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VARIAÇÕES EM CARACTERÍSTICAS REPRODUTIVAS DE AVES DO GÊNERO *TYRANNUS* AO LONGO DO ESPAÇO E TEMPO EM FUNÇÃO DO CLIMA

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BRASÍLIA - DF

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Tese apresentada ao programa de Pós-graduação em Ecologia, Instituto de Ciências Biológicas da Universidade de Brasília como requisito parcial para obtenção do título de Doutor em Ecologia.

Orientador: Dr. Miguel Ângelo Marini

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Tese de doutorado

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RESUMO GERAL

A grande variação geográfica de estratégias de sobrevivência e reprodução, intra- e interespecífica de aves compõe grande parte das discussões científicas desde metade do século passado. Várias hipóteses paralelas foram formuladas a fim de melhor explicar tais variações. No entanto, a forte covariação de atributos de história de vida das aves com o ambiente tem direcionado, tanto as questões quanto as respostas, a características ambientais cada vez mais diretas e mensuráveis. Clima, condições e variações climáticas são fatores importantes que têm potencial de responder sobre essa relação de causa e efeito. A variação residual nas características reprodutivas das aves. O tamanho da ninhada e ovos das aves, por representar um alto investimento, têm potencial de responder diretamente às condições climáticas de uma região ou de uma época. Apesar de bem estudada, não existe um consenso sobre as nuances entre as causas e efeitos das condições climáticas sobre o tamanho dos ovos e ninhadas de aves em grande escala. Como tese, defini que "características reprodutivas das espécies do gênero *Tyrannus*, mais especificamente o tamanho dos ovos e ninhadas, variam em função das condições climáticas em escalas espaciais e temporais". Reunimos informações de 1.358 ninhadas e 4.750 ovos de espécies do gênero *Tyrannus*, obtidas diretamente de 23 coleções ornitológicas ao redor do mundo, para responder como o clima atua na variação do tamanho de ninhadas e ovos das aves através de escalas espaciais e temporais.

No primeiro capítulo testamos a variação das características reprodutivas em função do clima, sub-climas e variáveis de temperatura e precipitação históricos com o objetivo de analisar a relação entre o tamanho das ninhadas e dos ovos das espécies de *Tyrannus* em diferentes escalas geoclimáticas. Ambas as características reprodutivas variam de acordo com os principais climas, climas regionais e condições locais de temperatura e precipitação. As regiões com maior variação climática tiveram as maiores ninhadas, mas os locais com invernos mais frios tiveram efeito oposto, enquanto o tamanho dos ovos das espécies de *Tyrannus* tende a aumentar em ambientes com períodos de seca menos extremos. A relação significativa entre ovos maiores e locais com temperaturas mais baixas pode explicar o aumento do tamanho dos ovos com a latitude.

No segundo capítulo usamos 1.145 ninhadas e 4.061 ovos de oito espécies de *Tyrannus* ao longo de 116 anos (1901-2016), para avaliar as relações entre os tamanhos das ninhadas e dos ovos as anomalias climáticas no ano que antecedeu a postura. A variação entre anos da temperatura e precipitação afetaram a taxas reprodutivas das espécies de *Tyrannus*. Os ovos e ninhadas de *Tyrannus* foram maiores em anos com condições climáticas mais estáveis. Próximo à reprodução, somente a temperatura teve efeito sobre a as variáveis reprodutivas dos *Tyrannus*, onde anos com maiores temperaturas resultaram em ninhadas maiores e ovos menores.

No terceiro capítulo, utilizamos os parâmetros ajustados de modelos estatísticos (α, β’s) obtidos no Capítulo 2, com o objetivo de projetar possíveis efeitos das mudanças climáticas nas características reprodutivas de *Tyrannus.* Geramos quatro cenários de Caminhos Socioeconômicos Compartilhados (*Shared Socio-Economic Pathways* - SSP), reunidos a partir de quatro Modelos Climáticos Globais (*General Circulation Model* - GCM) da versão seis do Projeto de Intercomparação de Modelos Acoplados (*Coupled Model Intercomparison Project* - CMIP6), tanto para as características reprodutivas, quanto para as variáveis de temperatura e precipitação entre os anos de 2020 e 2100. Os tamanhos da ninhada (TN) e ovos (TO) diminuíram em todos os cenários futuros (*e.g.* SSP5-8.5/2100; TN: β= -1.29, TO: β= -0.04), impulsionados principalmente pelo aumento dos parâmetros de temperatura e sazonalidade.

Os resultados deste trabalho corroboram minha tese de que “*características reprodutivas das espécies do gênero Tyrannus, mais especificamente o tamanho dos ovos e ninhadas, variam em função das condições climáticas em escalas espaciais e temporais”.* Além disso, há um impacto significativo das mudanças climáticas, com potencial para diminuir os ovos e ninhadas desse grupo alo longo do tempo. É importante destacar as implicações iminentes das mudanças climáticas locais na fisiologia das espécies, com diminuição da aptidão dos organismos que eclodem de ovos menores e possíveis perdas populacionais, mesmo para grupos amplamente distribuídos, como as espécies do gênero *Tyrannus*.

PALAVRAS-CHAVE

Biogeografia, clima, meteorologia, sazonalidade, mudanças climáticas, precipitação, temperatura, características reprodutivas, tamanho da ninhada, tamanho dos ovos, história de vida, *Tyrannus*

ABSTRACT

The wide geographic variation in birds' intra- and interspecific survival and reproductive strategies have been a significant part of scientific discussions since the middle of the last century. Several parallel hypotheses have been formulated to explain such variations better. However, the strong covariation of bird life-history traits with the environment has directed questions and answers to increasingly direct and measurable environmental characteristics. Climate, weather conditions, and variations in the weather are important factors that can potentially answer residual variation in bird reproductive traits. Because they represent a high investment, birds' clutch and egg sizes have the potential to respond directly to the climatic conditions of a region or season. Although well studied, there is no consensus on the nuances between the causes and effects of climatic conditions on these large-scale bird breeding traits. As a thesis, I defined that "breeding traits of Kingbirds (*Tyrannus* genus), specifically clutch and egg sizes, vary as a function of climatic conditions on spatial and temporal scales". We gathered information from 1,657 clutches and 5,644 eggs of Kingbirds species, obtained directly from 23 worldwide ornithological collections, to answer how climate acts on variation in clutch and egg size of birds across spatial and temporal scales.

In the first chapter, we tested the variation of breeding traits as a function of climate, sub-climates, and historical temperature and precipitation variables to analyze the relationship between clutch and egg sizes at different geoclimatic scales. Both breeding traits varied among climates, regional climates, and local temperature and precipitation conditions. Still, sites with colder winters had the opposite effect, where Kingbirds' egg size tended to increase in environments with less extreme drought periods. The significant relationship between the largest clutches with regions with greatest climatic variation and larger eggs with lower temperatures regions may explain the increase in these traits with latitude.

In the second chapter, we used 1,145 clutches and 4,061 eggs of Kingbirds, overlapped with weather time series over 116 years (1901-2016), to assess the relationships between breeding traits with climate anomalies in the year preceding laying. Interannual temperature and precipitation variation affected the reproductive traits of Kingbirds. Eggs and clutches were larger in years with more stable weather conditions. Precipitation variation was an essential variable to egg sizes, and only temperature affected these reproductive traits near breeding when years with higher temperatures resulted in larger clutches and smaller eggs.

In the third chapter, we used the fitted parameters of statistical models (α, β's) obtained in Chapter 2 to project possible effects of climate change on *Tyrannus* reproductive traits. We generated temperature and precipitation variables between the years 2020 and 2100 of four Shared Socio-Economic Pathways (SSP) scenarios, gathered from four General Circulation Models (GCM) of the sixty Coupled Model Intercomparison Project (CMIP6) for both reproductive traits. Clutch (CS) and egg (ES) sizes decreased in all future scenarios (e.g. SSP5-8.5/2100; CS: β= -1.29, ES: β= -0.04), driven primarily by increased temperature and seasonality parameters.

The results obtained support my thesis that "reproductive traits of Kingbirds, specifically egg and clutch size, vary as a function of climatic conditions over spatial and temporal scales". Furthermore, climate change has a significant impact, with the potential to decrease the eggs and clutches of this group over time. It is essential to highlight the imminent implications of local climate change on species physiology, with decreased fitness of organisms hatching from smaller eggs and possible population losses with decreasing clutch sizes, even for widely distributed groups such as species in the genus *Tyrannus*.

KEYWORDS

Biogeography, climate, weather, seasonality, climate change, precipitation, temperature, breeding traits, clutch size, egg size, life history, reproductive output, kingbirds, *Tyrannus*

INTRODUÇÃO GERAL

A grande diversidade de estratégias de sobrevivência e reprodução há muito tempo leva os ecólogos a questionar como cada espécie se adapta ao seu ambiente. Desde que os pesquisadores começaram a explorar e comparar regiões, eles começaram a perceber que o investimento de energia entre sobrevivência e reprodução muda de um lugar para outro, mesmo dentro de grupos relativamente relacionados (Brown & Lomolino 1998, Wallace 1876). A energia está disponível de forma diferente nos lugares, seja em quantidade, tempo e espaço, e os organismos têm que investir da melhor forma possível. Parte dessa diversificação ocorre porque o investimento na prole é caro, a energia disponível é limitada e a aptidão da prole aumenta com o investimento dos pais, em detrimento do investimento em sua sobrevivência (Bennett & Owens 2002, Krist 2011). O longo caminho para descrever a história vida das aves baseia-se principalmente em padrões espaciais mais evidentes, como uma mudança no tamanho corporal e no investimento reprodutivo ao longo da latitude (Blackburn et al. 1999, Moreau 1944, Ricklefs 2000). Com o foco na quantidade e forma que a energia flui em comunidades naturais (Rosenzweig 1968), fatores ambientais como a sazonalidade climática (Ashmole 1963), ganharam atenção por estarem diretamente relacionados à condição fisiológica de organismos com estratégias de resposta rápida. Atualmente, não como uma pergunta, mas como uma estrada pavimentada, sabemos que as características de história de vida tendem a ter uma forte correlação ambiental (Kuleska 1990) onde a reprodução tem um papel central na manutenção da população (Delgado et al. 2021, Newton 1998a) e o tamanho da ninhada é fundamental para o investimento reprodutivo das aves e uma das características mais documentadas de história da vida animal (Jetz et al. 2008). Mesmo que a seleção natural tenha definido os padrões espaciais do esforço reprodutivo (Lack 1947), uma parte da variação residual deve ser influenciada pelas condições que os organismos encontram durante seu ciclo reprodutivo (Martin 1987, Martin et al. 2006). No entanto, essa relação ainda permanece pouco conhecida e, consequentemente, não é possível explicar com confiança como e por que essa diversificação acontece (Bennett & Owens 2002).

A adaptação aos padrões climáticos locais é um dos muitos fatores que determinam a distribuição ou diversificação de espécies e populações (Boucher-Lalonde et al. 2014, Wallace 1876). De um ponto de vista regional, o clima é um pacote de condições dinâmicas que influencia diretamente o comportamento, a fisiologia, as fenologias e as características de história de vida (Gienapp et al. 2014). A sazonalidade climática é o ciclo ambiental mais pronunciado. A sazonalidade cria variações temporais nos recursos dos organismos para suas necessidades metabólicas, como crescimento e reprodução (Boyce 1979, Schultz & Halpert 1993), afetando fortemente a aptidão dos indivíduos (Boucher-Lalonde et al. 2014). É possível reconhecer que a adaptação às condições climáticas contribui na seleção e diversificação de estratégias migratórias e investimento reprodutivo em relação ao tamanho e ao número de descendentes (Jetz et al. 2008) e até mesmo a quantidade de energia a ser usada no atendimento à prole (Martin 1987). Em relação às características reprodutivas, as correlações com as condições locais são evidentes, mesmo para tamanho corporal constante, com tamanhos de ovos e de ninhadas variando entre as regiões (Martin et al. 2006). Consequentemente, essas espécies se adaptam à sazonalidade ambiental, ajustando sua fenologia para sincronizar com os padrões climáticos. Como resultado, essas espécies estarão no local e no tempo com a oferta de recursos no momento da demanda mais crítica (Mclean et al. 2016).

O tamanho da ninhada e o tamanho do ovo são, para as aves, componentes do investimento reprodutivo que têm uma forte correlação ambiental (Kuleska 1990, Ricklefs 2000). Em ambientes relativamente mais estáveis, o tamanho da prole individual deve estar mais próximo da seleção (Congdon & Gibbons 1987), o que sugere que a história evolutiva estabeleceu um limite para a variação desse atributo (Stearns 1989), apoiando a teoria de uma seleção estabilizadora (Wellmann 2023). Nesse caso, a pressão da seleção natural provavelmente reduz a variação no tamanho do ovo e da ninhada (Congdon & Gibbons 1987). Para justificar a variação latitudinal do tamanho da ninhada Ashmole (1963) baseou-se no efeito da sazonalidade climática. A sazonalidade climática é acentuada em latitudes mais altas, e o aumento da mortalidade nessas regiões é reflexo das condições de invernos mais rigorosos, afetando a densidade populacional e a quantidade de recursos alimentares *per capita* durante a estação reprodutiva. Essa oferta de recursos promove uma melhor nutrição das fêmeas que, por consequência, geram ninhadas maiores. Por outro lado, os estudos com suplementação de recursos podem não detectar essa covariação ambiental com o tamanho da ninhada, pois o investimento pode ocorrer na qualidade dos ovos e no aumento do sucesso reprodutivo (Martin 1987). O investimento em ovos em anos com condições ambientais diferentes exigirá, portanto, novas estratégias de investimento reprodutivo.

Os efeitos biológicos das mudanças climáticas ocorrem em vários níveis, desde as populações até ecossistemas. Muitos estudos mostram os efeitos das mudanças climáticas sobre a biodiversidade, com o objetivo de entender os processos e mitigar os efeitos sobre a biota (Aguiar et al. 2016, Bellard et al. 2012, Marini et al. 2009). As projeções mostram que vários grupos de organismos sofrerão com a perda de habitat e com a incompatibilidade entre suas demandas de energia e os recursos disponíveis (Aguiar et al. 2016, Durant et al. 2007, Kellermann & van Riper 2015, Marini et al. 2009, 2010). No entanto, os organismos que expressam maior plasticidade fenotípica, conseguem melhor se adequar a essas novas condições e minimizar os efeitos das mudanças climáticas (Bonamour et al. 2019). A falta de plasticidade para se adaptar a novos regimes climáticos pode se tornar uma ameaça, e até mesmo a causa, da extinção de espécies (Bonamour et al. 2019, Trautmann 2018). As mudanças necessárias na fenologia se tornaram um dos principais problemas das espécies em relação às mudanças ambientais (Bellard et al. 2012) quando os organismos já adaptados a determinadas condições de reprodução enfrentam dificuldades para ajustar suas fenologias às novas exigências.

Neste trabalho eu proponho a tese que: características reprodutivas das espécies do gênero *Tyrannus,* mais especificamente o tamanho dos ovos e ninhadas, variam em função das condições climáticas em escalas espaciais e temporais. O objetivo geral deste trabalho é testar o efeito do clima, condições e variáveis climáticas no tamanho das ninhadas e ovos de *Tyrannus*. Para avaliar essa tese, formulei os seguintes trabalhos, designados capítulos a seguir: Capítulo 1: *Multiple climatic effects on kingbirds (Tyrannus spp.) clutch and egg sizes along a continental scale* – onde eu testo a variação geoclimática dos atributos reprodutivos; Capítulo 2: *Differential short-term and long-term weather windows on breeding traits of Kingbirds* – onde eu analiso os efeitos da variação interanual de variáveis meteorológicas; e Capítulo 3: *Climate change model-based scenarios show a decrease in Tyrannus egg and clutch sizes by 2100* – onde eu faço projeções dos tamanhos de ovos e ninhadas em cenários climáticos futuros, baseados em parâmetros estatísticos ajustados de modelos sobre a sensibilidade climática das espécies de *Tyrannus,* expressados em seus atributos reprodutivos em dados históricos.

OBJETO DE ESTUDO: GÊNERO *Tyrannus*

O gênero *Tyrannus* (Kingbirds, em inglês) é um grupo da família Tyrannidae (Tyrant Flycatchers) composto por 13 espécies (Clements et al. 2022, Phillips 1994, Winkler et al. 2020). A maioria das espécies são cosmopolitas e apresentam grande adaptabilidade ao meio urbano, sendo encontradas facilmente habitando e nidificando nos centros das cidades. Assim como toda sua família, está restrito às Américas (Novo Mundo), porém se estendendo por uma grande amplitude latitudinal – desde a região central da Argentina (Río Negro) com *T. savana* (Jahn & Tuero 2020) até a região noroeste do Canadá (Yukon) com *T. tyrannus*, ausente, aparentemente, somente nas latitudes polares. Dentre as 13 espécies, somente *T. caudifasciatus* e *T. cubensis*, restritas ao Caribe não possuem nenhum comportamento migratório (Mobley & de Juana 2020, Peña & Navarro 2023). Dentre as 11 espécies que apresentam comportamento migratório, *T. niveigularis* e *T. albogularis* apresentam suas áreas de ocorrência somente na porção continental da América do Sul (Mobley 2020, Schulenberg & Johnson 2020), enquanto *T. vociferans* apresenta suas áreas de reprodução e invernada na América do Norte (Tweit & Tweit 2020). Como predomina dentro da família Tyrannidae, as espécies do gênero *Tyrannus* são insetívoros papa-moscas, de comportamento alimentar bem definido (Fitzpatrick 1981, 1980) e possuem tamanho corporal médio, variando entre 31,9 g (*T. savana*) e 93,6 g (*T. cubensis*) (Dunning 2007). Espécies desse gênero apresentam grande fidelidade de sítio de ninho entre anos, mostrando aparente adequabilidade com as condições ambientais a nível local e, por isso, a variação das condições climáticas em escala temporal deve ter reflexo em seus atributos de história de vida (Blancher & Robertson 1985, Murphy 1996).

1. MULTIPLE CLIMATIC EFFECTS ON KINGBIRDS (*TYRANNUS* SPP.) CLUTCH AND EGG SIZES ALONG A CONTINENTAL SCALE

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ABSTRACT

Changes in bird clutch and egg sizes across geographical gradients are issues often debated among ecologists, where latitudinal cline is a central issue in several discussions. There is an understanding that these patterns are primarily driven by climatic characteristics, where latitude acts as a proxy. Many studies attempt to analyse local climatic factors causing variation in life history traits but face methodological limitations. Here, as few studies have been able to, we achieve a robust dataset that covers a large territorial extent to answer this main biogeographical question. We approached the geographically widespread *Tyrannus* genus (kingbirds) and collected breeding data from 35 scientific egg collections in South and Central America, the USA, and Europe. After several data checking layers, including spatial, temporal and taxonomic checking, we analysed the relationship between kingbird's clutch and egg sizes with different climatic scales. The analyses of 1,358 clutches and 4,750 eggs confirmed that the kingbird's clutch and egg sizes increase towards the poles. Both breeding traits vary according to main climates, regional sub-climates, and local temperature and precipitation conditions. Regions with more climatic variation had the largest clutches, but sites with colder winters did not have the largest clutches. *Tyrannus* egg size increased in environments with less extreme dry periods. The significant relationship between larger eggs with sites with lower temperatures can explain the increase in egg size with latitude. Our findings suggest a robust correlation of residual variation in breeding traits with climatic conditions at both regional and local levels. Highly locally adapted species using climatic parameters as cues should also respond to interannual weather variations. With current discussions about climate change's effects on ecosystems, the insights provided in this work can assist in understanding how species will cope under future climate scenarios.

KEYWORDS Biogeography, breeding traits, climate, clutch size, egg size, latitudinal effect, life-history, reproductive output.

RESUMO

Mudanças em características reprodutivas das aves ao longo de gradientes geográficos são questões frequentemente debatidas entre os ecólogos, onde o gradiente latitudinal é uma questão central em várias discussões. Há um entendimento de que esses padrões são influenciados principalmente pelas condições climáticas, em que a latitude atua como um indicador. Muitos estudos procuram analisar os fatores climáticos locais que causam variação nas características de história de vida, mas enfrentam limitações metodológicas. Aqui, como poucos estudos foram capazes de fazer, conseguimos reunir um conjunto de dados robusto abrangendo uma grande extensão geográfica para responder a essa questão biogeográfica principal. Abordamos o gênero *Tyrannus* (Tyrannidae, papa-moscas), que possui uma ampla distribuição geográfica, e coletamos dados reprodutivos em 35 coleções científicas oológicas na América do Sul e Central, nos EUA e na Europa. Após várias camadas de verificação de dados, incluindo verificação espacial, temporal e taxonômica, analisamos a relação entre o tamanho das ninhadas e dos ovos das espécies de *Tyrannus* em diferentes escalas geoclimáticas. As análises de 1.358 ninhadas e 4.750 ovos confirmaram que os tamanhos das ninhadas e dos ovos dos *Tyrannus* aumentam em direção aos polos. Ambas as características reprodutivas variam de acordo com os principais climas, climas regionais e condições locais de temperatura e precipitação. As regiões com maior variação climática tiveram as maiores ninhadas, mas os locais com invernos mais frios tiveram efeito oposto, enquanto o tamanho dos ovos das espécies de *Tyrannus* tende a aumentar em ambientes com períodos de seca menos extremos. A relação significativa entre ovos maiores e locais com temperaturas mais baixas pode explicar o aumento do tamanho dos ovos com a latitude. Nossos resultados sugerem uma correlação robusta da variação residual das características reprodutivas com as condições climáticas, tanto em nível regional quanto local. Espécies altamente adaptadas localmente, que usam características climáticas do local de reprodução como pistas para eventos biológicos também devem responder às variações interanuais do clima. Com as discussões atuais sobre os efeitos das mudanças climáticas nos ecossistemas, os resultados fornecidos neste trabalho podem auxiliar na compreensão de como as espécies lidarão em possíveis cenários climáticos futuros.

1.1. INTRODUCTION

Investment in clutch and egg size are two main attributes of the life history of oviparous organisms (Carey 1996). Through the amount of nutrients invested in the eggs, parents must provide enough energy to the developing offspring to maximise the probability of their survival (Birkhead 2016, Congdon & Gibbons 1987, Martin 1987). In forming the eggs, females invest more than genetic materials that inform their evolutionary history but also by-products that show their physiological condition (Carey 1996, Williams & Groothuis 2015). This condition, in turn, will be related to the recent past of the organism, its ecological behaviour, and the environmental conditions in which the female finds herself at the egg-laying site (Martin 1987).

