20% of non-detections evenly across months, and then equated the number of detections and non-detections each month by randomly excluding records from the predominant group (i.e., non-detections). We used a temporal balanced dataset to validate models because we wanted to assess the model's ability to discriminate between areas of species presence and absence throughout the annual cycle. We assessed model performance using the True Skill Statistic (TSS) metric (Table S1.2), which provides a threshold-dependent measure of accuracy independent of prevalence applied for presence-absence predictions (Allouche *et al.*, 2006). TSS scores were calculated using an optimized threshold that maximizes the sum of sensitivity and specificity (Liu *et al.*, 2005).

After we fit each species' model, we predicted daily encounter rates across the calendar year (365 days) and averaged them per week (52 weeks). Predictions were generated within the centers of a regular grid with a cell resolution of *ca*. 2.5 x 2.5 km. To account for variation in detectability we included effort covariates in the prediction surface. Our predictions were for a 1 km traveling count conducted for 1 hour by a skilled observer. Because estimated distributions often contain cells with very low estimated encounter rates, some of which occur outside of species' traditional range boundaries, we applied two thresholding procedures to the predictions. We first used the maximum sum of sensitivity and specificity threshold value calculated for each model to generate a binary mask to exclude the estimates below this value. However, we did not apply this procedure to species whose estimates were almost fully excluded after thresholding (n = 6), due to low encounter rate estimates (Table S1.2). Since many estimates occurred outside species' traditional range boundaries, even after thresholding, we applied a second masking procedure based on the species breeding and non-breeding range maps provided by Birdlife International and Handbook of the Birds of the World (2019), and alpha hulls built from the EBD records not used to model species' distributions. We merged the range map polygons and alpha hull polygons and added a 100 km buffer to the resulting polygon. We chose this procedure to avoid underestimating species occurrence, as many species from our set have been recorded outside their traditional range boundaries. Alpha hulls were estimated using the *ahull* function in the R package *alphahull* (Pateiro-Lopez & Rodriguez-Casal, 2019). For species' seasonal range maps, see Appendix S2 in the Supporting Information.

Ecological productivity

We intersected species' weekly encounter rate estimates with three environmental variables commonly associated with ecological productivity: temperature, total precipitation, and vegetation greenness. Temperature and precipitation variables were derived from the ERA5 hourly single levels reanalysis data gridded at a 0.25° x 0.25° spatial resolution (Hersbach *et al.*, 2018). We extracted daily minimum, maximum, and mean temperature from the variable temperature of air at 2m above the surface (2m temperature), which we then averaged over the combined period 2002 to 2020. Daily temperatures for this period were then averaged across 7-day composite periods to generate weekly estimates. Total precipitation was calculated by summing the hourly total precipitation values for each day, which we then averaged over the same time period, for daily estimates, and summed across 7-day composite periods, for weekly estimates. Vegetation greenness was estimated using Enhanced Vegetation Index (EVI) from the MODIS instrument (Justice *et al.*, 1998) onboard the Terra (MOD13A2 V.006; Didan, 2015a) and Aqua satellites (MYD13A2 V.006; Didan, 2015b). EVI values were derived at a 10 x 10 km spatial resolution and daily temporal resolution for the combined period 2003 to 2020 following the procedure described in La Sorte and Graham (2021). We generated EVI weekly estimates following the same procedure we used to generate weekly temperature estimates.

Competition

We used two parameters to estimate seasonal differences in competition. The first was the area of each species' estimated breeding and non-breeding ranges to estimate seasonal differences in competition. Here, a decrease in range size from the non-breeding to breeding season would suggest an increase in intra- and inter-specific competition on the breeding grounds, and an increase in range size from the non-breeding to breeding season would suggest a decrease in intra- and inter-specific competition on the breeding grounds. The second parameter used was species richness of the tyrant flycatcher family within each of the 33 species' estimated breeding and non-breeding ranges. Here, an increase in species richness from the non-breeding to breeding season would suggest an increase in inter-specific competition on the breeding grounds, and a decrease in species richness from the non-breeding to breeding season would suggest a decrease in inter-specific competition on the breeding grounds

Breeding and non-breeding range maps were estimated for 25 species by aggregating species occurrence during the breeding and non-breeding periods within the Southern Hemisphere. Specifically, we averaged species' encounter rates during the months of November, December, and January for the breeding season and for the months of May, June, and July for the non-breeding season. Range sizes were derived from the cells where each species' encounter rate estimates were greater than zero (Table S1.3). We did not calculate the seasonal ranges for the species which we did not apply the threshold in the predictions (*n* = 6), because they had very low encounter rate values that overestimated species' range sizes. The estimates for two species were also not included because the predictions for their non-breeding periods were underestimated, presumably because of species' low conspicuousness during this period and field identification challenges (see Appendix S2, for species' seasonal range maps).

The species richness of tyrant flycatcher during the breeding and non-breeding seasons were estimated by overlaying the breeding and non-breeding range maps from 447 species of Tyrannidae available from BirdLife (BirdLife International & Handbook of the Birds of the World, 2019). Range maps are frequently used to estimate species richness of birds and other taxa, especially within data poor regions of the globe such as the tropics (Hawkins *et al.*, 2008). The range map polygons for the 447 species were first converted to rasters using the same spatial resolution as the species distribution models (2.5 x 2.5 km). We then overlapped all of the 447 rasters to estimate tyrant flycatcher species richness. Lastly, we calculated the weighted average species richness within each of the 25 species' breeding and non-breeding ranges using encounter rate estimates as a weighting factor (Table S1.3).

Analysis

Seasonal patterns of annual movement of each of the 33 species, and the associations with the three environmental variables, were estimated using the following approach. For each environmental variable, we first extracted weekly estimates of each variable using the same 2.5 x 2.5 km grid of points where the encounter rate estimates were made. We then calculated weighted averages of each variable for each species by week, using species weekly encounter rate estimates as the weighting factor. We also calculated the minimum and maximum values for each variable during the year across the set of encounter rate estimates for each of the 52 weeks of the year.

We used generalized additive mixed models (GAMMs) (Wood, 2017) to summarize each of the 33 species observed associations with each environmental variable. We included species as a random effect in each model to take into account among-species variation in their associations with the environmental variables. We also included a cyclic penalized cubic regression spline in each model to smoothly fit the last week of December with the first week of January. GAMMs were also applied separately to the minimum and maximum values of each variable with species included as a random effect. The predicted values from these two GAMM fits bounded the range of environmental conditions that occurred within each species weekly distributions across the annual cycle. We used the location of the observed GAMM fit relative to the minimum and maximum GAMM fits to determine the degree to which species tracked the annual maximum or minimum environmental conditions by week across the annual cycle. Species’ associations with maximum and minimum temperatures were similar to those documented for mean temperature, thus we only present the results for mean temperature.

We used the following approach to assess if range sizes and Tyrannidae species richness differed significantly between the breeding and non-breeding seasons for the studied species. For each of the 33 species, we subtracted the breeding season range size from the non-breeding season range size, and the breeding season Tyrannidae species richness from the non-breeding season Tyrannidae species richness. We then used one sample *t*-tests to determine if the differences in range size and species richness between the two seasons differed significantly from zero. Evidence that range sizes are larger during the breeding season (positive average difference) would suggest competition declines from the non-breeding to breeding seasons. Evidence that Tyrannidae species richness is lower during the breeding season (negative average difference) would suggest competition declines from the non-breeding to breeding seasons.

All analysis and data manipulations were conducted in R, version 4.1.1 (R Core Team, 2021). GAMMs were fit using the R package *gamm4* (Wood & Scheipl, 2020). One sample *t*-tests were performed using the R package *stats* (R Core Team, 2021). Spatial data preparation and analysis were conducted using the R package *raster* (Hijmans, 2021).

Results

Observed associations with mean temperature, total precipitation, and vegetation greenness followed similar patterns across the annual cycle on average for the 33 tyrant flycatcher species (Fig. 1). For all three environmental variables, associations were highest on average during the breeding season (December to February) and lowest on average during the non-breeding season (June to August; Fig. 1). During the non-breeding season species occurred in regions with slightly higher maximum total precipitation (Fig. 1b) and vegetation greenness (Fig. 1c) across the year. Mean temperature (Fig. 1a) and vegetation greenness (Fig. 1c) on the non-breeding grounds also had higher minimum values across the year. This suggests that the regions where these species spend the non-breeding season are slightly more productive compared to the same time of year in regions where they spend the breeding season.

During the breeding season, the 33 species were associated with regions where temperature, precipitation, and vegetation greenness were on average at their highest annual levels (Fig. 1). In contrast, during the non-breeding season, species occurred in regions where temperatures, precipitation, and vegetation greenness were on average at their lowest annual levels (Fig. 1). Patterns with precipitation differed slightly from those documented for temperature and vegetation greenness. In this case, species associations with precipitation were below the annual maximum on average during the breeding season and above the annual minimum on average during the non-breeding season (Fig. 1b). Thus, seasonal migration for these species resulted in associations with higher temperature, precipitation, and vegetation greenness during the breeding season close to the region's annual maximum, and lower temperature, precipitation, and vegetation greenness during the non-breeding season close to the region's annual minimum with little evidence that species occurred in regions across the annual cycle with different levels of environmental seasonality.

On the other hand, there were significant differences for the 25 tyrant flycatcher species in range size and Tyrannidae species richness between the breeding and non-breeding seasons. The size of species' breeding ranges was larger on average compared to the size of the non-breeding ranges (mean difference = 1,081,105 km^2; 95% CI = 15,265 to 2,146,945 km^2; t_{24} = 2.09, P = 0.0470), suggesting that competition on the non-breeding grounds was higher than on the breeding grounds. Tyrannidae species richness was lower on average within the breeding range compared to non-breeding range (mean difference = -2.91 species; 95% CI = -4.27 to -1.55 species; t_{24} = -4.42, P < 0.001) suggesting competition was higher on the non-breeding grounds than on the breeding grounds.

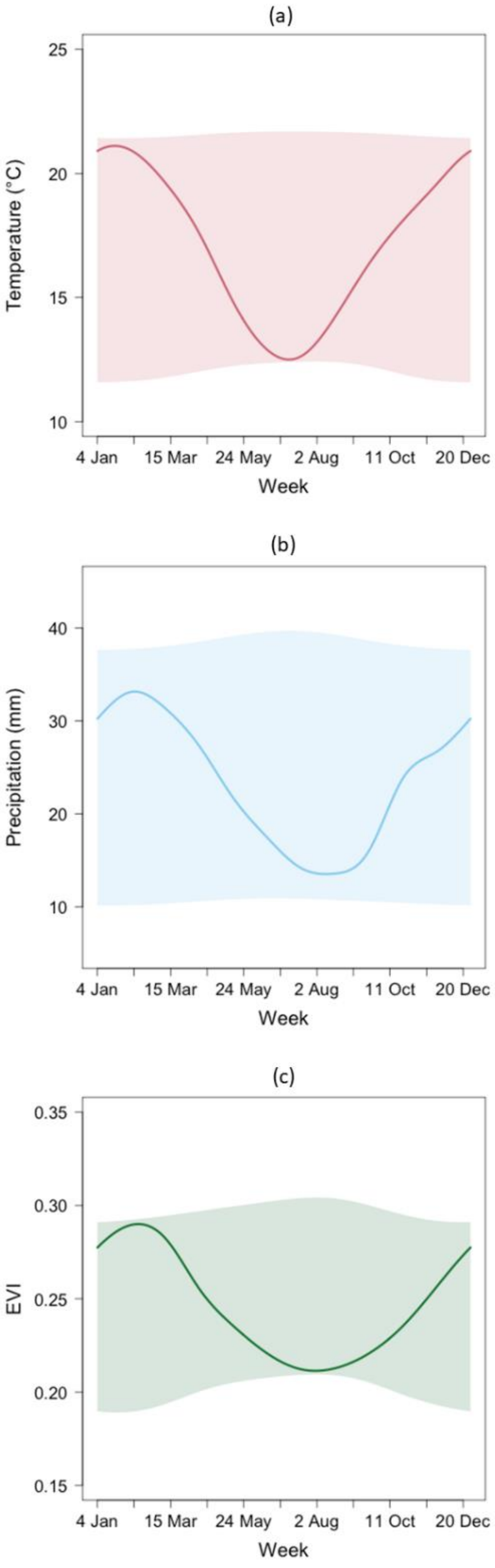


Figure 1. Observed associations with (a) mean temperature, (b) total precipitation, and (c) vegetation greenness (Enhanced Vegetation Index; EVI) for tyrant flycatcher species (n = 33) migrating within South America. The solid lines are the observed association fit using a generalized additive mixed model with species as a random effect. The bands estimate the range of possible associations available to species within their distributional range across the annual cycle. For these species, the breeding season occurs during the months November to January and the non-breeding season occurs during the months May to July.

Discussion

Our findings suggest that seasonal variation in competition on the non-breeding and breeding grounds play an important role in shaping the seasonal distributions of migratory birds in South America, with evidence of higher competition on the non-breeding grounds than on the breeding grounds. Compared to the breeding grounds, the non-breeding grounds were smaller and contained more tyrant flycatcher species. In contrast, we found little evidence that large-scale variation in temperature, precipitation and vegetation greenness drove seasonal bird migration within the region. Species´ weekly associations with seasonal variation in temperature, precipitation, and vegetation greenness did not completely follow our predictions. As we expected, species were associated with the region's annual maximum temperature, precipitation, and vegetation greenness during the breeding season, and with the region's annual minimum temperature, precipitation, and vegetation greenness during the non-breeding season. However, all regions where the species occurred displayed similar seasonality in temperature, precipitation, and vegetation greenness. Thus, if species stayed on their breeding or non-breeding grounds year-round, our findings suggest they would experience a similar range of environmental conditions, indicating that these species are not tracking the green wave of ecological productivity in the spring towards a resource surplus on their breeding grounds.

Our findings support the conclusion that competition is a central mechanism behind the ecology and evolution of seasonal bird migration in South America (Cox, 1968; Rappole & Jones, 2002; Somveille *et al.*, 2018; Powell *et al.*, 2021). Indeed, empirical studies suggest that food for migrant insectivorous birds is limiting at non-breeding sites (Sherry *et al.*, 2005; Brown & Sherry, 2006). In the Neotropics, the non-breeding season coincides with the tropical dry season, when there is a decline in arthropod abundance (Janzen & Schoener, 1968; Pinheiro *et al.*, 2002; Jahn *et al.*, 2010b), intensifying the potential for intra- (Marra, 2000) and inter-specific competition (Powell *et al.*, 2021). In a context of resource limitation, inter-specific competition plays a critical role in structuring migrant-resident bird communities, while intra-specific competition affects annual population dynamics (review in Dhondt, 2012). Highly competitive environments containing high densities of conspecifics and competitor species often have direct and indirect negative effects on fitness

(Gustafsson, 1987; Marra & Holmes, 2001; Powell *et al.*, 2021). Outcompeted individuals on the non-breeding grounds were reported to have lower annual survival, reduced body condition, lower annual return rates (Marra & Holmes, 2001), and higher predation exposure (Perez-Tris & Telleria, 2002). On the breeding ground, higher densities of conspecifics and competitor species negatively affects reproductive output (Gustafsson, 1987) and the number of recruits in the following year (Holmes, 2007), suggesting that breeding in the least crowded areas enhances fitness (Cox, 1968). For the tyrant flycatchers breeding in South America, the larger breeding ranges and the lower species richness on the breeding grounds points to a decrease in competition. If energy availability is the main cue determining species' distributions (Somveille *et al.*, 2018; Ng *et al.*, 2022), then migratory bird species might benefit from an energy surplus during the breeding season. Therefore, migration should be a progressively more favorable strategy, as competition depletes local energy supply on the non-breeding grounds (Somveille *et al.*, 2018).

Contrary to our expectations, we found little evidence that seasonal variation in ecological productivity associates with species' seasonal patterns of occurrence. The green-wave hypothesis was not supported by our findings due to the presence of similar levels of seasonality in environmental conditions, removing any opportunities for species to track increasing vegetation greenness in the spring. These findings differ from previous studies that associated seasonal variation in ecological productivity with migratory bird species occurrence (e.g., La Sorte et al., 2014; Thorup et al., 2017; Youngflesh et al., 2021). These studies were able to demonstrate that migratory bird species that breed in the Northern Hemisphere synchronize their seasonal movements with vegetation phenology, at least during spring migration. In our study, species occurred on the breeding grounds when vegetation greenness was at its annual maximum, as expected. However, we observed an opposite pattern when species occurred on their non-breeding grounds, with vegetation greenness close to its annual minimum. Similarly, migratory bird species that breed in North America and winter in tropics and subtropics occurred in these regions when vegetation greenness was at its annual minimum (La Sorte & Graham, 2021). This pattern diverged from other North American species and could be explained by the inherently low seasonality in vegetation greenness observed in the tropics and subtropics (La Sorte & Graham, 2021). The bird species considered in this study are mostly distributed in tropical and subtropical regions in South America across their annual cycle, which could explain the lack of associations between species' occurrence and vegetation greenness during the full annual cycle. Also, temperatures in South America are milder and less seasonal, compared to Northern America (Faaborg *et al.*, 2010a). South America, as well as other Southern continents, such as Africa and Oceania, occurs mainly in the mid-latitudes and, in the case of South America and Africa, their inland climates are buffered by the sea because of their triangular shape (Dingle, 2008; Faaborg *et al.*, 2010a). For example, the average difference in the mean midwinter temperatures between North and South America at 50° N and S latitude, respectively, is about 15°C, varying from -15°C in North America and 0°C in South America (Chesser, 1994). The species' distributional ranges had minimum mean temperatures above 10°C, and similar degrees of temperature seasonality across the annual cycle, suggesting that temperature might have little influence in the regions where species occur across the annual cycle.

In contrast, continents in the Southern Hemisphere have their climates largely characterized by wet-dry cycles, and winter distributions of migratory birds have often been suggested to be associated with rainfall patterns (Chesser, 2005; Dingle, 2008). Wet dry-cycles are mostly responsible for maintenance and variation of food resources in the Neotropical region, especially arthropods (Pinheiro *et al.*, 2002; Jahn *et al.*, 2010b). Indeed, most tyrant flycatcher species depend on small arthropods and flying insects for food (Fitzpatrick, 1980, 2019), which are less resilient to dry conditions (Janzen & Schoener, 1968) and whose abundance is correlated with rainfall (Jahn *et al.*, 2010b). Tyrant flycatcher species breeding in South America often migrate out of the breeding grounds during the dry season (Jahn *et al.*, 2010b; Lees, 2016) or display local movements within the non-breeding grounds according to rainfall patterns (MacPherson *et al.*, 2018). With the partial migrant Tropical Kingbird (*Tyrannus melancholicus*), individuals with higher energetic demands (i.e., large males) move out of the breeding grounds when its main insect prey decreases in abundance with decreases in rainfall (Jahn *et al.*, 2010a). Our divergent findings suggest that the species evaluated in our study might be less constrained by instantaneous availability of insects. In fact, arthropod availability during the non-breeding season in the Neotropics is dominated by small size classes, which are less seasonal and dependent on rainfall patterns than large, soft-bodied arthropods (review in Greenberg, 1995). Furthermore, patterns of fruit availability are more variable within tropical systems in the region and not necessarily related to precipitation (Jahn *et al.*, 2020). Tyrant flycatcher species that include fruits in their diets, such as species in the genus *Elaenia* (Marini & Cavalcanti, 1998), track fruit availability during the non-breeding season instead of insects, independent of rainfall patterns (Guaraldo *et al.*, 2016; Bravo *et al.*, 2017). The White-crested Elaenia (*Elaenia albiceps chilensis*), for instance, arrive in both the Atlantic Forest and Cerrado (Eastern and Central South America) during the dry season, when there is a low supply of insects, but a high quantity of nutritious fruits (Bravo *et al.*, 2017). The Lesser Elaenia (*Elaenia chiriquensis*) switch from insects to fruits during the non-breeding season (Guaraldo *et al.*, 2016), presumably diminishing dependence on rainfall.

Nevertheless, even though we found no evidence that species actively track vegetation greenness, temperature, and rainfall in their annual cycle, we observed that during the non-breeding season species tend to avoid regions with very low precipitation and that the annual minimum vegetation greenness and temperature in the non-breeding grounds were typically higher than the annual minimum in the breeding grounds. A similar pattern was observed in the Lesser Elaenia where individuals moved from one wintering ground to another when rainfall approached its lowest annual levels (Guaraldo *et al.*, 2021). Although species did not maintain associations with ecological productivity in their annual cycle, during the non-breeding season species likely tracked minimum levels of rainfall, and that in a certain degree they tended to move to a warmer and more productive environment.

Because species ranges are set by both abiotic and biotic factors (Louthan *et al.*, 2015), a virtue of our study is that we associated full annual cycle occurrence data with environmental variables and with proxy variables for species interactions. Yet the role of these factors in structuring distributions across the annual cycle needs to be clarified (Elsen *et al.*, 2017). A step forward would be to include biotic interactions in predictive spatial models to determine if they improve the quality of model predictions, for example, by using co-occurrence data (Urban *et al.*, 2013; Staniczenko *et al.*, 2017). Additionally, combining field data, such as observations of species' ecology and behavior, might help improve understanding on how intra- and inter-specific competition affect migrant distribution throughout the year. Here, we used range size and tyrant flycatcher species richness as proxy variables to represent intra- and inter-specific migration. However, the intensity of interactions may vary among species, with some species being better competitors than others or interacting directly with each other (Dhondt, 2012). Also, intensity may vary within a population, or a community based on density-dependent factors (Sherry *et al.*, 2005). Yet the large spatial extent of our study area, its low levels of survey completeness in eBird (La Sorte & Somveille, 2020), and gaps of knowledge of both basic patterns and mechanisms underlying bird migration in the Neotropics (Jahn *et al.*, 2020), prevented us from using these approaches. Although we could not demonstrate a correlation between macro-scale environmental cues and migrant distribution, a point that should be highlighted is that fine-scale changes in the environment can influence temporal and spatial variation in key resources, and drive seasonal bird distribution. Further studies using fine-scale tracking data, such as geolocator or satellite data, could help improve our understanding on how species occurrence and migration and breeding phenology interact with key environmental cues (e.g., Klaassen *et al.*, 2014; Stutchbury *et al.*, 2016; MacPherson *et al.*, 2018). Finally, our species set does not represent South American bird migration as a whole. Many of the species we studied here migrate within the Austral system, at lower latitudes, and only a few migrate in cooler regions, i.e., at high latitudes of the continent. The latter has distinct evolutionary and ecological patterns from the former (Joseph, 1997), and deserves further investigation.

Conclusion

Our results suggest competition is a central factor driving seasonal bird migration in South America, providing new insights into the ecology and evolution of bird migration in the region. We found evidence that bird species are subject to higher competition on the non-breeding grounds, driving migration out of these areas to the breeding grounds. Our study adds evidence to the hypothesis that bird migration originated as a response by juvenile birds to locate vacant breeding habitat (Cox, 1968; Rappole & Jones, 2002). However, the ecological factors affecting migration in South America differ from those occurring in the Northern Hemisphere. We found that biotic interactions were more likely to affect migration and that large-scale environmental seasonality has a secondary role as an ecological driver of migration in the region. Our findings emphasize the need to better understand the role of competition in the ecology and evolution of bird migration in South America. Finally, even though we have not found an association between climate variables and species' distribution, we highlight that interactions between species are critical to determine species ability to respond to environmental changes, and thus should be considered in predictive models on species response to future global changes (Wisz *et al.*, 2013).

CAPÍTULO 2

Clutch size associates with migration distance in South American land birds

Tamanho de ninhada associa-se com distância de migração em aves terrestres na América do Sul

Abstract

The association between migratory strategies and life history traits helps explain how migratory organisms balance, throughout their annual cycle, the energetic costs and survival risks with the benefits of migration. However, there is no consensus on how life history traits associate with migration, and on migrant's position at the slow-fast continuum of life history. Birds from different geographical regions, and thus subject to different selective pressures, are likely to show different patterns from each other. We used data from egg collections to investigate the relationship between reproduction and migration by assessing reproductive effort (clutch size) and reproductive investment (egg size) of 58 migratory and non-migratory tyrant flycatchers breeding in South America. We first compared clutch and egg size of migrants and non-migrants, and then we assessed how migrants balance these reproductive traits with migration distance. Despite high energy expenditure faced by migrants during their journey, migratory behavior was not a factor influencing clutch size and egg size. On the other hand, migration distance positively correlated with clutch size in migrants. Our study provides evidence that migratory behavior *per se* is a secondary factor affecting species' clutch size and egg size of birds in South America and might not be a determinant to place migrants in the slow-fast continuum of life history. It suggests that migratory distance, instead, correlates with reproductive traits. Thus, among tyrant flycatchers breeding in South America variation in migratory strategies might be more important than migratory behavior in interacting with life history traits. Integrating knowledge on migration and life history strategies is critical for predicting whether and how species migratory behavior could be influenced by human-induced changes in the environment, and for guiding future efforts aimed at the conservation of migratory organisms. This study also demonstrates the potential of museum egg collections to test ecological hypotheses that investigate large-scale variation in breeding parameters of birds.

Keywords: clutch size, egg size, life history, migration distance, oological collections, trade-offs.

Introduction

Birds are the most mobile organisms and have complex and varied forms of migration (Newton, 2010a), and thus are an important model for studies of migration ecology. Migration is an essential component of animal life history (Dingle & Drake, 2007), in which several behavioral, physiological, and morphological features evolved as adaptations to minimize costs and optimize fitness (Roff & Fairbairn, 2007; Blake *et al.*, 2013; Alerstam & Bäckman, 2018; Soriano-Redondo *et al.*, 2020). By traveling between two areas, migrants exploit seasonal peaks in resource abundance at the breeding grounds, and escape from unfavorable conditions, such as food shortage, harsh environmental conditions, and competition (Alerstam *et al.*, 2003). Despite taking advantage of their mobility to optimize energy acquisition, migrants need to cope with several costs in terms of time, energy expenditure and mortality risk (Alerstam & Lindström, 1990). Because of such elevated costs, the energy allocated for migration must be balanced with other activities such as reproduction, self-maintenance, and survival (Sibly *et al.*, 2012; Jahn *et al.*, 2017b; Soriano-Redondo *et al.*, 2020). Thus, life history strategies are expected to predict and mold migratory strategies of birds (Jahn *et al.*, 2020).

Despite many efforts to unveil how migratory species' life history traits interact with migration, there is no consensus on which position migratory birds occupy on the slow-fast continuum of life-history and on how life history traits associate with migration (see figures in Jahn *et al.*, 2020). On one hand, bird migration is suggested to occupy the fast end of the slow-fast continuum of life history (Soriano-Redondo *et al.*, 2020). Migration costs in terms of survival would incur in selective pressures in favor of life history strategies that ensure numerical compensation for migrants, e.g., earlier sexual maturity, and higher annual reproductive outputs (Soriano-Redondo *et al.*, 2020) with larger clutch sizes (Jetz *et al.*, 2008b), compared to non-migrants. On the other side, contrasting studies associate migration with the slow end of this continuum (Møller, 2007; Conklin *et al.*, 2017; Winger & Pegan, 2021). From this perspective, the costs of migrating are offset by its benefits (Buechley *et al.*, 2021), e.g., owing to the possibility of spending more time in benign environments with little abiotic mortality. This could result in positive fitness consequences, with typical characteristics of slow paces of life, e.g., high adult survival rates (Conklin *et al.*, 2017; Winger & Pegan, 2021), and lower rate of senescence (Møller, 2007). These contrasting strategies represent the result of a complex range of associations between intrinsic and extrinsic factors (Jetz *et al.*, 2008b; Sibly *et al.*, 2012; Soriano-Redondo *et al.*, 2020; Winger & Pegan, 2021), which should be accounted for when testing predictions for migratory and life history strategies (Jahn & Cueto, 2012; Jahn *et al.*, 2020).

Migration in the Southern Hemisphere occurs under milder and less seasonal climates and lacks geographical barriers in south-north direction (Chesser, 1994; Faaborg *et al.*, 2010a). These features result in shorter migration distances, higher diversity of migration routes and strategies, and in a larger number of species that undertake partial migrations, compared to systems located in the Northern Hemisphere (Chan, 2001; Jahn *et al.*, 2004; Dingle, 2008). Such patterns suggest that species migrating within the Neotropical region are less time-selected on migration and have a less risky strategy, as they experience lower selective pressures to arrive as early as possible in the breeding grounds (Jahn & Cueto, 2012; Jahn *et al.*, 2020). Migratory strategies that are less constrained in terms of time and adult mortality tend to result in slower and more flexible life-history strategies (Jahn *et al.*, 2020). This contrasts with most birds that breed in the Northern Hemisphere, which usually must cover longer distances (and have a potentially riskier strategy) and, as a consequence, have a tight schedule to fully accomplish activities, such as molting and breeding, within their annual cycle (Jahn & Cueto, 2012).

Large-scale comparative studies on the migration ecology of birds breeding in the Neotropical region are still rare (but see Chesser, 1998; Chesser & Levey, 1998; Heming & Marini, 2015), despite its remarkable variation with respect to routes, patterns of movement and strategies (Jahn *et al.*, 2020). Deepening knowledge on the migratory systems from this region holds a promising opportunity to improve understanding on the evolution of bird migration across the globe (Faaborg *et al.*, 2010a; Jahn & Cueto, 2012). However, the lack of systematized information on migration ecology and biology of Neotropical bird species (Heming *et al.*, 2013; Jahn *et al.*, 2020) represents a potential constraint for large-scale comparative studies in the region. In this regard, the use of secondary data has revealed to be an alternative to overcome this issue (Chesser, 1998; Remsen Jr., 2001; Møller & Fiedler, 2010; Heming *et al.*, 2013; Lees, 2016), and museum data have offered the possibility of covering several species, large spatial scales, and long time series in evolutionary and ecological studies (Collar *et al.*, 2003; Joseph, 2011; Marini *et al.*, 2020). Reproductive data, for example, are readily available in egg collections (Marini *et al.*, 2020), and can be source for studies investigating life history strategies of Neotropical birds.

Here, we aim to investigate how migratory strategies correlate with life-history strategies of tyrant flycatchers (Tyrannidae) breeding and migrating within South America. We tested two hypotheses about the associations between migration and reproductive traits (clutch size and egg size). The first is that migratory behavior (i.e. migratory x non-migratory behavior) does not predict life history strategies because migrants are not severely constrained in terms of time, and mortality risks. The second is that as time devoted to migration increases, in terms of migration distance, birds are selected for faster life history strategies. For this, we compiled reproductive data from dozens of egg collections for 58 migratory and non-migratory tyrant flycatchers breeding within South America (Table S1). First, we compared clutch size and egg size of migratory and non-migratory birds breeding in South America to assess how migratory behavior affects reproduction and test our first hypothesis. Then, we tested the relationships between clutch size and migration distance, and egg size and migration distance, among migrants only, to assess how different migratory strategies interacts with reproductive strategies and test our second hypothesis. Our expectation was that migrants and non-migrants had similar clutch size and egg size compared to non-migrants, and that migration distance will correlate positively with clutch size and decrease egg size. Besides focusing on one taxon and geographical region, we controlled for phylogenetic relatedness, breeding latitude, body mass, and nest type.