Among the most evident clinal variations in ecology is the change in biological traits as a function of latitude (Hut et al. 2013). The relationship between clutch size and the latitudinal gradient is a strong pattern in reproductive output where larger clutches are found at higher latitudes. This variation pattern is evident in animal body size (Stillwell 2010) and is the main variation factor for birds' clutch size (Jetz et al. 2008). Several assumptions have been proposed to explain this phenomenon (Lack 1947, Ricklefs 2000). However, the most accepted hypothesis is that the increase in clutch size is related to the seasonality of resources (Ashmole 1963, Griebeler et al. 2004, Lundblad & Conway 2021, Ricklefs 1980), where the physiological condition of the individuals is the central point. However, latitude is a proxy for the environmental conditions that exert pressure on the phenological adaptation of species, such as seasonality (Lundblad & Conway 2021) and day length (Hut et al. 2013). Since seasonality provides increased resources *per capita* during the breeding season, better-nourished parents can invest in larger clutches.

Like other seasonally adapted organisms, birds respond directly to environmental conditions through their life history parameters (Forchhammer et al. 1998, Kuleska 1990). The condition of the environment acts as a driver of organisms’ physiology, and it can help explain variations in breeding traits (Bêty et al. 2003, Christians 2002, Liu et al. 2018, Price & Liou 1989). Climate, and the inherent climatic seasonality (White & Hastings 2020), are key to bird phenology (Newton 1998b). Few bird groups reproduce year-round, even in tropical regions, where seasonality does not reach extreme conditions (Hau 2001). Migratory or not, birds must respond to climatic conditions at the breeding site (Ockendon et al. 2013).

Besides changes in clutch size, the increase in egg size across geographical gradients is still a well-debated question. Many ecologists argue that decreasing egg sizes could compensate for the increase in clutch size (Blackburn 1991), in which egg size would tend to decrease with increasing latitude. However, the positive relationship between egg and clutch sizes may indicate an environment with sufficient resource abundance for both reproductive outputs to increase (Hõrak et al. 1995). Also the positive relationship of eggs with latitude may also be explained due to the thermal potential of larger eggs in cold environments, which lose heat more slowly (Martin 2008). However, there are studies showing increased egg size with latitude (Stępniewski et al., 2021), while others find no effect (Guo & Lu 2022). Nonetheless, the variation of this trait is correlated with female body size (Bennett & Owens, 2002; Martin et al., 2006; Rahn et al., 1975) and incubation time (Rahn & Ar 1974). Since the body size of organisms within similar groups tends to be larger at higher latitudes (Blackburn et al. 1999, Stillwell 2010), the latitude increase could have a similar effect on eggs as on clutch size. That allometry pattern explains about 80% of egg size variation (Blackburn 1991). This ratio, considered a phylogenetic component, tends to maintain at high taxonomic levels, such as Order (Birchard & Deeming 2015). The resulting variation not explained by the phylogenetic component, the residual variation, tends to be influenced by ecological and environmental factors (Martin et al. 2006). Once the environment pressures a trait, it can respond independently of a trade-off, such as the supposed negative relationship between egg and clutch size (Blackburn 1991). Since clutch and egg size can change through space clines, environmental changes exert more influence on breeding traits than is known, requiring more understanding of this correlation.

Resource richness and abundance may be the essential factors in fine-tuning the timing of reproduction when females set the laying season so that hatching occurs when the greatest energetic demands of the offspring and more resources are available (Dunn & Winkler 2008, Welty 1982). Although studies have already diagnosed some of the residual variations in egg size – clutch size (Blackburn 1991, Martin 2008, Martin et al. 2006, Smith & Fretwell 1974), environmental conditions (Heming & Marini 2015, Martin 2008, Martin et al. 2006), migratory behaviour (Heming & Marini 2015) and geographical variation (Martin et al. 2006) – residual variation still seems to be not enough understood (Martin 2008, Martin et al. 2006). Furthermore, there is still a need to know how breeding traits can vary within a group of birds over time and space (Heming & Marini 2015).

Populations adapted to the climate of their breeding grounds tend to change their breeding traits when local temperature and precipitation change (Heming & Marini 2015). The climate is an assembly of conditions that include minimum, average, and maximum temperatures, and precipitation parameters. As each component of a climate can exert a different weight (van de Pol et al. 2016), the best way to evaluate how climate affects a trait would be a model that includes the combination of variables and respects the weight of each one. Once breeding traits of birds vary according to the environment (Christians 2002, Jetz et al. 2008), inevitably, climate change will bring new constraints on reproductive investment. Many studies have shown how the rise in temperatures stimulates birds to start the breeding season earlier (Both et al. 2004, Crick et al. 1997, Marrot et al. 2017, Visser et al. 2004). Moreover, there is evidence that increases in temperature can lead to changes in clutches (Both & Visser 2005, Tryjanowski et al. 2004) and egg sizes (Cady et al. 2019).

Despite increasing evidence showing the effects of climate change on breeding traits (Stevenson & Bryant 2000), studies have focused mainly on the reproductive phenology of species (Grudinskaya et al. 2022, Halupka et al. 2020, Shave et al. 2019), while the reproductive output (e.g., clutch size, egg size) was less frequently investigated (Crick 2004). Moreover, there is a significant discrepancy between the number of studies among regions, where the north-temperate systems are very well studied (Crick et al. 1997, Laaksonen et al. 2006, Winkler et al. 2002), and their results are often taken as references for the other biogeographic regions of the planet. However, north-temperate climates must not serve as a basis for studies in the equatorial regions, even for austral regions (Heming & Marini 2015), precisely because species tend to adapt their physiology to the conditions where they express their traits (Stutchbury & Morton 2001). Once we can gather extensive data from a monophyletic group spread over a substantial time and space range, we can assess common environmental predictors of spatial variation in life history traits.

We used a geographically widespread tyrant flycatcher genus and collected breeding data from scientific egg collections. This dataset covers their entire latitudinal range throughout almost all the American continent. This work aims to evaluate how residual variations in clutch and egg size of Kingbirds (*Tyrannus* species) are influenced by geo-climatic characteristics. We aim to answer how the clutches and egg sizes vary according to 1) latitude; 2) main climate (Köppen-Geiger climate classification; "KG"); 3) sub-climates within main KG climate classification; and 4) local long-term averages, i.e., historical climatic conditions based on temperature and precipitation parameters. Accordingly, we tested the hypotheses that clutch and egg size increase: a) with increasing latitude, b) in more seasonal climates and conditions (Köppen-Geiger), and c) at breeding sites with cooler and wet climatic parameters. Our premise is that these temperature conditions that increase reproductive output are characteristic of higher latitude regions. In contrast, precipitation conditions are related to high primary production and, therefore, the reason for the variation in reproduction.

1.2. METHODS

Database

We collected reproductive data from the Kingbird species (*Tyrannus* genus) in scientific egg collections. We choose the collections by researching and accessing the digitised and tabulated collections on their websites or scientific collection aggregators (*e.g.*, GBIF, VertNet). With the knowledge of the contents of most part these collections, we visited 35 museums in South America, the USA, and Europe (Supplementary material Tabela S1). We took a careful visual approach and inspected the eggs to confirm the main characteristics of the Tyrannidae family. Then we checked the data shown on the respective labels/cards. The visual inspection included the egg sizes, colours, mark patterns, and nest parasites within the egg set. With prior knowledge of the species, for this work, we ignored egg sets with possible changes in clutch size, either by nest parasitism, predation, or collecting bias. We only proceeded with those egg sets whose clutch size was reliable, even for the egg size analyses. In addition to clutch size, the records provided the laying location and date. Verifying the data's integrity with information on each species natural history patterns was crucial in matching the location with species distributions (BirdLife International 2020) and the laying date with their recorded phenology. The first taxonomic classification, whenever available, was essential to review taxonomic resolution, through synonymy, for the outdated taxonomic classifications of some collections. The taxonomic resolution for this group followed the order: (Sclater 1888), then (Cory & Hellmayr 1927), (Amadon et al. 1979), (Phillips 1994), and finally, we updated the species names (and subspecies when possible) following the eBird/Clements checklist (Clements et al. 2022).

We gathered pictures of eggs arranged in clutches on a black base with a ruler scale and their respective collection labels/cards. We extracted the egg dimensions from each image using *ImageJ* software (Schneider et al. 2012) associated with the *EggTools* add-on (Troscianko 2014). Besides the main dimensions (length, width, perimeter, and area), the process allowed us to extract the volume of the eggs (mm^3), which we treat here as "egg size." Establishing a maximum error of ±25km, we used the clutch collection site present in the cards to obtain the geocode (decimal latitude and longitude) through the ggmap package, established through the centroid of the locality, defined by Google Maps service (Kahle & Wickham 2013). Every locality, continent, or island that did not contain a geocode but provided localities with errors within these limits was integrated into our database. This error was defined to be compatible with the following climate information. With this level of resolution, we obtained climate conditions at the locality of egg-laying with the coordinates.

To classify the climate where the clutches were collected, we used the geo-climatic raster model of Köppen-Geiger (Kottek et al. 2006), available in shapefiles, according to its geographic position from clutch geocode. The combination of the five main climates (A – Equatorial climates, B – Arid climates, C – Warm temperate climates, D – Snow climates, and E - Polar climates) and temperature and precipitation parameters results in 31 possible climates (*e.g.*, Af – Equatorial rainforest, fully humid; Csa - Warm temperate climate with dry and hot summer and summer; Supplementary material Tabela S3, Figure 1.1). Equatorial climates (A) are characterised by high temperatures throughout the year in comparison with other climates, with average annual minimum temperatures ranging around 18 °C. Arid climates (B) are characterised by droughts with threshold precipitation below 10 mm. Warm temperate climates are characterised by average annual minimum temperatures ranging from -3 to 18 °C. Snow climates are classified by their average minimum temperature of around -3°C. The Köppen-Geiger was first established in the year 1900 after being updated between the 1950s, and 1960s has been updated frequently (Rubel et al. 2017). The data is made available digitally on the website http://koeppen-geiger.vu-wien.ac.at. Its climate models include historical temperature and precipitation indices with a monthly resolution of the entire land area of the planet, with a spatial resolution of 0.5 degrees latitude/longitude (Kottek et al. 2006).

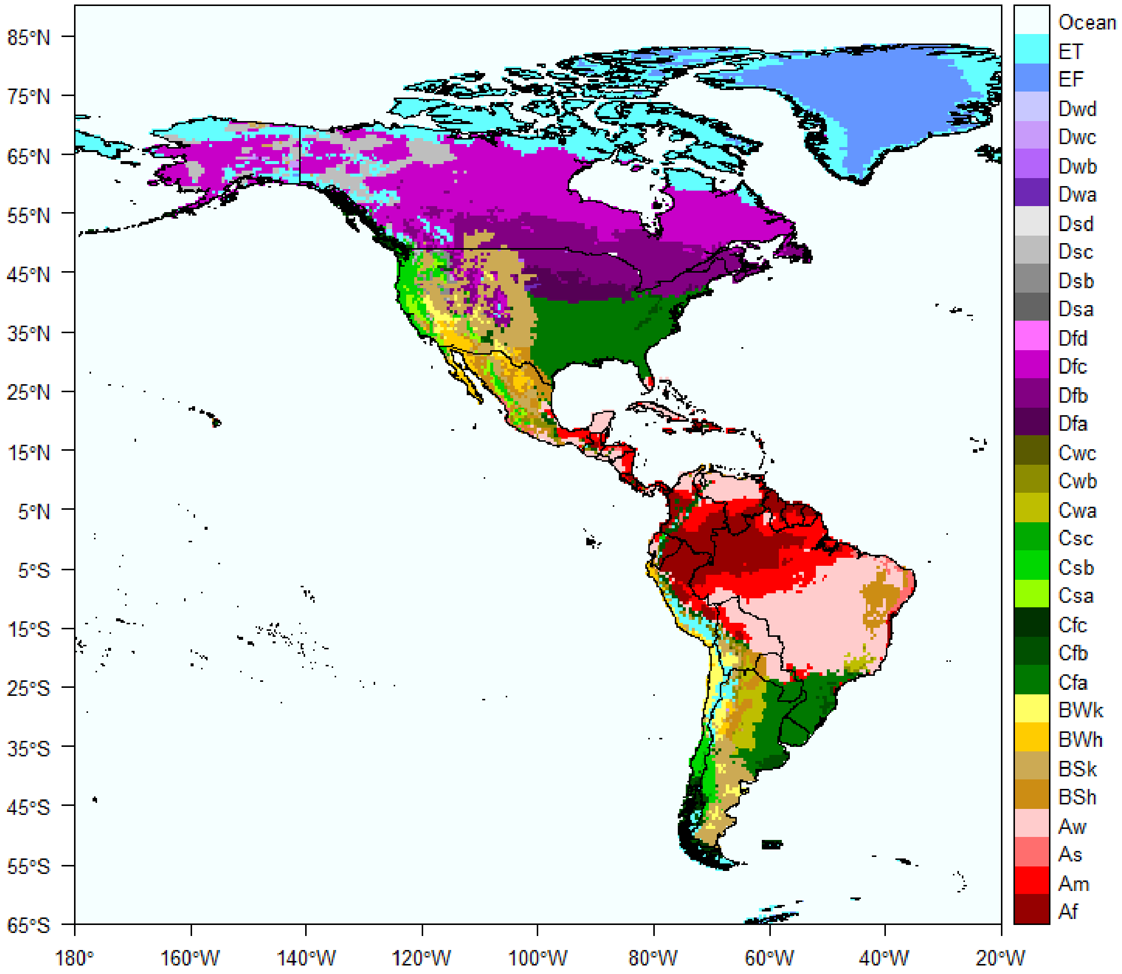

Figure 1.1 Map of the 31 Köppen-Geiger sub-climates of the Americas divided into five main climates (A – Equatorial climates, B – Arid climates, C – Warm temperate climates, D – Snow climates, and E – Polar climates) generated from observed temperature and precipitation data from 25 years (1986-2010). Source: Adapted from http://koeppen-geiger.vu-wien.ac.at

We gathered the local historical temperature and precipitation variables from WorldClim Bioclimatic Database (Fick & Hijmans 2017) at a 10-minute resolution to identify the local climate characteristics. We extracted the values of the following nine bioclimate variables: isothermality (Tiso), temperature seasonality (Tsea), maximum temperature of warmest month (Tmax), minimum temperature of coldest month (Tmin), annual mean temperature (Tmyr), annual precipitation (Pryr), precipitation of wettest month (Pmax), precipitation of driest month (Pmin), and precipitation seasonality (Psea), also using the geocode of the clutch collection site.

Statistics

We analysed the data using Linear Mixed Models (LMM). Since we aimed to observe geo-climatic variation across the entire *Tyrannus* genus, we set the species taxon as a random variable for the clutch and egg size analyses. Exclusively for egg size, recognising intraclutch dependence (Christians 2002), we used clutch identity to analyse climate effects on kingbirds' egg size. The analyses were divided into four geo-climatic scales: from largest to smallest – latitude, main climate, sub-climate, and local historical index of temperature and precipitation. For each geo-climatic category, a pair of analyses was performed for egg and clutch size as dependent variables. The latitudinal effect on clutch and egg size was evaluated using the absolute value of latitude, gathered from the site of the clutch collection, as a fixed variable. Then, we assessed the effect of climate on the reproductive output of Kingbirds in two steps. First, the effect of climate was analysed for the entire set of clutches and eggs using the main climates as a fixed variable, and, in the second step, within each main climate, we analysed the effect the sub-climate had on clutch and eggs, considering its characteristics among precipitation and temperature regimes.

We evaluate the smaller-scale climate effect by combining the local bioclimatic indices as fixed variables. To avoid multicollinearity among climate variables, we first estimated the pairwise Pearson's correlation coefficients and judged the high correlations ($|r| > 0.7$). Once we detect a correlation between a pair of variables, we exclude one of those, keeping the variable we thought was most important for the model. An initial model was established with all fixed variables. Then, assessing the weight and importance of each variable for the model using Akaike information criteria (AIC), we fitted the models by backward deletion, excluding less weighed variables to build the best-fixed structure, using maximum likelihood as a parameter (Zuur et al. 2009).

All continuous variables adopted in this work were standardised with a mean of zero and a standard deviation of one. Finally, we checked for overdispersion for each model, where no overdispersion was detected. All these steps, from the construction of the dataset to the analyses, were performed using the software R (R Core Team 2022) where we used the "lme4" package (Bates et al. 2015) to analyse the LMM associated with the "lmerTest" package (Kuznetsova et al. 2017) to calculate *p* values for each model output. Additionally, we calculated marginal and conditional R^2, obtaining the variance explained by the fixed effects and the variance of the fixed and random effects, respectively (Nakagawa & Schielzeth 2013).

1.3.RESULTS

Database

We gathered breeding records of 9529 eggs from 2931 clutches for all 13 Kingbird species. We were able to take pictures from 1657 clutches in the egg collections. After checking the taxonomy, consistent species-clutch sizes, and geographic distribution, we reached a set of 1358 clutches and 4750 eggs. Although, after observing the discrepancy in the number of clutches of each species, we chose to proceed with the analyses with only eight species. We removed the clutches of the following species from our data set: *Tyrannus niveigularis*, *T. crassirostris*, *T. cubensis*, *T. albogularis,* and *T. caudifasciatus*. Together, these species totalled only 36 clutches and 70 eggs. In our final dataset, therefore, we evaluated the variation by the climate of 1322 clutches and 4680 measured eggs from *Tyrannus melancholicus*, *T. savana*, *T. dominicensis*, *T. tyrannus*, *T. verticalis*, *T. couchii*, *T. vociferans,* and *T. forficatus* (Supplementary material Tabela S1), which covered the entire latitudinal extent of the genus' distribution in the American continent.

Statistics

The LMM revealed that clutch size had a significative and positive variation with absolute latitude (β = -0.25 ± 0.03, Table 1.1, Figure 1.2A).

Table 1.1 - A summary of the Linear Mixed Models investigating latitudinal variation in clutch and egg sizes of kingbirds. All variations were standardised with a mean of zero and a standard

deviation of one. Significant effects are classified by p-value ($p<0.05$; ** $p<0.01$; *** $p<0.001$). The marginal R^2 value represents the variance explained by fixed effects, and conditional R^2 represents the variance of the entire model.*

	Clutch size			**Egg size**		
Predictors	*Estimates*	*SE*	*CI*	*Estimates*	*SE*	*CI*
Intercept	0.06	0.19	-0.31 – 0.43	-0.03	0.3	-0.63 – 0.57
Absolute latitude	0.25 ***	0.03	0.19 – 0.32	0.10 ***	0.02	0.05 – 0.15
Marginal / Conditional R^2	0.068 / 0.366			0.009 / 0.892		

Kingbird's egg size also increased with latitude ($\beta = -0.10 \pm 0.02$, Table 1.1, Figure 1.2B).

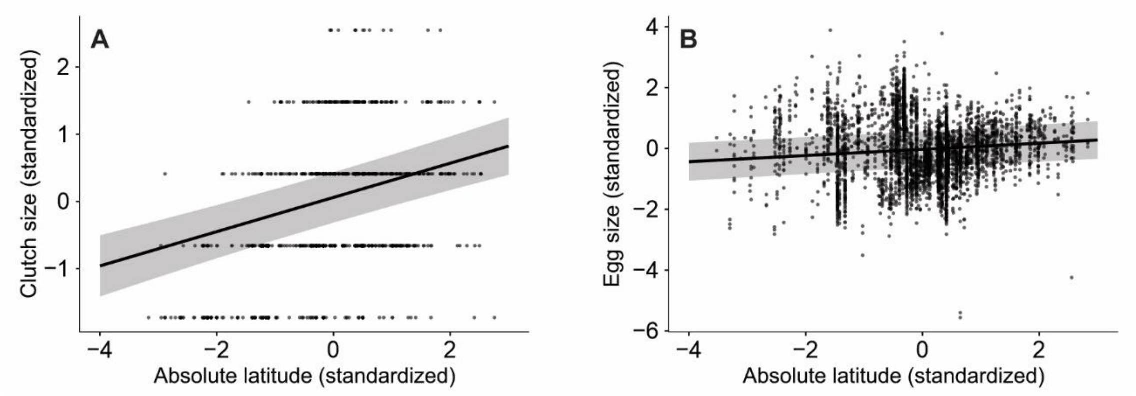

Figure 1.2 – Relationships between clutch size (A) and egg size (B) of kingbirds and absolute latitude by Linear Mixed Models (LMM). The shaded grey areas correspond to the 95% confidence intervals predicted.

The clutch size of kingbirds varied among the main climates (Table 1.2, Figure 1.3A). Taking the Equatorial climates as the intercept, where the clutches were smaller, the clutch sizes were larger in all other climates. Among all the main climates, the Snow climate had the largest clutches. Like clutch size, egg size was smaller in Equatorial climates and larger in Snow climates (Table 1.2, Figure 1.3B).

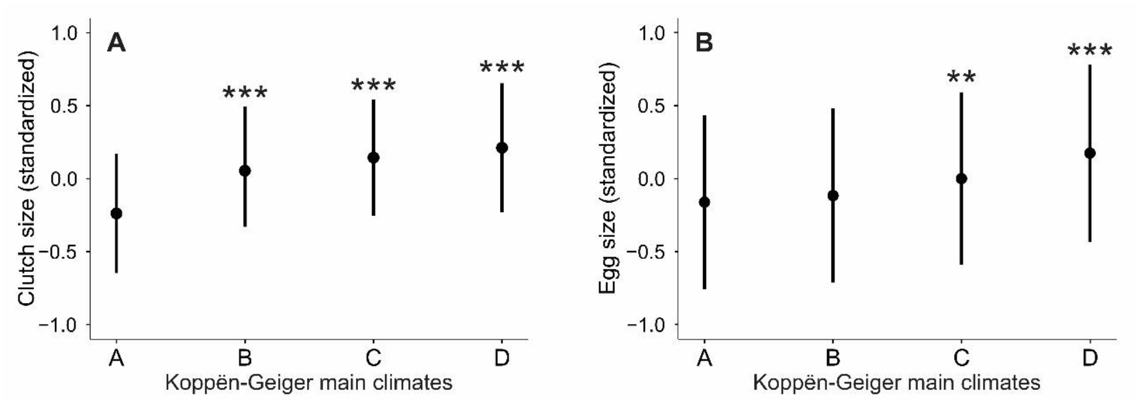

Figure 1.3 - Variation in the clutch (A) and egg sizes (B) of kingbird species in Equatorial (A), Arid (B), Warm temperate (C), and Snow (D) climates classified from (Kottek et al. 2006). *Clutch and egg size variations were standardised with a mean of zero and a standard deviation of one. Significant effects are classified by p-value (* $p<0.05$; ** $p<0.01$; *** $p<0.001$).*

Also, for egg size, there was no significant difference between Equatorial and Arid climates.