Methods

We studied migratory and non-migratory tyrant flycatchers breeding in South America. Using data from egg sets deposited in egg collections, we collected information on clutch size, egg size, and breeding location. After applying several qualitative filters to the data, we estimated the number of eggs in the clutch (i.e., clutch size) and the mean relative egg size of the clutch (i.e., egg size). Accounting for species phylogenetic relatedness, i.e., non-independence between species and their traits, we then modeled the relationship between each reproductive trait assessed (clutch size and egg size) and migratory behavior (i.e., migratory x non-migratory), and between each reproductive trait and migration distance. All modeled associations took into account intrinsic and extrinsic covariates known to affect reproduction.

Species Data Preparation

We selected for this study migratory tyrant flycatchers and their non-migratory congeners for which we had breeding data. The Tyrannidae family is largely distributed throughout the New World and comprises almost one third of the species migrating in the Austral system (Chesser, 1994; Stotz *et al.*, 1996). Also, tyrant flycatchers have their movement and seasonal distribution relatively well described when compared to other groups (e.g., Chesser, 1995; Somenzari *et al.*, 2018), and thus are a valuable model for this study. Defining which species migrate within the Neotropical region is a complex task since many species may have both migratory and non-migratory populations, and populations with both resident and migratory individuals (i.e., partial migrants) (Jahn *et al.*, 2012). So, we made a detailed review on the movement behavior of all tyrant flycatcher species occurring in the region, including the subspecies level, and analyzed their extent-of-occurrence range maps (see details below). We only included taxa (species or subspecies) with at least two clutch records. We excluded the taxa which we could not precisely classify their migratory behavior, either due to the lack of information regarding their distribution or to uncertainty in defining movement behavior, e.g., species that primarily undergo facultative irruptive or nomadic movements and partially migratory species which have both migratory and non-migratory individuals in the same population. The species selected for the study migrate: i) from south temperate region in South America towards northern areas (Austral system), and ii) from south to north within the tropical region in South America (Intratropical system).

Because many museum egg collections have outdated taxonomy, we reviewed the taxonomic classification of each clutch. We started from the oldest species name described in the museum labels or cards and checked synonyms in the chronological order of the museum catalogues from Sclater (1888), Cory and Hellmayr (1927), and Amadon et al. (1979). We then updated species names following eBird/Clements checklist (Clements *et al.*, 2019). Species name from phylogenetic and trait datasets (Jetz *et al.*, 2012; Wilman *et al.*, 2014; BirdLife International & Handbook of the Birds of the World, 2019) were also matched to eBird/Clements checklist classification.

Reproductive Investment Estimates

We estimated clutch size and egg size using egg sets deposited in 30 museum egg collections located in South America, North America, and Europe (see Supplementary Table S2 for museums list). Clutch sizes were defined using the number of eggs in the set. To avoid underestimated and overestimated clutch sizes, and because many sets may be the result of loss, incomplete clutch collecting, splitting for exchange or trade (review in Marini *et al.*, 2020), we applied some filters to the data and double-checked the number of eggs in the set with the information available at the museum labels. First, we excluded all egg sets with one egg, because this clutch size is highly uncommon for tyrant flycatchers. Second, we used estimates of maximum clutch size from the published literature to exclude oddly large clutch sizes. Third, we excluded all sets parasitized either by cowbirds (*Molothrus* sp.) or the Striped Cuckoo (*Tapera naevia*), because both taxa are known to eject host eggs from the nest (Soler, 2018).

We used relative egg size estimates because of the allometric relationship between egg mass and body mass (Huxley, 1927; Martin *et al.*, 2006; Birchard & Deeming, 2015). Relative egg size estimates were taken from the residuals of the linear log relationship between average egg volume per clutch and species' body mass (Figure S1). Egg volume was estimated from digital photographs taken at egg collections. We photographed egg sets together with their museum labels over a black background containing a metal ruler positioned at the height of the egg's largest width. We measured each egg photographed using the plugin Eggtools (Troscianko, 2014) in the software ImageJ (Schneider *et al.*, 2012). Eggtools calculates egg volume from digital images by fitting a model based on egg's curvature, and then calculating its volume by assuming a circular cross-section in the egg and splitting it into 10,000 long-axis slices. Average species' body masses (in grams) were compiled from Wilman et al. (2014) and, when missing, complemented from Birds of the World (Billerman *et al.*, 2020).

We used the clutches containing at least species identification and the locality of collection (Country, State/Province, or Municipality/County). As collectors used to collect egg sets in specific study sites and periods, we avoided including more than two clutches collected at the same period and site by randomly selecting clutches collected in the same site and week. Doubtful identifications were discarded considering the impossibility of checking or determining species identification of the egg sets with skin vouchers (Marini *et al.*, 2020).

Migration Ecology

Data on the migration ecology of Neotropical birds are scarce and sometimes inconclusive or undefined. We estimated migratory behavior, and migration distance using breeding location and several literature sources. Each clutch was classified according to the migratory behavior of the population from where it was collected, i.e., migrant (1) and non-migrant (0). We reviewed species and subspecies descriptions of movement behavior, and range maps available at Birds of the World (Billerman *et al.*, 2020) and Chesser (1995). As there were differences between populations of the same species, we worked at the subspecies level.

Migration distance was calculated by estimating the distance between the breeding location and the centroid of the non-breeding range. The geographical coordinates of the breeding location were extracted from the locality where the egg set was collected described in the museum label. When the description was incomplete and lacked any information about the locality of collection, we estimated the geographical coordinates by overlaying the limits of the locality available (e.g., Country or State/Province) with the species breeding range and extracting the centroid of the resulting polygon. If the polygon had a latitudinal and longitudinal variation of more than five degrees, we excluded the clutch from our analysis. Breeding and non-breeding range maps were derived from a global dataset of the World's bird species distributions containing polygons coded according to species known seasonality (resident, breeding season or non-breeding season) (BirdLife International & Handbook of the Birds of the World, 2019), and when necessary refined to the subspecies level based on the information available at Birds of the World (Billerman *et al.*, 2020) and Chesser (1995).

Intrinsic and Extrinsic Covariates

We included species' nest type and breeding latitude as covariates in the models, considering they affect the reproductive traits assessed in the study. Nest type was included because of its influence on species' reproductive effort and investment (Stearns, 1992; Jetz *et al.*, 2008b; Heming & Marini, 2015). Cavity nesters tend to have larger clutch and egg sizes than open nesters, and species with half-open nests tend to have intermediate clutch and egg sizes (Stearns, 1992; Jetz *et al.*, 2008b; Heming & Marini, 2015). Species nest type data were compiled from Birds of the World (Billerman *et al.*, 2020), and classified according to Jetz et al. (2008b): 1 = open, 2 = half-open, and 3 = closed nest.

Breeding latitude was included to account for the positive relationship between the latitudinal gradient and clutch size and the positive correlation with egg size (Stearns, 1992). We expected that latitude would affect migrants and non-migrants differently, as the former shifts geographical position during the non-breeding season. Thus, we assessed the interaction between breeding latitude and migratory behavior, as well. Breeding latitude was obtained from the geographical coordinates of the breeding location estimated as described previously. For analytical purposes, we adopted the absolute breeding latitude (herein breeding latitude).

Statistical Analyses

We used phylogenetic generalized least squares (PGLS) regression (Grafen, 1989; Pagel, 1999a) to model the relationships between clutch size and migratory behavior and migration distance, and relative egg size migratory behavior and migration distance, accounting for non-independence between species.

Potential phylogenetic signal in the response variable was controlled based on the estimation of the parameter Pagel's lambda (*λ*), which represents the degree to which the phylogenetic correlation matrix follows the Brownian motion model of evolution (Pagel, 1999b; Freckleton *et al.*, 2002). Values of λ range between 0 and 1, where 1 indicates that the trait of interest has evolved consistently with the Brownian motion model and has similar values among related species, and 0 indicates that trait values are unrelated among species. To account for intraspecific variation, we added into the phylogenetic tree, at the tip of each species branch, a hard polytomy with branches of length zero corresponding to one individual clutch each (Heming & Marini, 2015). Species phylogenetic information was extracted from Jetz et al. (2012). A consensus tree was inferred from a sample of 1,000 full backbone trees for the Tyrant flycatchers available in the Bird Tree website (birdtree.org). The final phylogenetic tree was obtained after we removed the branches corresponding to the species that we were not interested in. The phylogenetic correlation matrices, λ values, and the phylogenetic tree were estimated using the R package "*ape*" (Paradis & Schliep, 2019).

Each PGLS full model was first fitted with Residual Maximum Likelihood – REML, and then validated according to the assumptions of normality of the residuals, and homogeneity of the variances. We fitted models using the R package "*nlme*" (Pinheiro *et al.*, 2020). Before fitting the models, we inspected the distribution of each predictor to check for outliers and heteroscedasticity. We z-transformed all the response variables and predictors to get comparable coefficients (Mundry 2014). Predictors were checked for evidence of multi-collinearity following recommendations in Zuur et al. (2010). For this, we calculated variance inflation factors (VIFs) for each model using the R package *"car"* (Fox *et al.*, 2021). For information on potential multi-collinearity among predictors, see Table S3.

Results

We analyzed 58 bird species breeding in South America, 42 full or partial migratory species, and 16 non-migratory species (Table S1). Reproductive data were collected from a total of 957 clutches (migrant: n = 470 clutches; non-migrant: n = 487 clutches). Egg size values were estimated from part of this total, i.e., the clutches we photographed and measured (n = 813 clutches; migrant: n = 392 clutches; non-migrants: n = 421). Clutch size was obtained from 813 clutches (migrant: n = 408 clutches; non-migrant: n = 405), following the exclusion criteria we established previously.

Migratory behavior did not predict differences in the reproductive traits assessed between migrants and non-migrants. Both clutch size (Model I) and relative egg size (Model II) had no relationship with migratory behavior (Table 1), suggesting that migratory behavior is not a determinant factor influencing bird reproductive strategies, concerning clutch size and egg size. Breeding latitude had a positive relationship with clutch size, independently of migratory behavior and nest type (Table 1), and relative egg size was affected by nest type, independently of migratory behavior and breeding latitude (Table 1). The interaction between migratory behavior and breeding latitude had no relationships with clutch size and relative egg size.

Among migrants, clutch size had a positive relationship with migration distance, while relative egg size had no relationship with migration distance. Clutch size increased as migration distance increased and did not respond to breeding latitude or nest type (Model III; Figure 1A, Table 2). Relative egg size, again, was predicted only by nest type, where open nest has a tendency to have smaller egg than half-open nests (Model IV; Figure 1B, Table 2).

The extent of phylogenetic signal of the variables was strong in all models (Tables 1 and 2). Values from clutch size models were the lowest possibly because of the influence of other extrinsic factors on clutch size patterns. However, the λ values encountered in the study reflects an expected pattern in our dataset, i.e., that the reproductive traits values evaluated here have strong influence of phylogenetical factors. This suggests that, on average, closely related species have more similar clutch size and relative egg size than more distantly related species.

Table 1. Parameter estimates and tests from phylogenetic generalized least squares (PGLS) regression of clutch size (Model I) and relative egg size (Model I) as a function of migratory behavior for 58 migratory and non-migratory tyrant flycatcher species (see Table S1). Parameters in bold have significant coefficients. Relative egg size is defined as the residual of a simple linear regression between the log estimates of the average egg volume and species' body mass. The breeding latitude and nest type were included in the PGLS regression models as covariates. All response and predictor variables were standardized (see Methods for details). *P*-values < 0.05 are shown in bold.

Model/ Parameters	*k*	Estimate	SE	*t*	*P*
Model I (clutch size)	λ	0.44			
Intercept	β	-0.30	0.28	-1.07	0.2834
Migratory behavior	β	-0.08	0.10	-0.87	0.3860
Breeding latitude	**β**	**0.21**	**0.05**	**3.73**	**0.0002**
Nest type (half-open-closed)	β	0.32	0.21	1.51	0.1324
Nest type (half-open-open)	β	0.08	0.16	0.53	0.5937
Mig. behavior:Breeding latitude	β	-0.09	0.09	-1.02	0.3071
Model II (relative egg size)	λ	0.92			
Intercept	β	0.28	0.22	1.27	0.2042
Migratory behavior	β	0.00	0.03	0.02	0.9816
Breeding latitude	β	0.00	0.01	0.34	0.7356
Nest type (half-open-closed)	β	0.00	0.11	-0.03	0.9724
Nest type (half-open-open)	β	-0.35	0.06	-5.25	**<0.0001**
Mig. behavior:Breeding latitude	β	0.00	0.03	0.06	0.9506

Note: Model I: n = 53 species, 813 clutches (408 migrants, 405 non-migrants); Model II: n = 58 species, 813 clutches (392 migrants, 421 non-migrants).

Table 2. Parameter estimates and tests from phylogenetic generalized least squares (PGLS) regression of clutch size (Model III) and relative egg size (Model IV) as a function of migration distance for 37 migratory tyrant flycatcher species (see Table S1). Parameters in bold have significant coefficients. Relative egg size is defined as the residual of a simple linear regression between the log estimates of the average egg volume and species' body mass. The breeding latitude and nest type were included in the PGLS regression models as covariates. All response and predictor variables were standardized (see Methods for details). *P*-values < 0.05 are shown in bold.

Model/ Parameters	*k*	Estimate	SE	*t*	*P*
Model III (clutch size)	λ	0.48			
Intercept	β	-0.41	0.35	-1.17	0.2415
Migration distance	β	0.18	0.08	2.23	**0.0262**
Breeding latitude	β	0.01	0.07	0.13	0.8982
Nest type (half-open - closed)	β	-0.22	0.29	-0.75	0.4523
Nest type (half-open - open)	β	0.07	0.20	0.38	0.7004
Model IV (relative egg size)	λ	0.90			
Intercept	β	0.50	0.25	2.00	0.0458
Migration distance	β	0.05	0.03	1.35	0.1787
Breeding latitude	β	-0.01	0.03	-0.39	0.6938
Nest type (half-open - closed)	β	-0.02	0.13	-0.15	0.8826
Nest type (half-open - open)	β	-0.50	0.08	-6.50	**<0.0001**

Note: Model III: n = 33 species, 408 clutches; Model IV: n = 37 species, 392 clutches.

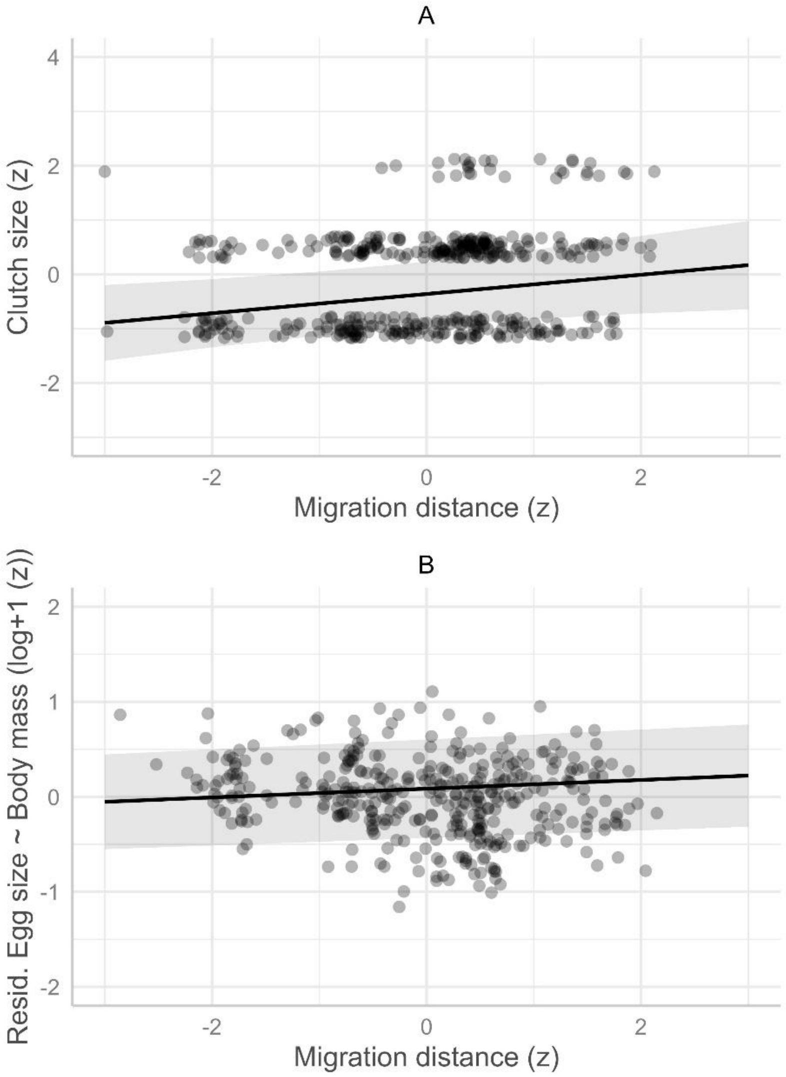


Figure 1. Observed (points) and predicted (line) values with 95% confidence intervals (grey fill) from phylogenetic generalized least squares (PGLS) regression of (**A**) clutch size and (**B**) relative egg size as a function of migration distance. The relationships were fit using data from 408 clutches of 33 species of migratory tyrant flytcatchers, for the clutch size model, and 392 clutches and 37 species, for the relative egg size model. Breeding latitude and nest type were included as covariates in the PGLS regression models. For additional details see Table 2. All response and predictor variables were standardized (see Methods for details).

Discussion

Our study provides evidence that clutch size and egg size of tyrant flycatchers breeding within South America have no relationship with migratory behavior, i.e., clutch size and egg size migrants and non-migrants are not different between each other. This could suggest that migratory behavior *per se* plays a secondary role in driving reproductive strategies of birds and might not be determinant to place migrants in the slow-fast continuum of life history. This result corroborates with our hypothesis that migrants are not severely constrained in terms of time, and mortality risks, compared to non-migrants. On the other side, we found a positive association between migration distance and clutch size. Aligned to our predictions, this could suggest that migratory strategies tyrant flycatchers breeding in South America, instead, might constrain migrants in terms of time and pressure reproduction in the direction of a faster strategy.

Our results suggest that despite migrants embrace a challenging and costly journey (Alves *et al.*, 2013; Lok *et al.*, 2015), migratory behavior may not be a factor that molds clutch size and egg size of birds. The intrinsic and extrinsic factors evaluated in the study explained, at least in part, the variation observed in clutch size and egg size. A study analyzing the determinants of clutch size variation in South America also failed to find an association of migratory behavior with clutch size, which was mainly explained by phylogenetic relatedness and habitat type (Yom-Tov *et al.*, 1994). In contrast, other studies suggest that migratory behavior is as much important as intrinsic factors such as body mass, and developmental mode; or extrinsic factors such as latitude, and climate to determine variation in life history traits (Böhning-Gaese *et al.*, 2000; Heming & Marini, 2015; Soriano-Redondo *et al.*, 2020). However, intrinsic and extrinsic factors affecting life history traits do not act in isolation, and may interact with each other (Jetz *et al.*, 2008b). Migratory behavior is closely related to seasonality and breeding latitude (Jetz *et al.*, 2008b; Winger & Pegan, 2021), and migratory species are likely to exhibit life history traits associated with these factors instead. Indeed, climatic factors are not responsible for driving migration in tyrant flycatchers (Sousa et al., Capítulo 1; but see Joseph, 1996), or determining clutch size of passerines (Yom-Tov *et al.*, 1994) in South America, possibly because of the milder and less seasonal climates found in the continent (Chesser, 1994; Faaborg *et al.*, 2010a). Also, South

America, as well as other Southern Hemisphere continents, lays in mid- rather than high-latitude compared to continents located in the Northern Hemisphere (Yom-Tov *et al.*, 1994). This suggests that birds migrating with in South American probably experience lower selective pressures due to weak climatic effects, which could explain the lack of correlation observed between migratory behavior and the reproductive traits analyzed.

On the other hand, the positive association between migration distance and clutch size suggests that time and energetic constraints can affect life history traits of South American migrants. Migration distance may affect the energetic balance of migrants owing to time constraints for completing all life-history events in the annual cycle (i.e., migration, reproduction and molting) (Jahn *et al.*, 2013a, 2017c; Paiva & Marini, 2013) and to the high amount of energy necessary for the journey (Wikelski *et al.*, 2003). Also, it may increase stochastic mortality during non-stationary periods due to longer exposure to predation and adverse environmental conditions (Klaassen *et al.*, 2014; Lok *et al.*, 2015). Several studies have suggested that migration distance incur in costs (Alerstam *et al.*, 2003; Klaassen *et al.*, 2014) that select for faster life history strategies (Alerstam *et al.*, 2003; Soriano-Redondo *et al.*, 2020). From this perspective, the positive association between clutch size and migration distance indicate that time and energetic constraints, as well as higher mortality risks, could select for faster life history strategies.

From another perspective, flying longer distances may enable reaching better areas in terms of availability of resources to breed or spend winter and imply in positive fitness consequences (Cox, 1968; Winger & Pegan, 2021). Studies have demonstrated that birds spending the breeding season in regions with higher availability of resources and/or lower competition have larger clutch sizes, fledge more young, and have lower nest predation (Gustafsson, 1987; Arcese & Smith, 1988; Martin & Martin, 2001; Holmes, 2007; Sousa et al. in prep., Capítulo 3). Also, favorable conditions experienced in low competitive non-breeding grounds are associated with larger clutch sizes later on the breeding season (Sousa et. al in prep, Capítulo 3). Thus, increasing investment in migration by flying longer distances could be a factor favoring chances of increasing reproductive output, and not necessarily a strategy that causes higher mortality (and larger clutch sizes) of migrants and pressures them towards the faster end of the slow-fast gradient. Corroborating with this argument, several studies have associated long distance migrations with high adult survival rates, because of the benefits provided by accessing high quality habitats (Böhning-Gaese et al., 2000; Winger & Pegan, 2021). This pattern has been more commonly reported for long-distance migrants (Böhning-Gaese *et al.*, 2000; Møller, 2007), including boreal migrants breeding in highly seasonal environments and flying extreme long distances (Conklin *et al.*, 2017; Winger & Pegan, 2021). Nevertheless, long distance migrations are least common in South America (Faaborg *et al.*, 2010a), and represent a small fraction of the species addressed in this study. This evidence suggest that migration distance is an important factor interacting with life history traits of migratory birds, and could increase chances of birds to have higher reproductive output.

Our study brought useful insights to the understanding of migration ecology in the Neotropics, however, our data enabled us to evaluate only two aspects of reproduction. Linking other traits to the parameters analyzed, such as the number of broods per year, adult survival, and longevity should support broader conclusions (Böhning-Gaese *et al.*, 2000; Soriano-Redondo *et al.*, 2020; Winger & Pegan, 2021). Additionally, including factors covarying with migratory behavior, such as developmental rate and diet, are essential to be addressed in future studies (Böhning-Gaese *et al.*, 2000; Cooney *et al.*, 2020; Minias & Włodarczyk, 2020). Our group-specific analysis, though, prevented us to make certain comparisons. Tyrant flycatchers in the Neotropics are altricial, mostly invertivores, and predominantly migrate in the Austral system (Chesser, 1994; Fitzpatrick, 2019). Nevertheless, studying one family alone enabled us to control cofounding effects that could have arisen from the variation in life history traits between different taxa. Besides, it helped coping with the limitations of data availability and knowledge on migration ecology in the region (Jahn *et al.*, 2020). Finally, comparisons with other migration systems (e.g., New World and Southern Hemisphere) could allow assessing different selective pressures that affect migrants and determine migratory strategies (Jahn & Cueto, 2012).

Conclusion

In conclusion, our study provides evidence that migratory behavior *per se* is a secondary factor affecting species' clutch size and egg size of birds in South America and might not be determinant to place migrants in the slow-fast continuum of life history. On the other side, it suggests that clutch size associates with migration distance, which could be either pre-adaptations or evolutionary consequences of time and energetic costs migration. However, comparative studies accounting for the energetic costs and benefits associated to migration, and the interaction with other life history traits, such as adult survival, longevity, and annual fecundity would help improving this understanding and enable further conclusions. As final remarks, we highlight that our study contributed to integrate knowledge on migration, and life history strategies, which is critical for predicting whether and how species could be affected by human-induced changes in the environment, and for guiding future efforts aimed at the conservation of migratory organisms. Also, this study consistently supported predictions on bird breeding biology by using data from museum egg collections, evidencing the potential of these kind of data to test ecological hypotheses and explore large-scale patterns in breeding traits of birds.

CAPÍTULO 3

Seasonal variation in competition affects clutch and egg size in migratory South American land birds

Variação sazonal na competição afeta o tamanho da ninhada e do ovo em aves migratórias terrestre da América do Sul

Abstract

Evidence suggests that competition across the annual may have several negative consequences for fitness, which can be expressed in the current phase or subsequently in the annual cycle. Migratory birds are thought to migrate to escape competition on the non-breeding grounds and avoid inclement weather on the breeding grounds and to breed in regions where the chances of survival and reproductive success are higher. We tested if clutch size and egg size responded to seasonal variation in competition in migratory birds breeding in South America. We compiled data on clutch size and relative egg size for 14 tyrant flycatcher species from museum egg collections and correlated them with the differences in species' range size estimates and in tyrant flycatcher species richness estimates between breeding and non-breeding seasons to test our competition predictions. We found evidence that larger breeding grounds relative to the non-breeding grounds, selects for larger clutch sizes, but smaller eggs. In contrast, decreasing species richness on the breeding grounds relative to the non-breeding grounds was associated with smaller clutch sizes. However, this could be the result of the higher competition in the non-breeding grounds, since the tyrant flycatcher species richness in the non-breeding ranges was on average higher than at the breeding ranges. We found evidence that the seasonal difference in competition between the breeding and non-breeding grounds enable species to increase clutch size and increase reproductive potential, presumably because of a surplus of resources provided by decreasing competition on the breeding grounds. Additionally, there is evidence that the high competition experienced during the non-breeding season affect subsequent reproduction by decreasing clutch size.

Keywords: Austral migration, clutch size, egg size, intra-specific competition, inter-specific competition, life history, Neotropical birds, seasonal bird migration.

Introduction

Birds are thought to migrate to escape competition on the non-breeding grounds and avoid inclement weather on the breeding grounds and to breed in regions where the chances of survival and reproductive success are higher (Cox, 1968; Rappole & Jones, 2002). The ecological and fitness consequences of inter- and intra-specific competition have been broadly documented in the literature, both for migratory and non-migratory birds (Marra & Holmes, 2001; Martin & Martin, 2001; Dhondt, 2012). However, most studies are local in extent, and focus on isolated communities or populations (e.g., Gustafsson, 1987; Marra & Holmes, 2001; Martin & Martin, 2001; Norris *et al.*, 2004; Powell *et al.*, 2021). Large-scale studies assessing the consequences of competition on bird communities are rare (but see Elsen *et al.*, 2017; Somveille *et al.*, 2018), and significant knowledge gaps remain in our understanding of the large-scale ecological patterns behind seasonal bird migration.

Competition during the breeding period may have several negative consequences for fitness, which can directly or indirectly affect reproductive success. Experimental studies that increase food supplies or remove conspecifics or remove competing species suggest that bird species breeding under reduced competition have larger clutch sizes, fledge more young, and have lower nest predation (Gustafsson, 1987; Arcese & Smith, 1988; Martin & Martin, 2001; Holmes, 2007). Additionally, indirect evidence suggests an inverse relationship between competition and reproductive success. As competition decreases there is an increase in the availability of preferred nest sites (i.e., sites less exposed to predation or with higher availability of nutritious and diverse food resources), higher nest feeding rates, larger fledglings, and a higher number of breeding attempts (Gustafsson, 1987; Martin & Martin, 2001; Perez-Tris & Telleria, 2002; Holmes, 2007). Thus, migrating to less competitive regions can provide a surplus of resources and increase fitness, and be a progressively more favorable strategy as competition depletes local energy supplies (Alves *et al.*, 2013; Somveille *et al.*, 2018; Winger *et al.*, 2019). However, reproductive success can also benefit through density-dependent effects, for example, through a reduction in nest predation mediated by higher nest (and species) diversity (Marini, 1997).

Similarly, migrants subject to higher competition in the non-breeding grounds may have fitness consequences that may carry-over to subsequent phases of the annual cycle (Akresh *et al.*, 2019; Powell *et al.*, 2021). Competition at the non-breeding grounds may force migratory species to occupy marginal habitats (Perez-Tris & Telleria, 2002), which may affect negatively annual survival, and annual return rates (Marra & Holmes, 2001; Powell *et al.*, 2021). Habitat limitation may also negatively affect migrant's physical condition and delay spring departure from the non-breeding grounds (Marra *et al.*, 1998; Akresh *et al.*, 2019; Powell *et al.*, 2021). These aspects may in turn lead to later arrival in the breeding grounds and to lower reproductive success (Norris *et al.*, 2004; Akresh *et al.*, 2019). Birds wintering in better quality territories, in contrast, may arrive earlier in the breeding grounds, guaranteeing better territories and more time and energy to reproduce (Tonra *et al.*, 2011; Bejarano & Jahn, 2018).

Bird migration in South America is thought to be mainly driven by competition, while large-scale climate variation exerts little influence on the geographical distribution patterns of species during their annual cycle (Capítulo 1; Sousa et al., in prep). Tyrant flycatcher species migrating and breeding within South America tend to have larger breeding ranges and lower species richness at the breeding grounds, compared to the non-breeding ranges, suggesting a seasonal decline in competition towards the breeding grounds (Capítulo 1; Sousa et al., in prep). Thus, higher seasonal variation in competition is expected to result in a surplus of resources in the breeding grounds, and potentially in a fitness increase.

Our study aims to assess the correlation between seasonal variation in competition and reproduction among 14 tyrant flycatcher species (Appendix S1; Table S1.1) that breed and migrate within South America. Because reproductive traits, such as clutch size and egg size, represent the outcomes of different interactions between individual life-history traits and its environment (Ricklefs, 2000), they have been useful to improve knowledge on how migratory bird species optimize migration, and on the potential energetic constraints experienced across the annual cycle (Norris *et al.*, 2004; Bejarano & Jahn, 2018; Akresh *et al.*, 2019; Winger & Pegan, 2021). We used two proxy variables to assess competition: seasonal variation in species' range size (i.e., the difference between species' breeding and the non-breeding ranges) and seasonal variation in tyrant flycatcher species richness in their seasonal ranges (i.e., the difference in species richness of tyrant flycatcher species within species' breeding and non-breeding ranges) (see Capítulo 1). Thus, we evaluated the response of each reproductive parameter (clutch size and egg size) to seasonal variation in each species' range size and to the seasonal variation in tyrant flycatcher species richness in their seasonal ranges. Our expectation is that clutch size and egg size will be on average larger as competition in the breeding grounds decreases, i.e., as species' breeding ranges increase in size and species' breeding ranges contain fewer tyrant flycatcher species, compared to their non-breeding ranges.

Methods

We compiled data on two reproductive traits, clutch size and relative egg size, for 14 tyrant-flycatcher species that breed and migrate within South America from museum egg collections (for details see Sousa et al., Capítulo 2). We used species' seasonal range estimates from Sousa et al. (Capítulo 1) to estimate seasonal variation in intra-specific competition, based on differences in the size of species' breeding and non-breeding ranges, and seasonal variation in inter-specific competition, based on tyrant flycatcher species richness within species' breeding and non-breeding ranges. We then examined the relationship between the two reproductive traits and seasonal variation in intra- and inter-specific competition after accounting for species phylogenetic relatedness; i.e., the non-independence between species and their traits, and other intrinsic and extrinsic factors. To dissociate the effects of competition at the breeding and at the non-breeding seasons, we also tested the relationship between the two reproductive traits and intra- and inter-specific competition in each season.

Species Data Preparation

We selected for analysis tyrant flycatcher (Tyrannidae) species that breed and migrate within South America for which we had breeding data (Table S1.1). Species selection followed the same procedure of Sousa et al. (Capítulo 1), and comprised species with clear seasonal movements (i.e., full migrants), and partial migrants that mostly displayed migratory behavior through their annual range. In addition, we included species with at least two clutch records in our reproductive dataset (see below).

Reproductive Investment Estimates

We estimated clutch size and relative egg size using 436 egg sets deposited in 27 museum egg collections located in South America, North America, and Europe compiled in Capítulo 2. Clutch size was estimated using 394 clutches, and relative egg size was estimated using 285 clutches. Clutch size was defined using the number of eggs in the set. To avoid under or over estimating clutch size due to egg loss, incomplete egg collecting, or splitting for exchange or trade (review in Marini *et al.*, 2020) we applied filters to the data and confirmed the number of eggs in the set with the museum labels. We first excluded all egg sets with one egg, because this clutch size is highly uncommon for tyrant flycatchers. Second, we used estimates of maximum clutch size from the literature to exclude unreasonably large clutch sizes.

We used relative egg size estimates because of the allometric relationship between egg mass and body mass (Huxley, 1927; Martin *et al.*, 2006; Birchard & Deeming, 2015). Relative egg size estimates were taken from the residuals of the linear log relationship between average egg volume per clutch and species' body mass (see Appendix S1, Figure S1.1). Average egg volume was estimated previously in Capítulo 2 from a digital photograph of the clutch taken at the collections. We photographed the clutches together with their museum labels over a black background containing a metal ruler positioned at the height of the egg's largest width. We measured each egg photographed using the plugin Eggtools (Troscianko, 2014) in the software ImageJ (Schneider *et al.*, 2012). Eggtools calculates egg volume from digital images by fitting a model based on egg's curvature, and then calculating its volume by assuming a circular cross-section in the egg and splitting it into 10,000 long-axis slices. Average species' body masses (in grams) were compiled from Wilman et al. (2014) and, when missing, complemented from Birds of the World (Billerman *et al.*, 2020).

All clutches parasitized either by cowbirds (*Molothrus* sp.) or the Striped Cuckoo (*Tapera naevia*) were excluded, because both taxa are known to eject host eggs from the nest (Soler, 2018). As collectors used to collect egg sets in specific study sites and periods, we avoided including more than two clutches collected at the same period (week) and site. Finally, doubtful identifications were discarded considering the impossibility of checking or determining species identification of the egg sets with skin vouchers (Marini *et al.*, 2020).

Because many museum egg collections have outdated taxonomy, we reviewed the taxonomic classification of each clutch following the same procedures of Capítulo 1. We started from the oldest species name described in museum labels or cards and checked synonyms in the chronological order of the museum catalogues from Sclater (1888), Cory and Hellmayr (1927), and Amadon et al. (1979). We then updated species names following eBird/Clements checklist (Clements *et al.*, 2019). Species name from phylogenetic and trait datasets (Jetz *et al.*, 2012; Wilman *et al.*, 2014; BirdLife International & Handbook of the Birds of the World, 2019) were also matched to eBird/Clements checklist classification.

Competition

We used the differences in the size of species' breeding and non-breeding ranges and in species richness of tyrant flycatchers between each species' breeding and non-breeding ranges as parameters to estimate seasonal differences in competition for the 14 species. Data were retrieved from Sousa et al. (Capítulo 1).

Intrinsic and Extrinsic Covariates

We included species' nest type and breeding latitude as covariates in the models, considering they affect the reproductive traits assessed in the study. Nest type was included because of its influence on species' reproductive effort and investment (Stearns, 1992; Jetz *et al.*, 2008b; Heming & Marini, 2015). Cavity nesters tend to have larger clutch and egg sizes than open nesters, and species with half-open nests tend to have intermediate clutch and egg sizes (Stearns, 1992; Jetz *et al.*, 2008b; Heming & Marini, 2015). Species nest type data were compiled from Birds of the World (Billerman *et al.*, 2020), and classified according to Jetz et al. (2008b): 1 = open, 2 = half-open, and 3 = closed nest.

Breeding latitude was included to account for the positive relationship between the latitudinal gradient and clutch size and the positive correlation with egg (Stearns, 1992). It was obtained from the geographical coordinates of the breeding location estimated as described in Capítulo 2. For analytical purposes, we adopted the absolute breeding latitude (herein breeding latitude).

Analysis

We used phylogenetic generalized least squares (PGLS) regression (Grafen, 1989; Pagel, 1999a) to model the relationships between clutch size and intra- and inter-specific competition, and relative egg size and intra- and inter-specific competition. We report the phylogenetic signal in the response variables using Pagel's lambda (λ), which estimates the degree to which the phylogenetic correlation matrix follows the Brownian motion model of evolution (Pagel, 1999a; Freckleton *et al.*, 2002). Values of λ range between 0 and 1, where 1 indicates that the trait of interest has evolved consistently with the Brownian motion model and has similar values among related species, and 0 indicates that trait values are unrelated among species. To account for intraspecific variation, we added to the tip of each branch of the phylogenetic tree a hard polytomy with branches of length zero corresponding to one individual clutch each (Heming & Marini, 2015). Species phylogenetic information was acquired from Jetz et al. (2012). A consensus tree was inferred from a sample of 1,000 full backbone trees for the Tyrant flycatchers available in the Bird Tree website (birdtree.org). The final phylogenetic tree was obtained after we removed the branches corresponding to the species that we were not interested in. The phylogenetic correlation matrices, λ values, and the phylogenetic tree were estimated using the R package "*ape*" (Paradis & Schliep, 2019).

Each PGLS full model was first fitted with Residual Maximum Likelihood (REML) and then validated according to the assumptions of normality of the residuals, and homogeneity of the variances. We fitted models using the R package "*nlme*" (Pinheiro *et al.*, 2020). Before fitting the models, we inspected the distribution of each predictor to check for outliers and heteroscedasticity. We *z*-transformed all the response variables and predictors to get comparable coefficients (Mundry 2014). Predictors were checked for evidence of multi-collinearity following recommendations in Zuur et al. (2010). For this, we calculated variance inflation factors (VIFs) for each model using the R package *"car"* (Fox *et al.*, 2021).

We used the same approach from Capítulo 1 to assess if range sizes and Tyrannidae species richness differed significantly between the breeding and non-breeding seasons for the studied species. For each species, we subtracted the breeding season range size from the non-breeding season range size, and the breeding season Tyrannidae species richness from the non-breeding season Tyrannidae species richness. We then used one sample *t*-tests to determine if the differences in range size and species richness between the two seasons differed significantly from zero.

All analysis and data manipulations were conducted in R, version 4.1.1 (R Core Team, 2021). Spatial data manipulations and summarizing reported in the methods were made using the R package *"raster"* (Hijmans, 2021). For details on the estimates for species' seasonal ranges, and tyrant flycatcher species richness at each range, see Table S1.1.

Results

Species' breeding ranges were larger on average than their non-breeding ranges (mean difference = 308,664 km^2; 95% CI = 47,033 to 570,294 km^2; $t_{13} = 2.55$, $P = 0.0242$). Similarly, tyrant flycatcher species richness was lower on average within the breeding range compared to non-breeding range (mean difference = -3.76 species; 95% CI = -5.82 to -1.70 species; $t_{13} = -3.95$, $P = 0.0016$). This suggests that competition declines on average from the non-breeding to the breeding seasons.

Clutch size had a positive association with seasonal variation in range size, i.e., the difference between species' breeding and non-breeding range sizes (Figure 1A; Table 1), and with breeding range size (Table 2), and no relationship with non-breeding range size (Table 3). These results suggest that as competition on the breeding grounds decreased relative to the non-breeding grounds, i.e., the breeding grounds increased in size, species invested in larger clutches.

In contrast, clutch size had a positive relationship (Figure 2A) with seasonal variation in tyrant flycatcher species richness, i.e., the difference between tyrant flycatcher species richness on the breeding grounds and the non-breeding grounds (Table 1). However, we found a marginal negative relationship of clutch size with species richness on the non-breeding grounds (Table 3) and no relationship on the breeding grounds (Table 2). Together, these results suggest that as species richness decreased in the non-breeding grounds relative to the breeding grounds, clutch size was negatively affected subsequently on the breeding season.

Relative egg size had a positive association with the seasonal variation in range size (Figure 1B; Table 1), and no relationships with seasonal variation in species richness (Table 1), or with range sizes and species richness within seasons (Tables 2 and 3). This suggests that as competition on the breeding grounds decreased relative to the non-breeding grounds, besides investing in larger clutches, species had smaller eggs. However, range size or species richness *per se* do not correlate with egg size. Other factors, i.e., nest type and phylogenetic signal, affected egg size instead (Tables 2 a 3).

The extent of phylogenetic signal of the variables assessed in the relative egg size models were strong (Tables 1-3). On average, closely related species had more similar relative egg size values than more distantly related species. In contrast, the clutch size model had a low phylogenetic signal, and thus low correlation among species (Table 1-3). Clutch size phylogenetic signal was low possibly because of the influence of factors not associated to phylogeny, such as extrinsic factors related to climate.

Table 1. Parameter estimates and tests from phylogenetic generalized least squares (PGLS) regression of clutch size and relative egg size as a function of estimated intra- and inter-specific competition for 14 migratory tyrant flycatcher species (see Table S1). Models fit clutch size (Model I) and relative egg size (Model II) as a function of the seasonal difference between species' breeding and non-breeding ranges (Breeding RS – Non-breeding RS) and to the seasonal difference in tyrant flycatcher species richness between species' breeding and non-breeding ranges (Breeding SR – Non-breeding SR). Relative egg size is defined as the residual of a simple linear regression between the log estimates of the average egg volume and species' body mass. The breeding latitude and nest type were included in the PGLS regression models as covariates. All response and predictor variables were standardized (see Methods for details). *P*-values < 0.05 are shown in bold.

Model/ Parameters	*k*	Estimate	SE	*t*	*P*
Model I (clutch size)	λ	0.09			
Intercept	β	-0.04	0.41	-0.09	0.9286
Breeding RS – Non-breeding RS	β	0.22	0.10	2.24	**0.0258**
Breeding SR – Non-breeding SR	β	0.20	0.06	3.31	**0.0010**
Latitude of breeding	β	0.10	0.06	1.63	0.1036
Nest type (half-open - closed)	β	-0.47	0.33	-1.43	0.1539
Nest type (half-open - open)	β	-0.16	0.33	-0.50	0.6187
Model II (relative egg size)	λ	0.96			
Intercept	β	-0.35	0.85	-0.41	0.6801
Breeding RS – Non-breeding RS	β	-0.37	0.18	-2.00	**0.0466**
Breeding SR – Non-breeding SR	β	0.16	0.09	1.74	0.0831
Latitude of breeding	β	0.04	0.03	1.41	0.1603
Nest type (half-open - closed)	β	0.30	0.25	1.20	0.2323
Nest type (half-open - open)	β	0.16	0.41	0.39	0.6970

Table 2. Parameter estimates and tests from phylogenetic generalized least squares (PGLS) regression of clutch size and relative egg size as a function of estimated intra- and inter-specific competition on the breeding season for 14 migratory tyrant flycatcher species (see Table S1). Models fit clutch size (Model I) and relative egg size (Model II) as a function of the species' breeding range sizes (Breeding RS) and the tyrant flycatcher species richness on breeding ranges (Breeding SR). Relative egg size is defined as the residual of a simple linear regression between the log estimates of the average egg volume and species' body mass. The breeding latitude and nest type were included in the PGLS regression models as covariates. All response and predictor variables were standardized (see Methods for details). *P*-values < 0.05 are shown in bold.

Model/ Parameters	*k*	Estimate	SE	*t*	*P*
Model I (clutch size)	λ	0.51			
Intercept	β	0.10	0.65	0.16	0.8727
Breeding RS	**β**	**0.37**	**0.18**	**2.05**	**0.0406**
Breeding SR	β	-0.24	0.24	-1.04	0.2975
Latitude of breeding	β	0.10	0.07	1.49	0.1358
Nest type (half-open - closed)	**β**	**-0.85**	**0.43**	**-1.98**	**0.0485**
Nest type (half-open - open)	β	-0.53	0.34	-1.58	0.1139
Model II (relative egg size)	λ	0.97			
Intercept	β	0.82	0.87	0.94	0.3464
Breeding RS	β	-0.07	0.14	-0.49	0.6266
Breeding SR	β	0.33	0.30	1.12	0.2642
Latitude of breeding	β	0.04	0.03	1.46	0.1462
Nest type (half-open - closed)	β	0.08	0.26	0.31	0.7163
Nest type (half-open - open)	**β**	**-0.52**	**0.19**	**-2.79**	**0.0056**

Table 3. Parameter estimates and tests from phylogenetic generalized least squares (PGLS) regression of clutch size and relative egg size as a function of estimated intra- and inter-specific competition on the non-breeding season for 14 migratory tyrant flycatcher species (see Table S1). Models fit clutch size (Model I) and relative egg size (Model II) as a function of the species' non-breeding range sizes (Non-breeding RS) and the tyrant flycatcher species richness on non-breeding ranges (Non-breeding SR). Relative egg size is defined as the residual of a simple linear regression between the log estimates of the average egg volume and species' body mass. The breeding latitude and nest type were included in the PGLS regression models as covariates. All response and predictor variables were standardized (see Methods for details). *P*-values < 0.05 are shown in bold.

Model/ Parameters	*k*	Estimate	SE	*t*	*P*
Model I (clutch size)	λ	0.58			
Intercept	β	-0.84	0.69	-1.21	0.2251
Non-breeding RS	β	0.16	0.14	1.15	0.2490
Non-breeding SR	β	-0.45	0.24	-1.91	0.0572
Latitude of breeding	β	0.10	0.06	1.55	0.1227
Nest type (half-open - closed)	β	-0.58	0.41	-1.43	0.1539
Nest type (half-open - open)	β	-0.17	0.31	-0.56	0.5756
Model II (relative egg size)	λ	0.97			
Intercept	β	0.87	0.94	0.93	0.3549
Non-breeding RS	β	0.00	0.14	-0.03	0.9727
Non-breeding SR	β	0.17	0.29	0.57	0.5668
Latitude of breeding	β	0.04	0.03	1.37	0.1701
Nest type (half-open - closed)	β	0.08	0.26	0.31	0.7585
Nest type (half-open - open)	**β**	**-0.70**	**0.17**	**-4.17**	**<0.0001**

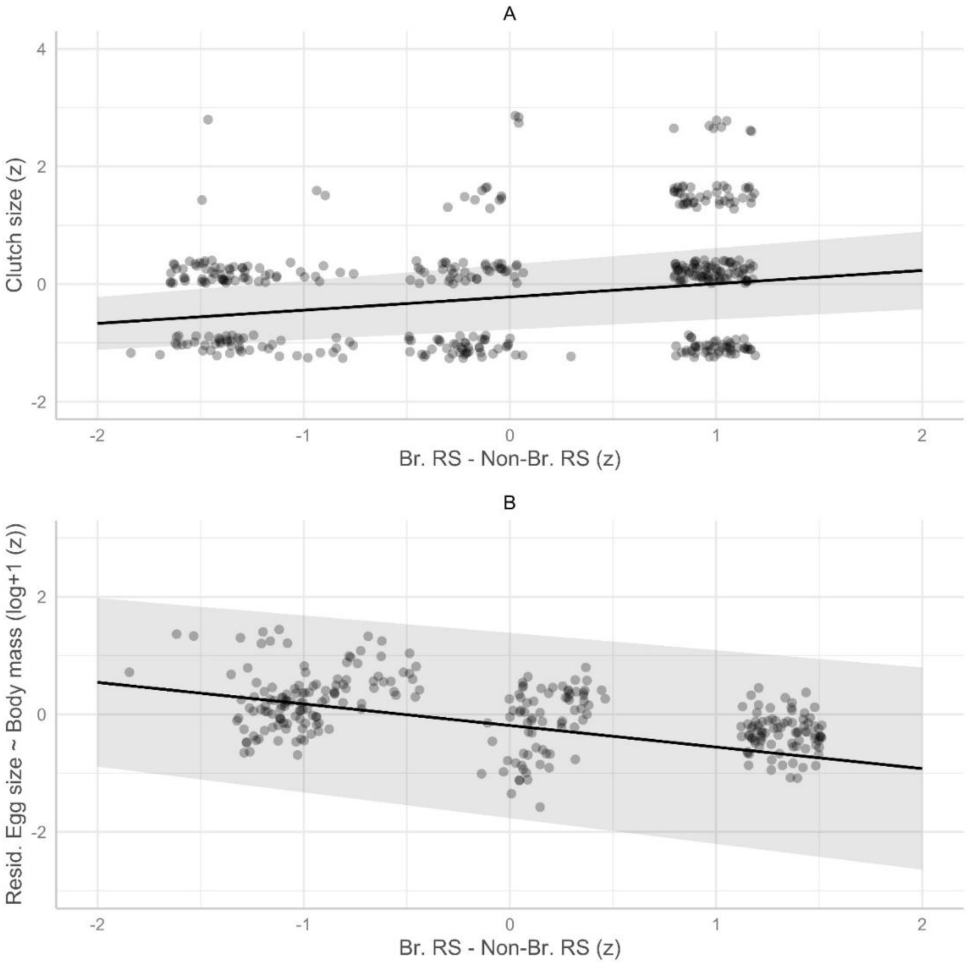


Figure 1. Observed (points) and predicted (line) values with 95% confidence intervals (grey fill) from phylogenetic generalized least squares (PGLS) regression of (**A**) clutch size and (**B**) relative egg size as a function of seasonal difference between species' breeding and non-breeding range size for 14 migratory tyrant flycatcher species (Table S1.1). Breeding latitude and nest type were included as covariates in the PGLS regression models. For additional details see Table 1. All response and predictor variables were standardized (see Methods for details).

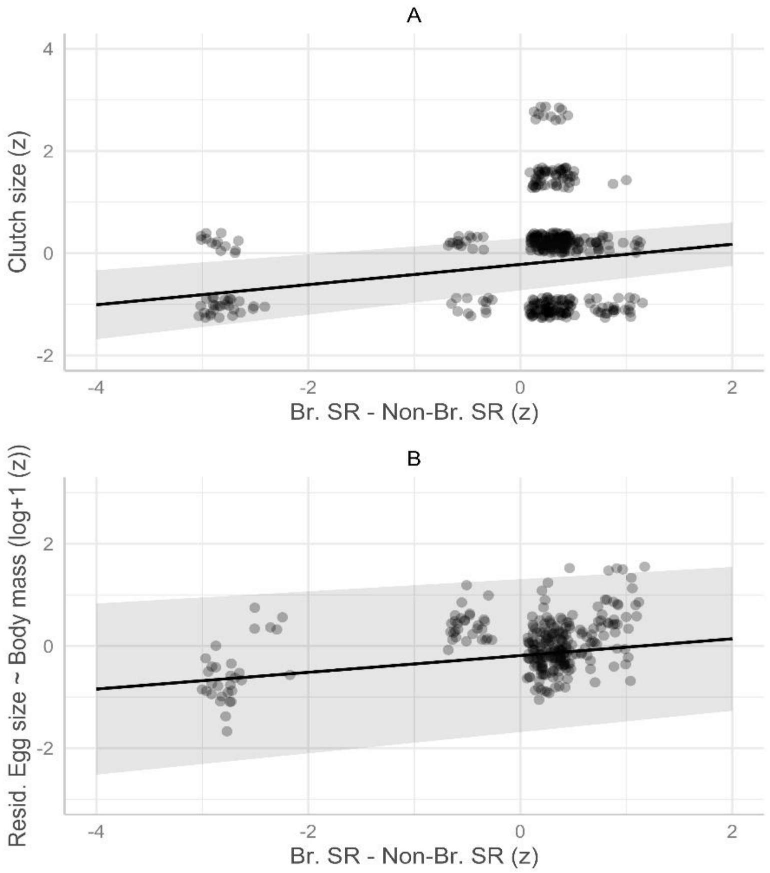


Figure 2. Observed (points) and predicted (line) values with 95% confidence intervals (grey fill) of phylogenetic generalized least squares (PGLS) regression of (**A**) clutch size and (**B**) relative egg size as a function of the seasonal difference in tyrant flycatcher species richness on species' breeding and non-breeding grounds for 14 migratory tyrant flytcatcher species (Table S1.1). Latitude of the breeding range and nest type were included as covariates in the (PGLS) regression models. For additional details see Table 1. All response and predictor variables were standardized (see Methods for details).

Discussion

Our findings suggest that competition on the breeding and the non-breeding grounds behaved differently on the reproduction strategies of tyrant-flycatchers breeding and migrating within South America. When the difference between the breeding and the non-breeding range size increased and species had more area to breed, species' clutch size increased, but egg size decreased. In contrast, when the number of tyrant flycatcher species on the non-breeding grounds decreased and the difference on species richness decreased relative to the breeding grounds, species' clutch size increased, and egg size did not change.

Our results suggest that species breeding in larger areas compared to the non-breeding grounds invest in larger clutch sizes, and in smaller egg sizes. Indeed, lower population density and higher food availability on the breeding grounds are associated with larger clutch sizes (Arcese & Smith, 1988; Jahn *et al.*, 2014) and higher reproductive success (Siikamaki, 1998), and clutch size can be the result of a strategic adjustment to local environmental conditions (Winkler & Allen, 1996). In contrast, the potential trade-off documented between clutch size and egg size was not expected. Despite this, the higher availability of food on the breeding grounds may improve offspring development (Martin, 1995), which could compensate for the smaller egg size and increase reproductive success (Martin, 1987). Additionally, the trade-off between clutch size and egg size could be explained by the high costs of egg production (Williams, 2005), and by the fact that birds reduce egg quality if subject to energetic constraints (Williams, 2001). Migratory birds may have limited energy reserves when arriving on their breeding grounds because of the costs associated with the journey (Wikelski *et al.*, 2003) and the costs incurred during the non-breeding season (Marra *et al.*, 1998). Decreases in parental energy reserves at the beginning of the reproductive event can increase dependence on exogenous resources or result in lower investment in current reproduction (e.g., smaller clutch size and egg size) (Martin, 1987). Therefore, the surplus of food available on the breeding grounds could be an essential part of the reproductive strategy of migrants because it could compensate for the energy expended during migration, without compromising current reproduction. As such, our results suggest that migrants take advantage of a surplus in resources available on their breeding grounds, rather than endogenous reserves, for meeting breeding demands and increasing fitness.

Our results for season differences in species richness contrasted with our initial expectations. The decrease in tyrant flycatcher species richness on the breeding grounds compared to the non-breeding grounds was associated to a decrease in species' clutch size. However, tyrant flycatcher species richness in the non-breeding ranges was on average higher than at the breeding ranges, and species' clutch size tended to decrease with increasing competition in the non-breeding grounds. Processes acting both during the breeding and non-breeding period are potentially influential in limiting or regulating populations of migratory birds (Holmes, 2007). The observed decrease in species' clutch size could be then the result of the higher competition experienced in the non-breeding grounds, considering that the effects observed during the breeding period should be a consequence of events experienced previously during the annual cycle (Marra *et al.*, 1998).

Our results demonstrate that to understand how different life-history strategies could affect population dynamics in migratory species, it is necessary to consider the factors that affect populations through the annual cycle – on the breeding grounds and on the non-breeding grounds, and even along migratory routes. Migratory birds have to manage energetically expensive activities, i.e., reproduction, molt, and migration, during the annual cycle through several trade-offs that mold migratory behavior (Hedenström, 2008). However, unraveling such complex questions represents a challenge to researchers and conservationists because it requires long-term studies across each species' annual cycle (review in Holmes, 2007). Yet, considering the large spatial extent of our study area, and gaps of knowledge of both basic patterns and mechanisms underlying bird migration in the Neotropics (Jahn *et al.*, 2020), our study was able to draw important conclusions on the potentiality of competition in affecting reproductive strategies of migratory bird species in South America. However, field data, such as observations of species' ecology and behavior, might help improve understanding on how intra- and inter-specific competition affect migrant reproductive strategies, in each phase of the annual cycle.

Conclusion

Our results corroborate the findings from a previous study that highlights the importance of the conditions on the breeding and non-breeding grounds in driving the seasonal migration of tyrant-flycatchers in South America (Sousa et al., in prep). We found evidence that the seasonal difference in competition between the breeding and non-breeding grounds enable species to increase clutch size and increase reproductive potential, presumably because of a surplus of resources provided by decreasing competition on the breeding grounds. Additionally, there is evidence that the high competition experienced during the non-breeding season can affect subsequent reproduction by decreasing clutch size. However, to fully understand the consequences of competition for the life history of migratory birds, further investigations are needed to dissociate the effects of competition on the breeding and at the non-breeding grounds.

CONSIDERAÇÕES FINAIS

Esta tese encontrou evidências de que a migração de tiranídeos na América do Sul é determinada pela variação sazonal na competição, e não pela variação sazonal do clima (Capítulo 1), e que essas espécies se beneficiam do adicional de recursos disponíveis nos sítios reprodutivos (Capítulo 3), mesmo quando investem mais na migração e esses custos se elevam (i.e., distância de migração) (Capítulo 2). Os Capítulos 2 e 3 sugerem que aves migratórias da região podem beneficiar-se em termos de tamanho de ninhada quando acessam áreas mais favoráveis ao longo do ciclo anual, e que por isso pode ser vantajoso investir mais em migração. Por outro lado, custos relacionados à competição nos sítios não-reprodutivos podem afetar negativamente a reprodução (Capítulo 3). Cabe ressaltar, ainda, que não encontrei evidências de que o comportamento de migrar ou não migrar seja em si um fator determinante para impor pressões seletivas que resultem em estratégias de história de vida mais rápidas, i.e., associadas a menores taxas sobrevivências e a maiores gastos energéticos durante a vida (Capítulo 2). Nesse mesmo contexto, o Capítulo 1 corrobora com esta tese ao apresentar evidências de que essas espécies migram para evitarem locais com alta competição e se reproduzirem em locais com maior disponibilidade de recursos.

Esta tese evidencia, ainda, as diferenças que a migração na América do Sul possui em relação à maior parte dos padrões migratórios observados em escala global. Encontrei evidências de que o clima da América do Sul exerce um papel secundário na migração de tiranídeos que se reproduzem na região. O clima mais ameno no continente, que em geral possui menores temperaturas e menor amplitude térmica ao longo do ano, é possivelmente um dos responsáveis pela baixa associação encontrada entre a distribuição de espécies migratórias e variações na temperatura, precipitação e no vigor da vegetação (*vegetation greenness*). Esse resultado é distinto dos padrões observados em sistemas temperados do Hemisfério Norte, os quais são caracterizados por temperaturas altamente sazonais e invernos rigorosos. Devido às diversas especificidades encontradas na migração da América do Sul, destaco a necessidade de aprofundamento sobre a relação da competição com a migração e de parâmetros de história de vida não avaliados aqui com a migração.

Por fim, destaco que este estudo testou hipóteses sobre padrões de larga-escala sobre a ecologia da migração e a biologia reprodutiva de espécies utilizando dados de coleções oológicas e de ciência cidadã. O uso desse tipo de dado demonstrou ser eficiente em regiões com lacunas de amostragem temporal e espacial, como a região Neotropical. Aprofundar em aspectos relacionados à interação entre as espécies e incorporá-los em estudos futuros é uma oportunidade de compreender a ecologia e a evolução da migração como um todo, e não somente a partir de um conjunto limitado de sistemas migratórios. Assim, é possível estimar com maior precisão como essas espécies estão respondendo às mudanças ambientais globais.

REFERÊNCIAS BIBLIOGRÁFICAS

Akresh, M.E., King, D.I. & Marra, P.P. (2019) Examining carry-over effects of winter habitat on breeding phenology and reproductive success in prairie warblers Setophaga discolor. *Journal of Avian Biology*, **50**, 1–13.

Alerstam, T. & Bäckman, J. (2018) Ecology of animal migration. *Current Biology*, **28**, R968–R972.

Alerstam, T., Hedenström, A. & Åkesson, S. (2003) Long-distance migration: evolution and determinants. *Oikos*, **103**, 247–260.

Alerstam, T. & Lindström, Å. (1990) *Optimal bird migration: the relative importance of time, energy, and safety*. *Bird Migration: Physiology and Ecophysiology* (ed. by E. Gwinner), pp. 331–351. Springer, Berlin, Germany.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.

Alves, J.A., Gunnarsson, T.G., Hayhow, D.B., Appleton, G.F., Potts, P.M., Sutherland, W.J. & Gill, J.A. (2013) Costs, benefits, and fitness consequences of different migratory strategies. *Ecology*, **94**, 11–17.

Amadon, D., Mayr, E., Snow, D.W., Traylor, Melvin A., Jr. & Zimmer, J.T. (1979) *Check-List of Birds of the World. Volume VIII*, (ed. by Jr. Traylor, Melvin A.) Museum of Comparative Zoology, Cambridge, USA.

Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J. & Jetz, W. (2018) A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data*, **5**, 180040.

Arcese, P. & Smith, J.N.M. (1988) Effects of population density and supplemental food on reproduction in song sparrows. *Source: Journal of Animal Ecology*, **57**, 119–136.

Areta, J.I. & Bodrati, A. (2010) Un sistema migratorio longitudinal dentro de la Selva Atlántica: movimientos estacionales y taxonomía del Tangará Cabeza Celeste (*Euphonia cyanocephala*) en Misiones (Argentina) y Paraguay. *Ornitologia Neotropical*, **21**, 71–86.

van Asch, M. & Visser, M.E. (2007) Phenology of forest caterpillars and their host trees: The importance of synchrony. *Annual Review of Entomology*, **52**, 37–55.

Bejarano, V. & Jahn, A.E. (2018) Relationship between arrival timing and breeding success of intra-tropical migratory Fork-tailed Flycatchers (Tyrannus savana). *Journal of Field Ornithology*, **89**, 109–116.