Table 1.2 - A summary of the Linear Mixed Models investigating variation in clutch and egg sizes of kingbirds as a function of the main Koppën-Geiger main climates. All variations were standardised with a mean of zero and a standard deviation of one. Significant effects are classified by p-value ($p<0.05$; ** $p<0.01$; *** $p<0.001$). The marginal R^2 value represents the variance explained by fixed effects, and conditional R^2 represents the variance of the entire model.*

	Clutch size			**Egg size**		
Predictors	*Estimates*	*SE*	*CI*	*Estimates*	*SE*	*CI*
[A] Equatorial climates (Intercept)	-0.24	0.21	-0.65 – 0.17	-0.16	0.3	-0.76 – 0.43
[B] Arid Climates	0.29^{***}	0.09	0.12 – 0.46	0.04	0.07	-0.08 – 0.17
[C] Warm Temperate climates	0.38^{***}	0.07	0.25 – 0.51	0.16^{**}	0.05	0.06 – 0.26
[D] Snow Climates	0.45^{***}	0.12	0.21 – 0.69	0.34^{***}	0.09	0.16 – 0.51
Marginal / Conditional R^2	0.025 / 0.359			0.007 / 0.890		

Among the Equatorial sub-climates, in equatorial with dry summer places (As), there was a significant positive variation in clutch size (Table 1.3).

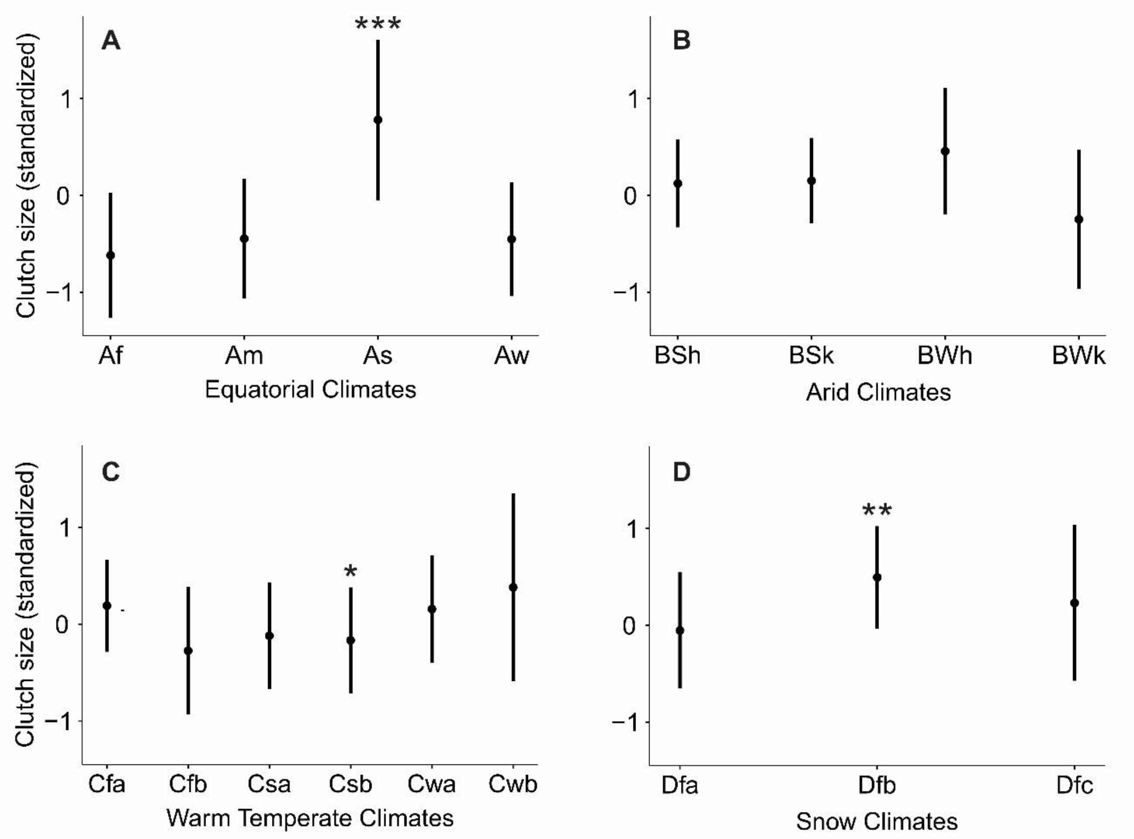

Figure 1.4 - Variation in the clutch size of kingbird species in sub-climates of Equatorial (A), Arid (B), Warm temperate (C), and Snow (D) climates, classified by (Kottek et al. 2006). *Clutch size variation was standardised with a mean of zero and a standard deviation of one. Significant effects are classified by p-value (* $p<0.05$*; ** $p<0.01$*; *** $p<0.001$*).*

The clutches were larger (Figure 1.5A), and the eggs were smaller (Figure 1.6A) in the As climate, a climate characterised by dry summers with minimum precipitation of less than 60 mm. Eggs were also smaller in the Aw climate (Figure 1.6A), where the major characteristic is dry winters, with average minimum precipitation rates of less than 60mm. Only egg size had significant variation between arid sub-climates (Table 1.3).

Table 1.3 - A summary of the Linear Mixed Models investigating variation in clutch and egg sizes of kingbirds as a function of the Koppën-Geiger sub-climates. All variations were standardised with a mean of zero and a standard deviation of one. Significant effects are classified by p-value ($p<0.05$; ** $p<0.01$; *** $p<0.001$). The marginal R^2 value represents the variance explained by fixed effects, and conditional R^2 represents the variance of the entire model.*

	Clutch size			**Egg size**		
Predictors	*Estimates*	*SE*	*CI*	*Estimates*	*SE*	*CI*
Equatorial climates						
Af (Intercept)	-0.62	0.33	-1.27 – 0.03	0.2	0.45	-0.69 – 1.08
Am	0.17	0.17	-0.17 – 0.52	0.01	0.15	-0.28 – 0.30
As	1.40 ***	0.33	0.75 – 2.05	-0.56 *	0.28	-1.10 – -0.01
Aw	0.17	0.16	-0.14 – 0.48	-0.34 *	0.13	-0.60 – -0.07
Marginal/ Conditional R^2	0.039 / 0.412			0.020 / 0.924		
Arid Climates						
BSh (Intercept)	0.12	0.23	-0.33 – 0.58	-0.35	0.28	-0.90 – 0.21
BSk	0.03	0.13	-0.23 – 0.29	0.21 **	0.08	0.05 – 0.37
BWh	0.33	0.27	-0.21 – 0.87	-0.15	0.16	-0.47 – 0.17
BWk	-0.37	0.31	-0.99 – 0.25	0.53 **	0.19	0.17 – 0.90
Marginal/ Conditional R^2	0.011 / 0.261			0.022 / 0.891		
Warm Temperate climates						
Cfa (Intercept)	0.19	0.24	-0.29 – 0.67	-0.01	0.33	-0.65 – 0.63
Cfb	-0.46	0.24	-0.94 – 0.01	0.35	0.18	-0.01 – 0.71
Csa	-0.31	0.18	-0.67 – 0.05	-0.16	0.14	-0.44 – 0.11
Csb	-0.36 *	0.18	-0.71 – -0.00	0.12	0.14	-0.15 – 0.39
Cwa	-0.03	0.16	-0.34 – 0.27	0.08	0.12	-0.16 – 0.31
Cwb	0.19	0.44	-0.67 – 1.05	-0.62	0.33	-1.27 – 0.03
Marginal/ Conditional R^2	0.021 / 0.460			0.007 / 0.892		
Snow Climates						
Dfa (Intercept)	-0.05	0.3	-0.65 – 0.55	-0.06	0.17	-0.40 – 0.28
Dfb	0.55 **	0.21	0.14 – 0.96	0.25	0.14	-0.02 – 0.52
Dfc	0.28	0.38	-0.48 – 1.05	0.66 **	0.25	0.17 – 1.16
Marginal/ Conditional R^2	0.069 / 0.200			0.052 / 0.579		

Kingbird eggs were larger in the BSk climate and even larger in the BWk climate (Figure 1.6B). These two Arid climates have in common the recording of average annual temperatures below 18°C and differ in precipitation rates. While BSk has a precipitation threshold between 5 and 10 mm, in the BWk climate, the species experiences a precipitation threshold of less than 5, characterising the region as desert. In Warm temperate climates, the clutch size was significantly smaller in the Csb climate (Table 1.3, Figure 1.5C), which is characterised by dry summers, with higher precipitation rates in winter and at least four months with average temperatures between 10 and 22 °C. In Snow climates, climate Dfb showed the largest clutches (Table 1.3), and climate Dfc was where eggs were significantly larger (Figure 1.6D). In common, these climates have high humidity and high precipitation and differ in summer temperatures. While Dfb has a warm summer, Dfc has a cool summer.

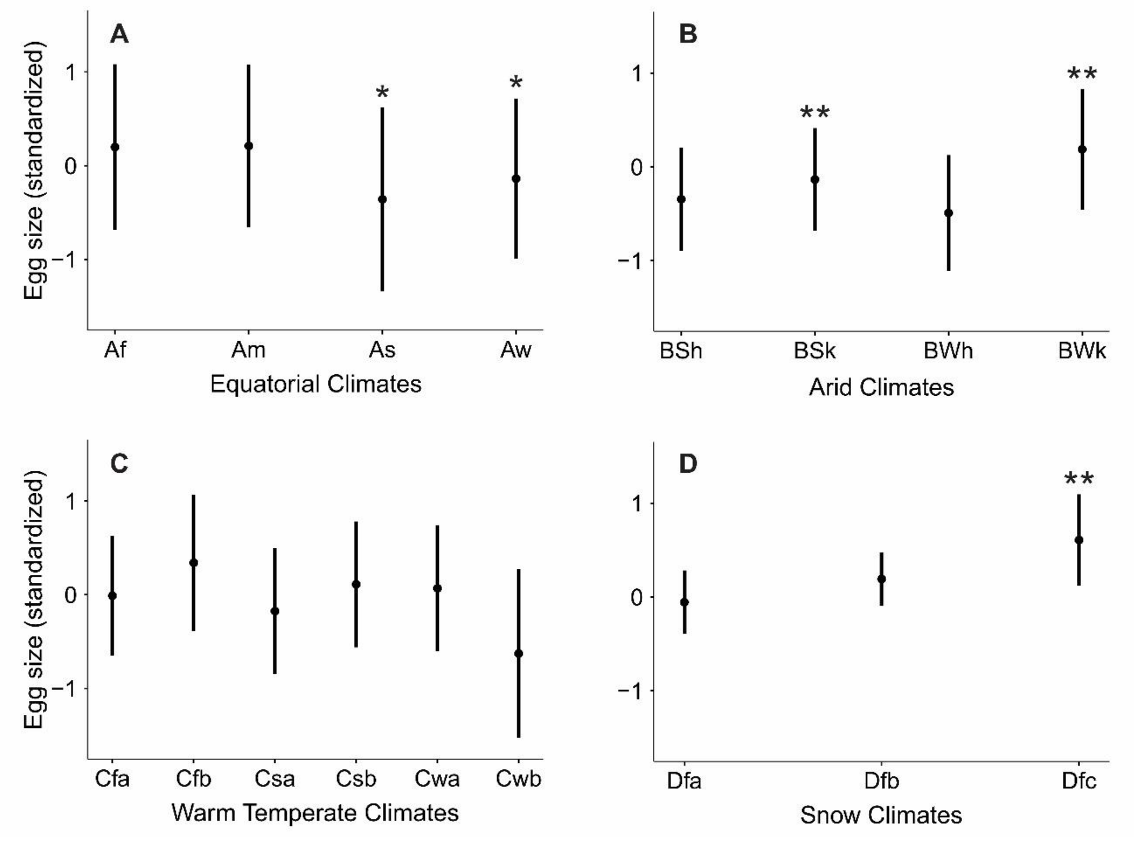

Figure 1.5 - Variation in the egg size of kingbird species in sub-climates of Equatorial (A), Arid (B), Warm temperate (C), and Snow (D) climates, classified by (Kottek et al. 2006). *Egg size variation was standardised with a mean of zero and a standard deviation of one. Significant effects are classified by p-value (* $p<0.05$; ** $p<0.01$; *** $p<0.001$).*

The LMM best-adjusted for clutch size was composed of three climatic variables, including isothermality (β = -0.42 ± 0.04; Table 1.4; Figure 1.7A), seasonality of precipitation (β = 0.18 ± 0.03; Table 1.4; Figure 1.7B), and minimum temperature of the coldest month (β = 0.11 ± 0.04; Table 1.4; Figure 1.7C).

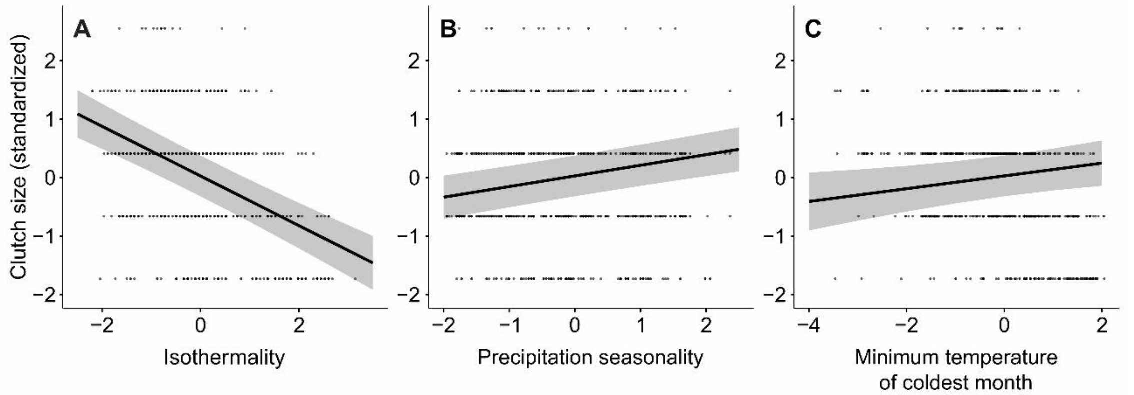

Figure 1.6 - Relationships between clutch size of kingbirds and climatic parameters by Linear Mixed Models (LMM). The backward selection resulted in the model with the variables (anomalies): (A) isothermality (Tiso), (B) precipitation seasonality (Psea), and (C) minimum temperature of the coldest month (Tmin). The shaded grey areas correspond to the 95% confidence intervals predicted.

In this model, all variables had significant coefficients and showed a marginal R^2 = 0.096 and a conditional R^2 = 0.367. This model indicated that the kingbird's clutch size is larger in locations with more stable annual temperatures, more distributed rainfall, and the coldest month of the year with higher minimum temperatures.

Table 1.4 - Linear mixed models, adjusted by the backward selection, for clutch and egg sizes and long-term mean parameters of precipitation and temperature. Significant effects are classified by p-value (p<0.05; ** p<0.01; *** p<0.001). The marginal R² value represents the variance explained by fixed effects, and conditional R² represents the variance of the entire model.*

	Clutch size			**Egg size**		
Predictors	*Estimates*	*SE*	*CI*	*Estimates*	*SE*	*CI*
Intercept	0.03	0.18	-0.32 – 0.37	-0.04	0.3	-0.62 – 0.55
Isot	-0.42 ***	0.04	-0.51 – -0.34	-	-	-
Pmin	-	-	-	0.10 ***	0.02	0.05 – 0.14
Pseas	0.18 ***	0.03	0.12 – 0.24	-	-	-
Tmax	-	-	-	-0.09 ***	0.02	-0.12 – -0.05
Tmin	0.11 *	0.04	0.02 – 0.20	-0.11 ***	0.02	-0.15 – -0.06
Marginal/ Conditional R^2	0.096 / 0.367			0.027 / 0.891		

For egg size, the best-adjusted LMM contained three variables, including precipitation of the driest month (β = 0.10 ± 0.02; Table 1.4; Figure 1.8A), maximum temperature of the warmest month (β = -0.09 ± 0.02; Table 1.4; Figure 1.8B), and minimum temperature of the coldest month (β = -0.11 ± 0.02; Table 1.4; Figure 1.8C). All three variables that compound the model were p-significant. These model coefficients show that kingbird's egg sizes are larger where the year's driest month has more rainfall and tends to be smaller where the warmest month have higher maximum temperatures and the coldest month have higher minimum temperatures. This model presented a marginal $R^2 = 0.027$ and conditional $R^2 = 0.891$.

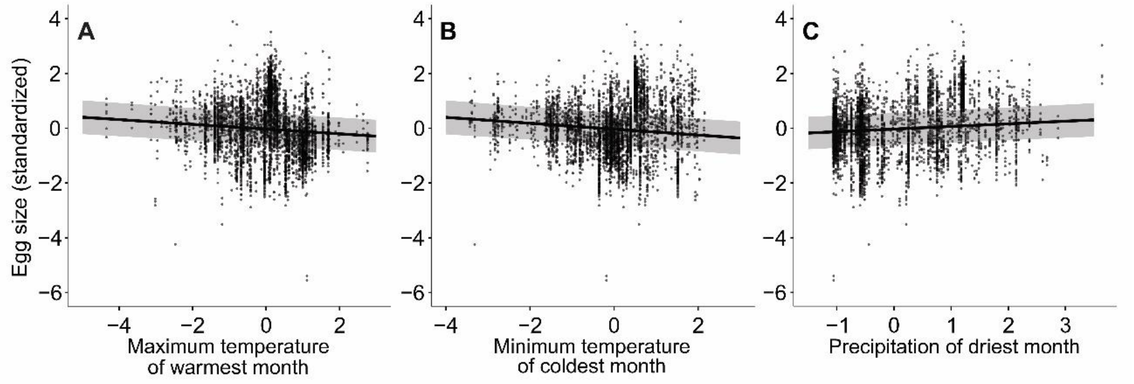

Figure 1.7 - Relationships between egg size of kingbirds and climatic parameters by Linear Mixed Models (LMM). The backward selection resulted in the model with the variables (anomalies): (A) maximum temperature of the warmest month (Tmax), (B) minimum temperature of the coldest month (Tmin), and (C) precipitation of driest month (Pmin). The shaded grey areas correspond to the 95% confidence intervals predicted.

1.4.DISCUSSION

Based on a dataset of 158 years (1858-2016), covering a latitude interval of 94° (37.9°S – 56.13°N) in the American continent, we analysed the variation in two breeding traits of eight kingbird species, clutch and egg size as a function of geo-climatic variables. We showed that kingbirds' clutch and egg sizes change not only with latitude but also with regional and local climates. Our results demonstrate that a great extent of the residual variation in these traits is due to adaptations to climatic conditions, both at regional and local levels, related or not to latitude variation.

The clutches of kingbirds were larger at sites with higher rainfall seasonality (Psea) and thermal variation (Tiso). It is already agreed that species inhabiting more seasonal environments tend to have larger clutches, especially concerning temperature variation (Jetz et al. 2008, Stevens 1989). The increase in seasonality with latitude is one of the most accepted explanations for bird clutch size among ornithologists (Ashmole 1963, Lundblad & Conway 2021). Ashmole's hypothesis considers that harsher winter conditions tend to leave individuals more vulnerable and susceptible to starvation and hypothermia, decreasing population density for the breeding season. However, the temperature variability parameter relevant for clutch size was not temperature seasonality (Tsea) but isothermality (Tiso). While the temperature seasonality measure is based on average temperatures, isothermality uses monthly and annual ranges, with maximum and minimum temperatures for each range (O'Donnell & Ignizio, 2012). Studies have shown that extreme temperatures have been a better predictor than average temperatures (Schaper et al. 2012) because these parameters have a higher potential to cause physiological stress in the species. Our results also show that clutches tend to be larger in environments with higher precipitation seasonality. Additionally, in Equatorial climates, kingbirds tend to have larger clutches in subclimates with dry summers (As).

Precipitation is an important primary productivity factor and crucial for increasing invertebrate populations (Pinheiro et al. 2002). It is, therefore, important to note that *Tyrannus* is a tyrant flycatcher genus and thus primarily insectivorous flycatchers (Fitzpatrick 1980, Murphy 1983b), which tends to correlate its reproductive output with insect abundance (Blancher & Robertson 1987), and the reproductive event is highly dependent on invertebrates as a protein source for egg development. Low seasonality of precipitation keeps insect populations at equilibrium throughout the year (Wolda 1988).

Furthermore, kingbirds at sites with higher precipitation in the drier months of the year (Pmin) had larger egg sizes. This means that more pronounced droughts, even if not occurring in the reproductive season, can affect egg size. Given that larger eggs generate larger chicks, higher-fitness offspring mean an excellent breeding season (Krist 2011). However, it is necessary to understand how egg composition, in addition to their size, can also ensure chick quality (Birchard & Deeming 2015). This result suggests a more direct relationship between precipitation and egg size. This time lag effect of the weather on breeding traits seems very important and deserves further consideration.

Sites with warmer winters, with higher minimum temperatures (>Tmin), had larger clutches and smaller eggs. As well as for local parameters, sub-climates with colder winter temperatures also presented smaller clutches (Csb). Breeding sites with higher maximum temperatures in the warmest month (Tmax) also had smaller eggs. Combined with this result, the arid subclimates where Kingbirds' eggs were largest were those with the lowest annual temperatures (BSk, BWk). Drier, warmer environments create a more significant challenge for eggs due to the dehydration process (Sauve et al., 2021). The high energy expenditure of birds can be justified in both cold and hot environments. In warmer environments the thermal potential can lead to dehydration, mainly in water-limited environments, such as arid regions (Sauve et al. 2021, Schifferli et al. 2014, Whitfield et al. 2015). However, in warm environments, productivity tends to lead to higher insect availability (Grüebler et al. 2008), main food resources of kingbirds.

The thermal potential of colder environments subjects female *Tyrannus*, as a unique parental incubator species (Blancher & Robertson 1985, Murphy 1996), to greater difficulties in maintaining optimum incubation temperature (Gillette et al. 2021), generating greater energy expenditure. Thus, the energy expenditure for heating and re-heating eggs in cold environments appears to be even higher than in warm environments. The premise that the low availability of resources triggered by lower temperatures leads to a decrease in the physiological conditions of the females, who would have lower body mass and consequently lay smaller eggs (Järvinen & Ylimaunu 1986), is refuted by our results. Larger chicks from larger eggs may show greater tolerance and resistance to heat loss in colder environments (Krist 2011). Larger eggs, which ensure greater fitness of offspring, when associated with an after-hatching attendance increase, must compensate for the lower resource conditions in cooler than in warmer environments (Gebhardt-Henrich & Richner 1998). Furthermore, in cooler climates, laying larger eggs have better heat conservation, allowing females more time outside the nest foraging and improving their condition (Gillette et al. 2021).

In Snow climates, *Tyrannus* only breeds in wet subclimates (Df*), but larger clutches occur only in subclimates that have warm summers (Dfb), while larger eggs are found in subclimates that have cool summers (Dfc). The high precipitation in this last subclimate, combined with the increased egg size in environments with more rain in the driest month of the year (>Pmin), also shows the importance of rainfall for kingbird's egg size, even though other studies have found no significant effect of precipitation for species in this group (Murphy 1983a). Even if precipitation occurs during winter, climatic events tend to influence individuals and populations in subsequent seasons (Marra et al. 2015). Kingbird's clutch sizes were largest in Snow climates, followed by Warm temperate and Arid climates, and were smallest in equatorial climates. This progression does not coincide with summer temperatures or precipitation but coincides with a decrease in winter temperatures. Higher latitude species tend to cover a higher latitudinal range and be better tolerant to temperature variation (Stevens 1989). In addition, local and regional sites with lower minimum winter temperatures tend to have smaller clutches. The progression of egg sizes followed the trend observed for clutch size, and Snow climates had the largest eggs. Particularly for egg size, Equatorial and Arid climates did not differ. Our findings so far indicate a combination of local factors that underlie the geographic variation in kingbird breeding traits.

The latitudinal variation in kingbird's clutch size corroborates again the pattern observed since Moreau (1944), increasing significantly toward the poles (Cody 1966). Environments with more seasonal climates and temperature variations promote larger clutches (Griebeler et al. 2004), and climate seasonality was a common factor among the climates and climatic conditions that caused *Tyrannus* to increase their clutches and high latitudes. However, harsher winter conditions do not promote larger clutches. Thus, even if winters are harsh and decrease population density (Lv et al. 2023), and increase per capita resource availability during the breeding season, the quality of resources in these locations does not provide the energy demands to increase the clutch size (Ockendon et al. 2013). Egg size followed the same trend as clutch size and increased with latitude. As an important factor for primary productivity, regions with milder winters can reflect in a breeding season with greater resource abundance but also high competitiveness (Newton 1998b). The progression of egg size with latitude appears to be negatively related to temperatures, as observed for other vertebrate groups (Feiner et al. 2016, Sheader 1996). Higher latitudes share the climatic characteristics that enable kingbirds lay larger eggs.

As the explanation of life history patterns is based on complex interactions of traits (Bennett & Owens 2002), the investment in clutch size can be correlated with adjustment in egg size (Roff & Fairbairn 2007, Stearns 1992), which depends on the short term strategy females will adopt when meeting the environmental conditions in the reproduction cycle (Aranzamendi et al. 2019). *Tyrannus* lacks a trade-off between clutch and egg sizes, varying among species in positive, negative, and no apparent trade-off. A trade-off in these traits tends to be a species-specific characteristic of *Tyrannus* and does not appear to be a general rule since most species already assessed do not show a correlation between clutch and egg size (Christians 2002, Sakai 2021).

It is important to note the potential effect of climate, weather conditions at the time and place of breeding, and their environmental consequences, on changes in the reproductive output of birds. In addition to the direct parental effect on clutch and egg size, much of the variation of an offspring trait is due to environmental impacts (Krist 2011). Eastern Kingbird (*T. tyrannus)*, for example, changes its reproductive performance interannually as a function of environmental quality (Blancher & Robertson 1985). Since species adapt their reproductive traits to a climate, interannual variation in climatic conditions tends to pressure the plasticity of their traits (Visser 2008). Kingbirds have characteristics that are dependent on climatic conditions. Members of this genus have high fidelity to the breeding site (Blancher & Robertson 1985, Murphy 1996) and select habitats based on climatic parameters, as is the case for *T. savana* and *T. tyrannus*, where temperature is a cue for breeding sites (MacPherson et al. 2018), and *T. savana* uses precipitation to select wintering sites (Jahn et al. 2013). In addition, heritability reinforces the relationship between species and local climate across generations (Christians 2002). It is essential, therefore, to know how climates define species' reproductive traits and how they respond to variations in climatic conditions.

Climate unpredictability is one of the most significant factors experienced by species through global climate change (Hansen et al., 2012), with negative effects on their fitness (McNamara et al. 2011). Kingbirds and other species are more responsive to extreme than average temperatures (Schaper et al. 2012). The extreme climate parameters will be most impacted by global climate change (Marcelino et al. 2020). Heat waves, droughts, and extreme rainfall are consequences of climate change and can affect birds depending on which stage of reproduction they experience these conditions (Cady et al. 2019, Sauve et al. 2021). Projections of future climate change scenarios show that birds are more vulnerable to future thermal stresses, greater even than mammals (Riddell et al. 2021).

In conclusion, our findings show that kingbirds clutch and egg sizes vary according to regional and local climate and that these correlations shed light on the latitudinal cline of reproductive investment. Still, it is not possible to assert whether the variation in investment in reproduction is a life history strategy or a physiological response (Dunn 2019, Martin & Mouton 2020). Therefore, more research relating climatic conditions to life history traits is indispensable (Christians 2002). Importantly, there is a recognition that species from different biogeographic regions may have common or divergent responses to climatic conditions and that responses of one species restricted to the Nearctic region are not necessarily similar to those by a Neotropical species. Here, we were looking for residual variation in clutch and egg sizes shared by a genus across a large latitudinal range, covering different biogeographic regions, climates, and local climatic conditions. For this, we accessed scientific egg collections, an important data source with robust and highly reliable information, and still poorly explored to answer ecological questions (Marini et al. 2020). Furthermore, long-term and longitudinal data is essential to understand the effects of global climate change on species reproduction (Järvinen 1994) and how their expressed traits will buffer future climatic conditions (McNamara et al. 2011, Sauve et al. 2021).

2. DIFFERENTIAL SHORT-TERM AND LONG-TERM WEATHER WINDOWS ON BREEDING TRAITS OF KINGBIRDS

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ABSTRACT

Natural selection defines a large part of species reproductive output, though fluctuations in temperature and precipitation can directly or indirectly influence birds' breeding traits. However, it is still unclear how weather conditions are used as cues by females to define their strategy for investing in the quality of their offspring. To assess weather effects on egg volume and clutch size, we used 1145 clutches and 4061 eggs of eight Kingbird species (*Tyrannus*) over 116 years (1901-2016) deposited in 35 ornithological collections. We used linear mixed models (LMM) to evaluate the relationships between egg (mm^3) and clutch sizes and weather anomalies (temperature and precipitation) of the year before laying (long-term time window) and the month before egg-laying (short-term time window). Temperature and precipitation variables affected the kingbird's reproductive output. The long-term window had the main effect on egg and clutch sizes. Kingbirds tended to be larger egg and clutch sizes in years with more stable weather conditions, while rainfall affect differently between these breeding traits. In the short-term window, only temperature parameters had an effect on the reproductive output of Kingbirds. The source of resources for egg production by *Tyrannus* species is probably affected by the fluctuation of precipitation and temperature, which alter ecosystem productivity in the long term and possibly change the phenology and availability of food supplies. Some climatic aspects may decrease while others tend to increase reproductive output. Still, the overall condition of these traits can only be defined by associating these variables and giving them the specific weight supplied by the statistical model. Given the rapid and increasing World climatic changes, it is necessary to understand the physiological limits involved in investing in offspring, their relationship with climate, and their consequences on population dynamics.

KEYWORDS

Weather, climate, climate change, kingbirds, egg size, clutch size, biogeography, seasonality

RESUMO

A seleção natural define grande parte das características reprodutivas das espécies, embora condições de temperatura e precipitação possam influenciar direta ou indiretamente a reprodução das aves. No entanto, ainda não está claro como as condições climáticas são usadas como pistas pelas fêmeas para definir sua estratégia de investimento na qualidade da prole. Para avaliar os efeitos do clima sobre o tamanho dos ovos e das ninhadas, usamos 1.145 ninhadas e 4.061 ovos de oito espécies de tiranídeos papa-moscas (aves do gênero *Tyrannus*) ao longo de 116 anos (1901-2016) depositados em 35 coleções ornitológicas. Utilizamos modelos lineares de efeitos mistos (MLEM) para avaliar as relações entre os tamanhos dos ovos (volume, mm^3) e das ninhadas e as anomalias climáticas (temperatura e precipitação) do ano anterior à postura (janela de tempo de longo prazo) e do mês anterior à postura dos ovos (janela de tempo de curto prazo). As variáveis de temperatura e precipitação afetaram a taxas reprodutivas das espécies de *Tyrannus* e a janela de longo prazo teve o principal efeito sobre o tamanho dos ovos e das ninhadas. As aves tenderam a ter ovos e ninhadas maiores em anos com condições climáticas mais estáveis, enquanto a precipitação afetou de forma diferente essas características reprodutivas. Na janela de curto prazo, somente os parâmetros de temperatura tiveram efeito sobre a taxa reprodutiva dos *Tyrannus*. A fonte de recursos para a produção de ovos pelas espécies de *Tyrannus* provavelmente é afetada pela flutuação da precipitação e da temperatura, que alteram a produtividade do ecossistema a longo prazo e possivelmente mudam a fenologia e a disponibilidade de recursos alimentares. Alguns aspectos climáticos podem diminuir, enquanto outros tendem a aumentar a produção reprodutiva. Ainda assim, a condição geral dessas características só pode ser definida associando-se essas variáveis e atribuindo-lhes o peso específico fornecido pelo modelo estatístico. Dadas as rápidas e crescentes mudanças climáticas mundiais, é necessário entender os limites fisiológicos envolvidos no investimento na prole, sua relação com o clima e suas consequências na dinâmica das populações.

2.1. INTRODUCTION

On the road to adaptation, birds' egg-laying seasons must be synchronised with the best conditions to provide the energetic demands of the female and the nestlings (McNamara et al. 2011). As organisms respond to environmental conditions through the plasticity of their life history traits (Forchhammer et al. 1998, Kuleska 1990), the interannual variation in climatic conditions, as an essential environmental aspect, tends to affect their reproductive traits (Töpfer 2018). Birds can lay larger clutches or eggs after experiencing good years or habitats as they are highly adapted to the local climate (Martin 1987). An increase in reproductive output could be partially related to an improvement in the physiological condition of females, which is provided by the climatic conditions encountered in their breeding area in the time of highest energy demand (Bêty et al. 2003, Christians 2002, Liu et al. 2018, Price & Liou 1989). Similarly, the reduced reproductive output may increase female longevity in years with adverse climatic conditions and thus reach the next breeding season (Edward & Chapman 2011, Martin 1987, Stearns 1992). Part of the normal variation in breeding traits can be dampened to a lesser degree but can impact those species with lower plasticity to environmental fluctuations (Perez et al. 2020). However, given site fidelity, the size of eggs and clutches may reflect a response to the weather that birds encounter during breeding. Thus, as components of the climatic conditions, temperature and precipitation changes can affect residual variation in breeding traits.

Birds use physical parameters as cues for almost their entire life, and the weather is one of the main factors driving bird phenology. Migratory species use climate conditions in habitat selection, such as temperature at breeding sites (MacPherson et al., 2018) or precipitation at their wintering sites (Jahn et al. 2013). Species use climate cues during fall (Therrien et al. 2017) and spring (Jenni & Kery 2003), when migration and weather conditions have been higher priority cues for breeding readiness (Crick et al. 1997), making day length a secondary factor (Boersma et al. 2022). Weather does not affect only movements but is an essential cue in the breeding season. Since laying dates can vary with temperatures (Crick & Sparks 1999, Crick et al. 1997) and rainfall (Aranzamendi et al. 2019), organisms can anticipate better conditions for their offspring with possible consequences for increased clutch size (Blancher & Robertson 1985, Selonen et al. 2021) and egg size (Christians 2002). The weather of a region during the year, influencing the quality of the environment through the quality of the resources or conditions, may affect species' reproductive output.

Every environment that organisms move through has the potential to affect their reproductive traits. Associated with income breeders (Ockendon et al. 2013), even migratory populations will use the resources of the breeding sites to increase their reproductive output (Selonen et al. 2021). Even winters reflect higher productivity and resource volume per capita during the reproductive season (Selonen et al. 2021). This correlation makes winter conditions at breeding sites important for migrants and residents when both will need resources for reproduction. During spring, conditions closer to the reproductive event reflect before, during, and after laying or incubation. These conditions can affect different aspects of reproduction, from breeding readiness (Boersma et al. 2022, Ockendon et al. 2013) with potential consequences on clutch size (Selonen et al. 2021), the delivery rate of food for the hatchlings (Schifferli et al. 2014) to direct influence on the recruitment rate of fledglings (Gullett et al. 2015). The weather conditions in the breeding season may reflect on the physiological needs and beyond their energy investment in the offspring to the detriment of the parents' survival (Schifferli et al. 2014, Stearns 1992). Thus, conditional on the weather conditions that occur throughout the year, birds' reproductive output can vary in egg size, clutch size, egg shape (Gómez-Bahamón et al. 2023, Stoddard et al. 2017) and the recruitment rate of fledglings as a function of clutch size (Gullett et al. 2015, Nägeli et al. 2022, Runge & Marra 2005, Selonen et al. 2021).

Different conditions during the year can result in a more favourable environment for breeding. Besides climatic variables, the time windows and the time it takes place can be critical in expressing breeding traits (van de Pol et al. 2016). Despite the evident correlation of species phenology with climate, it is not entirely clear which temporal variables are most important and how they interfere with each trait (Bevacqua et al. 2021, van de Pol et al. 2016). Conditions closer to the biological event have often been treated as more relevant (Schwartz & Liang 2019). Still, it is essential to evaluate in a complementary way how the conditions of the entire seasonal cycle (Runge & Marra 2005, Selonen et al. 2021), as well as those of the breeding season, affect species' reproductive output. With the date and place of a reproductive event (a clutch) and the necessary tools, estimating the pre-reproduction "year" conditions for these respective parents is achievable. Thus, it is possible to consider relative time windows and evaluate how the previous year's climatic conditions affected each female breeding trait (van de Pol & Cockburn 2011, van de Pol et al. 2016). Whether it is a difference of one month or more between laying events, two females can have relatively different years, reflected mainly by extreme weather events. What highlights the harsh weather and indices of temperature and precipitation variability is the direct influence on the phenological parameters of the species and requires rapid responses from organisms, but also long-term adaptation due to the potential effects of climate change (Thompson et al. 2013). Monthly precipitation and temperature data (Schwartz & Liang 2019) associated with the breeding site may provide sufficiently relevant information for analysing the weather's interference with the breeding traits of some groups (Trautmann 2018). Understanding temperature and precipitation and when they influence the reproductive output of birds will help us better understand how the environment can affect the structure of populations (Christians 2002, Runge & Marra 2005).

In recent decades, organisms have experienced increasingly broad climatic anomalies and more frequent extreme weather events (Hansen et al. 2012). Consequently, it has been known since the middle of the last century that climate changes have influenced birds' life history traits (Crick 2004). There is increased interest in the effect of recent and relatively rapid climate change on breeding patterns in birds (Bennett & Owens 2002), and recent studies have evaluated their interference in the reproduction of modern birds (Dunn & Møller 2019). Climate anomalies, variations in climate variables relative to a baseline (Chen et al. 2021), represent the interannual variation from the conditions to which the organisms are adapted, which can create another layer of temporal complexity for the organisms to establish themselves. Climate change will likely go beyond an increase in average temperatures, stressing the effects of increased climate variability and extreme conditions. Extreme weather events during the breeding season can adversely affect birds (van de Pol et al. 2010), and severely dry and cold weather tends to decrease the volume of resources during the year that could be invested in eggs (Simmons et al. 2004). By the most apparent responses to climatic maximum and minimum, it is possible, at this moment, to understand how the climatic extremes can affect species' responses to climatic fluctuations, especially what interference these extremes have on their breeding traits. Interannual climate variation can change reproductive output, an important factor affecting population maintenance, which brings us to the importance of better understanding these processes in the face of the consequences of climate change. Despite this, how interannual climate variation alters birds' clutch size and egg volume is not fully understood, especially in tropical regions (Aranzamendi et al. 2019).

We propose in this paper to clarify how weather conditions at the breeding site can alter the breeding traits of Kingbirds (*Tyrannus*). Specifically, we will answer the following questions: 1) how do weather variables affect egg volume and clutch size in short and long-term windows; 2) which time window - short-term (month of laying and a month before); long term (a year before laying) - tends to affect more egg and clutch sizes of the *Tyrannus* species. We tested the following hypotheses: (1) an increase in precipitation over the long and short terms tends to increase egg and clutch sizes; (2) an increase in temperature tends to increase egg and clutch sizes in the long term and tends to decrease egg size and increase clutch sizes in the short term; (3) an increase in precipitation seasonality tends to decrease egg size but increase clutch size; (4) an increase in isothermality tends to increase egg size and decrease clutch size; (5) that harsher conditions of the year – coldest and driest months – decrease egg and clutch sizes and; (6) the long-term time window tends to affect reproductive output more than the short-term window. To achieve these goals, we built statistical models separately for clutch and egg sizes on different time windows. Our models are Kingbirds (*Tyrannus spp.),* a genus of New World flycatchers, primarily insectivorous flycatchers (Fitzpatrick 1980), single-parent incubators with high breeding site fidelity (Blancher & Robertson 1985, Murphy 1996) and distributed throughout almost all the American continent.

2.2. METHODS

Database

We gathered reproductive data from Kingbird species on visits to ornithological collections and natural history museums in South America, the USA, and Europe (Supplementary material Tabela S1). At the collections, we applied a visual inspection to confirm the main Tyrannidae characteristics for each egg set and the matching with their labels. We also checked egg sizes, colours, and mark patterns, looking for misidentifications and eggs from nest parasites within the set. All the clutches that could somehow bias clutch size and the individuality of the clutch, like nest parasitism and predation, were noted. We arranged the eggs in clutches on a black base and a ruler scale, levelled them horizontally, and took digital pictures with their respective museum labels/cards. Date, site, collector, and first taxonomic classification were crucial for resolving the outdated taxonomy diagnosed in most collections. Starting from the site and date of collection of the specimens, we were able to conduct a taxonomic validation/synonymisation, following: Sclater (1888), then Cory and Hellmayr (1927), Amadon et al. (1979), Phillips (1994), and lastly updated the species names following eBird/Clements check-list (Clements et al. 2022). To extract egg dimensions, we used the photos obtained from the collections using ImageJ software (Schneider et al. 2012). We associated the software with the EggTools package (Troscianko 2014), where we could extract egg volume (mm^3), treated in this study as egg size, based on the primary dimensions of the egg (maximum length and width).

We took the collection site of the clutch to obtain the geocode through the *ggmap* package, established by the centroid point from the place by Google Maps service (Kahle & Wickham 2013). So, we set a spatial error of ±25km for those clutches that did not have a precise collection site. Therefore, clutches that did not report the site but came from islands or provinces were smaller than the error we included in the data set. This spatial resolution allowed us to extract weather conditions at the time and locality of egg-laying using the coordinates.

Climate variables

The interannual climate variations, characterised here by climatic anomalies, are the deviation of weather conditions and laying dates from the historical climate average. We extracted this variation through the difference between each weather record – time series (TS) – regarding the laying date and the historical value for the same variable – long-term mean (LTM) – defined by the average of the variables for the period from 1970 and 2000. We gathered the long-term means from WorldClim Bioclimatic Database (Fick & Hijmans 2017) and used the time series from the Centre for Environmental Data Analyses (CEDA) (Harris et al. 2020). We obtained temperature and precipitation time series for 12 months from CEDA, starting from the laying month and the 11 previous months of each clutch (Figure 2.1). Then, two time windows were defined – A long-term window (annual anomalies) which variables were: minimum temperature of the coldest month (Anom.Tmin), the maximum temperature of the warmest month (Anom.Tmax), annual isothermality (Anom.Tiso), precipitation of the driest month (Anom.Pmin), precipitation of the wettest month (Anom.Pmax), and the annual precipitation seasonality (Anom.Pseas); And a short-term window (the laying month and the previous month) which variables were: maximum and minimum temperatures (Anom.Tmx.m; Anom.Tmxm1; Anom.Tmn.m; Anom.Tmnm1) and the accumulated rainfall for these months (Anom.Pre.m; Anom.Prm1). – We independently took the LTM attributed for the short-time window and calculated the time series average for the specific month between 1970 and 2000. All minimum and maximum temperature metrics were defined in degrees celsius (°C), while minimum and maximum precipitation metrics were in cubic millimetres (mm^3). The minimum and maximum monthly temperature values reflect the daily average of these parameters, while precipitation reflects the accumulated values for the respective months. The index defined for precipitation seasonality is expressed as a percentage (%), a ratio of the monthly and annual precipitation indices, which can be read as a coefficient of variation. Finally, isothermality, also expressed as a percentage (%), quantifies the oscillation among minimum and maximum monthly and annual temperatures of the year under analysis (O'Donnell and Ignizio 2012). To avoid multicollinearity among the explanatory variables, we estimated the pairwise Pearson’s correlation coefficients (Supplementary material Figura S4), and we judged the high correlations ($|r| > 0.7$) for each of the combinations individually. In this case, we included only one of the most relevant variables in the model.