Bennett, P.M. & Owens, I.P.F. (2002) *Evolutionary ecology of birds: life histories, mating systems and extinction*, Oxford University Press, New York, USA.

Berthold, P. (1993) *Bird migration: a general survey*, Oxford University Press, New York, USA.

Billerman, S.M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S. & (Editors) (2022) *Birds of the World*, (ed. by S. M. Billerman), B. K. Keeney), P. G. Rodewald), and T. S. Schulenberg) Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Billerman, S.M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S. & (Editors) (2020) Birds of the World.

Birchard, G.F. & Deeming, D.C. (2015) *Egg allometry: influences of phylogeny and the altricial-precocial continuum*. *Nests, Eggs & Incubation: New Ideas About Avian Reproduction* (ed. by D.C. Deeming) and S.J. Reynolds), pp. 97–112. Oxford University Press Oxford, Oxford, UK.

BirdLife International & Handbook of the Birds of the World (2019) Bird species distribution maps of the world. Version 2019.1.

Blake, S., Yackulic, C.B., Cabrera, F., Tapia, W., Gibbs, J.P., Kümmeth, F. & Wikelski, M. (2013) Vegetation dynamics drive segregation by body size in Galapagos tortoises migrating across altitudinal gradients. *Journal of Animal Ecology*, **82**, 310–321.

Böhning-Gaese, K., Halbe, B., Lemoine, N. & Oberrath, R. (2000) Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. *Evolutionary Ecology Research*, **2**, 823–839.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.

Bravo, S.P., Cueto, V.R. & Gorosito, C.A. (2017) Migratory timing, rate, routes and wintering areas of White-crested Elaenia (*Elaenia albiceps chilensis*), a key seed disperser for Patagonian forest regeneration. *PLoS ONE*, **12**, e0170188.

Briedis, M., Bauer, S., Adamík, P., Alves, J.A., Costa, J.S., Emmenegger, T., Gustafsson, L., Koleček, J., Krist, M., Liechti, F., Lisovski, S., Meier, C.M., Procházka, P. & Hahn, S. (2020) Broad-scale patterns of the Afro-Palaearctic landbird migration. *Global Ecology and Biogeography*, **29**, 722–735.

Brown, D.R. & Sherry, T.W. (2006) Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia*, **149**, 22–32.

Buechley, E.R., Oppel, S., Efrat, R., Phipps, W.L., Carbonell Alanís, I., Álvarez, E., Andreotti, A., Arkumarev, V., Berger-Tal, O., Bermejo Bermejo, A., Bounas, A., Ceccolini, G., Cenerini, A., Dobrev, V., Duriez, O., García, J., García-Ripollés, C., Galán, M., Gil, A., Giraud, L., Hatzofe, O., Iglesias-Lebrija, J.J., Karyakin, I., Kobierzycki, E., Kret, E., Loercher, F., López-López, P., Miller, Y., Mueller, T., Nikolov, S.C., de la Puente, J., Sapir, N., Saravia, V., Şekercioğlu, Ç.H., Sillett, T.S., Tavares, J., Urios, V. & Marra, P.P. (2021) Differential survival throughout the full annual cycle of a migratory bird presents a life-history trade-off. *Journal of Animal Ecology*, **90**, 1228–1238.

Chan, K. (2001) Partial migration in Australian landbirds: a review. *Emu - Austral Ornithology*, **101**, 281–292.

Chapman, B.B., Brönmark, C., Nilsson, J.-Å.Å. & Hansson, L.-A.A. (2011) The ecology and evolution of partial migration. *Oikos*, **120**, 1764–1775.

Chen, C., Liaw, A. & Breiman, L. (2004) Using random forest to learn imbalanced data. *University of California, Berkeley*, 1–12.

Chesser, R.T. (1995) *Biogeographic, ecological, and evolutionary aspects of South American austral migration, with special reference to the family Tyrannidae*, Ph.D. dissertation, Lousiana State University and Agricultural & Mechanical College, Baton Rouge, USA.

Chesser, R.T. (1998) Further perspectives on the breeding distribution of migratory birds: South American austral migrant flycatchers. *Journal of Animal Ecology*, **67**, 69–77.

Chesser, R.T. (1994) Migration in South America: an overview of the Austral system. *Bird Conservation International*, **4**, 91–107.

Chesser, R.T. (2005) Seasonal distribution and ecology of South American austral migrant flycatchers. *Birds of two worlds: the ecology and evolution of migration*, 168–181.

Chesser, R.T. & Levey, D.J. (1998) Austral migrants and the evolution of migration in New World birds: diet, habitat, and migration revisited. *The American Naturalist*, **152**, 311–319.

Clements, J.F., Schulenberg, T.S., Iliff, M.J., Roberson, D., Fredericks, T.A., Sullivan, B.L., Wood, C.L., Billerman, S.M., Fredericks, T.A., Sullivan, B.L. & Wood, C.L. (2019) The eBird/Clements Checklist of Birds of the World: v2019.

Collar, N., Fisher, C. & Feare, C. (2003) Why museums matter: avian archives in an age of extinction. *Bulletin of the British Ornithologists' Club Supplement A*, **123**, 1–360.

Conklin, J.R., Senner, N.R., Battley, P.F. & Piersma, T. (2017) Extreme migration and the individual quality spectrum. *Journal of Avian Biology*, **48**, 19–36.

Cooney, C.R., Sheard, C., Clark, A.D., Healy, S.D., Liker, A., Street, S.E., Troisi, C.A., Thomas, G.H., Székely, T., Hemmings, N. & Wright, A.E. (2020) Ecology and allometry predict the evolution of avian developmental durations. *Nature Communications*, **11**, 2383.

Cory, C.B. & Hellmayr, C.E. (1927) *Catalogue of Birds of the Americas and the Adjacent Islands in Field Museum of Natural History. Vol. XIII*, (ed. by W.H. Osgood) Field Museum of Natural History, Chicago, USA.

Cox, G.W. (1968) The role of competition in the evolution of migration. *Evolution*, **22**, 180–192.

Danielson, J.J. & Gesch, D.B. (2011) Global multi-resolution terrain elevation data 2010 (GMTED2010).

Dhondt, A.A. (2012) *Interspecific competition in birds*, Oxford University Press, New York, US.

Dias, R.I., Vianna, V.R. & Araújo, R. (2021) Annual movements of four South American tyrant flycatchers: uncovering intratropical migration patterns. *Bird Study*, **68**, 76–89.

Didan, K. (2015a) MOD13A2 MODIS/Terra Vegetation Indices 16-Day L3 Global 1km SIN Grid V006 [Data set].

Didan, K. (2015b) MYD13A2 MODIS/Aqua Vegetation Indices 16-Day L3 Global 1km SIN Grid V006 [Data set].

Dingle, H. (2006) Animal migration: is there a common migratory syndrome? *Journal of Ornithology*, **147**, 212–220.

Dingle, H. (2008) Bird migration in the southern hemisphere: a review comparing continents. *Emu - Austral Ornithology*, **108**, 341–359.

Dingle, H. (2014) *Migration: the biology of life on the move*, Oxford University Press, USA.

Dingle, H. & Drake, V.A. (2007) What is migration? *BioScience*, **57**, 113–121.

Drent, R.H., Ebbinge, B.S. & Weijand, B. (1978) Balancing the energy budgets of Arctic-breeding geese throughout the annual cycle: a progress report. *Verh. Ornithologischen Ges. Bayern*, **23**, 239–264.

Elsen, P.R., Tingley, M.W., Kalyanaraman, R., Ramesh, K. & Wilcove, D.S. (2017) The role of competition, ecotones, and temperature in the elevational distribution of Himalayan birds. *Ecology*, **98**, 337–348.

Faaborg, J., Holmes, R.T., Anders, A.D., Bildstein, K.L., Dugger, K.M., Gauthreaux, S.A., Heglund, P., Hobson, K.A., Jahn, A.E., Johnson, D.H., Latta, S.C., Levey, D.J., Marra, P.P., Merkord, C.L., Erica, N.O.L., Rothstein, S.I., Sherry, T.W., Scott Sillett, T., Thompson, F.R., Warnock, N., Faaborg, J., Holmes, R.T., Anders, A.D., Bildstein, K.L., Dugger, K.M., Gauthreaux, S.A., Heglund, P., Hobson, K.A., Jahn, A.E., Johnson, D.H., Latta, S.C., Levey, D.J., Marra, P.P., Merkord, C.L., Nol, E., Rothstein, S.I., Sherry, T.W., Sillett, T.S., Thompson, F.R. & Warnock, N. (2010a) Recent advances in understanding migration systems of New World land birds. *Ecological Monographs*, **80**, 3–48.

Faaborg, J., Holmes, R.T., Anders, A.D., Bildstein, K.L., Dugger, K.M., Gauthreaux, S.A., Heglund, P., Hobson, K.A., Jahn, A.E., Johnson, D.H., Latta, S.C., Levey, D.J., Marra, P.P., Merkord, C.L., Nol, E., Rothstein, S.I., Sherry, T.W., Sillett, T.S., Thompson, F.R. & Warnock, N. (2010b) Conserving migratory landbirds in the New World: do we know enough? *Ecological Applications*, **20**, 398–418.

Fitzpatrick, J. (2019) *Tyrant-flycatchers (Tyrannidae)*. *Handbook of the Birds of the World Alive* (ed. by J. del Hoyo), A. Elliott), J. Sargatal), D.A. Christie), and E. de Juana), Lynx Edicions, Barcelona, Spain.

Fitzpatrick, J.W. (1980) Foraging behavior of Neotropical Tyrant flycatchers. *Condor*, **82**, 43–57.

Forrest, J.R.K. & Thomson, J.D. (2011) An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecological Monographs*, **81**, 469–491.

Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-Bovy, G., Bolker, B., Ellison, S., Firth, D. & Friendly, M. (2021) *car*: An R companion to applied regression.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**, 712–726.

Friedl, M. & Sulla-Menashe, D. (2019) MCD12Q1 MODIS/Terra+Aqua Land Cover Type Yearly L3 Global 500m SIN Grid V006 [Data set].

Gorleri, F.C., Hochachka, W.M. & Areta, J.I. (2021) Distribution models using semi-structured community science data outperform unstructured-data models for a data-poor species, the Plain Tyrannulet. *Ornithological Applications*, **123**, 1–17.

Grafen, A. (1989) The phylogenetic regression. *Phil. Trans. Soc. R. Lond. B*, **326**, 119–157.

Greenberg, R. (1986) Competition in migrant birds in the nonbreeding season. *Current ornithology. Vol. 3*, 281–307.

Greenberg, R. (1995) Insectivorous migratory birds in tropical ecosystems: the breeding currency hypothesis. *Journal of Avian Biology*, **26**, 260–264.

Greenberg, R. & Marra, P. (2005) *Birds of two worlds: the ecology and evolution of migration*, JHU Press, Baltimore, USA.

Griffioen, P.A. & Clarke, M.F. (2002) Large-scale bird-movement patterns evident in eastern Australian atlas data. *Emu - Austral Ornithology*, **102**, 99–125.

Guaraldo, A.C., Bravo, S.P., Bridge, E. & Marini, M.Â. (2021) Longitudinal and cyclic poleward migration of a South American intratropical migrant Flycatcher, the Lesser Elaenia (*Elaenia chiriquensis*). *Ornitología Neotropical*, **32**, 94–102.

Guaraldo, A.D.C. (2014) Ecologia comparada de Tiranídeos (Aves) residentes e migratórios.

Guaraldo, A.D.C., Kelly, J.F. & Marini, M.Â. (2016) Contrasting annual cycles of an intratropical migrant and a tropical resident bird. *Journal of Ornithology*, **157**, 695–705.

Gustafsson, L. (1987) Interspecific competition lowers fitness in Collared flycatchers *Ficedula albicollis*: an experimental demonstration. *Ecology*, **68**, 291–296.

Hawkins, B.A., Rueda, M. & Rodríguez, M.Á. (2008) What do range maps and surveys tell us about diversity patterns? *Folia Geobotanica*, **43**, 345–355.

Hayes, F.E. (1995) Definitions for migrant birds: what is a Neotropical migrant? *The Auk*, **112**, 521–523.

Hedenström, A. (2008) Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions pf The Royal Society B*, **363**, 287–299.

Heming, N.M., Greeney, H.F. & Marini, M.Â. (2013) Breeding biology research and data availability for New World flycatchers. *Natureza & Conservação*, **11**, 54–58.

Heming, N.M. & Marini, M.Â. (2015) Ecological and environmental factors related to variation in egg size of New World flycatchers. *Journal of Avian Biology*, **46**, 352–360.

Hersbach, H., Bell, B., Berrisford, P., Biavati, G., Horányi, A., Muñoz Sabater, J., Nicolas, J., Peubey, C., Radu, R., Rozum, I., Schepers, D., Simmons, A., Soci, C., Dee, D. & Thépaut, J.-N. (2018) ERA5 hourly data on single levels from 1979 to present.

Hijmans, R.J. (2021) *raster*: Geographic data analysis and modeling.

Holmes, R.T. (2007) Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. *Ibis*, **149**, 2–13.

Huxley, J.S. (1927) On the Relation between Egg-weight and Body-weight in Birds. *Journal of the Linnean Society of London, Zoology*, **36**, 457–466.

Jahn, A.E., Bejarano, V., Cueto, V.R., di Giacomo, A.S. & Fontana, C.S. (2017a) Movement ecology research to advance conservation of South America's grassland migratory birds. *Perspectives in Ecology and Conservation*, **15**, 209–215.

Jahn, A.E., Bejarano, V., Guzmán, M.B., Brown, L.M., Carvalho Provinciato, I.C., Cereghetti, J., Cueto, V.R., Giraldo, J.I., Gómez-Bahamón, V., Husak, M.S., LePage, H.K., MacPherson, M., Marini, M.Â., Pizo, M.A., Quickle, A., Roeder, D. v., Sarasola, J.H. & Tuero, D.T. (2017b) Molting while breeding? Lessons from New World Tyrannus Flycatchers. *Journal of Ornithology*, **158**, 1061–1072.

Jahn, A.E., Bejarano, V., Guzmán, M.B., Brown, L.M., Carvalho Provinciato, I.C., Cereghetti, J., Cueto, V.R., Giraldo, J.I., Gómez-Bahamón, V., Husak, M.S., LePage, H.K., MacPherson, M., Marini, M.Â., Pizo, M.A., Quickle, A., Roeder, D. V., Sarasola, J.H. & Tuero, D.T. (2017c) Molting while breeding? Lessons from New World Tyrannus Flycatchers. *Journal of Ornithology*, **158**, 1061–1072.

Jahn, A.E., Bravo, S.P., Cueto, V.R., Levey, D.J. & Morales, M. v. (2012) Patterns of partial avian migration in northern and southern temperate latitudes of the New World. *Emu - Austral Ornithology*, **112**, 17–22.

Jahn, A.E. & Cueto, V.R. (2012) The potential for comparative research across New World bird migration systems. *Journal of Ornithology*, **153**, 199–205.

Jahn, A.E., Cueto, V.R., Fontana, C.S., Guaraldo, A.C., Levey, D.J., Marra, P.P. & Ryder, T.B. (2020) Bird migration within the Neotropics. *The Auk*, **137**, 1–23.

Jahn, A.E., Cueto, V.R., Fox, J.W., Husak, M.S., Kim, D.H., Landoll, D. V., Ledezma, J.P., LePage, H.K., Levey, D.J., Murphy, M.T. & Renfrew, R.B. (2013a) Migration timing and wintering areas of three species of flycatchers (*Tyrannus*) breeding in the Great Plains of North America. *The Auk*, **130**, 247–257.

Jahn, A.E., Cueto, V.R., Sagario, M.C., Matnani, A.M., Vidoz, J.Q., De Casenave, J.L. & Di Giacomo, A.G. (2009) Breeding and winter site fidelity among eleven Neotropical austral migrant bird species. *Ornitologia Neotropical*, **20**, 275–283.

Jahn, A.E., Levey, D.J., Cueto, V.R., Ledezma, J.P., Tuero, D.T., Fox, J.W. & Masson, D. (2013b) Long-distance bird migration within South America revealed by light-level geolocators. *The Auk*, **130**, 223–229.

Jahn, A.E., Levey, D.J., Hostetler, J.A. & Mamani, A.M. (2010a) Determinants of partial bird migration in the amazon basin. *Journal of Animal Ecology*, **79**, 983–992.

Jahn, A.E., Levey, D.J., Mamani, A.M., Saldias, M., Alcoba, A., Ledezma, M.J., Flores, B., Vidoz, J.Q. & Hilarion, F. (2010b) Seasonal differences in rainfall, food availability, and the foraging behavior of Tropical Kingbirds in the southern Amazon Basin. *Journal of Field Ornithology*, **81**, 340–348.

Jahn, A.E., Levey, D.J. & Smith, K.G. (2004) Reflections across hemispheres: a system-wide approach to New World bird migration. *The Auk*, **121**, 1005–1013.

Jahn, A.E., Tuero, D.T., Mamani, A.M., Bejarano, V., Masson, D.A. & Aguilar, E. (2014) Drivers of clutch-size in Fork-tailed Flycatchers (Tyrannus savana) at temperate and tropical latitudes in South America. *Emu*, **114**, 337–342.

Janzen, D.H. & Schoener, T.W. (1968) Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology*, **49**, 96–110.

Jetz, W., Freckleton, R.P. & McKechnie, A.E. (2008a) Environment, migratory tendency, phylogeny and basal metabolic rate in birds. *PLoS ONE*, **3**, e3261.

Jetz, W., Sekercioglu, C.H. & Böhning-Gaese, K. (2008b) The worldwide variation in avian clutch size across species and space. *PLoS Biology*, **6**, 2650–2657.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444–448.

Johnston, A., Hochachka, W.M., Strimas-Mackey, M.E., Ruiz Gutierrez, V., Robinson, O.J., Miller, E.T., Auer, T., Kelling, S.T. & Fink, D. (2021) Analytical guidelines to increase the value of community science data: An example using eBird data to estimate species distributions. *Diversity and Distributions*, **00**, 1–13.

Johnston, A., Moran, N., Musgrove, A., Fink, D. & Baillie, S.R. (2020) Estimating species distributions from spatially biased citizen science data. *Ecological Modelling*, **422**, 108927.

Joseph, L. (2011) Museum collections in ornithology: today’s record of avian biodiversity for tomorrow’s world. *Emu*, **111**, i–xii.

Joseph, L. (1996) Preliminary climatic overview of migration patterns in South American Austral migrant Passerines. *Ecotropica*, **2**, 185–193.

Joseph, L. (1997) Towards a broader view of neotropical migrants: consequences of a re-examination of austral migration. *Ornitología Neotropical*, **8**, 31–36.

Justice, C.O., Vermote, E., Townshend, J.R.G., Defries, R., Roy, D.P., Hall, D.K., Salomonson, V. v, Privette, J.L., Riggs, G., Strahler, A., Lucht, W., Myneni, R.B., Knyazikhin, Y., Running, S.W., Nemani, R.R., Wan, Z., Huete, A.R., Leeuwen, W. van, Wolfe, R.E., Giglio, L., Muller, J., Lewis, P. & Barnsley, M.J. (1998) The Moderate Resolution Imaging Spectroradiometer (MODIS): land remote sensing for global change research. *IEEE Transactions on Geoscience and Remote Sensing*, **36**, 1228–1249.

Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.M., Bairlein, F. & Alerstam, T. (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, **83**, 176–184.

Lack, D. (1960) The influence of weather on passerine migration. A Review. *The Auk*, **77**, 171–209.

Lack, D. (1954) *The natural regulation of animal numbers*, The Clarendon Press, Oxford, UK.

La Sorte, F.A. & Fink, D. (2017) Migration distance, ecological barriers and en-route variation in the migratory behaviour of terrestrial bird populations. *Global Ecology and Biogeography*, **26**, 216–227.

La Sorte, F.A., Fink, D., Hochachka, W.M., DeLong, J.P. & Kelling, S. (2014) Spring phenology of ecological productivity contributes to the use of looped migration strategies by birds. *Proceedings of the Royal Society B: Biological Sciences*, **281**.

La Sorte, F.A. & Graham, C.H. (2021) Phenological synchronization of seasonal bird migration with vegetation greenness across dietary guilds. *Journal of Animal Ecology*, **90**, 343–355.

La Sorte, F.A. & Somveille, M. (2020) Survey completeness of a global citizen-science database of bird occurrence. *Ecography*, **43**, 34–43.

Lees, A.C. (2016) Evidence for longitudinal migration by a “sedentary” Brazilian flycatcher, the Ash-throated Casiornis. *Journal of Field Ornithology*, **87**, 251–259.

Lehikoinen, E. & Sparks, T.H. (2010) *Changes in migration*. *Effects of climate change on birds* (ed. by A.P. Moller), W. Fiedler), and P. Berthold), pp. 89–112. Oxford University Press, USA, New York.

Levey, D.J. (1994) Why we should adopt a broader view of Neotropical migrants. *The Auk*, **111**, 233–136.

Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.

Lok, T., Overdijk, O. & Piersma, T. (2015) The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biology Letters*, **11**, 20140944.

Louthan, A.M., Doak, D.F. & Angert, A.L. (2015) Where and When do Species Interactions Set Range Limits? *Trends in Ecology and Evolution*, **30**, 780–792.

MacPherson, M.P., Murphy, M.T., Kim, D.H., Jahn, A.E., Cueto, V.R.V.R., Tuero, D.T., Hill, E.D., Murphy, M.T., Kim, D.H., Cueto, V.R.V.R., Tuero, D.T. & Hill, E.D. (2018) Follow the rain? Environmental drivers of Tyrannus migration across the New World. *The Auk*, **135**, 881–894.

Marini, M.Â. (1997) Predation-mediated bird nest diversity: an experimental test. *Canadian Journal of Zoology*, **75**, 317–323.

Marini, M.Â., Barbet-Massin, M., Lopes, L.E. & Jiguet, F. (2013) Geographic and seasonal distribution of the Cock-tailed Tyrant (*Alectrurus tricolor*) inferred from niche modeling. *Journal of Ornithology*, **154**, 393–402.

Marini, M.A. & Cavalcanti, R.B. (1998) Frugivory by *Elaenia* flycatchers. *Hornero*, **15**, 47–50.

Marini, M.Â., Hall, L., Bates, J., Steinheimer, F.D., McGowan, R., Silveira, L.F., Lijtmaer, D.A., Tubaro, P.L., Córdoba-Córdoba, S., Gamauf, A., Greeney, H.F., Schweizer, M., Kamminga, P., Cibois, A., Vallotton, L., Russell, D., Robinson, S.K., Sweet, P.R., Frahnert, S., Corado, R. & Heming, N.M. (2020) The five million bird eggs in the world's museum collections are an invaluable and underused resource. *The Auk: Ornithological Advances*, **137**, 1–7.

Marra, P.P. (2000) The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology*, **11**, 299–308.

Marra, P.P., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, **282**, 1884–1886.

Marra, P.P. & Holmes, R.T. (2001) Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *The Auk*, **118**, 92–104.

Martin, P.R. & Martin, T.E. (2001) *Ecological and fitness consequences of species coexistence: a removal experiment with Wood Warblers*,.

Martin, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65**, 101–127.

Martin, T.E. (1987) Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics*, **18**, 453–487.

Martin, T.E., Bassar, R.D., Bassar, S.K., Fontaine, J.J., Lloyd, P., Mathewson, H.A., Niklison, A.M. & Chalfoun, A. (2006) Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution*, **60**, 390–398.

Minias, P. & Włodarczyk, R. (2020) Avian developmental rates are constrained by latitude and migratoriness – A global analysis. *Journal of Biogeography*, **47**, 2156–2167.

Møller, A.P. (2007) Senescence in relation to latitude and migration in birds. *Journal of Evolutionary Biology*, **20**, 750–757.

Møller, A.P. & Fiedler, W. (2010) *Long-term time series of ornithological data*. *Effects of Climate Change on Birds* (ed. by A.P. Møller), W. Fiedler), and P. Berthold), pp. 33–38. Oxford University Press, New York, USA.

Newton, I. (2010a) *Bird Migration*, HarperCollins Publishers, London, UK.

Newton, I. (2012) Obligate and facultative migration in birds: ecological aspects. *Journal of Ornithology*, **153**, 171–180.

Newton, I. (2010b) *The migration ecology of birds*, Elsevier, London.

Ng, W.H., Fink, D., La Sorte, F.A., Auer, T., Hochachka, W.M., Johnston, A. & Dokter, A.M. (2022) Continental-scale biomass redistribution by migratory birds in response to seasonal variation in productivity. *Global Ecology and Biogeography*, **31**, 727–739.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliffe, L.M. (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 59–64.

Owen, M. (1980) *Wild geese of the world: their life history and ecology*, Batsford, London, UK.

Pagel, M. (1999a) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

Pagel, M. (1999b) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

Paiva, L. V. & Marini, M.Â. (2013) Timing of migration and breeding of the Lesser Elaenia (*Elaenia chiriquensis*) in a Neotropical savanna. *The Wilson Journal of Ornithology*, **125**, 116–120.

Paradis, E. & Schliep, K. (2019) *ape* 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, **35**, 526–528.

Pateiro-Lopez, B. & Rodriguez-Casal, A. (2019) *alphahull*: Generalization of the convex hull of a sample of points in the plane.

Perez-Tris, J. & Telleria, J.L. (2002) Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. *Journal of Animal Ecology*, **71**, 211–224.

Pinheiro, F., Diniz, I.R., Coelho, D. & Bandeira, M.P.S. (2002) Seasonal pattern of insect abundance in the Brazilian cerrado. *Austral Ecology*, **27**, 132–136.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2020) *nlme*: Linear and nonlinear mixed effects models.

Pinho, J.B., Aragona, M., Hakamada, K.Y.P. & Marini, M.Â. (2017) Migration patterns and seasonal forest use by birds in the Brazilian Pantanal. *Bird Conservation International*, **27**, 371–387.

Powell, L.L., Ames, E.M., Wright, J.R., Matthiopoulos, J. & Marra, P.P. (2021) Interspecific competition between resident and wintering birds: experimental evidence and consequences of coexistence. *Ecology*, **102**, e03208.

Pya, N. (2021) *scam*: Shape constrained additive models.

R Core Team (2021) R: a language and environment for statistical computing.

Rappole, J.H. (2013) *The avian migrant: the biology of bird migration*, Columbia University Press, New York, USA.

Rappole, J.H. & Jones, P. (2002) Evolution of old and new world migration systems. *Ardea*, **90**, 525–537.

Remsen Jr., J.V. (2001) True winter range of the Veery (*Catharus fuscescens*): lessons for determining winter ranges of species that winter in the tropics. *The Auk*, **118**, 838–848.

Ricklefs, R.E. (2000) Density dependence, evolutionary optimization, and the diversification of avian life histories. *The Condor*, **102**, 9–22.

Robinson, O.J., Ruiz-Gutierrez, V. & Fink, D. (2018) Correcting for bias in distribution modelling for rare species using citizen science data. *Diversity and Distributions*, **24**, 460–472.

Roff, D.A. & Fairbairn, D.J. (2007) The evolution and genetics of migration in insects. *BioScience*, **57**, 155–164.

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, **9**, 671–675.

Schubert, S.C., Manica, L.T. & Guaraldo, A.D.C. (2019) Revealing the potential of a huge citizen-science platform to study bird migration. *Emu*, **119**, 364–373.

Sclater, P.L. (1888) *Catalogue of the Birds in the British Museum. Volume XIV*, Taylor & Francis, London, UK.

Sherry, T.W., Johnson, M.D. & Strong, A.M. (2005) *Does winter food limit populations of migratory birds? Birds of Two Worlds: The Ecology and Evolution of Migration* (ed. by R.R. Greenberg) and P.P. Marra), pp. 414–425.

Sibly, R.M., Witt, C.C., Wright, N.A., Venditti, C., Jetz, W. & Brown, J.H. (2012) Energetics, lifestyle, and reproduction in birds. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 10937–10941.

Sick, H. (1997) *Ornitologia Brasileira*, Nova Fronteira, Rio de Janeiro.

Siikamaki, P. (1998) Limitation of reproductive success by food availability and breeding time in Pied Flycatchers. *Ecology*, **79**, 1789–1796.

Soler, M. (2018) *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*, Springer, Cham, Switzerland.

Somveille, M., Manica, A., Butchart, S.H.M. & Rodrigues, A.S.L. (2013) Mapping Global Diversity Patterns for Migratory Birds. *PLoS ONE*, **8**.

Somveille, M., Manica, A. & Rodrigues, A.S.L.L. (2019) Where the wild birds go: explaining the differences in migratory destinations across terrestrial bird species. *Ecography*, **42**, 225–236.

Somveille, M., Rodrigues, A.S.L. & Manica, A. (2018) Energy efficiency drives the global seasonal distribution of birds. *Nature Ecology and Evolution*, **2**, 962–969.

Somveille, M., Rodrigues, A.S.L. & Manica, A. (2015) Why do birds migrate? A macroecological perspective. *Global Ecology and Biogeography*, **24**, 664–674.

Soriano-Redondo, A., Gutiérrez, J.S., Hodgson, D. & Bearhop, S. (2020) Migrant birds and mammals live faster than residents. *Nature Communications*, **11**, 1–8.

Staniczenko, P.P.A., Sivasubramaniam, P., Suttle, K.B. & Pearson, R.G. (2017) Linking macroecology and community ecology: refining predictions of species distributions using biotic interaction networks. *Ecology Letters*, **20**, 693–707.

Stearns, S.C. (1992) *The Evolution of Life Histories*, Oxford University Press, New York, USA.

Stotz, D.F., Fitzpatrick, J.W., Parker III, T.A. & Moskovits, D.K. (1996) *Neotropical Birds: Ecology and Conservation*, The University of Chicago Press, London, UK.

Strimas-Mackey, M., Hochachka, W.M., Ruiz-Gutierrez, V., Robinson, O.J., Miller, E.T., Auer, T., Kelling, S., Fink, D. & Johnston, A. (2020) *Best Practices for Using eBird Data. Version 1.0.*, Cornell Laboratory of Ornithology, Ithaca, NY.

Stutchbury, B.J.M., Siddiqui, R., Applegate, K., Hvenegaard, G.T., Mammenga, P., Mickle, N., Pearman, M., Ray, J.D., Savage, A., Shaheen, T. & Fraser, K.C. (2016) Ecological causes and consequences of intratropical migration in temperate-breeding migratory birds. *The American Naturalist*, **188**, S28–S40.

Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D. & Kelling, S. (2009) eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, **142**, 2282–2292.

Thorup, K., Tøttrup, A.P., Willemoes, M., Klaassen, R.H.G., Strandberg, R., Vega, M.L., Dasari, H.P., Araújo, M.B., Wikelski, M. & Rahbek, C. (2017) Resource tracking within and across continents in long-distance bird migrants. *Science Advances*, **3**, e1601360.

Tonra, C.M., Marra, P.P. & Holberton, R.L. (2011) Migration phenology and winter habitat quality are related to circulating androgen in a long-distance migratory bird. *Journal of Avian Biology*, **42**, 397–404.