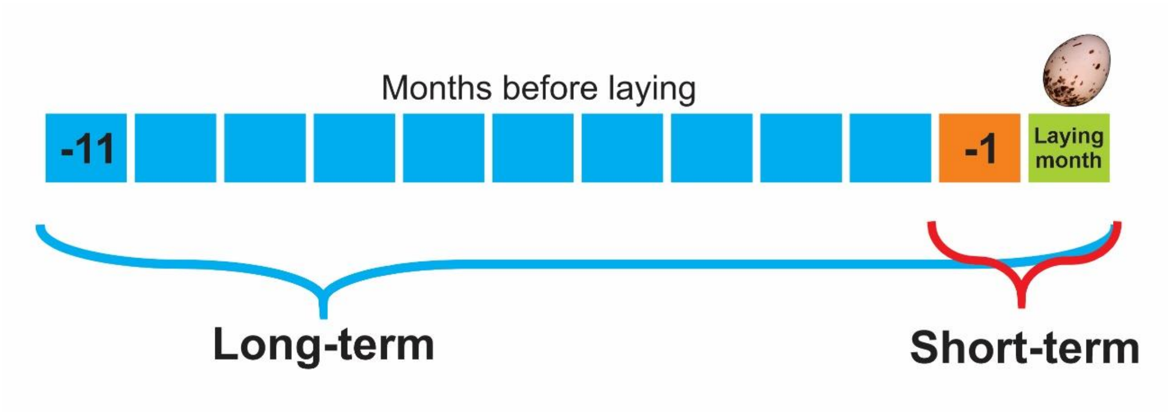

Figure 2.1 - Weather windows assessed in the effects on clutch and egg size of kingbirds: (a) long-term window (minimum temperature of the coldest month (Anom.Tmin); maximum temperature of the warmest month (Anom.Tmax); precipitation of the driest month (Anom.Pmin); precipitation of the wettest month (Anom.Pmax); annual isotermality (Anom.Tiso); annual precipitation seasonality (Anom.Pseas)); and (b) short-term window (maximum temperature of previous month Anom.Tmxm1; minimum temperature of previous month (Anom.Tmnm1); precipitation of previous month (Anom.Prm1); maximum temperature of laying month (Anom.Tmx.m); minimum temperature of laying month (Anom.Tmn.m); precipitation of laying month (Anom.Pre.m))

Statistics

We first checked the variation of the breeding dataset spatially, temporally, and by taxonomy using linear models. Thus, we considered grouping and tendencies as random variables to remove effects outside this work's scope and improve data independence. So, as a random variable, we identified and set the climate polygon based on the Köppen-Geiger climate classification (KG) (Kottek et al. 2006) as a population parameter and controlled the spatial variation effect (intercept). Additionally, since we considered that it is not justified to establish a complex nested phylogenic structure, we included "*Species*" as a random effect (intercept) and the possibility of a temporal trend through the interaction "*Species*Year*" (slope). We also considered the possibility of intraclutch pseudoreplication in the egg size analyses. We solved this issue by identifying the eggs belonging to the same female with the "clutch ID". We also included the interaction between "Species*Clutch size" after verifying that the relationship between the eggs and clutch size varies among the *Tyrannus* species (slope) (Christians 2002). Neither the migration status set for each subspecies nor mean body mass nor the interaction of these variables (Migration status*Mean species body mass) significantly affected the distribution of clutch and egg sizes of the *Tyrannus* species.

After checking data distribution, we set to evaluate the relationship between breeding traits and climate anomalies through Linear Mixed Models (LMMs). We performed the analyses in four steps. First, we assessed the long-term effects on egg size and clutch size. Then, in the third step, we used the short-time variables to evaluate the effects of the conditions of the laying month and the previous month on egg size and, ultimately, in the fourth step, on clutch sizes. We constructed each model by combining fixed variables, determined by the climatic anomalies and egg size (mm^3) and clutch size as dependent variables (Table 2.1). We fitted both models using the Akaike information criteria (AIC) for backward deletion, adjusting the model excluding variables to obtain the optimal fixed structure by maximum likelihood (Zuur et al. 2009). All the continuous variables were standardised to mean zero and standard deviation equal to one, and the significance threshold was set at $\alpha = 0.05$ for all models.

Table 2.1 – Variables used to build the global model of the effect of climate anomalies on Kingbird egg and clutch size

Response variable	Fixed structure	Random structure
Egg size (long-term)	Anom.Pmax + Anom.Pmin + Anom.Pseas + Anom.Tiso + Anom.Tmax + Anom.Tmin	• Species • Latitudinal syndrome (by species) • Climate by KG • Time effect (by species) • Clutch size trade-off (by species) • Female ID
Egg size (short-term)	Anom.Tmx.m + Anom.Tmn.m + Anom.Tmxm1 + Anom.Tmnm1 + Anom.Pre.m + Anom.Prem1	
Clutch size (long-term)	Anom.Pmax + Anom.Pmin + Anom.Pseas + Anom.Tiso + Anom.Tmax + Anom.Tmin	• Species • Latitudinal syndrome (by species) • Climate by KG • Time effect (by species)
Clutch size (short-term)	Anom.Tmx.m + Anom.Tmn.m + Anom.Tmxm1 + Anom.Tmnm1 + Anom.Pre.m + Anom.Prem1	

Additionally, we checked the residuals for overdispersion, and no overdispersion was detected. All these steps were applied using the software R (R Core Team, 2022), where we used the "*lme4*" package (Bates et al., 2015) to analyse the LMM. We associated it with the "*lmerTest*" package (Kuznetsova et al. 2017) to calculate *p* values for each model output. To identify how much the final model of each time window contributed to the variation in reproductive traits, we calculated marginal R^2, where we obtained the variance explained by the fixed effects, and the conditional R^2, which gave us the variance of the fixed and random effects (Nakagawa & Schielzeth 2013).

2.3. RESULTS

Dataset

We gathered a dataset of 2931 clutches and 9529 eggs among the 13 Kingbird species. Of this set, 1657 clutches were photographed at the egg collections, totalling 5644 photographed eggs. After filtering by inconsistency in the taxonomy, clutch sizes, geographic distribution, and overlaps with climate time series, we reached a set of 1156 clutches that included photographs of 4097 eggs (Supporting information Table S2). Then, because of the discrepancy in species data, we chose to proceed with the analyses with only eight species. In the end, therefore, we analysed 1145 clutches and 4061 eggs covering almost the entire genus in terms of geographical distribution (Supporting information Figure S1), which we consider robust to evaluate the effects of weather parameters in the breeding traits of Kingbirds.

The dataset included breeding events over 116 years (1901-2016) at sites with monthly rainfall indexes ranging from total drought in the driest month of the year (0 mm^3) up to 784.3 mm^3 in the year's wettest month. These indexes resulted in rainfall anomalies of -55 to 94.4 mm^3 in the driest month and -382.1 to 293.2 mm^3 in the year's wettest month. Concerning the laying month, 32 clutches were laid in a month with a minimal rainfall index (*e.g.,* San Diego, California, USA, 1950; 0 mm^3). On the other hand, three clutches were laid in months with rainfall indexes higher than 500 mm^3. The laying month's highest rainfall index (562.1 mm^3) was registered for a *T. melancholichus* at Oaxaca, Mexico, in 1961. Three hundred and ten clutches were at sites with precipitation seasonality higher than 100%. This index varied between 17.43 and 213.87% and presented anomalies between -21.77 and 148.56%.

Extreme temperatures varied between -34.4 °C (Manitoba, Canada, 1907) and 42.5 °C (North Dakota, United States, 1931). Temperature anomalies for the coldest month varied between -6.6 and 11.6 °C, and for the warmest month of the year, between -9.9 to 10 °C. The weather in the laying months presented minimal temperatures ranging between 0.5 and 24.5 °C and warmest temperatures between 12.1 and 38.8 °C. These values resulted in anomalies of the coldest temperatures between -3.6 and 3.0 °C and the warmest temperatures between -4.9 and 5.2 °C. The registered isothermality contrasted

21.06 for the highest variation in the temperature up to 83.72 for the most increased stability in the annual temperatures.

Long-term window

The top model for egg size in the long-term window contained four variables, including *Anom.Pmin* ($\beta = 0.046 \pm 0.023$; Figure 2.2B), *Anom.Pseas* ($\beta = -0.052 \pm 0.025$; Figure 2.2A), *Anom.Pmax* ($\beta = -0.009 \pm 0.021$; Figure 2.2C) and *Anom.Tmax* ($\beta = 0.016 \pm 0.020$; Figure 2.2D), in which only the first two variables had significant coefficients. These model coefficients (Table 2.2) indicate that kingbirds' egg sizes increase with more precipitation in the driest month and decrease in years with more seasonal rainfall, respectively. This model presented a conditional $R^2 = 0.920$ and marginal $R^2 = 0.002$.

Table 2.2 - Linear mixed models, adjusted by the backward selection, for egg and clutch sizes for climate anomalies in the long-term window. Significant effects are in bold. The marginal R² value represents the variance explained by fixed effects, and the entire model explains the conditional R².

	Estimate	SE	t value	P value
Egg size				
Marginal *R²* = 0.002		Conditional *R²* = 0.920		
Intercept	-0.304	0.267	-1.137	0.29
Anom.Pmin	**0.046**	**0.023**	**1.963**	**< 0.05**
Anom.Pseas	**-0.052**	**0.025**	**-2.119**	**< 0.05**
Anom.Pmax	-0.009	0.021	-0.420	0.67
Anom.Tmax	0.016	0.020	0.837	0.40
Clutch size				
Marginal *R²* = 0.001		Conditional *R²* = 0.988		
Intercept	-0.130	0.316	-0.413	0.70
Anom.Pmax	**-0.067**	**0.026**	**-2.583**	**< 0.05**
Anom.Pseas	**-0.064**	**0.030**	**-2.160**	**< 0.05**
Anom.Tmin	**-0.056**	**0.024**	**-2.288**	**< 0.05**
Anom.Tiso	**0.225**	**0.041**	**5.438**	**< 0.05**

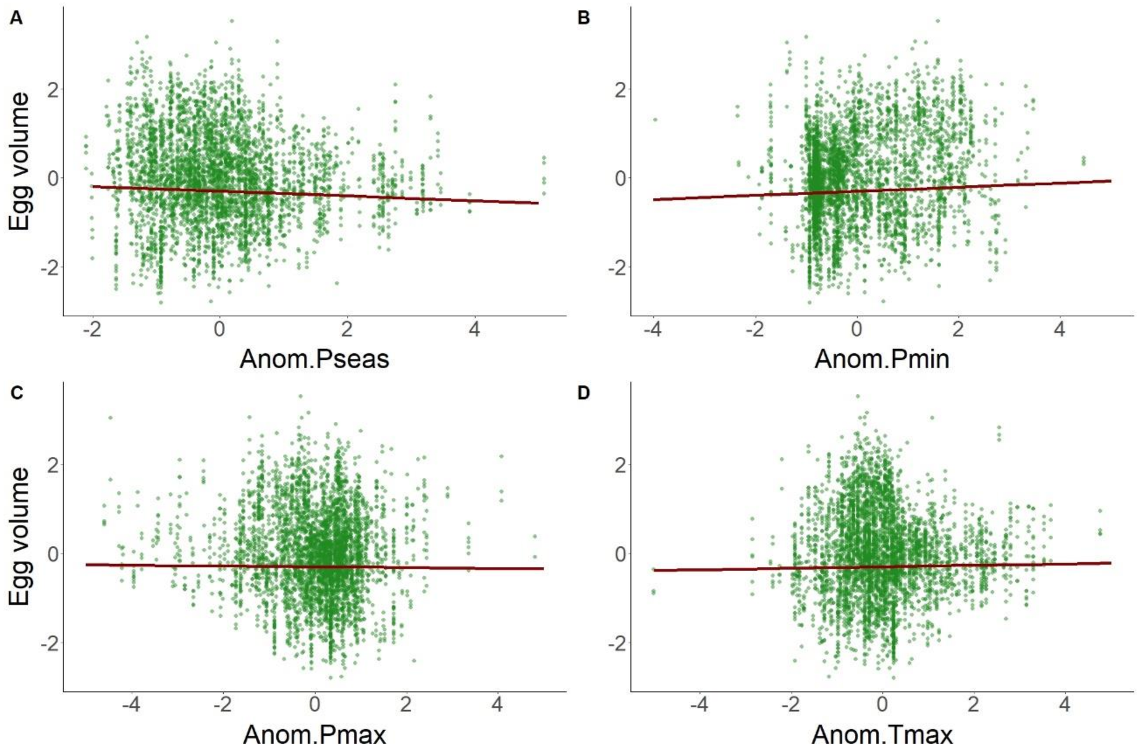

Figure 2.2 - Relationships between egg size of Kingbird species and long-term window weather conditions by Linear Mixed Models (LMM). The backward selection resulted in the model with the variables (anomalies): (A) precipitation seasonality (Anom.Pseas), (B) minimum precipitation of the driest month (Anom.Pmin), (C) maximum precipitation of the wettest month (Anom.Pmax), and (D) maximum temperature of the warmest month (Anom.Tmax).

The best-adjusted model for Kingbirds clutch size at the long-term window comprised four variables, including *Anom.Pmax* (β = -0.067 ± 0.026; Figure 2.3B), *Anom.Pseas* (β = -0.064 ± 0.030; Figure 2.3A), *Anom.Tiso* (β = 0.225 ± 0.041; Figure 3C) and *Anom.Tmin* (β = -0.056 ± 0.024; Figure 2.3D), in which all the variables had significant coefficients and showed a marginal $R^2 = 0.001$ and a conditional $R^2 = 0.988$. This model indicates that Kingbirds tended to decrease clutch sizes in years with more precipitation in the wettest months, in years with more seasonal rainfall and lower temperatures in the coldest month and increase clutch sizes in years with smaller temperature variation, respectively (Table 2.2).

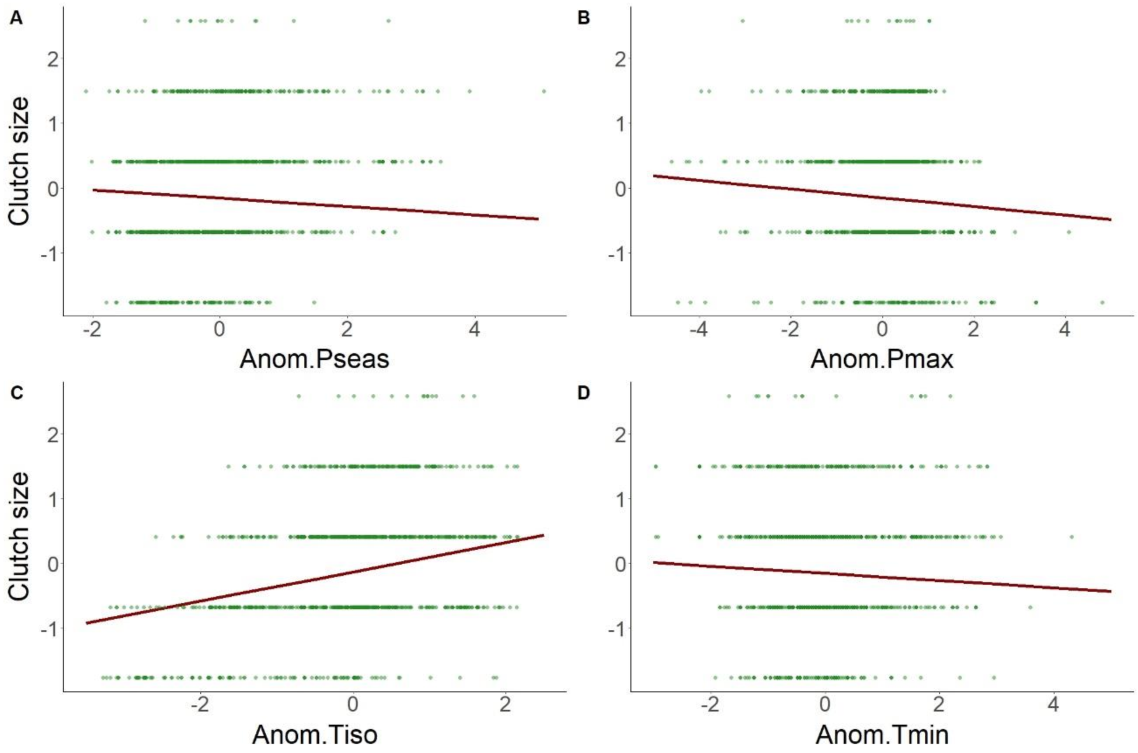

Figure 2.3 - Relationships between the clutch size of Kingbird species and long-term window weather conditions by Linear Mixed Models (LMM). The backward selection resulted in the model with the variables (anomalies): (A) precipitation seasonality (Anom.Pseas), (B) maximum precipitation of the wettest month (Anom.Pmin), (C) isothermality (Anom.Tiso), and (D) minimum temperature of the coldest month (Anom.Tmin).

Short-term window

Each top model for egg size and clutch size in the short-term window contained only one temperature variable. The top model for egg size included the *Anom.Tmxm1* ($\beta = -0.033 \pm 0.017$; Figure 2.4) means a tendency for smaller eggs when maximum temperatures were above the historical average in the month preceding laying. The short-term model for egg size presented a marginal $R^2 = 0.0008$ and conditional $R^2 = 0.916$. For clutch size, the variable that composed the top model was *Anom.Tmnm1* ($\beta = 0.050 \pm 0.023$; Figure 2.5), indicating increased clutch size when minimum temperatures were higher in the month before laying. The short-term model showed a marginal $R^2 = 0.002$ for clutch size and conditional $R^2 = 0.481$. Both short-term models had significant coefficients (Table 2.2).

Table 2.3 - Linear mixed models, adjusted by the backward selection, for egg and clutch sizes for climate anomalies in the short-term window. Significant effects are in bold. The marginal R^2 value represents the variance explained by fixed effects, and the entire model explains the conditional R^2.

	Estimate	SE	t value	p-value
Egg size				
Marginal $R^2 = 0.0008$		Conditional $R^2 = 0.916$		
Intercept	-0.305	0.297	-1.029	0.34
Anom.Tmxm1	**-0.033**	**0.017**	**-1.970**	**< 0.05**
Clutch size				
Marginal $R^2 = 0.002$		Conditional $R^2 = 0.481$		
Intercept			0.518	0.62
Anom.Tmnm1			**2.195**	**< 0.05**

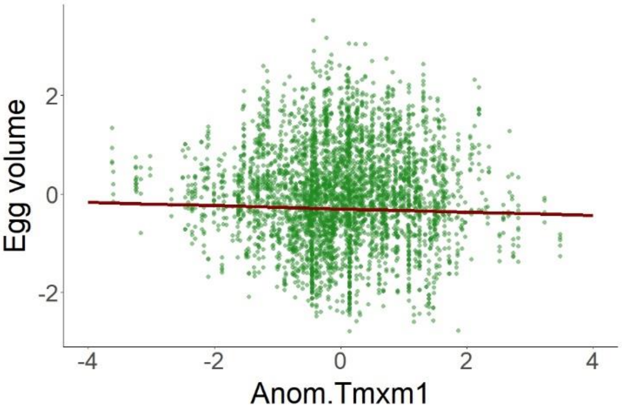

Figure 2.4 - Relationships between egg size of Kingbird species and short-term window weather conditions by Linear Mixed Models (LMM). The backward selection resulted in the model with the variable (anomalies): maximum temperature of the month before laying (Anom.Tmxm1).

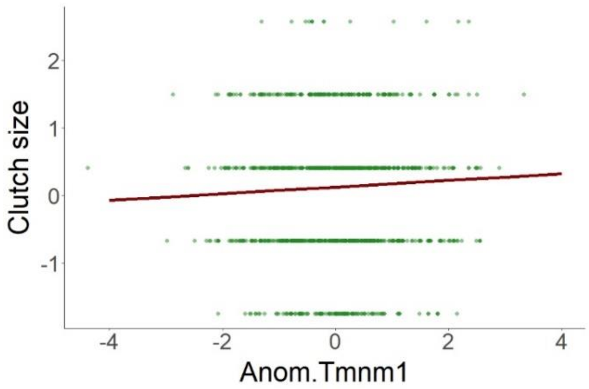

Figure 2.5 - Relationships between the clutch size of Kingbird species and short-term window weather conditions by Linear Mixed Models (LMM). The backward selection resulted in the model with the variable (anomalies): minimum temperature of the month before laying (Anom.Tmnm1).

2.4. DISCUSSION

Based on a dataset of 116 years for the whole of America's distribution, we associated weather variables for the year and months preceding the breeding event and two breeding traits of eight kingbird species. We simultaneously analysed whether and how weather conditions influence (a) egg size in short- and long terms; and (b) clutch size in short- and long terms. Our results show that Kingbird egg and clutch sizes are influenced by the interannual climate variation at the breeding site, regardless of whether conditions occur before or during the breeding season. Precipitation and temperature year parameters interfered with clutch and egg size reproductive output.

Our analyses showed that over the year (eleven months before the month of the laying event), temperature and precipitation conditions potentially change the clutch size of Kingbirds, while only annual rainfall affected egg size. The long-term time window best explained the variation in breeding traits in kingbirds, corroborating our hypothesis. The long-term time window tends to be more relevant for several species (Cady et al. 2019). Effects on birds can be correlated with breeding site conditions of the last year or previous years before laying, even when away from the site (Selonen et al. 2021) (Norris & Taylor 2006). This result shows the greater importance of environmental conditions during the entire seasonal cycle than requirements only during breeding. *Tyrannus's* needs during the breeding season reflected that annual pre-breeding weather was important for egg and clutch size. Larger egg size occurred when the year preceding laying had lower precipitation seasonality, which can also be interpreted as the year with less concentrated and more spread rainfall. This condition agrees with the fact that *Tyrannus* also has larger eggs in years with the rainiest drier months. Clutch size also tends to increase in more stable years, with less precipitation seasonality and more isothermality. In addition, clutch size tends to be larger in years with less rainfall in the wettest month and lower temperatures in the coldest months.

The temperature was the only variable affecting the egg or clutch size of Kingbirds in the short-term window. The association of temperature with reproduction is known to affect breeding phenology, where spring temperature before the breeding season usually explains the variation in laying dates (Crick et al. 1997, Ockendon et al. 2013, Schaper et al. 2012). Temperature parameters in the month before laying had effects on egg and clutch sizes. The increase in maximum temperature in the month before laying led Kingbirds to lay smaller eggs, similar to that already found by Heming & Marini (2015) for tyrant flycatchers. In contrast, the increase in the minimum temperature in the month preceding the laying led Kingbirds to lay more eggs. Goławski (2008) assumed that the clutch and egg size of red-backed shrike (*Lanius collurio*) could be affected by weather conditions up to four days before laying but found no effect, while Barkowska et al. (2003) found temperature effects on egg size variation in tree sparrow (*Passer montanus*) eggs from seven days before the first egg until the third egg of the clutch was laid. Precipitation had a low weight in our model in the short term, though, in some cases, it can predict growth and body mass increase and is directly related to breeding readiness and moulting (Aranzamendi et al. 2019).

Based on R^2 values, long-term conditions had a better fit in our models than short-term conditions, but the conditions during the breeding season can still be important in some aspects. Other physiological processes, such as moulting (van de Pol & Cockburn 2011), demand high energy and can be more related to long-term conditions where precipitation is crucial to increase food resources. At the same time, temperature may have a more direct, short-term influence (Gillette et al. 2021). One possible explanation is that precipitation has a more substantial ecosystem effect by influencing long-term environmental conditions through ecosystem productivity. It is, therefore, essential to understanding how weather conditions throughout the year can affect organisms, primarily through their most important food resources (Aranzamendi et al. 2019). Meanwhile, the temperature can more immediately affect the relationship between individuals and their environment, such as changes in clutch size (Järvinen & Ylimaunu 1986) and incubation behaviour (Schöll et al. 2020).