Troscianko, J. (2014) A simple tool for calculating egg shape, volume and surface area from digital images. *Ibis*, **156**, 874–878.

Urban, M.C., Zarnetske, P.L. & Skelly, D.K. (2013) Moving forward: dispersal and species interactions determine biotic responses to climate change. *Annals of the New York Academy of Sciences*, **1297**, 44–60.

U.S. Department of State (2013) Detailed World Polygons (LSIB), South America. *U.S. Department of State. Humanitarian Information Unit*.

Vaughan, I.P. & Ormerod, S.J. (2005) The continuing challenges of testing species distribution models. *Journal of Applied Ecology*, **42**, 720–730.

Watts, H.E., Cornelius, J.M., Fudickar, A.M., Pérez, J. & Ramenofsky, M. (2018) Understanding variation in migratory movements: a mechanistic approach. *General and Comparative Endocrinology*, **256**, 112–122.

Webster, M.S. (2017) *The extended specimen*. *The Extended Specimen: Emerging Frontiers in Collections-based Ornithological Research* (ed. by M.S. Webster), pp. 1–9. Taylor & Francis, Boca Raton.

van Wijk, R.E., Kölzsch, A., Kruckenberg, H., Ebbinge, B.S., Müskens, G.J.D.M. & Nolet, B.A. (2012) Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos*, **121**, 655–664.

Wikelski, M., Tarlow, E.M., Raim, A., Diehl, R.H., Larkin, R.P. & Visser, G.H. (2003) Costs of migration in free-flying songbirds. *Nature*, **423**, 704–704.

Wikiaves (2022) WikiAves, a Enciclopédia das Aves do Brasil.

Williams, T.D. (2001) Experimental manipulation of female reproduction reveals an intraspecific egg size clutch size trade-off. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 423–428.

Williams, T.D. (2005) Mechanisms underlying the costs of egg production. *BioScience*, **55**, 39–48.

Wilman, H., Belmaker, J., Simpson, J., de La Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: species-level foraging attributes of the world’s birds and mammals. *Ecology*, **95**, 2027.

Winger, B.M., Auteri, G.G., Pegan, T.M. & Weeks, B.C. (2019) A long winter for the Red Queen: rethinking the evolution of seasonal migration. *Biological Reviews*, **94**, 737–752.

Winger, B.M. & Pegan, T.M. (2021) Migration distance is a fundamental axis of the slow-fast continuum of life history in boreal birds. *Ornithology*, **138**, ukab043.

Winkler, D.W. & Allen, P.E. (1996) The seasonal decline in Tree Swallow clutch size: physiological constraint or strategic adjustment? *Ecology*, **77**, 922–932.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P. & Svenning, J.-C. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, **88**, 15–30.

Wood, S. & Scheipl, F. (2020) gamm4: Generalized Additive Mixed Models using “mgcv” abd “lme4.”

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, **73**, 3–36.

Wood, S.N. (2017) *Generalized additive models: an introduction with R*, 2nd ed. Chapman and Hall/CRC.

Wright, M.N. & Ziegler, A. (2017) *ranger*: A fast implementation of random forests for high dimensional data in C++ and R. *Journal of Statistical Software*, **77**, 1–17.

Yom-Tov, Y., Christie, M.I. & Iglesias, G.J. (1994) Clutch size in passerines of southern South America. *The Condor*, **96**, 170–177.

Youngflesh, C., Socolar, J., Amaral, B.R., Arab, A., Guralnick, R.P., Hurlbert, A.H., LaFrance, R., Mayor, S.J., Miller, D.A.W. & Tingley, M.W. (2021) Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. *Nature Ecology and Evolution*.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

APÊNDICES

Capítulo 1

Appendix S1

Table S1.1. Tyrant flycatcher species breeding and migrating within South America used in the study.

Species	**English-name**	**Migratory status***
Agriornis micropterus	Gray-bellied Shrike-Tyrant	partial
Agriornis murinus	Lesser Shrike-Tyrant	full
Anairetes flavirostris	Yellow-billed Tit-tyrant	partial
Colorhamphus parvirostris	Patagonian Tyrant	full
Elaenia albiceps	White-crested Elaenia	partial
Elaenia chiriquensis	Lesser Elaenia	partial
Elaenia parvirostris	Small-billed Elaenia	full
Elaenia spectabilis	Large Elaenia	full
Elaenia strepera	Slaty Elaenia	full
Empidonomus aurantioatrocristatus	Crowned Slaty Flycatcher	partial
Empidonomus varius	Variegated Flycatcher	partial
Hymenops perspicillatus	Spectacled Tyrant	partial
Inezia inornata	Plain Tyrannulet	partial
Knipolegus hudsoni	Hudson's Black-Tyrant	full
Lessonia rufa	Austral Negrito	full
Muscisaxicola albilora	White-browed Ground-Tyrant	full
Muscisaxicola capistratus	Cinnamon-bellied Ground-Tyrant	full
Muscisaxicola cinereus	Cinereous Ground-Tyrant	partial
Muscisaxicola flavinucha	Ochre-naped Ground-Tyrant	full
Muscisaxicola frontalis	Black-fronted Ground-Tyrant	full
Muscisaxicola maclovianus	Dark-faced Ground-Tyrant	partial
Myiarchus swainsoni	Swainson's Flycatcher	partial
Myiodynastes maculatus	Streaked Flycatcher	partial
Neoxolmis coronatus	Black-crowned Monjita	full
Neoxolmis rubetra	Rusty-backed Monjita	partial
Neoxolmis rufiventris	Chocolate-vented Tyrant	full
Pseudocolopteryx acutipennis	Subtropical Doradito	full
Pseudocolopteryx dinelliana	Dinelli's Doradito	partial
Pseudocolopteryx flaviventris	Warbling Doradito	full
Serpophaga griseicapilla	Straneck's Tyrannulet	full
Tyrannus albogularis	White-throated Kingbird	partial
Tyrannus melancholicus	Tropical Kingbird	partial
Tyrannus savana	Fork-tailed Flycatcher	partial

* Classification based on literature review of species' distributions and behavior (Chesser, 1995; Billerman *et al.*, 2020).

Table S1.2. Performance of encounter rate balanced random forest models based on eBird occurrence information for 33 tyrant flycatcher species. Model predictions were calibrated using the random forest and modeled the observed encounter rate against the predicted probabilities with a generalized additive model (GAM) constrained to be monotonically increasing. Models were validated using a semi-independent dataset containing an equal number of detections and non-detections for each month and were assessed using the True Skill Statistic (TSS) metric. TSS scores were calculated using an optimized threshold that maximizes the sum of sensitivity and specificity.

Species	**TSS**	**Sensitivity**	**Specificity**
Agriornis micropterus	0.6918	0.7358	0.9560
*Agriornis murinus**	0.6981	0.7547	0.9434
Anairetes flavirostris	0.8468	0.9091	0.9377
Colorhamphus parvirostris	0.7626	0.8741	0.8885
Elaenia albiceps	0.5854	0.7636	0.8218
Elaenia chiriquensis	0.5452	0.6968	0.8484
Elaenia parvirostris	0.4752	0.7196	0.7556
Elaenia spectabilis	0.5968	0.7325	0.8643
*Elaenia strepera**	0.6538	0.6538	1.0000
Empidonomus aurantioatrocristatus	0.6777	0.8208	0.8569
Empidonomus varius	0.6162	0.7908	0.8254
Hymenops perspicillatus	0.7345	0.9019	0.8326
Inezia inornata	0.6296	0.6543	0.9753
*Knipolegus hudsoni**	0.3000	0.3250	0.9750
Lessonia rufa	0.7629	0.8988	0.8642
Muscisaxicola albilora	0.8022	0.8242	0.9780
Muscisaxicola capistratus	0.6885	0.7213	0.9672
Muscisaxicola cinereus	0.9224	0.9569	0.9655
Muscisaxicola flavinucha	0.9091	0.9091	1.0000
Muscisaxicola frontalis	0.6571	0.6571	1.0000
Muscisaxicola maclovianus	0.7430	0.8969	0.8461
Myiarchus swainsoni	0.5523	0.7462	0.8061
Myiodynastes maculatus	0.5769	0.8556	0.7213
*Neoxolmis coronatus**	0.6316	0.6579	0.9737
*Neoxolmis rubetra**	0.6512	0.6744	0.9767
*Neoxolmis rufiventris**	0.4340	0.4340	1.0000
Pseudocolopteryx acutipennis	0.7753	0.7865	0.9888
Pseudocolopteryx dinelliana	0.8226	0.8226	1.0000
Pseudocolopteryx flaviventris	0.7273	0.8182	0.9091
Serpophaga griseicapilla	0.7203	0.8531	0.8672
Tyrannus albogularis	0.6283	0.6702	0.9581
Tyrannus melancholicus	0.4860	0.8172	0.6688
Tyrannus savana	0.5032	0.7332	0.7701

*Species with very low encounter rate estimates, and whose predictions were not thresholded.

Table S1.3. Seasonal range sizes and tyrant flycatcher species richness at the breeding and non-breeding grounds of 25 migratory tyrant flycatchers breeding and migrating within South America. Range sizes were estimated based on where each species' encounter rate estimates were greater than zero during the months of November, December, and January, for the breeding season, and the months of May, June, and July, for the non-breeding season. Species richness at each season represents the weighted average species richness of the Tyrannidae family (BirdLife International & Handbook of the Birds of the World, 2019) in the breeding and non-breeding ranges.

Species*	**Range size (km^2)**		**Species richness**	
	Breeding	**Non-breeding**	**Breeding**	**Non-breeding**
Agriornis micropterus	80,631	165,675	25.15	28.36
Anairetes flavirostris	1,527,956	2,072,463	19.42	20.87
Colorhamphus parvirostris	205,344	562,225	8.33	9.19
Elaenia chiriquensis	1,877,763	3,980,225	57.80	56.53
Elaenia parvirostris	8,262,838	3,374,163	50.16	53.03
Empidonomus aurantioatrocristatus	10,561,488	6,430,644	51.42	63.60
Empidonomus varius	8,355,419	7,771,444	58.15	61.21
Hymenops perspicillatus	3,601,906	2,746,838	29.98	35.30
Inezia inornata	584,106	966,863	47.00	51.62
Lessonia rufa	1,575,275	1,278,969	18.21	20.52
Muscisaxicola albilora	966,994	809,694	14.05	14.67
Muscisaxicola capistratus	535,713	86,538	16.87	15.38
Muscisaxicola cinereus	903,594	1,017,000	15.52	16.18
Muscisaxicola flavinucha	917,106	892,288	12.73	13.91
Muscisaxicola frontalis	564,438	630,706	12.35	12.78
Muscisaxicola maclovianus	563,981	2,037,544	8.60	11.57
Myiarchus swainsoni	15,843,700	9,908,194	56.62	61.59
Myiodynastes maculatus	15,831,219	13,784,663	57.92	59.04
Pseudocolopteryx acutipennis	191,894	161,094	37.51	37.11
Pseudocolopteryx dinelliana	49,831	138,431	36.70	39.27
Pseudocolopteryx flaviventris	687,756	329,488	34.12	35.45
Serpophaga griseicapilla	523,356	2,489,425	29.89	37.32
Tyrannus albogularis	1,372,375	166,200	56.71	67.43
Tyrannus melancholicus	15,886,469	11,151,825	56.82	59.77
Tyrannus savana	11,634,294	3,125,219	47.03	50.13

*The ranges for *Agriornis murinus, Elaenia strepera, Knipolegus hudsoni, Neoxolmis coronatus, Neoxolmis rubetra* and *Neoxolmis rufiventris* were not estimated because we did not apply the threshold in the model predictions (see main text for explanation), and the very low encounter rate values overestimated species' range sizes. The estimates for *Elaenia albiceps* and *Elaenia spectabilis* were also not included because the predictions generated for their non-breeding periods were underestimated, presumably because of species' low conspicuousness during this period and field identification challenges.

References

Billerman, S. M., Keeney, B. K., Rodewald, P. G., Schulenberg, T. S., & (Editors). (2020). Birds of the World. Cornell Laboratory of Ornithology. https://birdsoftheworld.org/bow/home

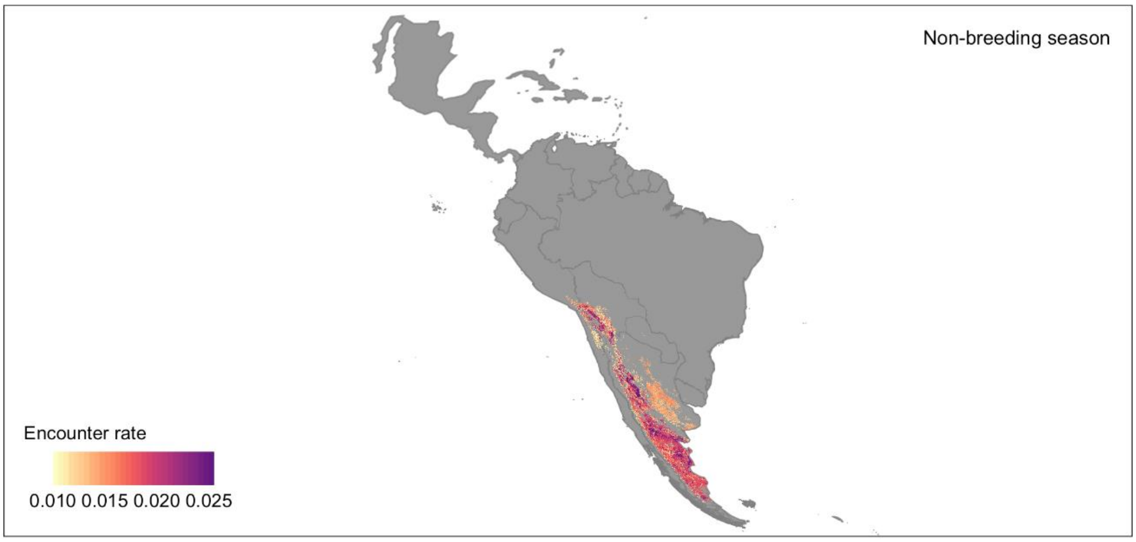
BirdLife International, & Handbook of the Birds of the World. (2019). Bird species distribution maps of the world. Version 2019.1. http://datazone.birdlife.org/species/requestdis

Chesser, R. T. (1995). Biogeographic, ecological, and evolutionary aspects of South American austral migration, with special reference to the family Tyrannidae. Ph.D. dissertation, Lousiana State University and Agricultural & Mechanical College. https://digitalcommons.lsu.edu/gradschool_disstheses

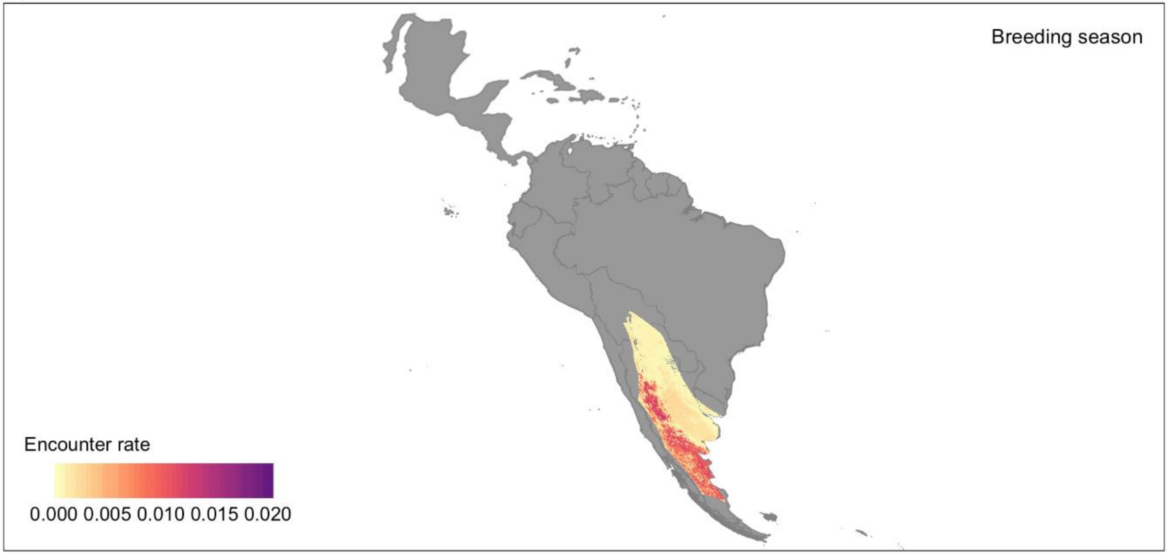
Appendix S2

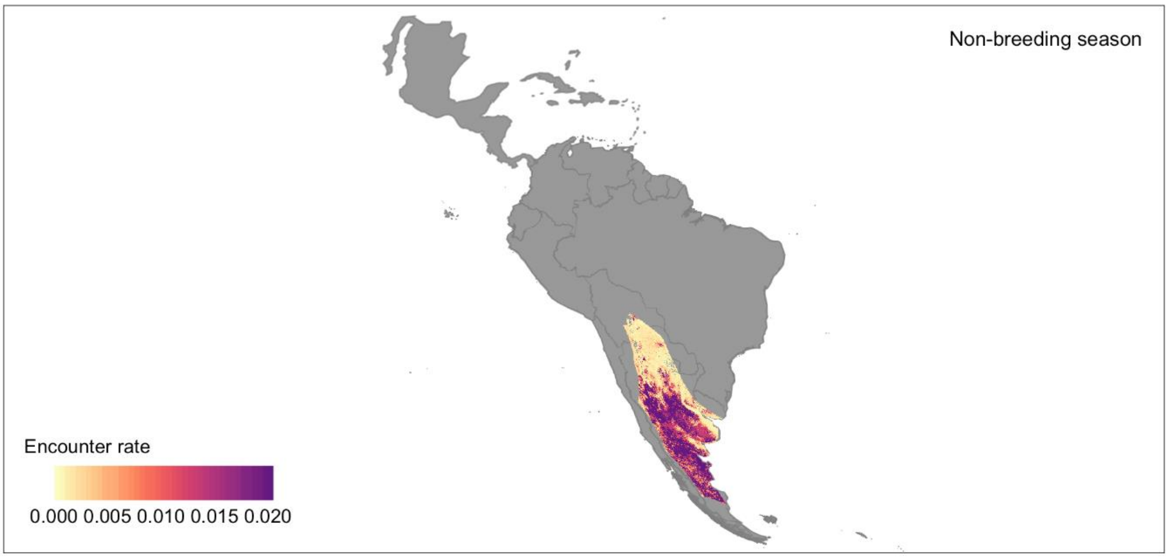
Tyrant flycatcher species' seasonal range maps

Agriornis micropterus

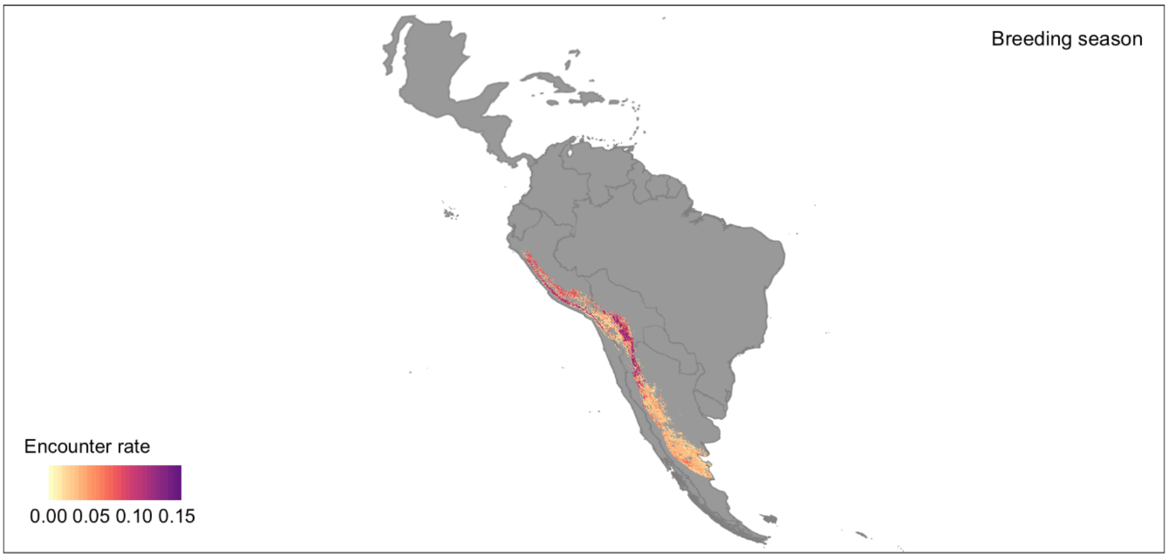


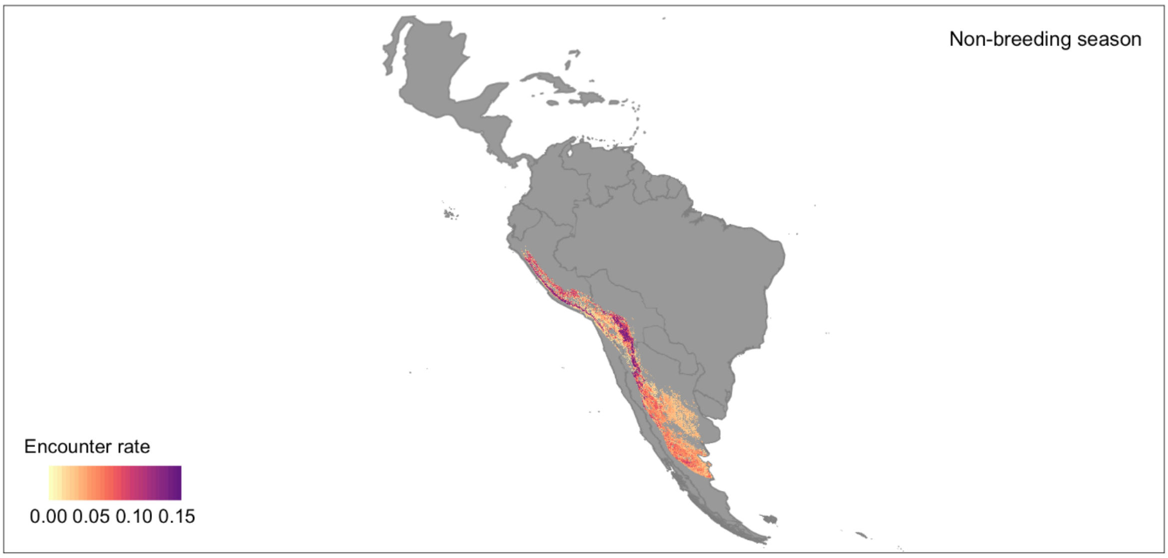
Agriornis murinus





Anairetes flavirostris





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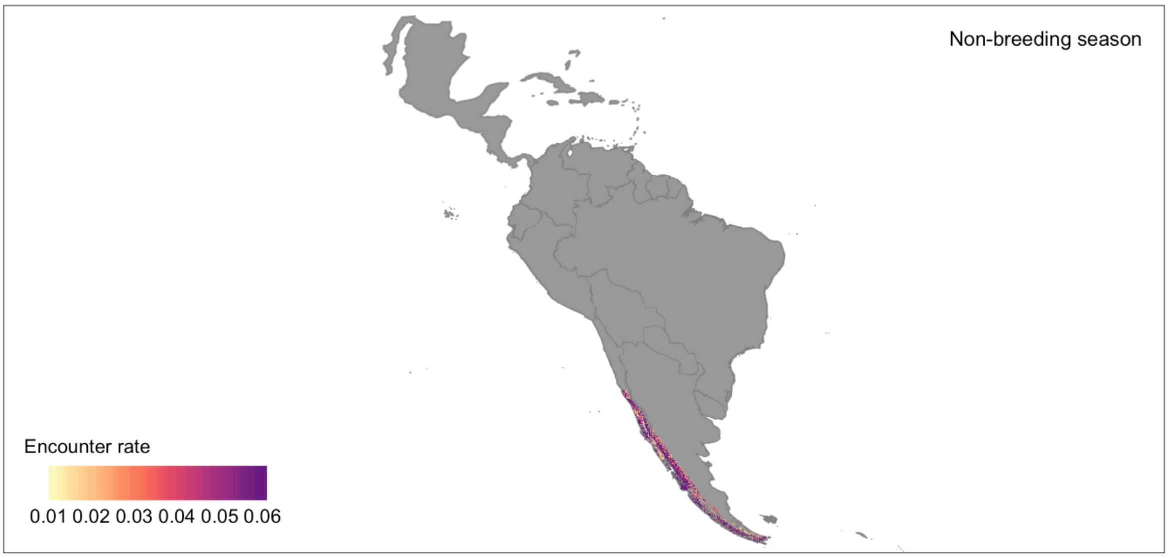

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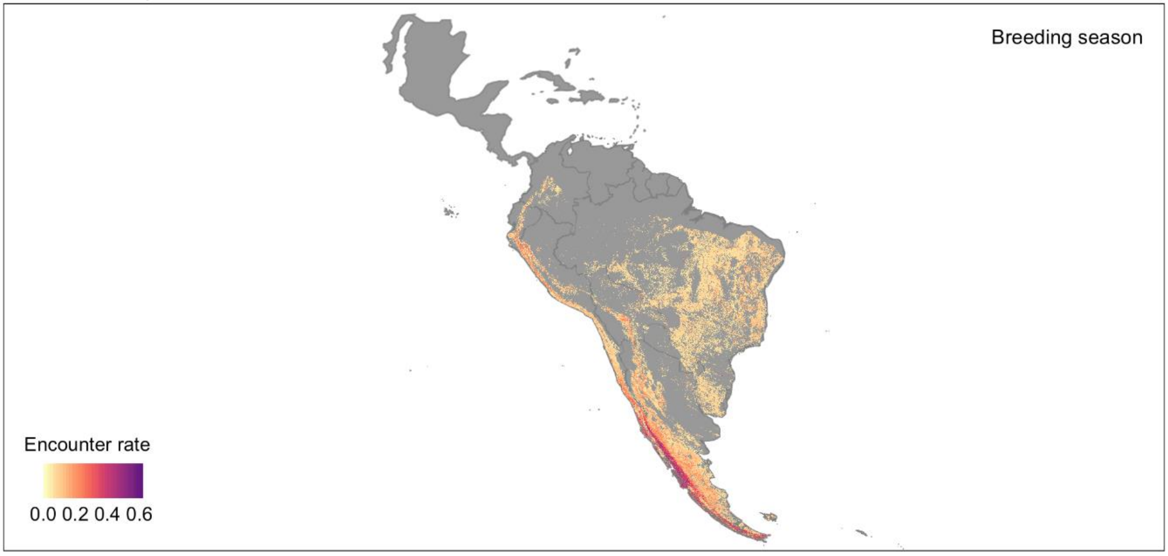

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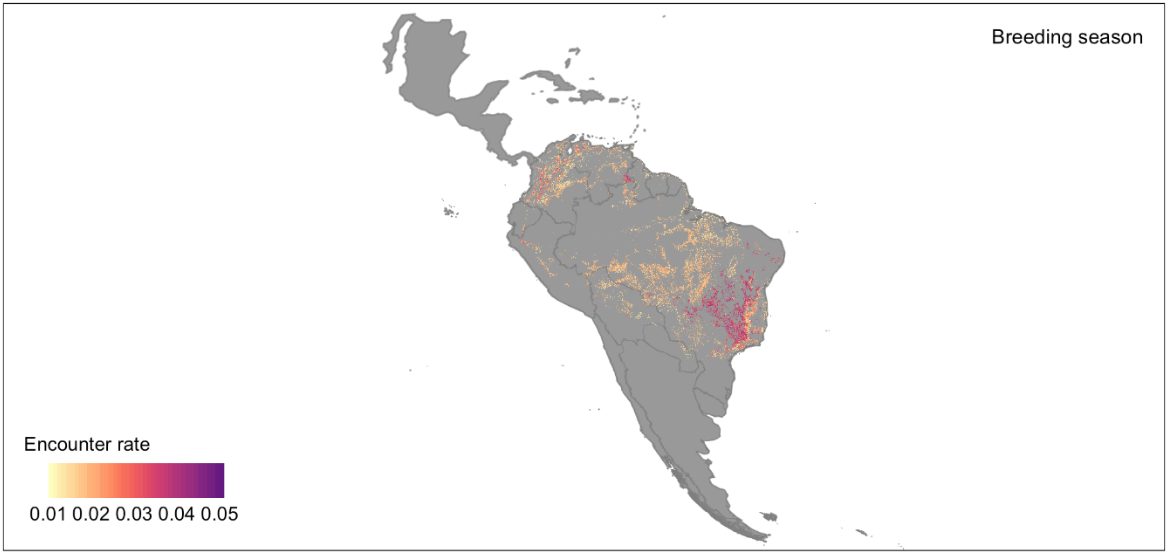

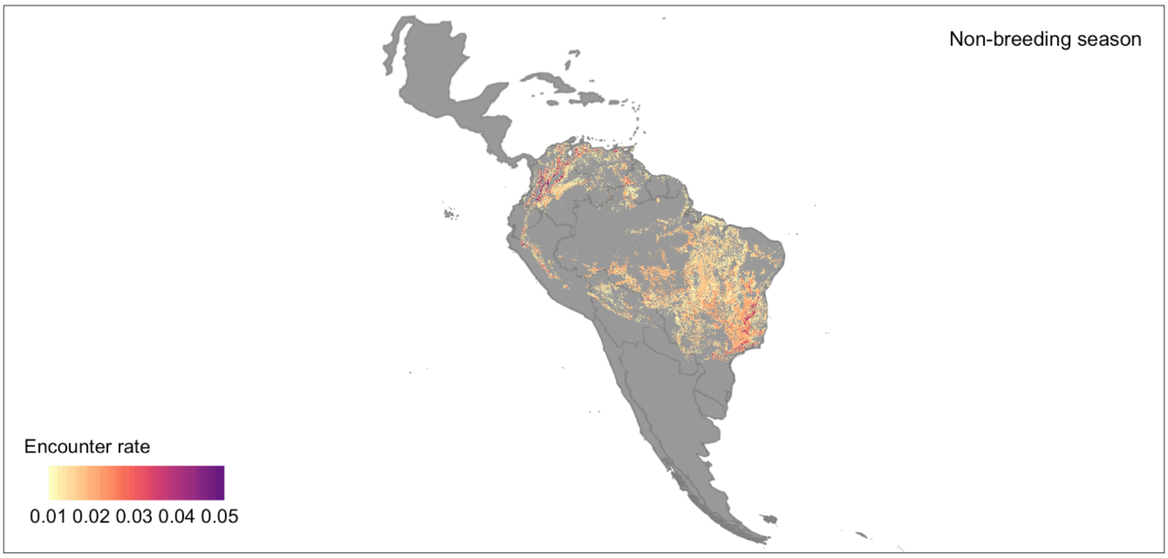

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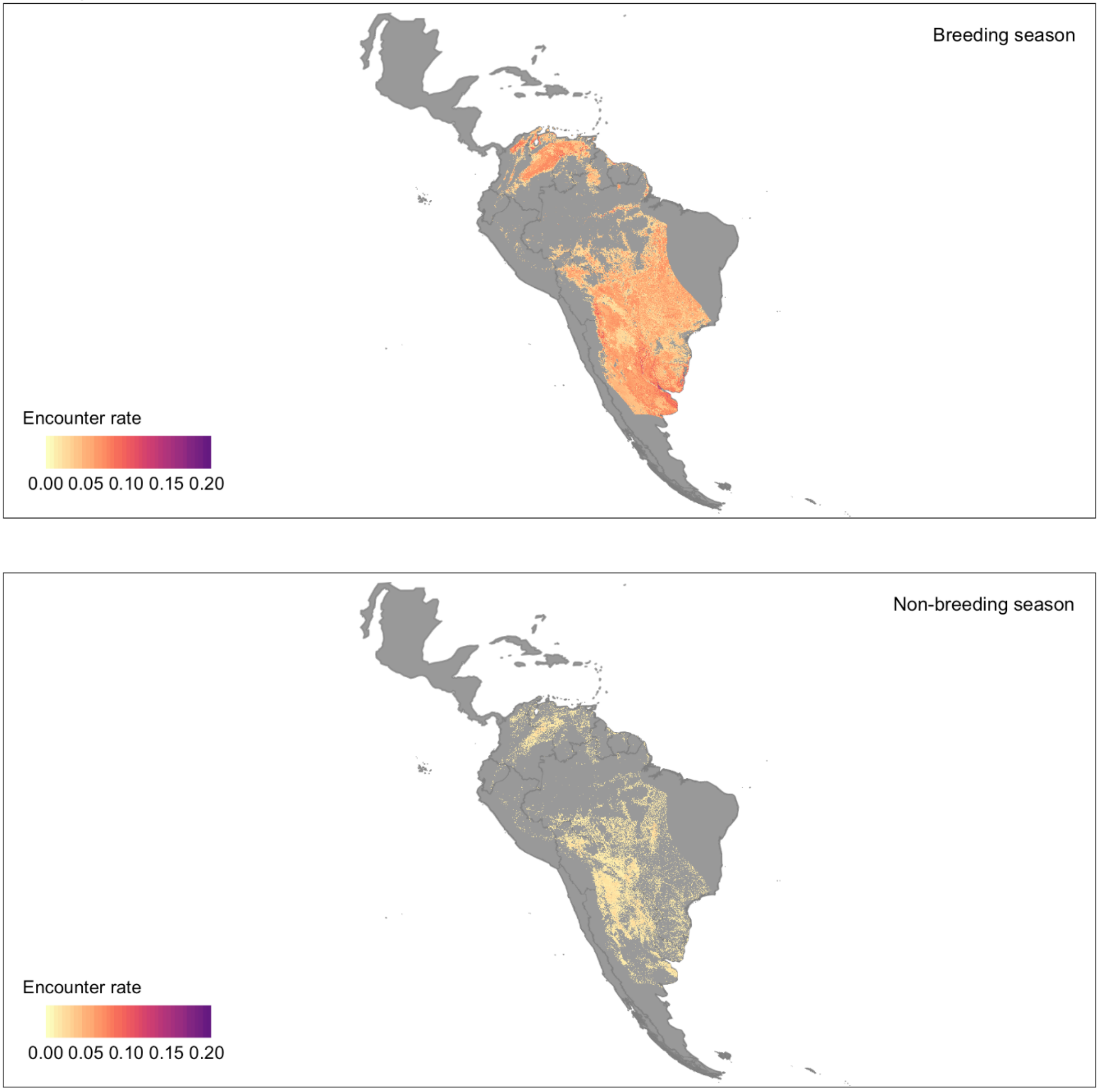

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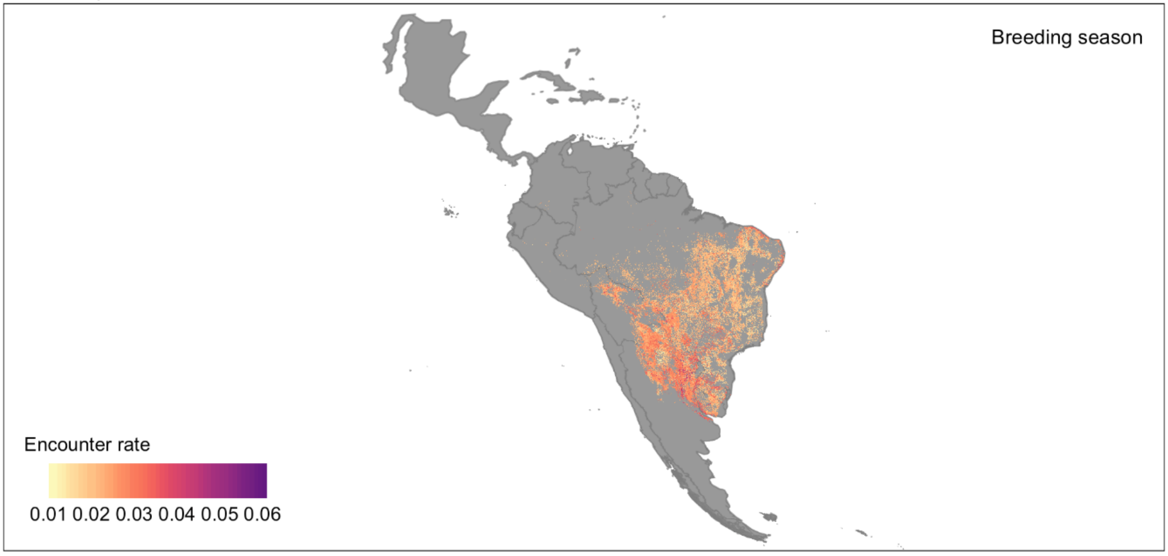

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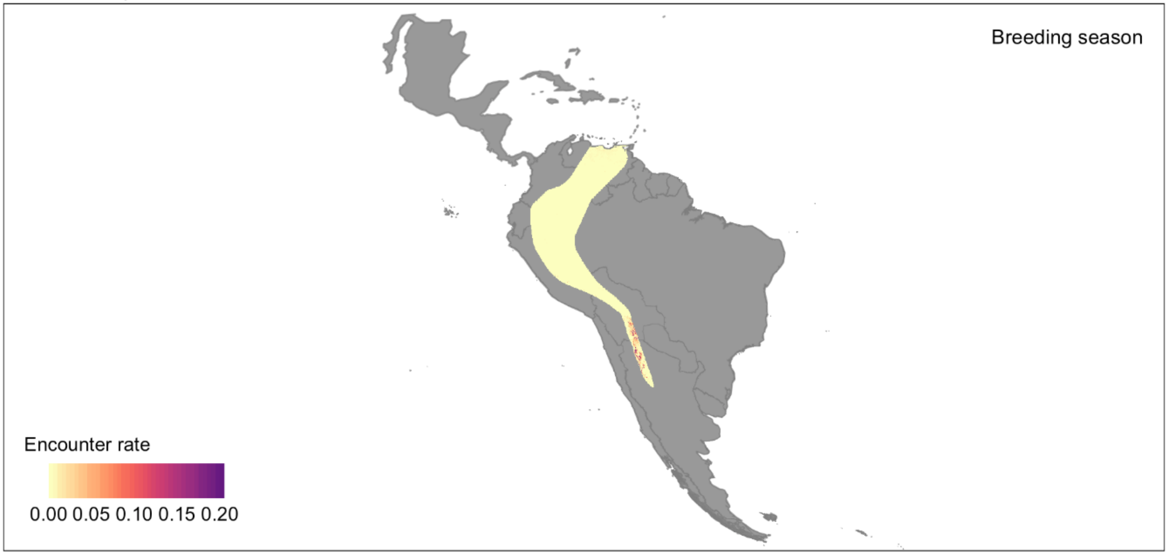

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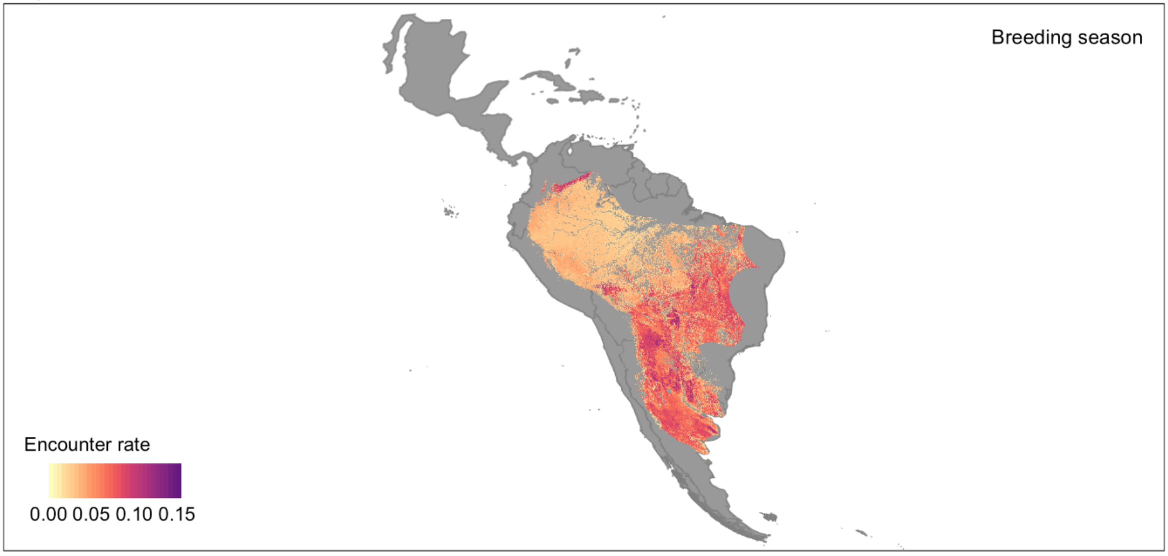

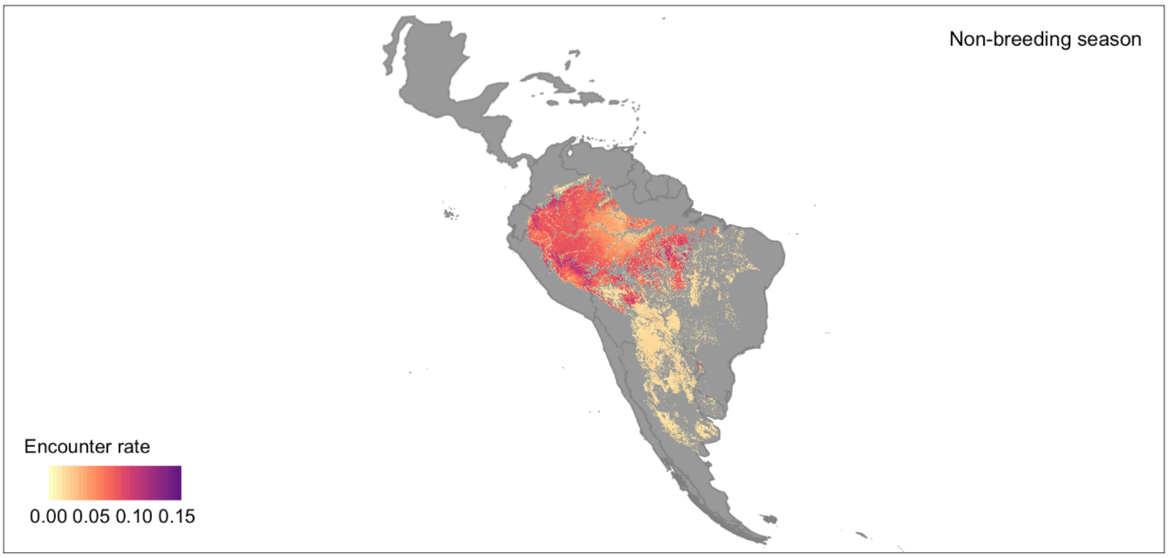

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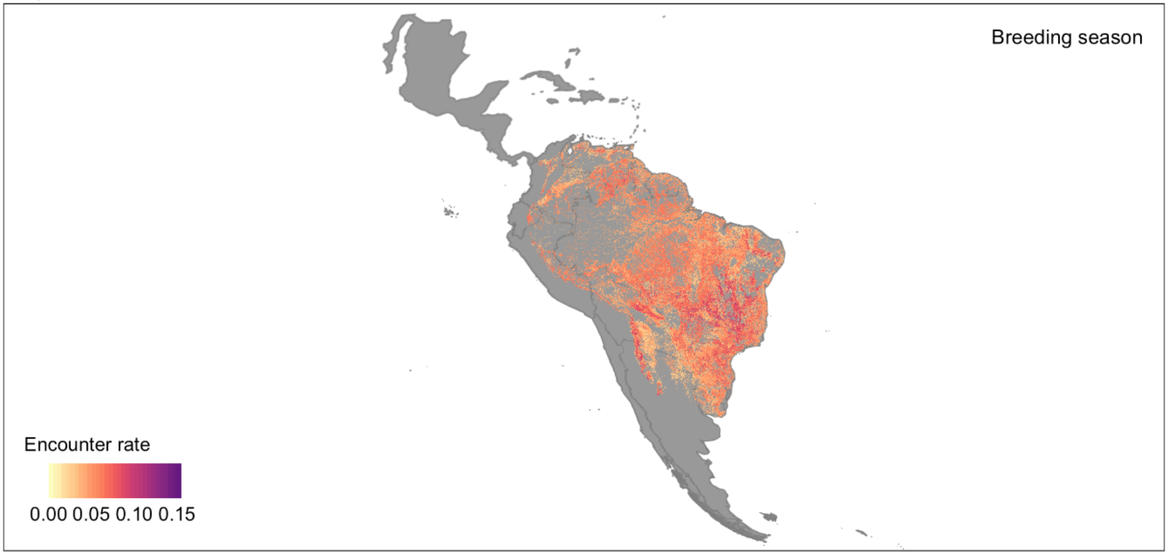

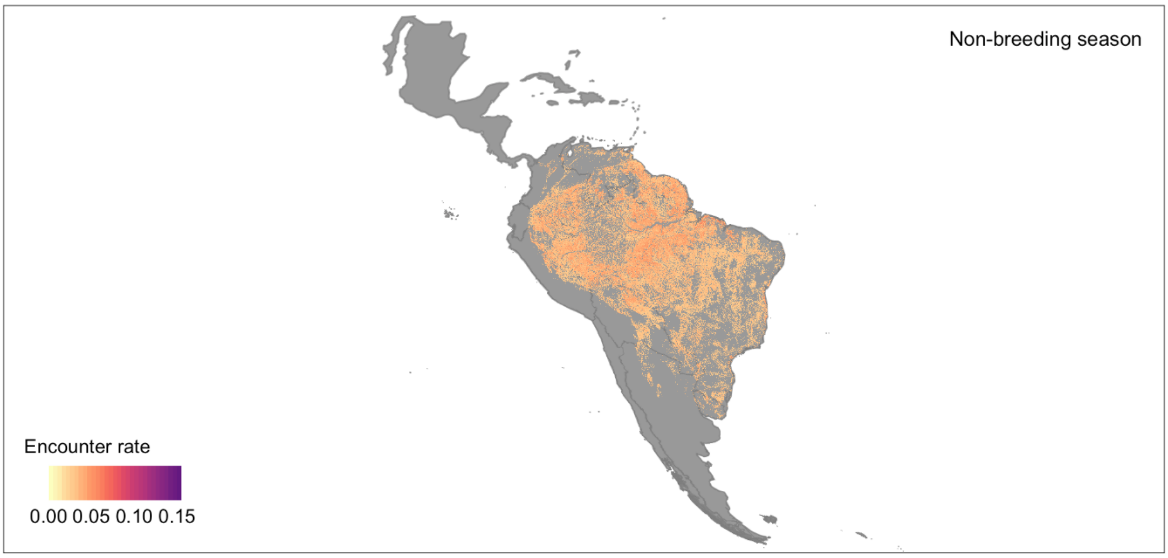

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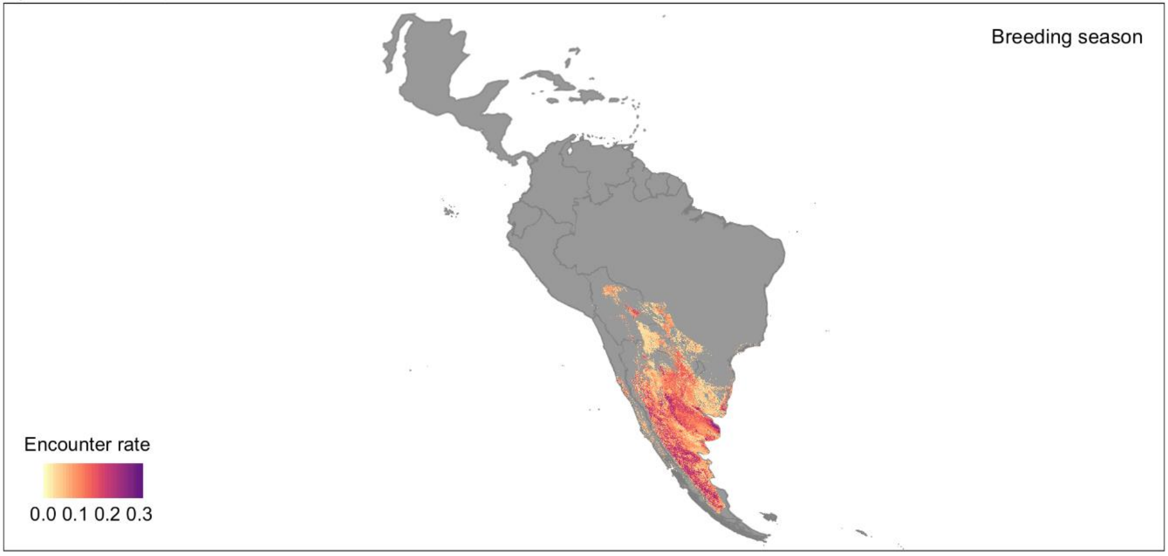

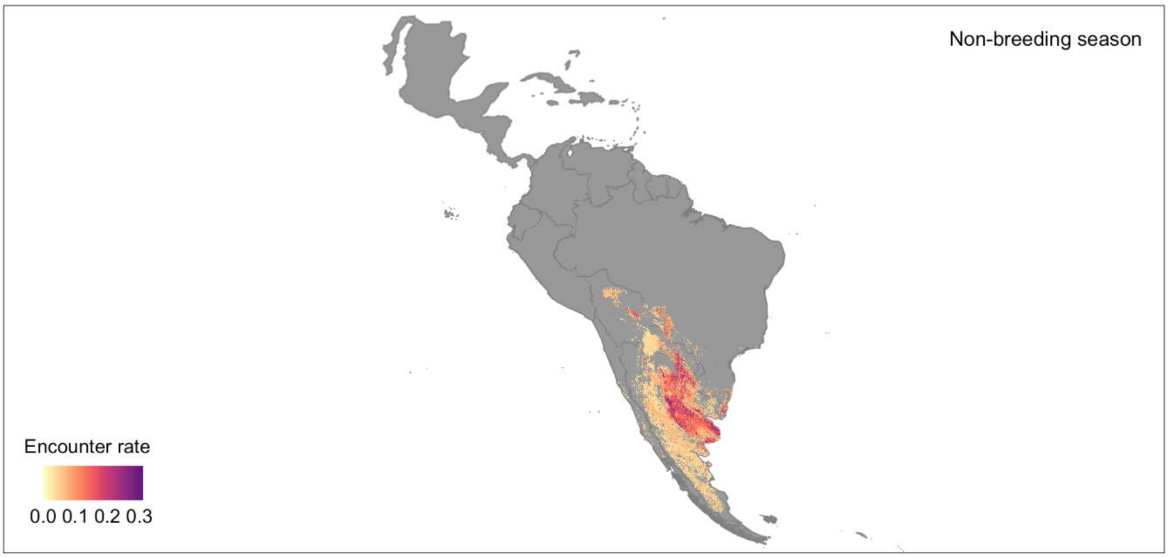

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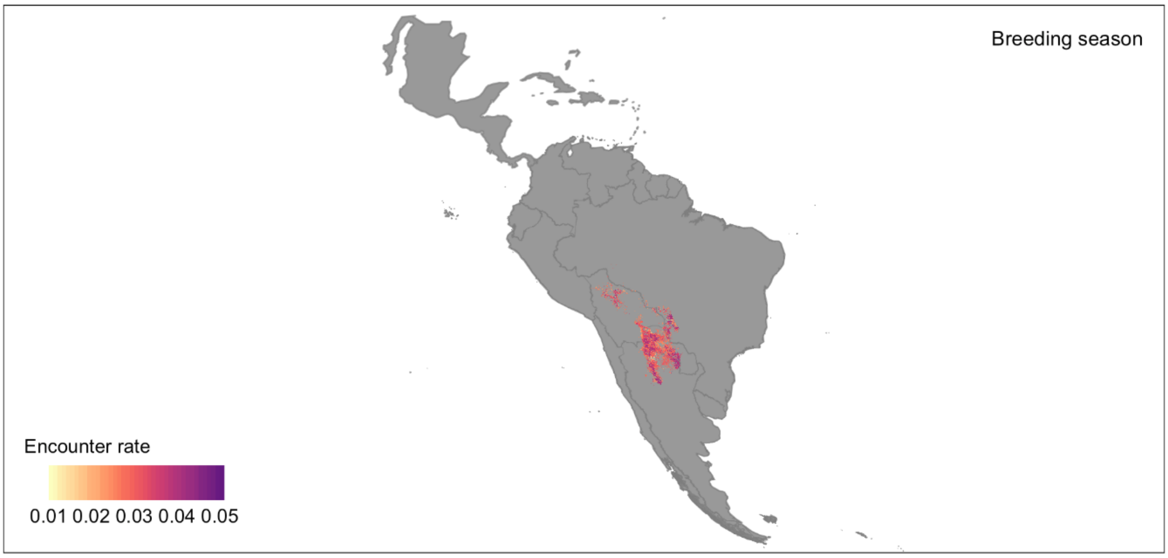

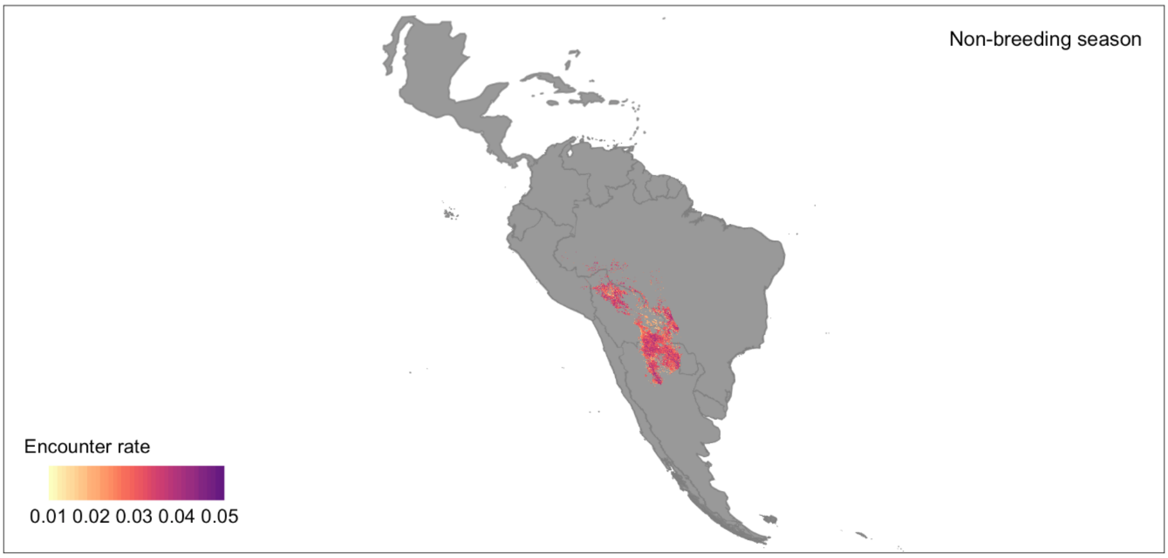

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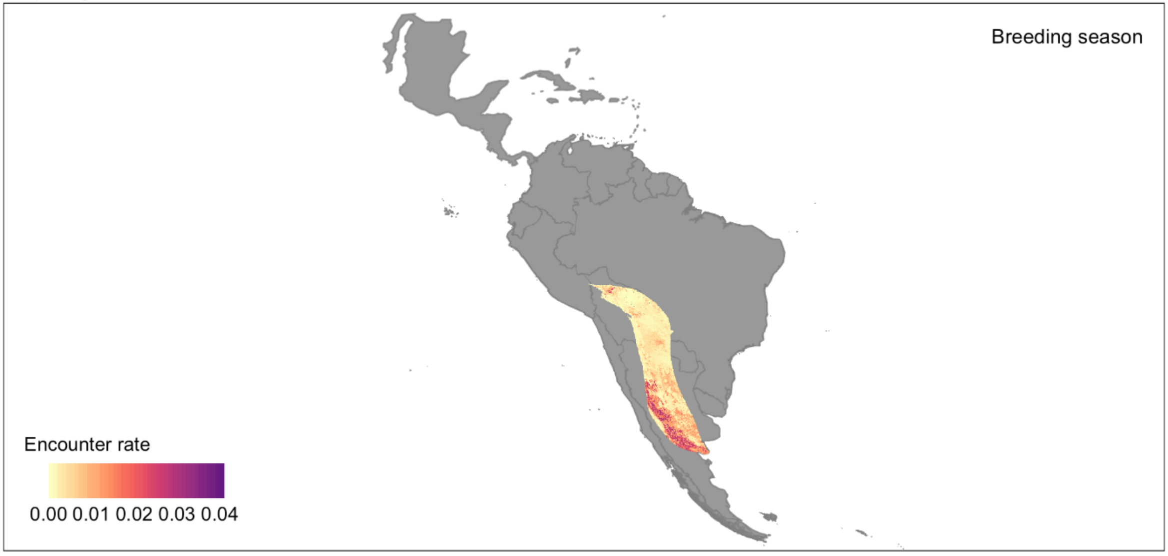
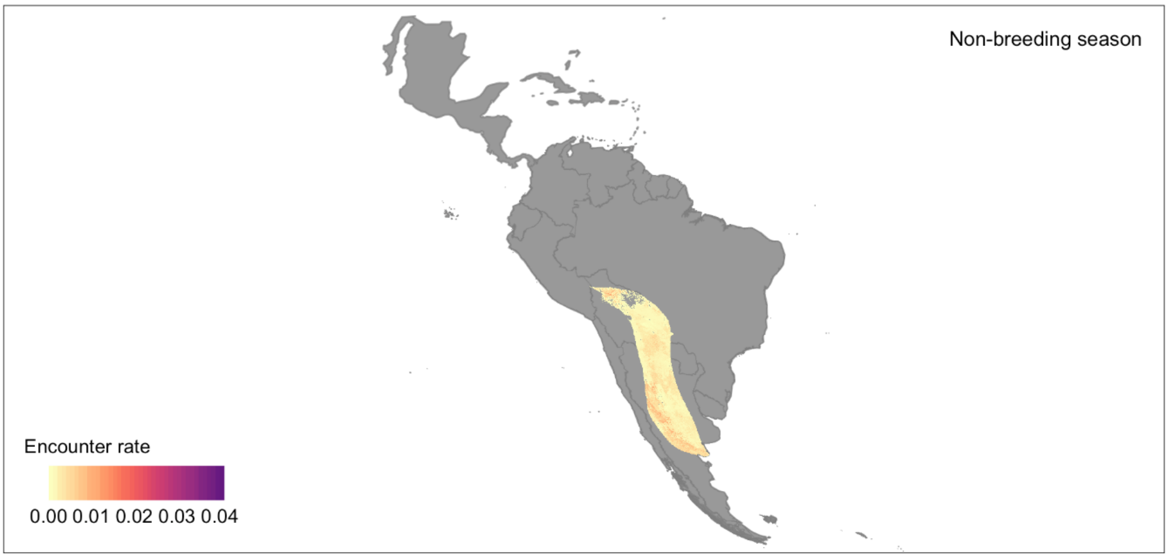
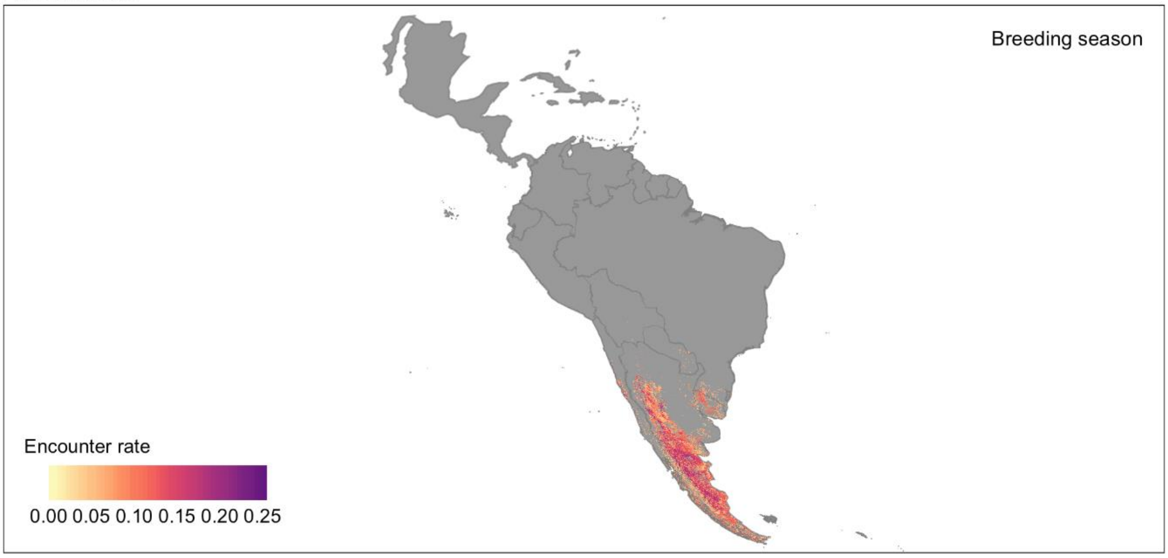
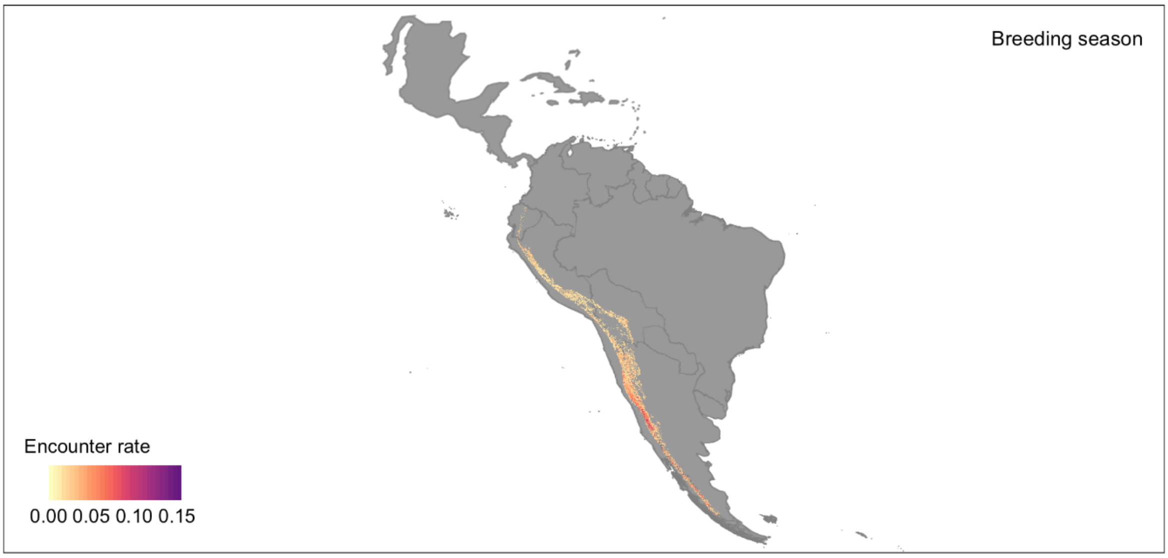