Studies focusing only on short-term windows found significant relationships between reproductive output and weather conditions, both for temperature (Nägeli et al., 2022; van de Pol & Cockburn, 2011) and precipitation (Aranzamendi et al. 2019). Although, since it is difficult to detect the short-term effects of weather on egg size (Christians 2002, Griffith et al. 2020, Nager & Van Noordwijk 1992, Thomson & Hadfield 2017), our study was able to detect these effects. Breeding traits can be expressed in different time lags (Runge & Marra 2005, van de Pol & Cockburn 2011) that become evident when approached independently and with specific resolutions. When evaluating the expression of an environmental factor in an attribute, it is essential to consider different and flexible time windows (van de Pol et al. 2016). According to Cady et al. (2019), even though drought conditions are unfavourable for the species in general, the western kingbird (*T. verticalis*) responded most strongly to drought at a month temporal window, while scissor-tailed-flycatcher (*T. forficatus*) responded most strongly to the year-window. Here, we have chosen to approach other time windows relative to the month of laying. However, more studies on the effects of non-breeding seasons (Runge & Marra 2005), including wintering sites, for those migratory birds, will be able to clarify further this meaningful relationship (Selonen et al. 2021).

Precipitation was an important weather variable for the expression of *Tyrannus* breeding traits. Kingbirds tend to have larger eggs and clutches in years with better distribution and less seasonal rainfall. Moreover, the driest month of the year negatively affects egg size when precipitation is below historical averages, resulting in more pronounced droughts. Precipitation in non-breeding seasons can improve growth rates and increase the body mass of organisms breeding in the following reproductive season (Sauve et al. 2021). Precipitation is essential for increasing protein resources and fundamental for reproduction, even for primarily non-invertivore species (Hau 2001). Precipitation during the wettest season increases productivity, nest success, and fecundity of puaiohi (*Myadestes palmeri*) (Fantle-Lepczyk et al. 2016). As primary production following rainfall tends to influence the development of insects (Tidon 2006, Wolda 1988, 1978), we expected that the increase in precipitation, regardless of the time window, would increase egg and clutch sizes. A potential controversial point to highlight, however, is that increased rainfall in the wettest months affects clutch size negatively. Extra rain close to the reproductive event can create difficulties for the incubation of large clutches, causing the females to spend more energy reheating the eggs during foraging intervals (Gillette et al. 2021). However, precipitation was neither a relevant variable for clutch nor egg size in the short-term window, as reported for *T. tyrannus* (Murphy 1983a). Clutch size seems to be a much more complex component, varying even among species, with a significant trade-off bias with other traits when compared to egg size.

The temperature had no significant influence on egg size at the long-term window. Although, at the short-term window, the increase in the maximum temperature in the month before laying had a negative effect on the egg size, corroborating our hypothesis. Organisms tend to expend more energy when the environment is warmer (Schifferli et al. 2014) and can compromise the resources for the production of eggs. Moreover, despite promoting productivity and insect availability (Grüebler et al. 2008), a warming environment can leave parents, nestlings, and eggs vulnerable to dehydration, mainly in water-limited environments (Sauve et al. 2021, Whitfield et al. 2015). On the other hand, low temperatures also increase energy expenditure since they require higher incubation attendance to heat and re-warm the eggs and reduce food supplies. Smaller eggs could occur in colder years because the cold weather subjects females to less productive environments, which tend to decrease their body mass (Järvinen & Ylimaunu 1986). Temperatures beyond the optimum, whether higher or lower, can lead to higher energy expenditure and create challenges for the offspring's development. Laying larger eggs and paying more attention to the offspring should compensate for the lower resource availability in cold environments (Gebhardt-Henrich & Richner 1998). Clutches with larger eggs can be essential in incubation, whose heat potential promotes slower cooling and can decrease the energy expenditure in incubation (Gillette et al. 2021).

As for the short-term time window, temperature positively affected the clutch size of Kingbirds, which increased with a higher minimum temperature of the month before laying, corroborating our hypothesis. Higher temperatures close to laying are also favourable for the clutch size of the Red-cockaded Woodpecker (*Dryobates borealis*) (Fullerton et al. 2021). For the migratory Pied Flycatcher (*Ficedula hypoleuca*), the temperature during wintering positively affected reproductive output, having an even stronger effect on fledglings' survival when coupled with precipitation during the breeding season (Selonen et al. 2021). Even though precipitation is an essential factor driving the increase of invertebrates, once rainfall is unpredictable, the rise of temperature can predict arthropod supply (Ockendon et al. 2013, Tökölyi et al. 2012). Furthermore, the low resources supply associated with the low temperatures decreases nestlings' survival (Blancher & Robertson 1985, Nägeli et al. 2022). However, warmer temperatures resulted in slower growth and smaller nestlings for Eastern Kingbird (*T. tyrannus*) (Murphy 1985, Sauve et al. 2021). In addition, for Kingbirds, the uniparental incubator behaviour represents an extra energy cost for females compared to biparental incubators (Schöll et al. 2020). Besides being a physiological response, laying smaller clutches in adverse conditions can be an adaptation for a better investment of resources, ensuring the survival of the own parents. However, Martin & Mouton (2020) consider it impossible to assert whether the variation in investment in reproduction is a life history strategy or a physiological response.

We found that Kingbirds' clutches and eggs tend to be larger in years with more stable weather conditions. Precipitation seasonality negatively affected breeding traits in egg and clutch sizes. In addition, temperature variation also affected clutch size, which tended to be larger in years with higher isothermal indices. Although environmental stability is expected to be inversely proportional to the clutch size of Passeriformes (Ashmole 1963, Cody 1966), there is evidence for the opposite effect in some species (e.g., Young, 1994, Winkler et al., 2002). But our findings still support the importance of resource seasonality overruling the short-time conditions of the breeding season (Jetz et al. 2008). Despite the suggestion that a minimum abundance of food resources for insectivores may be enough for reproduction (Aranzamendi et al., 2019), it appears to limit reproductive output and increase variation in egg and clutch sizes of Kingbirds. Better-nourished females will have a larger relative mass and lay larger eggs, resulting in larger nestlings (Christians 2002, Järvinen & Ylimaunu 1986), which have higher quality and fitness (Krist 2011).

Less extreme weather conditions in the year before breeding have contradictory effects on the breeding traits. For egg size, less extreme drought in the driest month of the year increased egg size. Reducing energy expenditure in direct response to precipitation levels instead of interrupting reproduction can buffer the effects of droughts (Martin & Mouton 2020). Kingbirds' clutch size, in turn, tends to decrease in years with higher minimum temperatures in the coldest months. Somehow, colder winters can guarantee better conditions for the populations in the following months. From the Ashmole hypothesis perspective (Ashmole 1963, Ricklefs 1980), harsh winters act as population control, guaranteeing greater per capita resources during the reproductive season.

A large part of our data set comprises species with some migratory behaviour. We assert that for the population dynamics of migrants, it is essential to consider the weather in regions where individuals are currently inhabiting (Selonen et al. 2021). Conditions faced by migratory species during breeding, migration, and overwintering periods are essential to understanding the dynamics of these populations (Runge & Marra 2005). It is important to study winter conditions for the wintering, breeding, and stopover sites during migration (Selonen et al., 2021) and the carry-over effects to better understand the seasonal interactions (Runge & Marra 2005). These conditions are valid even for migratory species affected by places not yet visited (Selonen et al. 2021). The breeding ground's temperature could explain more about clutch size than precipitation at the wintering ground (Ockendon et al. 2013). This correlation agrees with the results of two migratory species in our dataset (*T. savana* and *T. tyrannus*), where temperature cues these species to select their breeding grounds (MacPherson et al. 2018). However, since our pre-analyses found no effect of migratory status on *Tyrannus* reproductive output, we assumed that carry-over would not have a more significant effect.

The multi-year compilation of climate variables can be used as a predictor of the quality of the environment (Norris & Taylor 2006), with direct effects on reproductive output. Here we observed that different aspects of the same variable (e.g., maximum and minimum temperature) can affect a trait differently (Sauve et al. 2021). Climate averages are usually the most widely used predictors in studies (van de Pol et al. 2016), which can mask the effects of extreme temperature and precipitation conditions. When we consider climate anomalies, we highlight how much and how the deviation from climatic patterns can alter the investment among Kingbirds species.

The species-environment relationship may have physiological and behavioural aspects influencing life history strategies. It is essential to highlight that individual foraging behaviour and the different landscape characteristics at the nest site may confer different ways of coping with weather conditions. Kingbird species show high breeding site fidelity (Murphy 1996), which could mean that the species are adapted to the breeding site climate. Climatic condition is a complex set of factors between precipitation and temperature that, when taken together, generally proves more relevant (van de Pol & Cockburn 2011). That is why constructing a model by backward selection and not by testing independent variables was adopted here. A good example is the more pronounced effect of high temperature with higher precipitation in the reproductive output of pied flycatcher (*Ficedula hypoleuca*) (Selonen et al. 2021). Working by associating data from natural history collections and climate databases may allow us to explore different scenarios on the date of the reproductive event. Still, this data may present information gaps for groups with migratory behaviours due to the lack of knowledge of their place of origin. Without this information, one solution is to create climate averages for their region of population origin, but this requires a broad knowledge of each population that is unavailable.

It is essential to know how climate affects the reproductive patterns of many taxa (Hau 2001). Even when the weather does not indicate changes in the reproductive output of birds, it may be affecting the availability of resources for breeding (Morrissey et al. 2020). Precipitation increases the body size of female white-shouldered fairywren (*Malurus alboscapulatus*), which declines throughout the nesting period without changes in egg sizes, meaning a more significant investment in offspring by females (Boersma et al. 2022). When dealing with low rainfall rates, males, on the other hand, invest less in reproduction in favour of moulting (Boersma et al. 2022). The heating of the experimental nests caused tree swallows to increase their body mass and time in the nest since the females in the heated treatment had lower energy expenditure (Ardia et al. 2009). When analysing other oviparous, with the increasing annual rainfall, the striped plateau lizard (*Sceloporus virgatus*) increased body and clutch size (Abell, 1999), while the clutch size of common five-lined skinks (*Plestiodon fasciatus*) was positively associated with the mean annual temperature and with mean annual precipitation (Morrissey et al. 2020). Keeping clutch size within the average and ensuring the offspring's survival even under adverse conditions may depend on the strategy of the species (Martin & Mouton 2020). Instead, egg size is correlated with offspring quality, faster growth, decreasing the vulnerability of the young, and increasing the survival of chicks (Krist 2011). Since larger eggs increase the fitness of the chicks, this will contribute directly to population maintenance (Järvinen 1994).

Studies involving weather have become frequent due to the imminent impacts related to climate change. To know how climate change will affect species, it is essential first to understand the best environmental predictors associated with physiological, behavioural, life-history, demographic, population, species, and community responses (van de Pol et al. 2016). Future population projections in the face of climate change need an understanding of the current vulnerability of species under current conditions (Martin & Mouton 2020). The speed of climate change may not offer enough time for species to adjust to new conditions in the region (Järvinen 1994, Trautmann 2018). As soon as the breeding site does not offer the best conditions due to biotic interactions, extreme weather, and food availability, the population may be limited to occupying a few local patches (Boucher-Lalonde et al. 2014). Identifying the climatic variables and the time windows allow us to better project future climatic conditions and their impact on the traits of these species that will face new environmental conditions. Our results in this work add an essential layer of understanding about species' relationship with weather conditions, which will potentially be impacted by climate change. Once year-specific weather conditions can explain variations in egg and clutch size (Järvinen & Ylimaunu 1986), the interaction of species with the weather could mean how difficult it will be to cope with climate change (Sauve et al. 2021). Even species that inhabit warmer and more arid regions will be negatively impacted by the average temperature increase (Riddell et al. 2021). Once a weather condition affects reproductive rates, it will affect population size (Selonen et al. 2021). Identifying the climatic variables and the time windows allow us to better project future climatic conditions and their impact on the traits of these species that will face new environmental conditions.

About our findings, we highlight that: (1) the final sample size, which we based on our analysis, we considered highly robust for detecting large patterns; (Bennett & Owens 2002), and (2) we were able to detect how the interannual climate variation influences the breeding traits of a bird group distributed throughout almost the entire American continent. Our results show that Kingbirds change their breeding according to the year's weather conditions. This work helps us understand how species reduce reproduction under adverse conditions (Martin & Mouton 2020), which may provide directions for future studies of other life-history traits. The reproductive effort is a complex component in life history, which must interact with the age and breeding experience of the parents (McCleery et al. 2008). It is affected by the trade-off between investment in the offspring at the expense of the parents' survival. We highlight the egg collections' relevance in providing a well-documented and widely geographically distributed database. Considering sources of primary information on morphology and geographic distribution (Marini et al. 2020, Töpfer 2018), egg collections are still little explored and can help answer a wide range of questions, from life history to effects of climate change (Xiao et al. 2017).

CAPÍTULO 3:

3. CLIMATE CHANGE MODEL-BASED SCENARIOS SHOW A DECREASE IN *TYRANNUS* EGG AND CLUTCH SIZES BY 2100

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ABSTRACT

In the face of ongoing climatic changes, many studies have reported the effects of shifts in temperature and precipitation regimes on the biological traits of birds. Despite the robust estimates of future climate scenarios, the few projections for the reproductive traits of birds are based mainly on phenological changes. We established clutch and egg sizes projections to visualize climate change effects on reproductive output in a tyrant flycatcher genus (Kingbirds, *Tyrannus* ssp). We relied on estimated parameters of statistical models (α, β), where we detected the effects of weather variables on 4,061 eggs and 1,145 clutches of Kingbirds gathered from 23 worldwide egg collections. Based on four Shared Socio-economic Pathways scenarios (SSP), ensembled from four Global Climate Models (GCMs) of Coupled Model Intercomparison Project (CMIP6), we generated 68 scenarios for each breeding trait between 2020 and 2100. Clutch (CS) and egg (ES) sizes decreased in the end in all future scenarios (*e.g.*, SSP5-8.5/2100; ES: β= -0.002, p<0.001; CS: β= -0.04, p<0.01), driven mainly by increasing temperature and seasonality parameters. The projections based on the most pessimistic model (SSP5-8.5) predict the most pronounced changes in breeding traits. Kingbirds show a close relationship between their reproductive output and the climatic conditions of their breeding grounds. It is important to highlight the imminent implications of the local climate change on species' physiology, with decreased fitness of organisms hatching from smaller eggs and potential population losses, even for widely distributed groups such as Kingbirds.

RESUMO

Diante das iminentes mudanças climáticas, muitos estudos já relataram os efeitos das mudanças nos regimes de temperatura e precipitação sobre os padrões biológicos das aves. Apesar das estimativas robustas para cenários climáticos futuros, as poucas projeções para os atributos reprodutivos das aves baseiam-se principalmente em mudanças na fenologia. Estabelecemos projeções de tamanhos de ninhadas e ovos para estimar os efeitos das mudanças climáticas sobre a reprodução de um gênero de tiranídeos a partir de parâmetros ajustados por modelos estatísticos (α, β), nos quais detectamos os efeitos de variáveis climáticas em 4.061 ovos e 1.145 ninhadas de espécies de *Tyrannus* coletados em 23 coleções de ovos. Com base em quatro cenários de Caminhos Socioeconômicos Compartilhados (*Shared Socio-Economic Pathways* - SSP), reunidos a partir de quatro Modelos Climáticos Globais (*General Circulation Model* - GCM) do Projeto de Intercomparação de Modelos Acoplados (*Coupled Model Intercomparison Project* - CMIP6), geramos 68 cenários para cada atributo reprodutivo entre os anos de 2020 e 2100. Os tamanhos da ninhada (CS) e ovos (ES) diminuíram em todos os cenários futuros (*e.g.* SSP5-8.5/2100; ES: β= -0.001, p<0.001; CS: β= -0.04, p<0.001), impulsionados principalmente pelo aumento dos parâmetros de temperatura e sazonalidade. As projeções baseadas nos modelos SSP5-8.5, o modelo mais pessimista, são onde as mudanças nos atributos reprodutivos são mais acentuadas. As espécies de *Tyrannus* mostram uma relação estreita entre seus atributos reprodutivos e as condições climáticas nos seus locais de reprodução, e aqui nossos resultados mostram um impacto significativo das mudanças climáticas em seu investimento reprodutivo. É importante destacar as implicações iminentes das mudanças climáticas locais na fisiologia das espécies, com diminuição da aptidão dos organismos que eclodem de ovos menores e possíveis perdas populacionais, mesmo para grupos amplamente distribuídos, como as espécies de *Tyrannus*.

3.1. INTRODUCTION

Climate change is one of the most worrying environmental problems of the 21st century. An average increase of up to 4.4ºC is predicted for up to 2100 in the most extreme scenario (IPCC 2021) and tends to alter the climatic dynamics of the whole Planet. Its effects are not only on average temperatures on Earth but also on changes in biogeochemical cycles (Ciais et al. 2013), ocean dynamics (Church et al. 2013) and seasonality of rainfall regimes/patterns (Feng et al. 2013, Lee et al. 2021, Vera et al. 2006). As a consequence, there are increases in extreme events such as droughts, storms and fires (Bellard et al. 2012, Chou & Lan 2012, Dore 2005, Easterling et al. 2000, Lee et al. 2021, Seneviratne et al. 2021). The impact on the biotic environment is indubitable. Since some species are less physiologically sensitive to climate change, many use physical and climatic cues to express their biological traits. In general, the climatic conditions in scenarios of future changes have the potential to affect species persistence in many ways (Lovejoy & Hannah 2019).

The influence of climate on birds has been known for decades, and the effects of changing climate dynamics on birds can already be seen (Crick 2004). Climate changes have affected birds' metabolic and behavioural patterns (Dakin et al. 2016) and have been related to direct and indirect influences on ecological interactions (Crick 2004, Hoover & Tylianakis 2012, Walther et al. 2002), reproductive parameters (e.g., breeding success) and, consequently, in population sizes (Brown et al. 1999, Crick 2004, Newton 1998a, Stevenson & Bryant 2000). Changes in the breeding phenology of some bird species have also been identified as relevant and a potential threat (Trautmann 2018). In many cases, the laying dates of birds are related to spring temperatures, which are advancing with warmer spring temperatures (Crick et al. 1997, McCleery & Perrins 1998, Potti 2009).

The expected climate change effects may generate further adverse conditions for birds. To understand the effects of how the future will unfold, it is necessary to quantify climatic sensitivity of species (van de Pol & Bailey 2019). In the case of climate change, an essential step is to know how species deal with the conditions at the time of their interaction with the environment. Temperature and precipitation are important variables for the interaction of birds with the environment and can act in different ways and time windows on biological traits (van de Pol et al. 2016). A large, comprehensive dataset at both temporal and spatial scales can show how species' life history traits correlate with environmental conditions.. In this context, one way to assess biological responses to climate change is through climate anomalies. Since species adapt to climate averages, where they express their traits, the temporal variation in these conditions can show how plastic the traits of these species are. This plasticity can show how much environmental change each species will endure as different conditions progress.

GCMs are a valuable and elaborate tools, actually updated by the sixth Assessment Report version (AR6; IPCC 2021), allowing us to project future weather conditions. With the evolution of simulations throughout the phases of the Coupled Model Intercomparison Project (CMIP), the models have become accessible to the scientific community as projections become increasingly reliable, allowing better knowledge of the climate dynamics of the past, present and future (Eyring et al. 2016, Stouffer et al. 2017). As a product of the CMIP6, the Shared Socioeconomic Pathways framework (SSP) include regional forces such as land use, air quality public policies, and non-CO_2 greenhouse gas emissions (O’Neill et al. 2014). Even though the sixth and latest phase of the CMIP is underway and has more analytical layers that make climate projections more reliable (Eyring et al. 2016), few studies have explored the new CMIP6 scenarios and their effects on birds' biological traits. In addition, climate projections have been made mainly concerning changes in species distribution in complex models supported by high-level processing algorithms (Marini et al. 2009). And so far, no study has investigated these scenarios regarding bird reproductive output. Bird clutch and egg sizes have a strong relationship with temporal and spatial climatic conditions and are expected to be strongly affected by the worsening effects of climate change.

Based on recent climate change models, this study aimed to evaluate the potential effect of future weather conditions on egg and clutch sizes of Kingbirds of the *Tyrannus* genus. Based on previous analyses, this group responds to different climates across space and weather through interannual variations in climatic conditions. Based on these results, we hypothesise that higher temperature increase scenarios and more variable climatic conditions, through seasonality index, with higher greenhouse gas emissions (SSP models), will have more prominent negative effects on clutch and egg size.

3.2. METHODS

Database

We collected breeding data of species of the *Tyrannus* genus gathered from ornithological collections and natural history museums in South America, the USA, and Europe (Supplementary material Table S1). For each egg set, we applied a series of inspections to improve the robustness of the data. We visually checked the matching with their labels/cards to search for eggs from nest parasites, checking the clutch size and date and site of collection. Then we resolved the outdated taxonomy following Tyrannidae catalogues and taxonomy checklists (Amadon et al. 1979, Clements et al. 2022, Cory & Hellmayr 1927, Phillips 1994, Sclater 1888). We extracted egg size (egg volume, mm^3) from the pictures obtained from the collections using ImageJ software (Schneider et al. 2012) associated with the EggTools package (Troscianko 2014).

Using Linear Mixed Models (LMM), we separately analysed the effects of interannual variation in weather conditions on the egg and clutch size of eight *Tyrannus* species (Capítulo 2). We used three precipitation and three temperature anomalies as fixed variables. For each category, we defined four extreme year weather variables – precipitation of the driest month (Anom.Pmin), precipitation of the wettest month (Anom.Pmax), minimum temperature of the coldest month (Anom.Tmin), and the maximum temperature of the warmest month (Anom.Tmax) – and two annual weather variable – isothermality (Anom.Tiso), and the precipitation seasonality (Anom.Pseas). Data independence was corrected using “species” as taxonomic grouping, “year” as a temporal trend, the “absolute latitude” and Köppen-Geiger geographical climates (KG) population grouping and, only for egg size analyses, the “clutch ID” as intraclutch correlation. With all the continuous variables standardised to mean zero and standard deviation equal to one, we fitted both models for backward deletion, excluding variables to achieve the best fixed structure, via the Akaike information criteria (Zuur et al. 2009). Four weather variables compound each of the fitted models (Table 3.2).

Future projections

Projections of future climate scenarios were performed in the period between the years 2020 and 2100 based on raster files in the Earth System Grid Federation (ESGF) archive (https://esgf-node.llnl.gov/projects/cmip6/) (Eyring et al. 2019). To maintain cohesion with previous analyses of the influence of climate anomalies on egg and clutch sizes of *Tyrannus* species, we established the same criteria for variable selections. Thus, we filtered the monthly time-scale and spatial projections with a 1º Longitude × 1º Latitude grid to obtain the minimum and maximum temperatures and precipitation data. Following the example of Yue et al. (2021), we only used the first realisation (r1i1p1f1) of each GCM compatible with the established scales to maintain consistency among the scenarios in the database. Four integrated SSP and RCP scenarios: SSP1-2.6 (SSP1 + RCP2.6), SSP2-4.5 (SSP2 + RCP4.5) SSP3-7.0 (SSP3 + RCP7.0) and SSP5-8.5 (SSP5 + RCP8.5), were used in this study. Of these scenarios, one represents the most optimistic climate change model, with a lower emission scenario (SSP1-2.6), two intermediate scenarios (SSP2-4.5 and SSP3-7.0), and one more pessimistic scenario, with a forecast of higher greenhouse gas emissions (SSP5-8.5). With their established settings, we extracted these scenarios from 4 GCMs (INM-CM5-0, MRI-ESM2-0, GFDL-ESM4, CAS-ESM2-0; Table 3.1).

Table 3.1 - List of the CMIP6 GCMs used in this study

Model	Institution /Country	Reference
INM-CM5-0	Institute of Numerical Mathematics (INM) / Russia	(Volodin et al. 2019)
MRI-ESM2-0	Meteorological Research Institute (MPI) / Japan	(Yukimoto et al. 2019)
GFDL-ESM4	National Oceanic and Atmospheric Administration, Geophysical Fluid Dynamics Laboratory (NOAA-GFDL) / USA	(Guo et al. 2018)
CAS-ESM2-0	Chinese Academy of Sciences (CAS) / China	(Chai 2020)

For each SSP scenario, we extracted six weather variables (Table 3.2) over 17 (every five years) different periods between 2020 and 2100. Taking the original breeding dataset used to analyse the effect of weather on the reproductive characteristics of *Tyrannus* species, we used the location and month of recording of each clutch to mirror the specific annual interval between 2020 to 2100. Temperature values, obtained in degrees Kelvin (ºK), were converted to degrees Celsius (ºC), and the precipitation values, obtained as the monthly average of kilograms per square meter per second ($kg/m^2/s$), were converted to monthly accumulated cubic millimetres (mm^3/m). We made an ensemble average of the GCMs for each variable. From this average, we calculated the climate anomalies from the mean historical climate values (LTM - long-term mean), taken between 1970 and 2000, extracted from the WorldClim Bioclimatic Database (Fick & Hijmans 2017). Finally, to determine the compatibility between the previous analyses and the projections, all anomalies' variables were standardised to mean zero and standard deviation equal to one.

For future statistical downscaling projections, the breeding traits were simulated based on the parameters of the fitted LMM (Table 3.2, *see chapter2*), reconstructing the models by checking the intercept (α-values) and the weight of each climate anomaly (β-values) for each scenario. The effects of each variable in the projected scenarios were determined individually for each egg (egg size projections) and clutch (clutch size projections) by randomising the value from a normal distribution, where the estimated values of α and β were taken as the mean, and their respective standard error (SE) values were taken as standard deviation.

Table 3.2 - Linear mixed models, adjusted by the backward selection, for egg and clutch sizes of Tyrannus species for climate anomalies. Significant effects are in bold.

	Estimate	SE	P value
Egg size			
Intercept	-0.304	0.267	0.289
Anom.Pmin	**0.046**	**0.023**	**0.049**
Anom.Pseas	**-0.052**	**0.025**	**0.034**
Anom.Pmax	-0.009	0.021	0.675
Anom.Tmax	0.016	0.020	0.40
Clutch size			
Intercept	-0.130	0.316	0.698
Anom.Pmax	**-0.067**	**0.026**	**0.009**
Anom.Pseas	**-0.064**	**0.030**	**0.031**
Anom.Tmin	**-0.056**	**0.024**	**0.000**
Anom.Tiso	**0.225**	**0.041**	**0.022**

To assess changing climate parameters and residual variation in reproductive outputs over time, we performed linear models taking each of the egg and clutch size and climate anomalies associated with each breeding trait as dependent variables while time (Year) was treated as a continuous variable, was defined as the independent variable. We judged the trends statistically significant for linear models with a $P < 0.05$.

3.3.RESULTS

Using six weather anomalies, we projected 4097 egg sizes and 1202 clutch sizes in 17 different years for four climate scenarios in an 80-year interval, totalling 68-year/SSP scenarios for each breeding trait.

Future changes in weather variables

All variables showed some significant time trend in at least one SSP scenario, except for Anom.Pmin (Figure 3.1B) (Table 3.3). The temporal effects on precipitation occurred in the other two variables, Pmax and Pseas. In all scenarios, Pmax showed a positive effect with time (Table 3.3, Figure 3.1A). However, in three of four scenarios, did the wettest month precipitation increase significantly (SSP1-2.6, $\beta= 0.13$, $p<0.05$; SSP3-7.0, $\beta=0.33$, $p<0.001$; SSP5-8.5, $\beta=0.43$, $p<0.05$). As for the seasonality of precipitation, there was a positive trend in all scenarios, but only two were significant (SSP1-2.6, $\beta=0.03$, $p<0.01$; SSP5-8.5, $\beta=0.04$, $p<0.001$).

Table 3.3 – Trends of precipitation of the wettest month (Anom.Pmax), precipitation of the driest month (Anom.Pmin), precipitation seasonality (Anom.Pseas), maximum temperature of the warmest month (Anom.Tmax), minimum temperature of the coldest month (Anom.Tmin) and isothermality (Anom.Tiso) analysed by linear models. Significant effects are classified by p-value
(* $p<0.05$; ** $p<0.01$; *** $p<0.001$)

Anomalies	SSP scenario	Intercept α	Estimates β	CI
Pmax	**1-2.6**	**-208.74**	**0.13** *	**0.02 – 0.24**
	2-4.5	-174.72	0.11	-0.00 – 0.23
	3-7.0	**-613.82** ***	**0.33** ***	**0.21 – 0.44**
	5-8.5	**-818.35** ***	**0.43** ***	**0.31 – 0.55**
Pmin	1-2.6	-16.16	-0.002	-0.03 – 0.02
	2-4.5	-25.97	0.001	-0.02 – 0.02
	3-7.0	-27.27	0.002	-0.02 – 0.02
	5-8.5	-21.77	0.001	-0.02 – 0.02
Pseas	**1-2.6**	**-24.2**	**0.03** **	**0.01 – 0.06**
	2-4.5	8.99	0.02	-0.01 – 0.04
	3-7.0	6.35	0.02	-0.01 – 0.04
	5-8.5	**-39.8**	**0.04** ***	**0.02 – 0.06**
Tmax	**1-2.6**	**-19.53** *	**0.01** *	**0.00 – 0.02**
	2-4.5	**-49.81** ***	**0.02** ***	**0.02 – 0.03**
	3-7.0	**-85.99** ***	**0.04** ***	**0.03 – 0.05**
	5-8.5	**-116.46** ***	**0.06** ***	**0.05 – 0.07**
Tmin	**1-2.6**	**-26.18** **	**0.01** *	**0.00 – 0.02**
	2-4.5	**-64.87** ***	**0.03** ***	**0.02 – 0.04**
	3-7.0	**-100.06** ***	**0.05** ***	**0.04 – 0.05**
	5-8.5	**-124.71** ***	**0.06** ***	**0.05 – 0.07**
Tiso	1-2.6	14.08 *	0.01	-0.00 – 0.01
	2-4.5	23.83 ***	0.00	-0.01 – 0.01
	3-7.0	**42.38** ***	**-0.01** **	**-0.01 – -0.00**
	5-8.5	38.23 ***	-0.01	-0.01 – 0.00

Time had the most evident effects in the temperature variables. Tmin had a positive trend reaching higher values in 2100 (Table 3.3, Figure 3.1F), and the coefficients were increasingly higher for the more drastic scenarios (SSP1-2.6, β= 0.01, p<0.05; SSP2-4.5, β= 0.03, p<0.001; SSP3-7.0, β=0.05, p<0.001; SSP5-8.5, β=0.06, p<0.001). Tmax scenarios were also positively progressive in the scenarios of higher greenhouse gas emissions (Table 3.3, Figure 3.1E). The maximum temperature of the warmest month tended to increase under all projected scenarios (SSP1-2.6, β= 0.01, p<0.05; SSP2-4.5, β= 0.02, p<0.001; SSP3-7.0, β=0.04, p<0.001; SSP5-8.5, β=0.06, p<0.001). Isothermality trends varied among the scenarios (Table 3.3, Figure 3.1D). However, only the SSP3-7.0 scenario, where isothermality tends to decrease, had a significant statistical effect (β=0.01, p<0.01).

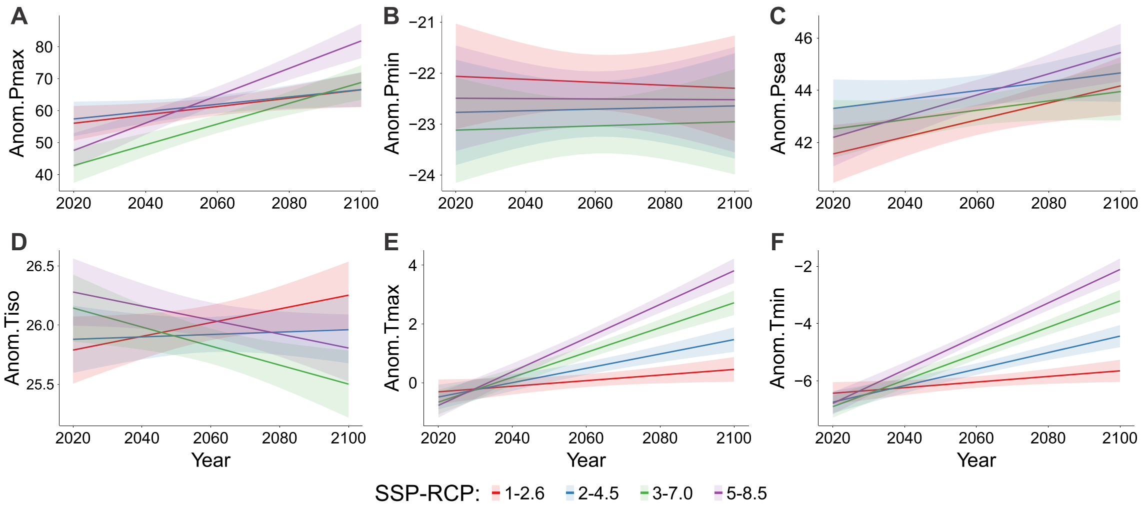


Figure 3.1 – Temporal trends for six climate anomalies with potential effects on egg and clutch sizes of Tyrannus *species in four SSP scenarios (1-2.6, red; 2-4.5, blue; 3-7.0, green; and 5-8.5, purple).*

Future changes in breeding traits

Kingbirds' breeding traits decreased in all future scenarios (Table 3.4). For clutch size, the coefficient slopes were progressively more negative from the most optimistic to the most drastic scenario (Figure 3.2B), reaching the lowest coefficient in the SSP5-8.5 scenarios (SSP1-2.6, β= 0.01, p<0.01; SSP2-4.5, β= 0.01, p<0.001; SSP3-7.0, β=0.03, p<0.001; SSP5-8.5, β=0.04, p<0.001). Kingbirds' egg size also tended to decrease in all scenarios, reaching the lowest values in the SSP5-8.5 scenario by 2100 (Figure 3.2A). However, unlike clutch size, the intermediate SSP2-4.5 scenario showed the coefficient with the slightest slope (SSP1-2.6, β= 0.002, $p<0.001$; SSP2-4.5, β= 0.0008, $p<0.05$; SSP3-7.0, β=0.0002, $p<0.001$; SSP5-8.5, β=0.001, $p<0.001$).

Table 3.4 – Temporal trends of clutch and egg size of Tyrannus analysed by linear models. Significant effects are classified by p-value (p<0.05; ** p<0.01; *** p<0.001)*

	Clutch size			Egg size		
SSP Scenario	***Intercept* α**	***Estimates* β**	***CI***	***Intercept* α**	***Estimates* β**	***CI***
1-2.6	18.35 **	-0.01 **	-0.02 – -0.00	0.48	-0.002 ***	-0.004 – -0.001
2-4.5	23.48 ***	-0.01 ***	-0.02 – -0.01	-1.42	-0.0008 *	-0.003 – -0.000
3-7.0	66.23 ***	-0.03 ***	-0.04 – -0.03	0.00	-0.0002 ***	-0.004 – -0.001
5-8.5	77.53 ***	-0.04 ***	-0.04 – -0.03	3.05 *	-0.001 ***	-0.005 – -0.002

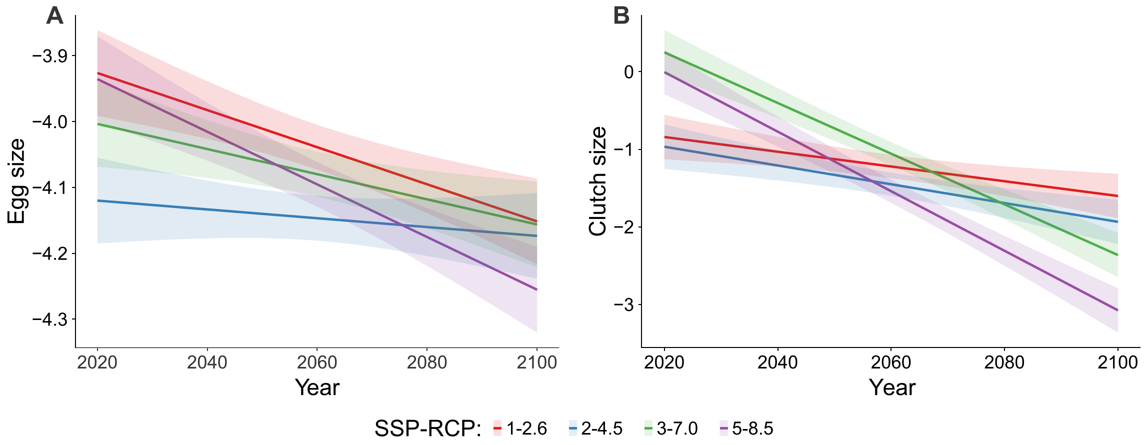


Figure 3.2 – Temporal trends for egg and clutch sizes between the years 2020 and 2100 in four SSP scenarios (1-2.6, red; 2-4.5, blue; 3-7.0, green; and 5-8.5, purple)

3.4. DISCUSSION

We observed time changes in clutch and egg sizes throughout all projected scenarios. Regardless of future climate conditions, our models show that the size of Kingbird clutches and eggs will decrease significantly and reach the lowest values by 2100.

Tyrannus clutch size decreased progressively from the mildest to the most extreme model. The statistical model used for downscaling clutch size of Kingbirds is composed of two temperature variables and two precipitation variables. *Tyrannus* tends to decrease clutch size with an increase in the minimum temperature in the year's coldest month. Progressively, as expected, these variables tend to increase by the year 2100. In addition, years with more significant temperature variability will also negatively affect clutch size. Even though only one scenario for isothermality had a statistically significant negative result, this variable has the highest coefficient among the variables for clutch size. Therefore, even a minor variation will have an increased effect on this reproductive trait. Like Tiso, the Pseas increase scenarios will decrease *Tyrannus'* clutch size. Seasonality is only one of many explanations for the changes in clutch size among regions (Jetz et al. 2008, Lundblad & Conway 2021, Stevens 1989). However, our models show the opposite, and therefore the more significant climatic variation, the smaller clutch sizes of Kingbirds will be.

Kingbirds' egg size decreased significantly throughout the years under all projected scenarios. The statistical models used for downscaling egg size comprise three precipitation variables and one temperature variable, where only Pmin and Pseas had p-significant coefficients and, therefore, more expressive β-coefficients. Kingbirds tend to decrease their eggs in warmer environments and years with warmer temperature anomalies in birds (Heming & Marini 2015, Tryjanowski et al. 2004) and other taxa, as reef fishes and amphipods (Kokita 2003, Sheader 1996). The egg size projections resemble precipitation seasonality models, but in an inversely proportional way (Figures 3.1C and 3.2A). While Kingbirds tend to lay larger eggs in more climatically stable years, what we project in the future scenarios is increased climate variability, especially with increased seasonality. Conversely, the strong effect of Pmin indices in egg size will not be apparent, as the projections showed no significant change over time for this weather variable. Overall, precipitation regimes in future scenarios will be more complex and less linear, which may be the result of variation among GCM models.

Tmax and Tmin increase progressively over the next century, even for the most optimistic scenario (Figures 3.1E and 3.1F). General warming scenarios are expected and robust and bring the challenge of species that respond directly to environmental temperature in their traits (Sauve et al. 2021, Schifferli et al. 2014, Whitfield et al. 2015). However, isothermality does not have the same behaviour, and only one scenario showed a statistically significant trend. In this scenario, isothermality tends to decrease, causing an increase in annual temperature variation, negatively affecting Kingbird’s clutch size. Some predictions include an increase in annual temperature variability in future scenarios, with different regional effects, where the most significant reduction in variability is expected in winter temperatures at mid and high latitudes (Lee et al. 2021).

The weather scenarios showed regions that should not face a continuous and progressive drought over time but large increasing volumes of concentrated rainfall during the wettest time window of the year, as demonstrated by the Pmin and Pmax time trend results. However, even with no linear trend, fluctuations can cause stochastic drought events (IPCC 2021). Drought affects bird populations by dehydration (Albright et al. 2010, Riddell et al. 2021), even in arid regions (Roberts et al. 2021). Rainfall is also an essential cue for breeding energetics demands because it increases invertivore food (Hau 2001). Hence, food limitation is a crucial factor in the variation of the surviving-fecundity trade-off (Martin 1995) and tends to explain a relevant part of the variation in egg size (Barkowska et al. 2003). These stochastic events can compromise their fitness for subsequent breeding seasons, influencing reproductive or survival rates, even if they do not have fatal effects on breeding individuals (Marra et al. 2015). The rainfall index increases directly with temperatures (Lee et al. 2021). However, the increase will be different among regions. Precipitation tends to increase in the extratropical areas (30-90º latitude) and decrease in the subtropical regions (Lee et al., 2021), including arid areas. Knowledge about how species’ will responding to drought will be essential for conservation policies (Cady et al. 2019).

Our study shows that this increase will be seasonal, in line with the positive trends in Pseas over time. Precipitation seasonality is expected to increase in all SSP scenarios up to 2100 in high latitudes and humid regions and decrease in arid (subtropical) regions (Lee et al. 2021). Moreover, although not captured in our models, cycles of the El Niño Southern Oscillation (ENSO) will cause a significant increase in the amplitude of rainfall variability over the 21st century in the four SSP scenarios (Lee et al. 2021). ENSO effects can already be seen in birds’ reproduction (Englert Duursma et al. 2018) and survival (Wolfe et al. 2015). In general, precipitation seems to be a more complex component, with temperature as one of its components of variation. Still, its importance in breeding traits further reinforces the need to understand its dynamics in future scenarios.

The breeding traits studied here will directly reflect the effects of environmental conditions on their parents (Krist, 2011), where the possibility of maintainingclutch and egg size will be compromised at the cost of physiological conditions (Christians 2002). Kingbirds tend to have high nest site fidelity, and this characteristic can be reinforced when the environment provides suitable conditions for breeding success in previous years (Blancher & Robertson 1985). Then, offspring may experience similar environmental conditions as their parents, inflating the trait's apparent heritability (Christians 2002). A search for new areas when previously established ones are of poorer quality or weather conditions are unfavourable (Cady et al. 2019) is a mechanism that can be compromised in future scenarios where there are predicted changes in suitable habitats for the species (Marini et al. 2009).

Genetically-determined reproductive characteristics will suffer less interference in more favourable environments and conditions (Sauve et al. 2021). However, species with higher survival rates have lower reproductive rates under adverse conditions (Martin & Mouton 2020), prioritising their survival. Clutch size is directly related to the number of fledglings, meaning that population density may decrease in unfavourable scenarios for large clutches (Selonen et al. 2021). Additionally, *Tyrannus* does not show a correlation between egg and clutch size, as already examined for most species (Christians 2002, Sakai 2021). Therefore an increase in egg size is not expected as a trade-off to increase chicks' survival probability. Since larger eggs give rise to higher fitness organisms (Krist 2011) and larger clutches increase reproductive rates, smaller chicks from smaller clutches (Sakai 2021), can result a relevant stress on reproduction (Delgado et al. 2021).

In summary, this study reinforces the probability of adverse effects of climate change on bird traits, a projected decrease of clutch and egg sizes. The climate scenarios presented here show adverse conditions for reproduction, mainly due to increasing temperatures and climate variability. Despite the increased complexity in the construction of projections, the models obtained in GCMs assembled and interpolated still need caution due to the complexity of climate models and can still be biased in some points (Yue et al. 2021). On the other hand, we reinforce that this work was designed using only ornithological databases and collections, building a unique, robust dataset that empirical results are unlikely to achieve. Ornithological collections can provide robust information on species' life history traits and their sensitivity to climate variables, which allows for assessing the effects of environmental changes on these traits (Marini et al. 2020, Møller & Hochachka 2019). Finding the impact of climate change only reinforces the need for urgent changes in climate change policies, either for populations or species. The inertia in these policies stresses, even more, the problems described above, with consequences for human populations and ecosystems in general (Diffenbaugh & Field 2013, Walther et al. 2002).

CONCLUSÃO GERAL

Testamos se (e como) o tamanho das ninhadas e ovos das espécies do gênero *Tyrannus* variam em função de variáveis climáticas, em dimensões espaciais e temporais. Para responder essa pergunta recorremos às coleções ornitológicas dispersas pelo mundo, uma fonte de dados ainda pouco explorada e que nos permitiu checar a integridade de cada ninhada e ovo disponível. Ao final, reunimos informações de 9.529 ovos de 2.931 ninhadas. Desse conjunto, fotografamos 1.657 ninhadas, das quais 4.750 ovos foram medidos individualmente. Identificamos e removemos, sempre que possível, as variações residuais causadas pelas diferenças entre populações, espécies e os padrões espaciais e temporais nas características reprodutivas. Bancos de dados climáticos e meteorológicos de alta qualidade nos permitiram obter informações regionais e temporais para o passado, e projeções de cenários climáticos futuros. Conseguimos assim reunir um banco de dados reprodutivo/climático singular e robusto que nos permitiu responder três de várias perguntas possíveis de se fazer com essa informação.