Lessonia rufa

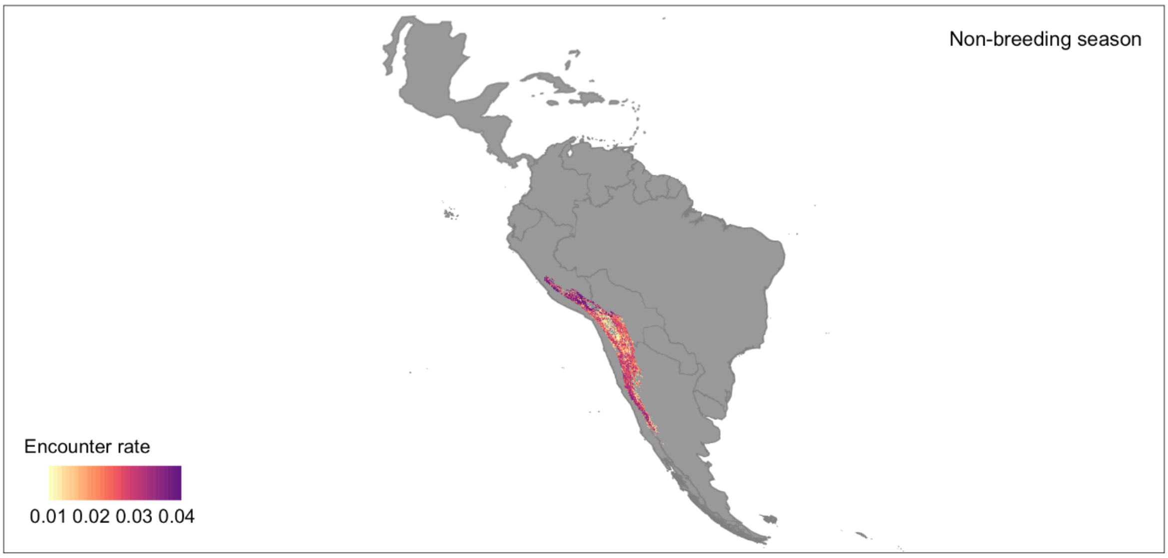


Muscisaxicola albilora



Muscisaxicola capistratus

Muscisaxicola cinereus



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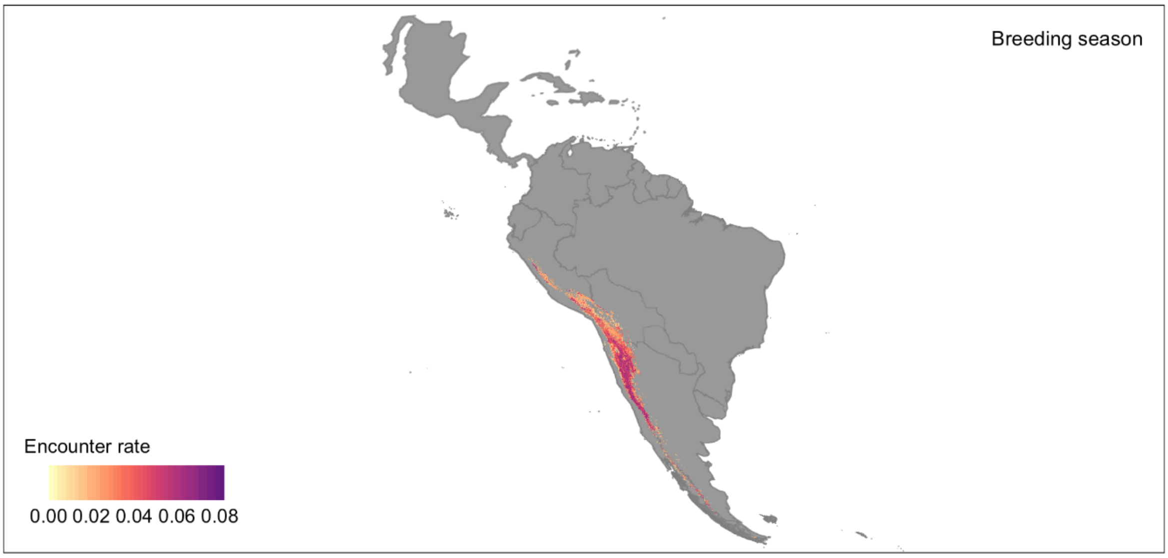
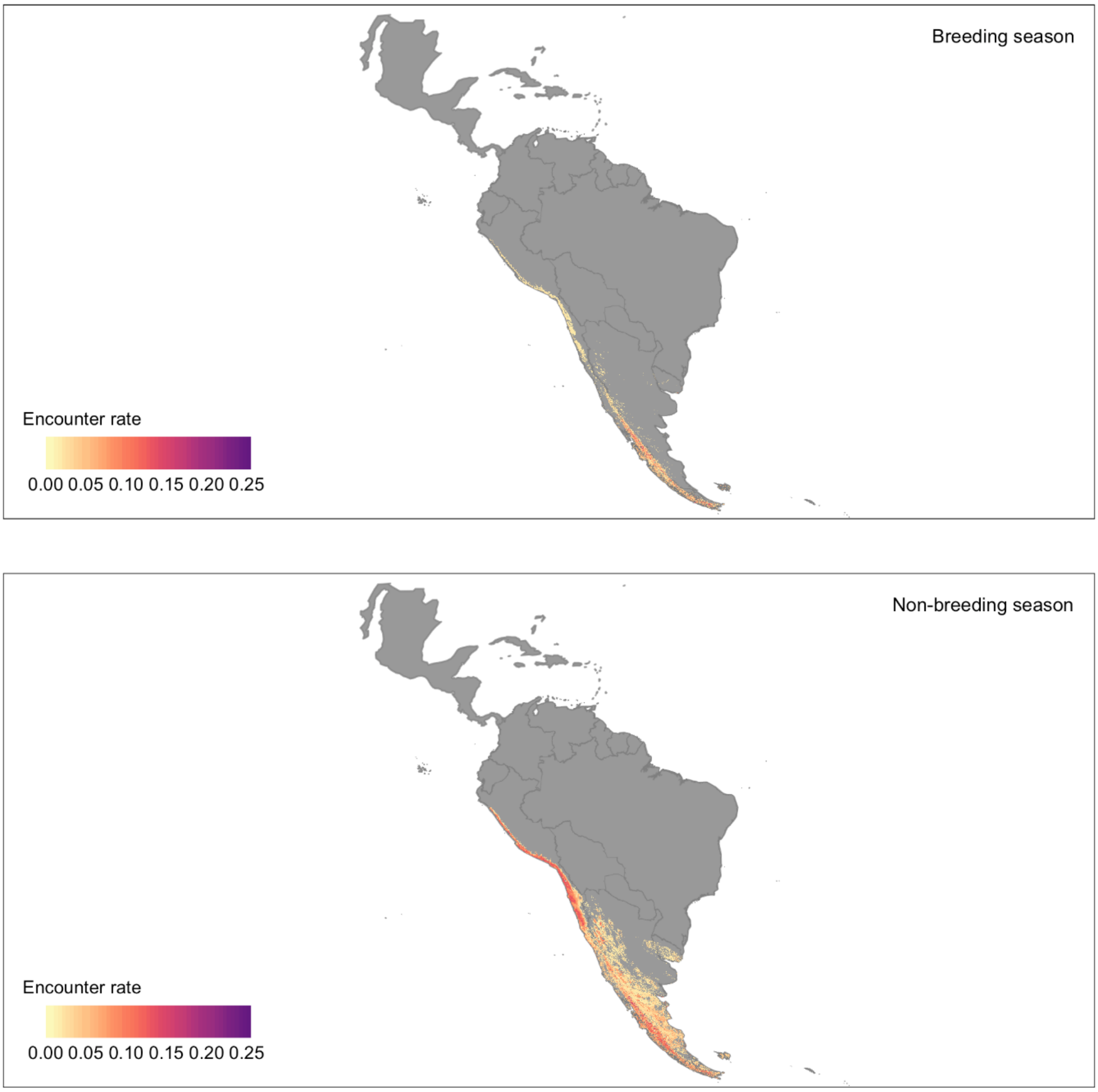
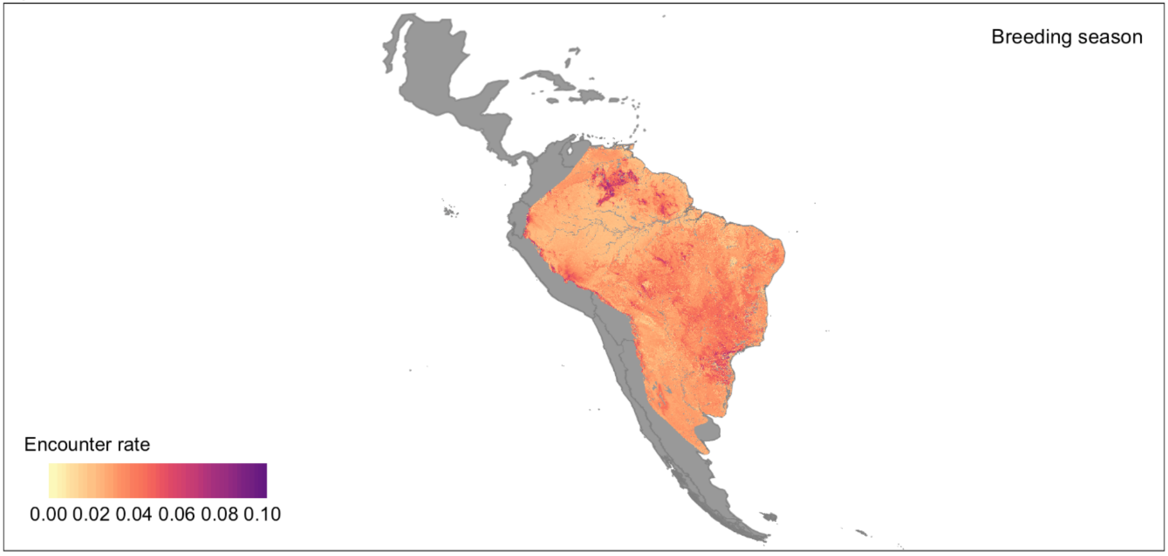


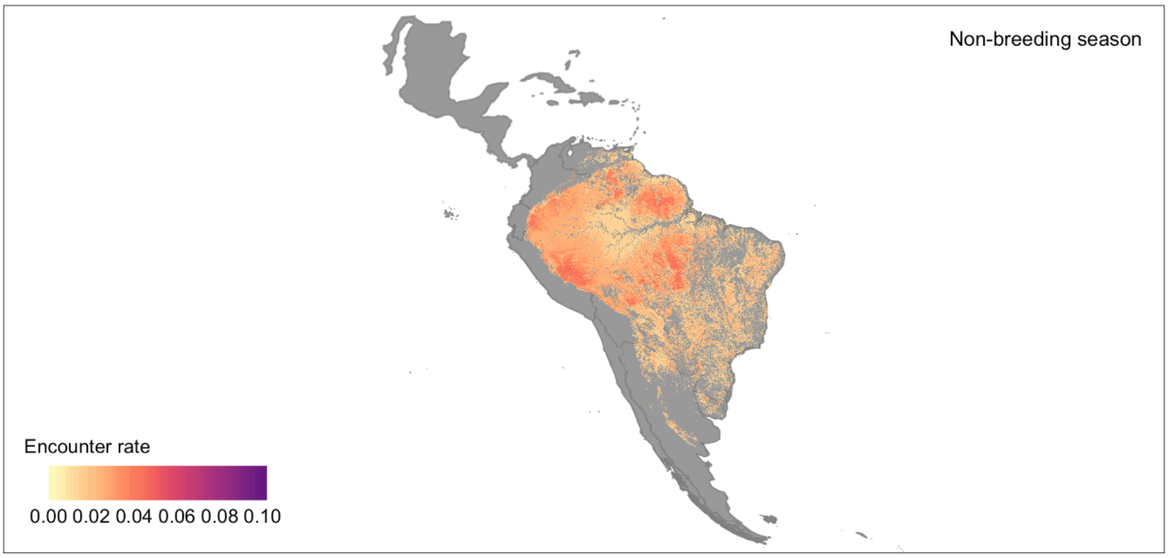
Muscisaxicola frontalis

Muscisaxicola maclovianus



Myiarchus swainsoni





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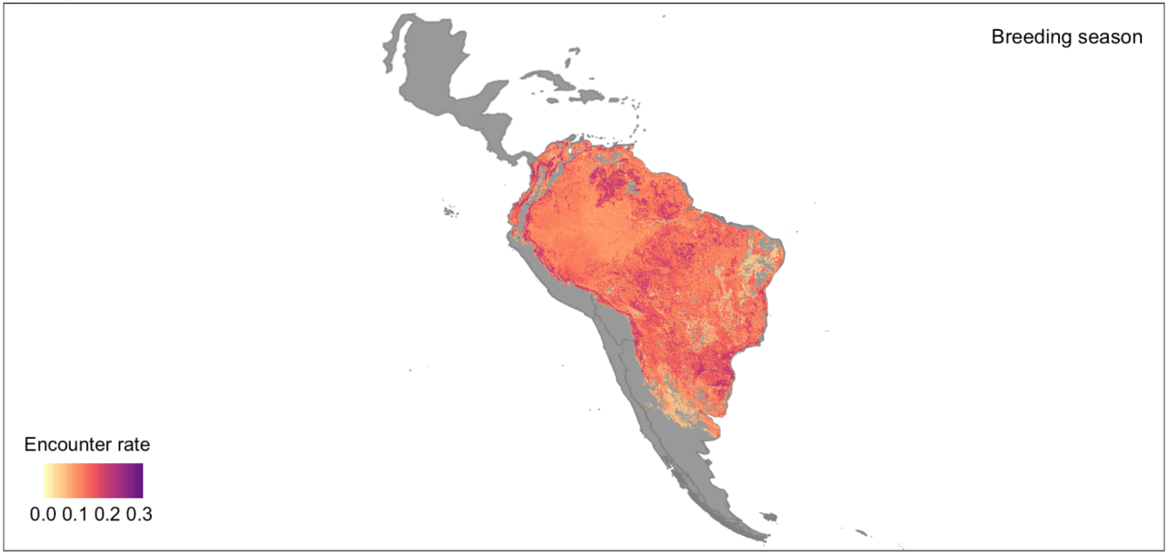
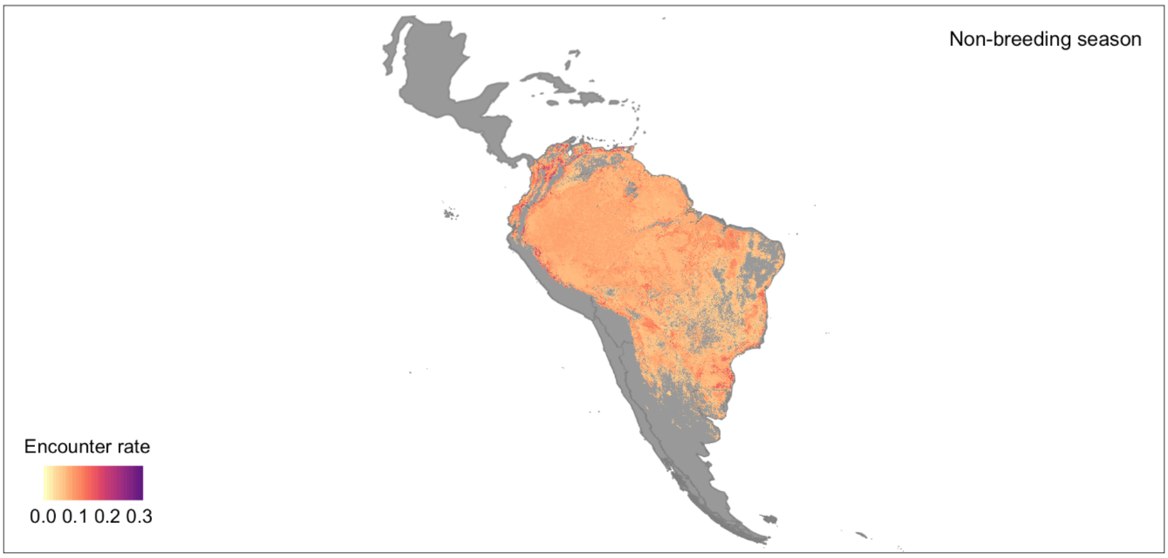
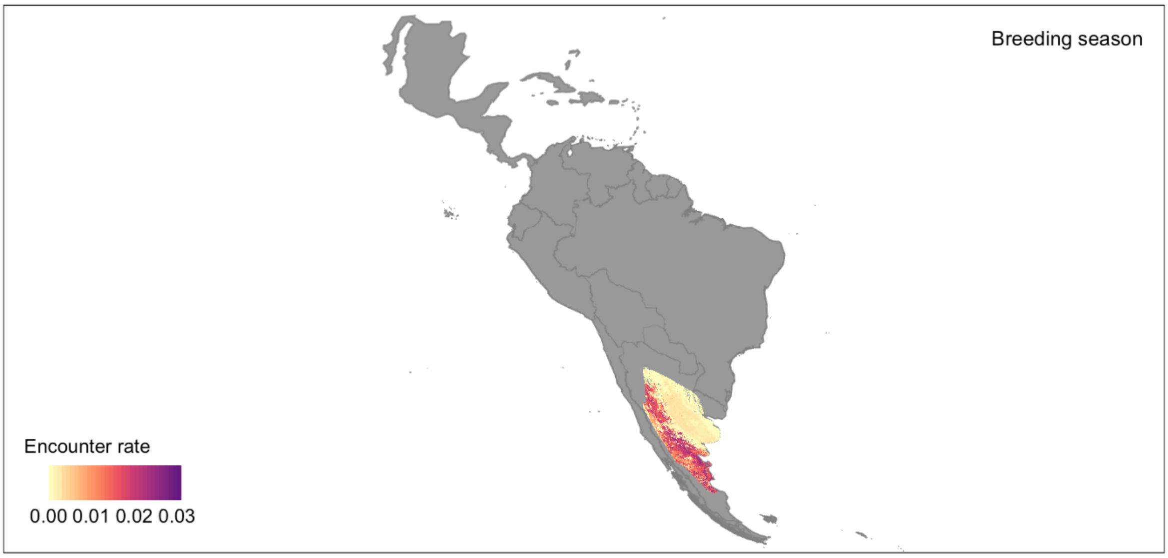
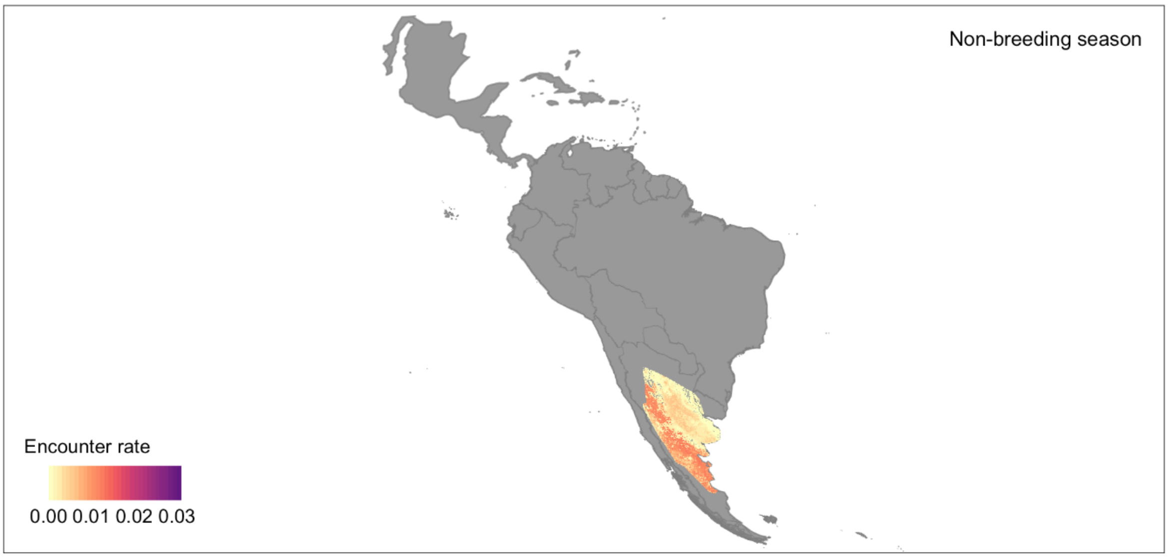


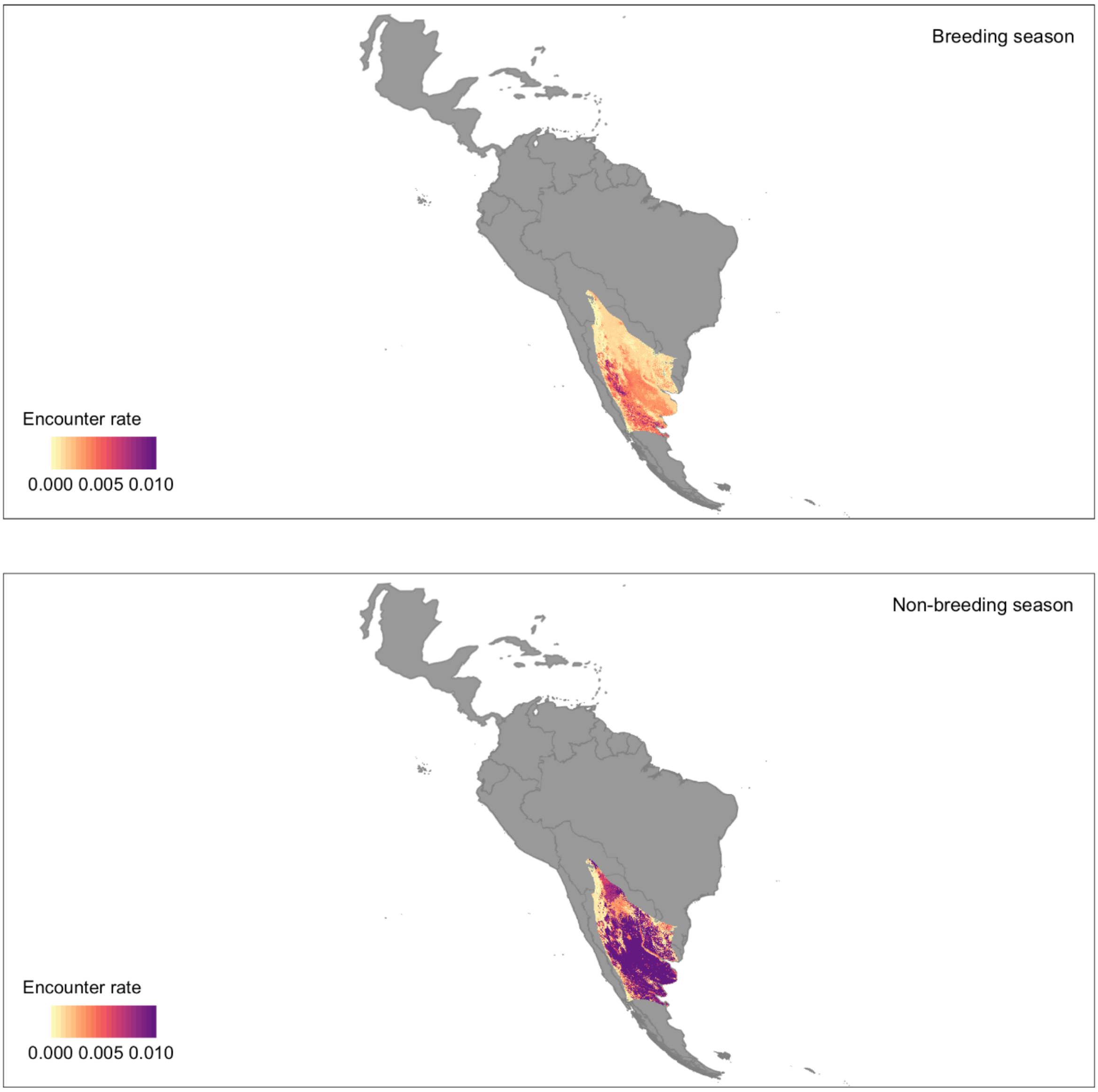


Neoxolmis rubetra

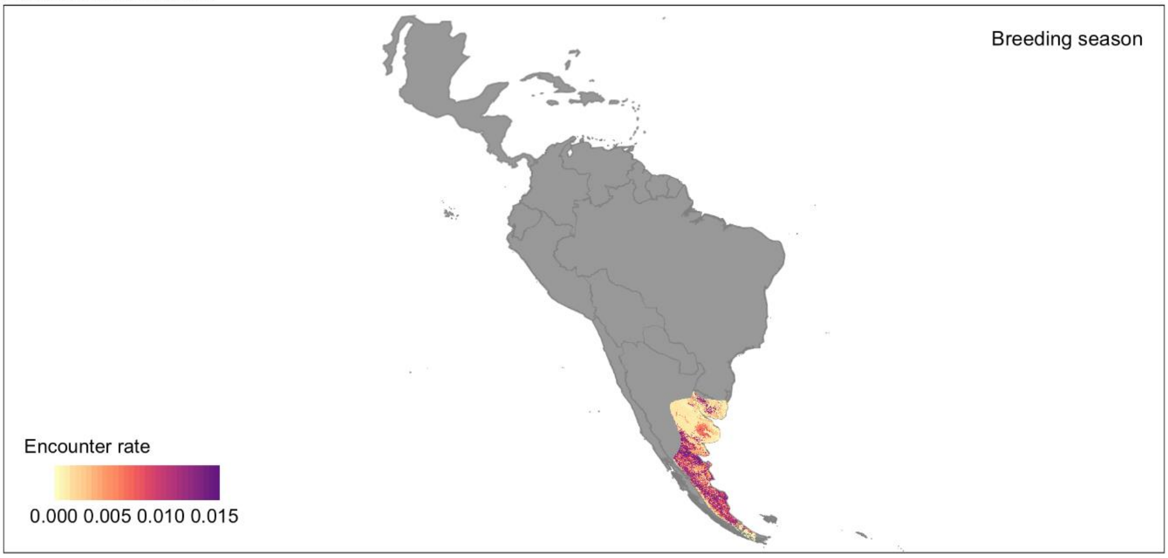


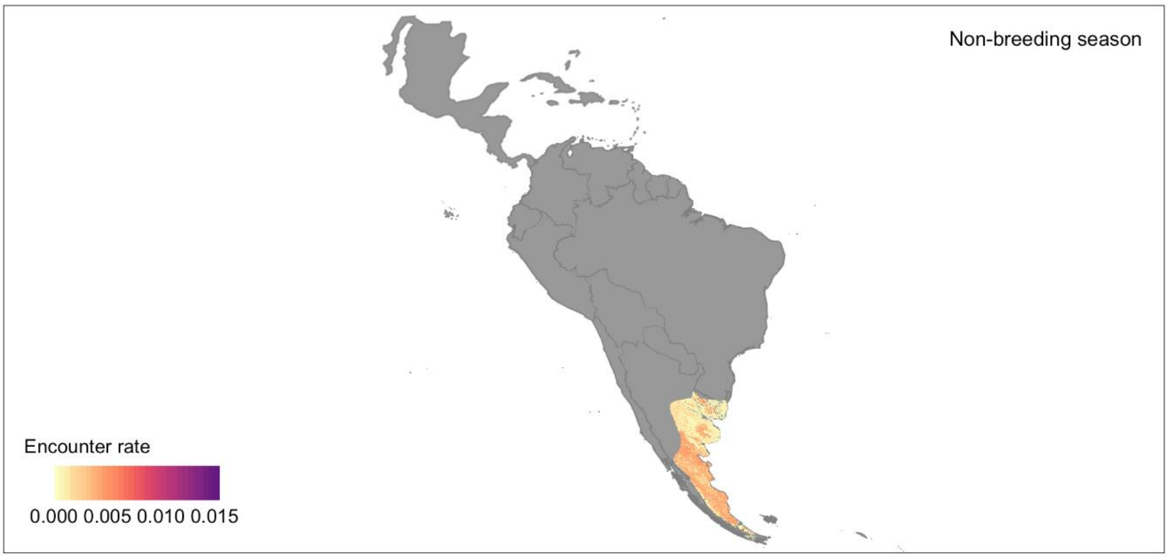


Neoxolmis coronatus



Neoxolmis rufiventris



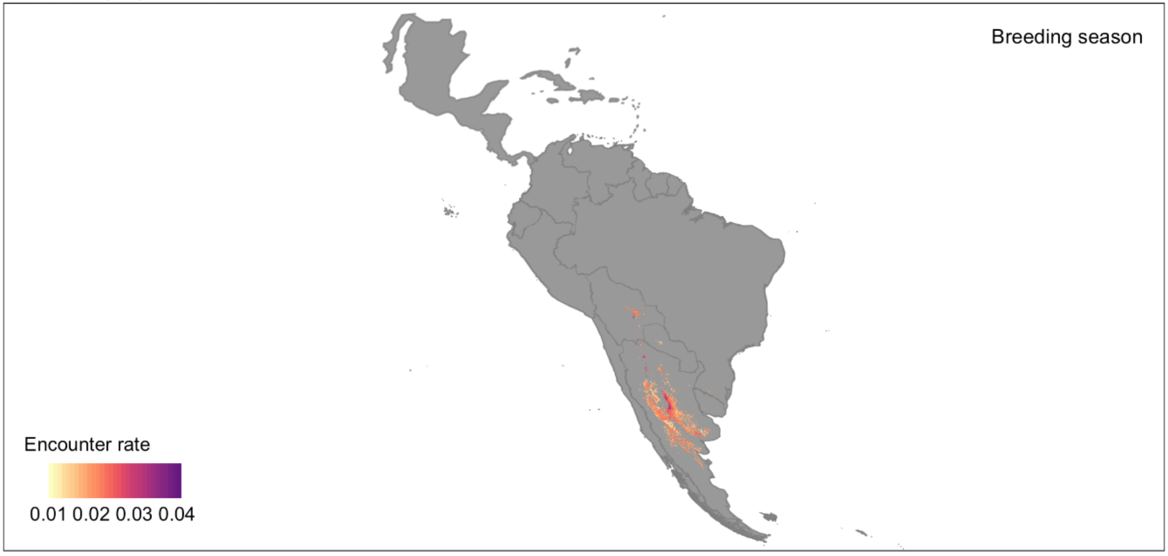


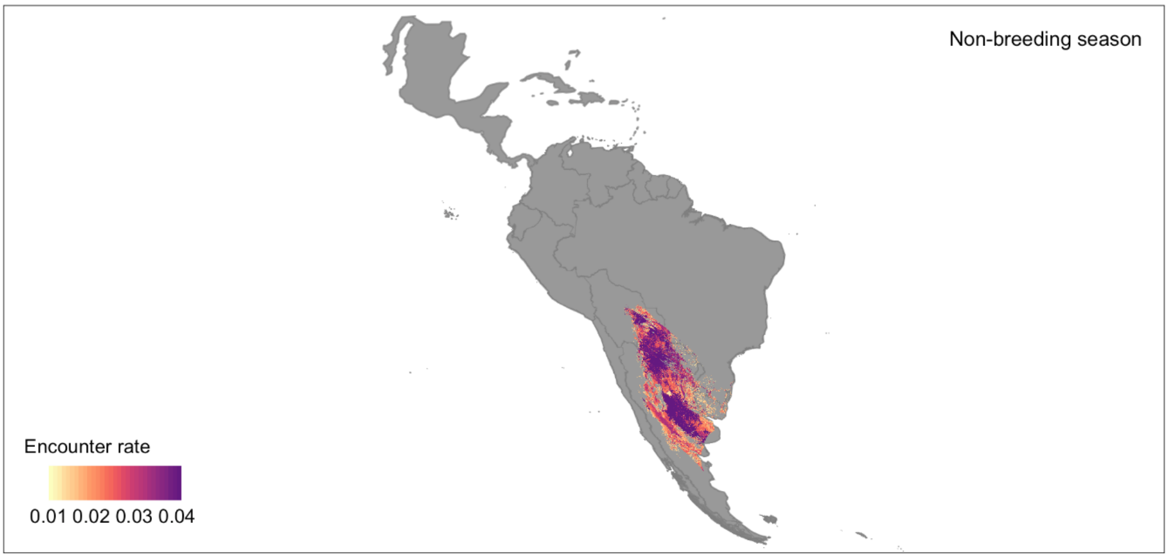
Pseudocolopteryx acutipennis

Pseudocolopteryx dinelliana

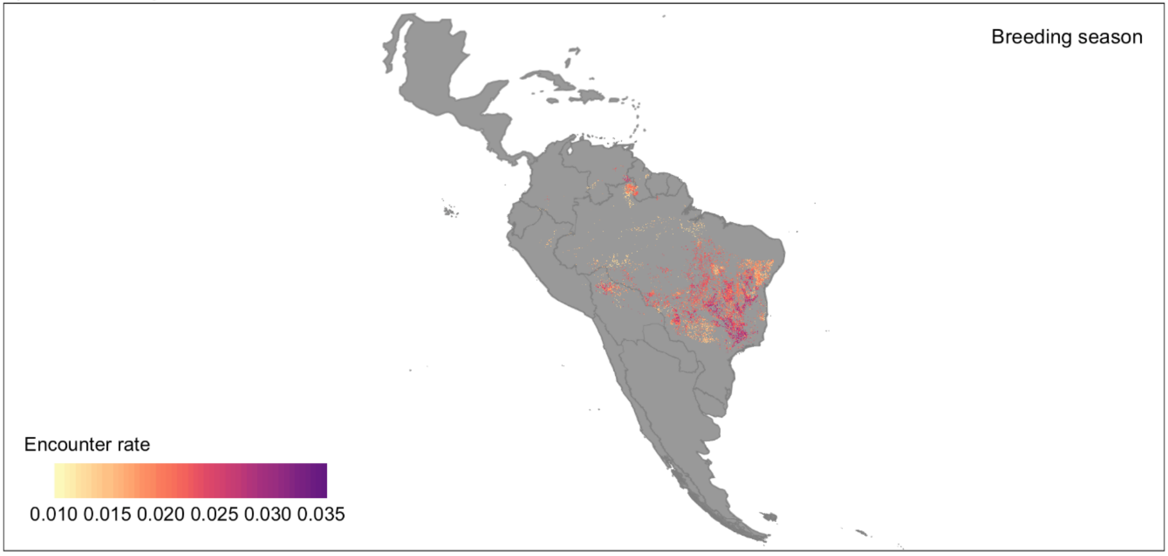
Pseudocolopteryx flaviventris

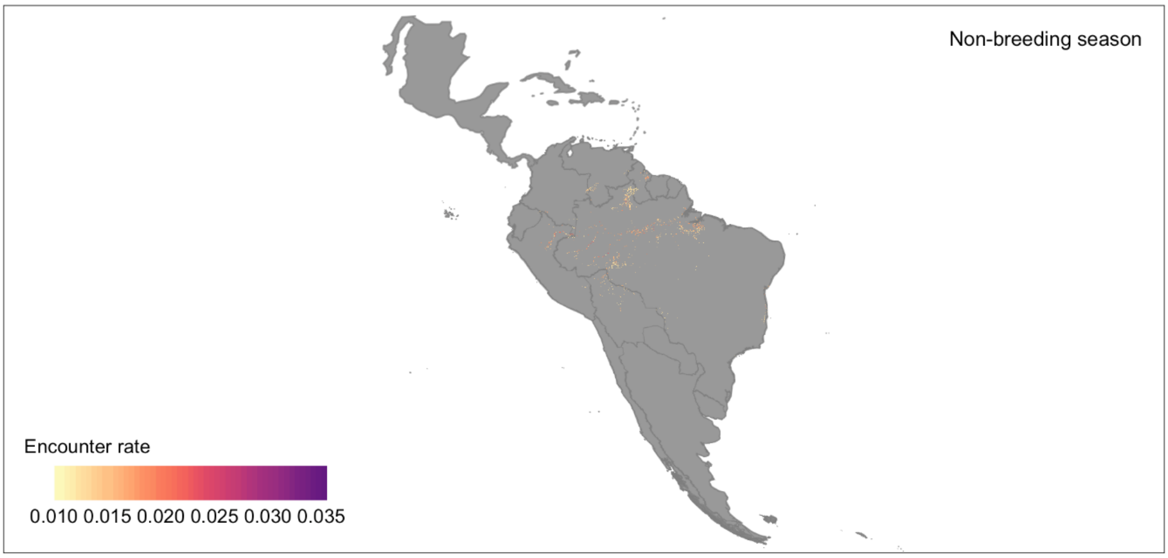
Serpophaga griseicapilla





Tyrannus albogularis





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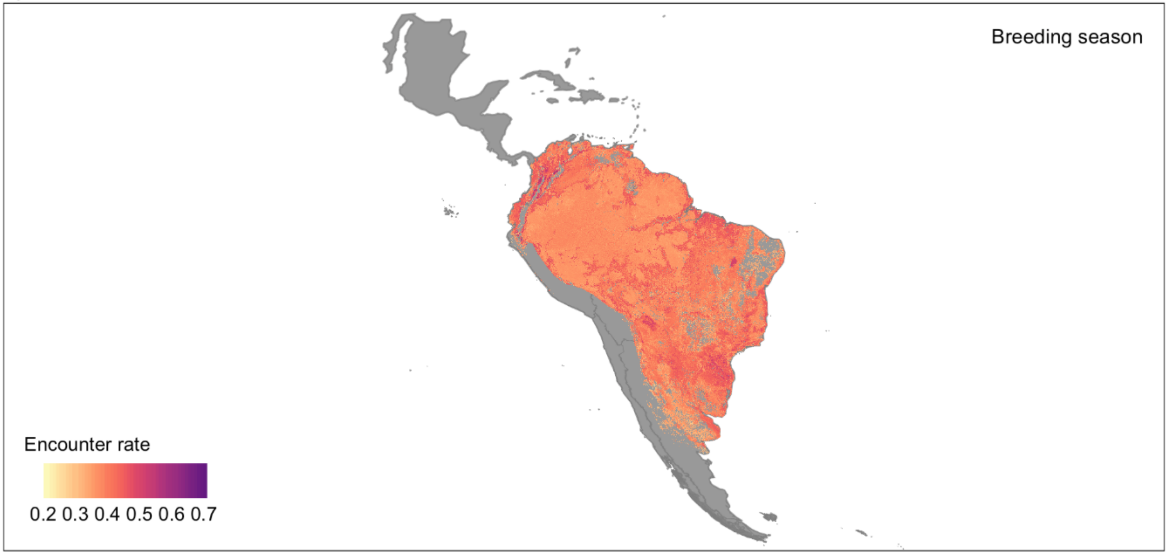
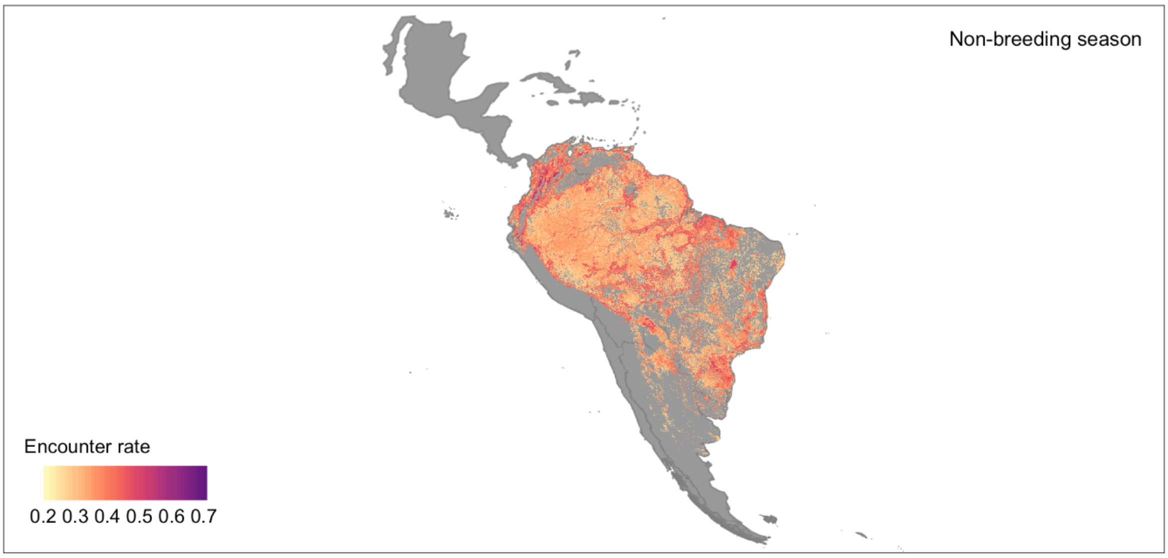
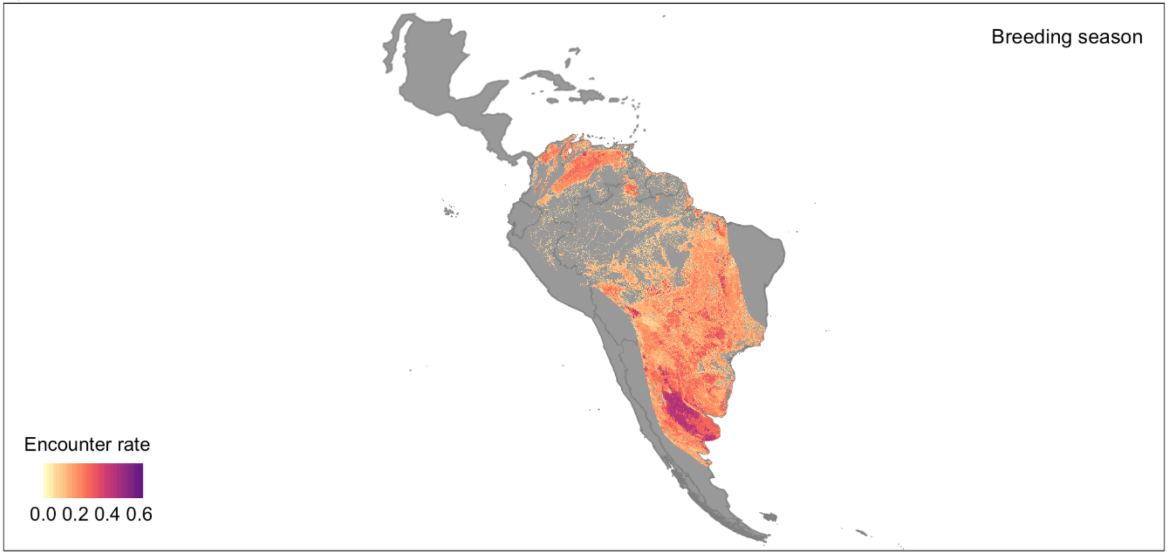
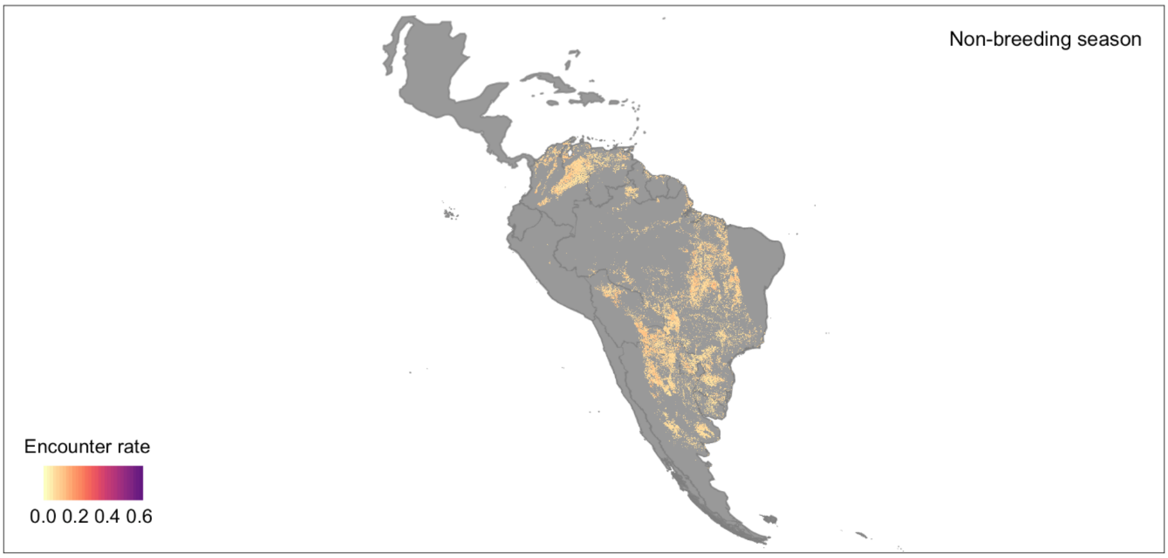




Tyrannus savana





Capítulo 2

Supplemental material

Table S1. Tyrant-flycatcher species analysed in the study, movement type (sedentary, partial migrant, full migrant), and number of clutches analysed.

Species	English name	Movement type	*n*
Agriornis lividus	Great Shrike-Tyrant	Sedentary	5
Agriornis montanus	Black-billed Shrike-Tyrant	Partial	4
Anairetes flavirostris	Yellow-billed Tit-tyrant	Partial	3
Anairetes parulus	Tufted Tit-tyrant	Partial	22
Cnemotriccus fuscatus	Fuscous Flycatcher	Partial	7
Colorhamphus parvirostris	Patagonian Tyrant	Full	3
Empidonomus aurantioatrocristatus	Crowned Slaty Flycatcher	Partial	20
Empidonomus varius	Variegated Flycatcher	Partial	21
Fluvicola albiventer	Black-backed Water-Tyrant	Full	19
Fluvicola nengeta	Masked Water-Tyrant	Sedentary	6
Fluvicola pica	Pied Water-Tyrant	Sedentary	11
Heteroxolmis dominicana	Black-and-white Monjita	Sedentary	3
Hirundinea ferruginea	Cliff Flycatcher	Partial	8
Hymenops perspicillatus	Spectacled Tyrant	Partial	35
Knipolegus aterrimus	White-winged Black-Tyrant	Partial	7
Knipolegus cabanisi	Plumbeous Black-tyrant	Sedentary	6
Knipolegus cyanirostris	Blue-billed Black-Tyrant	Partial	5
Knipolegus lophotes	Crested Black-Tyrant	Sedentary	7
Knipolegus striaticeps	Cinereous Tyrant	Partial	7
Lathrotriccus euleri	Euler's Flycatcher	Partial	8
Legatus leucophaius	Piratic Flycatcher	Partial	14
Lessonia oreas	Andean Negrito	Partial	4
Lessonia rufa	Austral Negrito	Full	31
Muscisaxicola albilora	White-browed Ground-Tyrant	Full	3
Muscisaxicola flavinucha	Ochre-naped Ground-Tyrant	Full	4
Muscisaxicola maclovianus	Dark-faced Ground-Tyrant	Partial	3
Muscisaxicola maculirostris	Spot-billed Ground-Tyrant	Partial	9
Myiarchus ferox	Short-crested Flycatcher	Sedentary	22
Myiarchus swainsoni	Swainson's Flycatcher	Partial	7
Myiarchus tyrannulus	Brown-crested Flycatcher	Partial	20
Myiodynastes bairdii	Baird's Flycatcher	Sedentary	5
Myiodynastes chrysocephalus	Golden-crowned Flycatcher	Sedentary	6
Myiodynastes maculatus	Streaked Flycatcher	Partial	32
Myiopagis gaimardii	Forest Elaenia	Sedentary	4

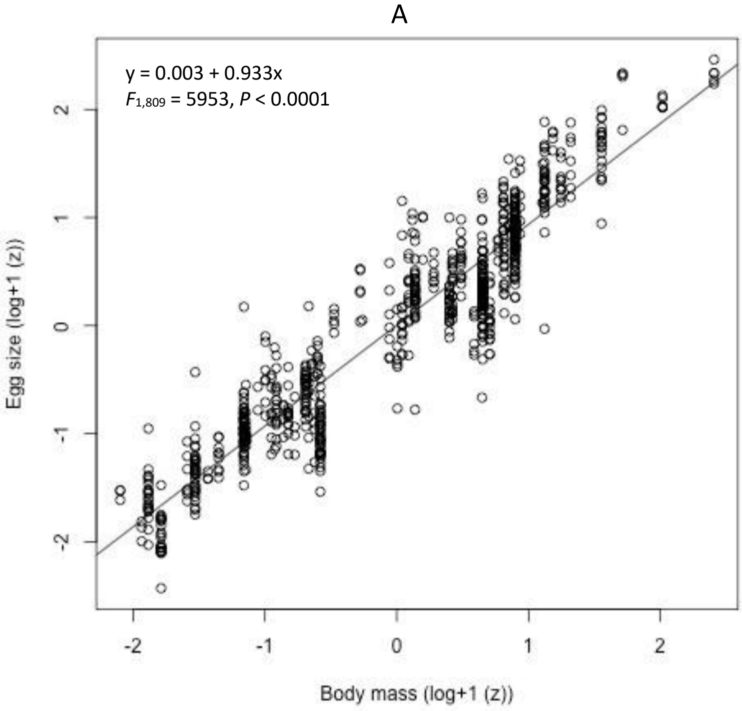
Myiopagis viridicata	Greenish Elaenia	Partial	2
Myiophobus fasciatus	Bran-colored Flycatcher	Partial	63
Myiophobus flavicans	Flavescent Flycatcher	Sedentary	4
Nengetus cinereus	Gray Monjita	Sedentary	24
Neoxolmis coronatus	Black-crowned Monjita	Full	12
Neoxolmis rufiventris	Chocolate-vented Tyrant	Full	6
Phaeomyias murina	Mouse-colored Tyrannulet	Partial	14
Pseudocolopteryx citreola	Ticking Doradito	Full	9
Pseudocolopteryx flaviventris	Warbling Doradito	Full	8
Pyrocephalus rubinus	Vermilion Flycatcher	Partial	52
Pyrope pyrope	Fire-eyed Diucon	Partial	18
Satrapa icterophrys	Yellow-browed Tyrant	Partial	22
Serpophaga cinerea	Torrent Tyrannulet	Sedentary	3
Serpophaga munda	White-bellied Tyrannulet	Partial	3
Serpophaga subcristata	White-crested Tyrannulet	Partial	30
Sublegatus arenarum	Northern Scrub-flycatcher	Sedentary	4
Sublegatus modestus	Southern Scrub-flycatcher	Partial	9
Tachuris rubrigastra	Many-colored Rush-tyrant	Partial	35
Tyrannus albogularis	White-throated Kingbird	Full(?)	6
Tyrannus melancholicus	Tropical Kingbird	Partial	113
Tyrannus niveigularis	Snowy-throated Kingbird	Partial	5
Tyrannus savana	Fork-tailed Flycatcher	Partial	112
Xolmis irupero	White Monjita	Sedentary	24
Xolmis velatus	White-rumped Monjita	Sedentary	7

Table S2. Scientific museums, and location where reproductive data were collected.

Museum	City	Abbreviation
American Museum of Natural History	New York, USA	AMNH
California Academy of Sciences	San Francisco, USA	CAS
Coleção Ornitológica Marcelo Bagno, Universidade de Brasília	Brasília, Brazil	COMB
Cris-River Regional Museum	Oradea, Romania	CRRP
Delaware Museum of Natural History	Wilmington, USA	DMNH
Fundação Zoobotânica do Rio Grande do Sul	Porto Alegre, Brazil	FZB
Instituto de Investigaciones de Recursos Biológicos "Alexander von Humboldt"	Vila de Leyva, Colombia	IAvH
Museo Argentino de Ciencias Naturales	Buenos Aires, Argentina	MACN
Museo de La Plata	La Plata, Argentina	MLP
Museu de Ciências e Tecnologia da PUCRS	Porto Alegre, Brazil	PUCRS
Museu de Zoologia da UFRRJ	Seropédica, Brazil	UFRRJ
Museu de Zoologia da USP	São Paulo, Brazil	MZUSP
Museu do Ceará + Aquasis	Fortaleza, Brazil	MC
Museu Nacional	Rio de Janeiro, Brazil	MN
Museu Paraense Emilio Goeldi	Belém, Brazil	MPEG
Muséum d'Histoire Naturelle de Genève	Geneva, Switzerland	MHNG
Museum für Naturkunde	Berlin, Germany	ZMB
Muséum National d'Histoire Naturelle	Paris, France	MNHN
Museum of Comparative Zoology, Harvard University	Cambridge, USA	MCZ
Museum of Vertebrate Zoology	Berkeley, USA	MVZ
National Museum of Natural History	Washington, D.C., USA	USNM
National Museums Scotland	Edinburgh, UK	NMS
Naturalis, Nationaal Natuurhistorisch Museum	Leiden, The Netherlands	NBCN
Naturhistorisches Museum Bern	Bern, Switzerland	NMBE
Naturhistorisches Museum Wien	Vienna, Austria	NMW
San Bernardino County Museum	Redlands, USA	SBCM
Staatliches Naturhistorisches Museum	Braunschweig, Germany	SNMB
The Natural History Museum	Tring, UK	NHM
Western Foundation of Vertebrate Zoology	Camarillo, USA	WFVZ
Zentralmagazin Naturwissenschaftlicher Sammlungen, Martin Luther University Halle-Wittenberg	Halle (Saale), Germany	MLUH

Table S3. Variance inflation factors (VIF) for the models assessed in the study.

	VIF	df
Model I		
Migratory behavior	1.43	1
Body mass	1.11	1
Latitude of breeding	1.43	1
Nest type	1.21	2
Model II		
Migratory behavior	1.44	1
Body mass	1.09	1
Latitude of breeding	1.46	1
Nest type	1.18	2
Model II		
Migration distance	1.08	1
Body mass	1.17	1
Latitude of breeding	1.05	1
Nest type	1.14	2
Model IV		
Migration distance	1.10	1
Body mass	1.12	1
Latitude of breeding	1.05	1
Nest type	1.14	2



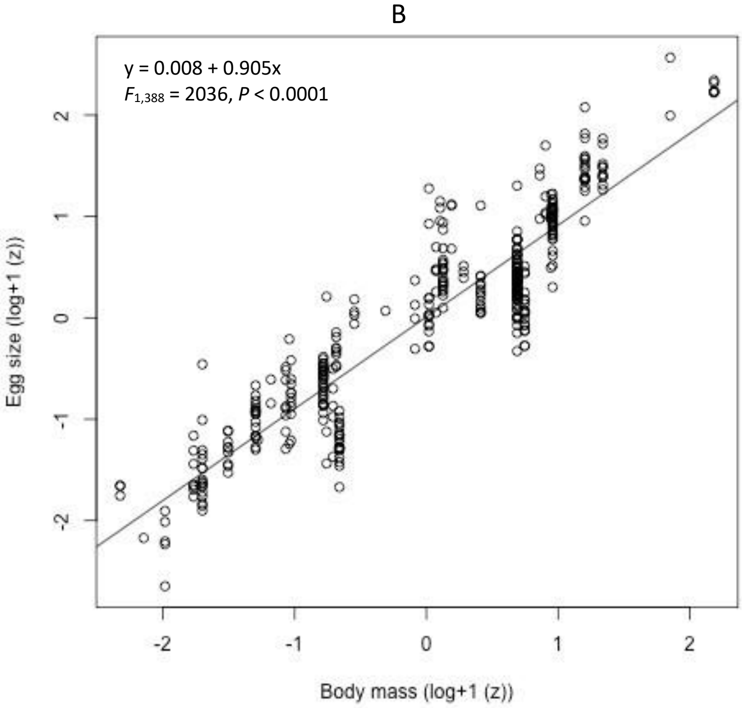


Figure S1. Linear log relationship between average egg volume per clutch and average body mass of (A) 58 migratory and non-migratory, and (B) 33 migratory tyrant flycatcher species breeding in South America. Average species' body masses were compiled from Wilman et al. (2014) and, when missing, complemented from Birds of the World (Billerman *et al.*, 2020). All variables were standardized.

References

Billerman, S.M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S. & (Editors) (2020) Birds of the World.

Wilman, H., Belmaker, J., Simpson, J., de La Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. Ecology, **95**, 2027.

Capítulo 3

Appendix S1

Table S1.1. Tyrant flycatcher species breeding and migrating within South America used in the study. Seasonal range sizes and tyrant flycatcher species richness at the breeding and non-breeding grounds were taken from Capítulo 2 (Sousa et al., in prep). Migratory status classification was based on literature review of species' distributions and behavior (Chesser, 1995; Billerman *et al.*, 2020).

Species	**Range size (km^2)**		**Species richness**		**Migratory status**
	Breeding	**Non-breeding**	**Breeding**	**Non-breeding**	
Colorhamphus parvirostris	8.33	9.19	205343.75	562225.00	full
Empidonomus aurantioatrocristatus	51.42	63.60	10561487.50	6430643.75	partial
Empidonomus varius	58.15	61.21	8355418.75	7771443.75	partial
Hymenops perspicillatus	29.98	35.30	3601906.25	2746837.50	partial
Lessonia rufa	18.21	20.52	1575275.00	1278968.75	full
Muscisaxicola albilora	14.05	14.67	966993.75	809693.75	full
Muscisaxicola flavinucha	12.73	13.91	917106.25	892287.50	full
Muscisaxicola maclovianus	8.60	11.57	563981.25	2037543.75	partial
Myiarchus swainsoni	56.62	61.59	15843700.00	9908193.75	partial
Myiodynastes maculatus	57.92	59.04	15831218.75	13784662.50	partial
Pseudocolopteryx flaviventris	34.12	35.45	687756.25	329487.50	full
Tyrannus albogularis	56.71	67.43	1372375.00	166200.00	partial
Tyrannus melancholicus	56.82	59.77	15886468.75	11151825.00	partial
Tyrannus savana	47.03	50.13	11634293.75	3125218.75	partial

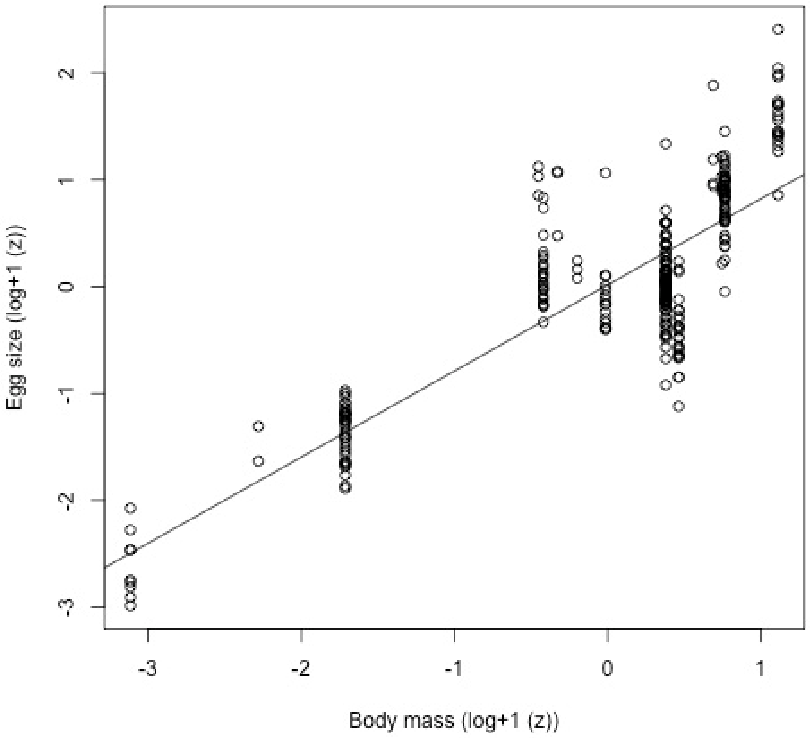


Figure S1.1. Linear log relationship (y = 0.016 + 0.805x) between average egg volume per clutch (n = 285 clutches) and average body mass of 14 tyrant flycatcher species that migrate and breed in South America. Average species' body masses were compiled from Wilman et al. (2014) and, when missing, complemented from Birds of the World (Billerman *et al.*, 2020). All variables were standardized.

References

Billerman, S.M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S. & (Editors) (2020) Birds of the World.

Chesser, R.T. (1995) *Biogeographic, ecological, and evolutionary aspects of South American austral migration, with special reference to the family Tyrannidae*, Ph.D. dissertation, Lousiana State University and Agricultural & Mechanical College, Baton Rouge, USA.

Wilman, H., Belmaker, J., Simpson, J., de La Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. Ecology, **95**, 2027.