No primeiro capítulo analisamos os padrões geoclimáticos das características reprodutivas do gênero *Tyrannus*, com objetivo de compreender melhor a variação espacial do tamanho de ninhadas e ovos. Encontramos resultados que correspondem a padrões debatidos a décadas por ecólogos, como o aumento do tamanho das ninhadas em função da latitude. As ninhadas e ovos das espécies de *Tyrannus* aumentam em função da latitude, mas também respondem aos padrões de temperatura e precipitação característicos de altas latitudes. Então, no nosso ponto de vista, parte da variação latitudinal no tamanho das ninhadas e ovos ocorre em função do clima.

No segundo capítulo avaliamos o efeito da variação interanual das condições climáticas nas características reprodutivas, assumindo que as espécies de *Tyrannus* são adaptadas ao clima do seu local de reprodução, e a variação entre anos afetaria esses atributos. Como muitas ninhadas foram coletadas antes de 1900, e como os dados meteorológicos não estão disponíveis para o período anterior ao século 20, nosso conjunto de dados foi menor para o Capítulo 2. Ainda com um conjunto de dados robusto, composto por 1.156 ninhadas e 4.097 ovos, conseguimos observar que o tamanho das ninhadas e ovos das espécies de *Tyrannus* variam entre anos, principalmente em função das condições climáticas a longo prazo. A variação das características reprodutivas pode ocorrer em função das condições climáticas através de respostas plásticas das espécies, sem que haja efeitos mais drásticos. No entanto é preciso maior conhecimento sobre o limite fisiológico das espécies frente às variações do clima, bem como qual o limite fisiológico mínimo para que o tamanho dos ovos dê origem a filhotes viáveis. A resolução mensal para dados meteorológicos não foi uma barreira para encontrarmos relações gerais entre as condições climáticas e a variação nas características reprodutivas das espécies de *Tyrannus*, mas o aumento da resolução, com a disponibilidade de dados diários, poderá permitir uma perspectiva mais refinada sobre a relação dos organismos com o clima.

No terceiro capítulo, nos baseamos na sensibilidade à variação das condições climáticas das espécies, analisada no Capítulo 2, para avaliar os impactos das condições climáticas futuras. Em quatro cenários de mudanças climáticas (cenários SSP), as condições climáticas terão impacto negativo no tamanho de ovos e ninhadas das espécies de *Tyrannus*. Ovos maiores não só dão origem a filhotes maiores, mas também com mais chances de sobrevivência, enquanto ninhadas maiores aumentam a probabilidade de sucesso reprodutivo. Além disso, projeções têm sido feitas usando algoritmos e *machine learning*, para avaliar as mudanças na distribuição das espécies. Embora não estejam voltadas para as variações de características reprodutivas, as mudanças no habitat terão efeitos sobre a reprodução de *Tyrannus*, principalmente por se tratar de um grupo com alta fidelidade ao sítio de reprodução, características que permite transmitir padrões reprodutivos entre as gerações. As condições e as características do ambiente em que o organismo se encontra refletem em sua reprodução, e uma mudança forçada, em um intervalo muito menor do que a seleção natural atua, terá potencial de afetar negativamente a estrutura das populações.

Muito tem se discutido sobre o potencial efeito das mudanças climáticas sobre as espécies e ecossistemas, além da economia, saúde e bem-estar da população humana. No entanto, muitas discussões deveriam dar espaço a políticas concretas para um caminho de retorno. É esperado que mudanças na evolução das mudanças climáticas sejam sentidas com um atraso de no mínimo 20 anos após a redução das emissões de gases estufa. Essa contagem regressiva, no entanto, só começará a partir de ações efetivas.

De forma geral *Tyrannus* tendem a responder a variáveis de temperatura e precipitação. Quanto aos índices de temperatura, é importante ressaltar que *Tyrannus* coloca ovos maiores em climas e sub-climas de invernos frios, regiões e locais com temperaturas mais baixas e em anos que as temperaturas próximas à reprodução são menores. Nesta perspectiva, mesmo sem abordar as demais variáveis, é factível esperar que o aumento das temperaturas causadas pelas mudanças climáticas afetaria negativamente o tamanho dos ovos a curto e longo prazo.

Cada uma das variáveis que afetam as características reprodutivas aqui encontradas, compõe a reposta para a principal pergunta desse trabalho final de doutorado. Ao final deste trabalho, portanto, eu concluo que os resultados obtidos nesses três capítulos corroboram minha tese de que "*o tamanho dos ovos e ninhadas das espécies do gênero* Tyrannus *variam em função das condições climáticas no espaço e tempo*".

REFERÊNCIAS BIBLIOGRÁFICAS

Abell, A. J. (1999). Variation in Clutch Size and Offspring Size Relative to Environmental Conditions in the Lizard *Sceloporus virgatus*. Journal of Herpetology 33:173–180.

Aguiar, L. M. S., E. Bernard, V. Ribeiro, R. B. Machado, and G. Jones (2016). Should I stay or should I go? Climate change effects on the future of Neotropical savannah bats. Global Ecology and Conservation 5:22–33.

Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, C. H. Flather, P. D. Culbert, B. D. Wardlow, and V. C. Radeloff (2010). Effects of drought on avian community structure. Global Change Biology 16:2158–2170.

Amadon, D., E. Mayr, D. W. Snow, M. A. Traylor Jr., and J. T. Zimmer (1979). Volume 8. In Check-list of birds of the world (Jr. Traylor, Melvin A., Editor). Museum of Comparative Zoology, Cambridge.

Aranzamendi, N. H., M. L. Hall, S. A. Kingma, M. van de Pol, and A. Peters (2019). Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. Journal of Animal Ecology 88:1799–1811.

Ardia, D. R., J. H. Pérez, E. K. Chad, M. A. Voss, and E. D. Clotfelter (2009). Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behaviour. Journal of Animal Ecology 78:4–13.

Ashmole, N. P. (1963). The regulation of numbers of oceanic tropical birds. Ibis 103:458–473.

Barkowska, M., J. Pinowski, and B. Pinowska (2003). The Effect of Trends in Ambient Temperature on Egg Volume in the Tree Sparrow Passer montanus . Acta Ornithologica 38:5–13.

Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp (2012). Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

Bennett, P. M., and I. P. F. Owens (2002). Evolutionary ecology of birds: life histories, mating systems and extinction. 1st edition. Oxford University Press, Oxford.

Bêty, J., G. Gauthier, and J. F. Giroux (2003). Body condition, migration, and timing of reproduction in snow geese: a test of condition-dependent model of optimal clutch size. The American Naturalist 162:110–121.

Bevacqua, E., C. de Michele, C. Manning, A. Couasnon, A. F. S. Ribeiro, A. M. Ramos, E. Vignotto, A. Bastos, S. Blesić, F. Durante, J. Hillier, et al. (2021). Guidelines for Studying Diverse Types of Compound Weather and Climate Events. Earth's Future 9:1–23.

Birchard, G. F., and D. C. Deeming (2015). Egg allometry: influences of phylogeny and the altricial- precocial continuum. In Nests, Eggs, and Incubation - New Ideas About Avian Reproduction (D. C. Deeming and S. J. Reynolds, Editors). 1st edition. Oxford University Press, Oxford, pp. 97–112.

BirdLife International (2020). BirdLife data zone. [Online.] Available at http://www.birdlife.org/datazone/home.

Birkhead, T. R. (2016). The most perfect thing: Inside (and outside) a bird's egg. 1st edition. Bloomsbury Publishing, London.

Blackburn, T. M. (1991). An interspecific relationship between egg size and clutch size in birds. The Auk 108:973–977.

Blackburn, T. M., K. J. Gaston, N. Loder, and N. Centre (1999). Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and Distributions 5:165–174.

Blancher, P. J., and R. J. Robertson (1985). Site Consistency in Kingbird Breeding Performance: Implications for Site Fidelity. Journal of Animal Ecology 54:1017–1027.

Blancher, P. J., and R. J. Robertson (1987). Effect of Food Supply on the Breeding Biology of Western Kingbirds. Ecology 68:723–732.

Boersma, J., E. D. Enbody, J. Karubian, H. E. Watts, and H. Schwabl (2022). Drought disrupts year-round breeding readiness in a tropical songbird. Avian Conservation and Ecology 17:art44.

Bonamour, S., L.-M. Chevin, A. Charmantier, and C. Teplitsky (2019). Phenotypic plasticity in response to climate change: the importance of cue variation. Philosophical Transactions of the Royal Society B: Biological Sciences 374:20180178.

Both, C., A. V. Artemyev, B. Blaauw, R. J. Cowie, A. J. Dekhuijzen, T. Eeva, A. Enemar, L. Gustafsson, E. V. Ivankina, A. Järvinen, N. B. Metcalfe, et al. (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society B: Biological Sciences 271:1657–1662.

Both, C., and M. E. Visser (2005). The effect of climate change on the correlation between avian life-history traits. Global Change Biology 11:1606–1613.

Boucher-Lalonde, V., A. Morin, and D. J. Currie (2014). A consistent occupancy-climate relationship across birds and mammals of the Americas. Oikos 123:1029–1036.

Boyce, M. S. (1979). Seasonality and patterns of natural selection for life histories. The American Naturalist 114:569–583.

Brown, J. H., and M. V. Lomolino (1998). Biogeography. 2nd edition. Sinauer Associates, Sunderland.

Brown, J. L., S. H. Li, and N. Bhagabati (1999). Long-term trend toward earlier breeding in an American bird: a response to global warming? Proceedings of the National Academy of Sciences of the United States of America 96:5565–5569.

Cady, S. M., T. J. O’Connell, S. R. Loss, N. E. Jaffe, and C. A. Davis (2019). Species-specific and temporal scale-dependent responses of birds to drought. Global Change Biology 25:2691–2702.

Carey, C. (1996). Female reproductive energetics. In Avian energetics and nutritional ecology (C. Carey, Editor). Springer, Boston, pp. 324–374.

Chai, Z. (2020). CAS CAS-ESM2.0 model output prepared for CMIP6 CMIP. [Online.] Available at https://doi.org/10.22033/ESGF/CMIP6.1944.

Chen, D., M. Rojas, B. H. Samset, K. Cobb, A. D. Niang, P. Edwards, S. Emori, S. H. Faria, E. Hawkins, P. Hope, P. Huybrechts, et al. (2021). Framing, Context, and Methods. In Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, et al., Editors). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 147–286.

Chou, C., and C. W. Lan (2012). Changes in the annual range of precipitation under global warming. Journal of Climate 25:222–235.

Christians, J. K. (2002). Avian egg size: variation within species and inflexibility within individuals. Biological reviews of the Cambridge Philosophical Society 77:1–26.

Church, J. A., P. U. Clark, A. Cazenave, J. M. Gregory, S. Jevrejeva, A. Levermann, M. A. Merrifield, G. A. Milne, R. S. Nerem, P. D. Nunn, A. J. Payne, et al. (2013). Sea level change. In Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (T. F. Stocker, D. Qin, G.-K. Plattner, M. M. B. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P. M. Midgley, Editors). Cambridge University Press, Cambridge, pp. 1137–1216.

Ciais, P., C. Sabine, G. Bala, L. Bopp, V. Brovkin, J. Canadell, A. Chhabra, R. DeFries, J. Galloway, M. Heimann, C. Jones, et al. (2013). Carbon and Other Biogeochemical Cycles. In Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (T. F. Stocker, D. Qin, G.-K. Plattner, M. M. B. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P. M. Midgley, Editors). Cambridge University Press, Cambridge, pp. 465–570.

Clements, J. F., T. S. Schulenberg, M. J. Iliff, T. A. Fredericks, J. A. Gerbracht, D. Lepage, S. M. Billerman, B. L. Sullivan, and C. L. Wood (2022). The eBird/Clements checklist of birds of the world: v2022. *Comstock Pub. Associates/Cornell University Press*. [Online.] Available at http://www.birds.cornell.edu/clementschecklist/download/.

Cody, M. L. (1966). A general theory of clutch size. Evolution 20:174–184.

Congdon, J. D., and J. W. Gibbons (1987). Morphological constraint on egg size: a challenge to optimal egg size theory? Proceedings of the National Academy of Sciences 84:4145–4147.

Cory, C. B., and C. E. Hellmayr (1927). Tyrannidae. Field Museum of Natural History.

Crick, H. Q. P. (2004). The impact of climate change on birds. Ibis 146:48–56.

Crick, H. Q. P., C. Dudley, D. E. Glue, and D. L. Thomson (1997). UK birds are laying eggs earlier. Nature 388:526–527.

Crick, H. Q. P., and T. H. Sparks (1999). Climate change related to egg-laying trends. Nature 399:423–424.

Dakin, R., J. Q. Ouyang, Á. Z. Lendvai, M. F. Haussmann, I. T. Moore, and F. Bonier (2016). Weather matters: Begging calls are temperature and size-dependent signals of offspring state. Behaviour 153:871–896.

Delgado, S., N. Zorrozua, and J. Arizaga (2021). No evidence of habitat effect on clutch size, egg quality, and hatching success of the Yellow-legged Gull *Larus michahellis* at a micro-spatial scale. Marine Ornithology 49:241–246.

Diffenbaugh, N. S., and C. B. Field (2013). Changes in ecologically critical terrestrial climate conditions. Science 341:486–92.

Dore, M. H. I. (2005). Climate change and changes in global precipitation patterns: What do we know? Environment International 31:1167–1181.

Dunn, P. O. (2019). Changes in timing of breeding and reproductive success in birds. In Effects of Climate Change on Birds (P. O. Dunn and A. P. Møller, Editors). Second. Oxford University Press, Oxford, pp. 108–119.

Dunn, P. O., and A. P. Møller (2019). Effects of Climate Change on Birds. Second edi. Oxford University Press, Oxford.

Dunn, P. O., and D. W. Winkler (2008). Effects of climate change on timing of breeding and reproductive success in birds. In Effects of climate change on birds. pp. 113–128.

Dunning, J. B. Jr. (2007). CRC Handbook of Avian Body Masses. 2nd edition. CRC Press, Boca Raton.

Durant, J. M., D. Hjermann, G. Ottersen, and N. C. Stenseth (2007). Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33:271–283.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns (2000). Climate extremes: Observations, modeling, and impacts. Science 289:2068–2074.

Edward, D. A., and T. Chapman (2011). Mechanisms underlying reproductive trade-offs: Costs of reproduction. In Mechanisms of Life History Evolution. The Genetics and Physiology of Life History Traits and Trade-Offs (T. Flatt and A. Heyland, Editors). 1st edition. Oxford University Press, New York, pp. 137–152.

Englert Duursma, D., R. V. Gallagher, and S. C. Griffith (2018). Effects of El Niño Southern Oscillation on avian breeding phenology. Diversity and Distributions 24:1061–1071.

Eyring, V., S. Bony, G. A. Meehl, C. A. Senior, B. Stevens, R. J. Stouffer, and K. E. Taylor (2016). Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. Geoscientific Model Development 9:1937–1958.

Eyring, V., P. M. Cox, G. M. Flato, P. J. Gleckler, G. Abramowitz, P. Caldwell, W. D. Collins, B. K. Gier, A. D. Hall, F. M. Hoffman, G. C. Hurtt, et al. (2019).

Taking climate model evaluation to the next level. Nature Climate Change 9:102–110.

Fantle-Lepczyk, J., A. Taylor, D. Duffy, L. H. Crampton, and S. Conant (2016). Weather influences on nest success of the endangered Puaiohi (*Myadestes palmeri*). Wilson Journal of Ornithology 128:43–55.

Feiner, Z. S., H. Wang, D. W. Einhouse, J. R. Jackson, E. S. Rutherford, C. Schelb, C. S. Vandergoot, T. G. Zorn, and T. O. Höök (2016). Thermal environment and maternal effects shape egg size in a freshwater fish. Ecosphere 7.

Feng, X., A. Porporato, and I. Rodriguez-Iturbe (2013). Changes in rainfall seasonality in the tropics. Nature Climate Change 3:811–815.

Fick, S. E., and R. J. Hijmans (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

Fitzpatrick, J. W. (1980). Foraging behavior of neotropical tyrant flycatchers. Condor 82:43–57.

Fitzpatrick, J. W. (1981). Search strategies of tyrant flycatchers. Animal Behaviour 29:810–821.

Forchhammer, M. C., E. Post, and N. C. Stenseth (1998). Breeding phenology and climate. Nature 391:29–30.

Fullerton, M. R., J. R. Walters, R. E. Will, and S. R. Loss (2021). Interannual climate variation influences nest initiation date and nest productivity of the Red-cockaded Woodpecker at the northwestern edge of its range. Ornithological Applications 123:1–17.

Gebhardt-Henrich, S., and H. Richner (1998). Causes of growth variation and its consequences for ?tness. In Avian growth and development (J. M. Starck and R. E. Ricklefs, Editors). Oxford University Press, pp. 324–339.

Gienapp, P., T. E. Reed, and M. E. Visser (2014). Why climate change will invariably alter selection pressures on phenology. Proceedings of the Royal Society B: Biological Sciences 281:20141611–20141611.

Gillette, S. M., A. L. Klehr, and M. T. Murphy (2021). Variation in incubation length and hatching asynchrony in Eastern Kingbirds: Weather eclipses female effects. Ornithology 138:1–15.

Goławski, A. (2008). No Evidence of Weather Effect Found on the Clutch Size, Eggs Sizes and their Hatchability in the Red-Backed Shrike Lanius collurio in Eastern Poland . Annales Zoologici Fennici 45:513–520.

Gómez-Bahamón, V., E. R. Chen, D. T. Tuero, M. de las N. Sabio, K. Tkach, M. Assis, N. M. Heming, M. Â. Marini, and J. M. Bates (2023). Egg shape variation across the distribution of the partially migratory fork-tailed flycatcher *Tyrannus savana*. Journal of Avian Biology:e03006.

Griebeler, E. M., T. Caprano, and K. Böhning-Gaese (2004). Evolution of clutch size along latitudinal gradients: Revisiting Ashmole’s hypothesis. Evolutionary Ecology Research 6:679–694.

Griffith, S. C., S. C. Andrew, L. S. C. McCowan, L. L. Hurley, D. Englert Duursma, K. L. Buchanan, and M. M. Mariette (2020). Egg size is unrelated to ambient temperature in the opportunistically breeding zebra finch. Journal of Avian Biology 51:1–14.

Grudinskaya, V., S. Samsonov, E. Galkina, A. Grabovsky, T. Makarova, T. Vaytina, S. Fedotova, and D. Shitikov (2022). Effects of spring weather on laying dates, clutch size, and nest survival of ground-nesting passerines in abandoned fields. Avian Conservation and Ecology 17:art8.

Grüebler, M. U., M. Morand, and B. Naef-Daenzer (2008). A predictive model of the density of airborne insects in agricultural environments. Agriculture, Ecosystems and Environment 123:75–80.

Gullett, P. R., B. J. Hatchwell, R. A. Robinson, and K. L. Evans (2015). Breeding season weather determines long-tailed tit reproductive success through impacts on recruitment. Journal of Avian Biology 46:441–451.

Guo, H., J. G. John, C. Blanton, C. McHugh, S. Nikonov, A. Radhakrishnan, K. Rand, N. T. Zadeh, V. Balaji, J. Durachta, C. Dupuis, et al. (2018). NOAA-GFDL GFDL-CM4 model output. [Online.] Available at https://doi.org/10.22033/ESGF/CMIP6.1402.

Guo, Y., and X. Lu (2022). Clutch size of passerines increases with latitude in China, but egg size is conserved. Ibis 164:1063–1072.

Halupka, L., B. Czyż, and C. M. Macias Dominguez (2020). The effect of climate change on laying dates, clutch size and productivity of Eurasian Coots Fulica atra. International Journal of Biometeorology 64:1857–1863.

Hansen, J., M. Sato, and R. Ruedy (2012). Perception of climate change. Proceedings of the National Academy of Sciences 109:E2415–E2423.

Harris, I., T. J. Osborn, P. Jones, and D. Lister (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. Scientific Data 7:1–18.

Hau, M. (2001). Timing of Breeding in Variable Environments: Tropical Birds as Model Systems. Hormones and Behavior 40:281–290.

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

Hoover, S. E. R., and J. M. Tylianakis (2012). Species interactions. In Behavioural responses to a changing world (U. Candolin and B. B. M. Wong, Editors). 1st edition. Oxford University Press, Oxford, pp. 129–142.

Hõrak, P., R. Mänd, I. Ots, and A. Leivits (1995). Egg size in the Great Tit *Parus major*: individual, habitat and geographic differencess. Ornis Fennica 72:97–114.

Hut, R. A., S. Paolucci, R. Dor, C. P. Kyriacou, and S. Daan (2013). Latitudinal clines: an evolutionary view on biological rhythms. Proceedings of the Royal Society B: Biological Sciences 280:20130433.

IPCC (2021). Summary for Policymakers. In Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, et al., Editors). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jahn, A. E., V. R. Cueto, J. W. Fox, M. S. Husak, D. H. Kim, D. v. Landoll, J. P. Ledezma, H. K. LePage, D. J. Levey, M. T. Murphy, and R. B. Renfrew (2013). 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, Alex. E., and D. T. Tuero (2020). Fork-tailed Flycatcher (*Tyrannus savana*). In Birds of the World (T. S. Schulenberg, Editor). Cornell Lab of Ornithology.

Järvinen, A. (1994). Global warming and egg size of birds. Ecography 17:108–110.

Järvinen, A., and J. Ylimaunu (1986). Intraclutch Egg-Size Variation in Birds: Physiological Responses of Individuals to Fluctuations in Environmental Conditions. The Auk 103:235–237.

Jenni, L., and M. Kery (2003). Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proceedings of the Royal Society B: Biological Sciences 270:1467–1471.

Jetz, W., C. H. Sekercioglu, and K. Böhning-Gaese (2008). The Worldwide Variation in Avian Clutch Size across Species and Space. PLoS Biology 6:e303.

Kahle, D., and H. Wickham (2013). ggmap: Spatial Visualization with ggplot2. The R Journal 5:144–161.

Kellermann, J. L., and C. van Riper (2015). Detecting mismatches of bird migration stopover and tree phenology in response to changing climate. Oecologia 178:1227–1238.

Kokita, T. (2003). Potential latitudinal variation in egg size and number of a geographically widespread reef fish, revealed by common-environment experiments. Marine Biology 143:593–601.

Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel (2006). World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15:259–263.

Krist, M. (2011). Egg size and offspring quality: A meta-analysis in birds. Biological Reviews 86:692–716.

Kuleska, G. (1990). An analysis of clutch size in New World passerine birds. Ibis 132:407–422.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen (2017). lmerTest package: tests in linear mixed effects models. Journal of statistical software 82:1–26.

Laaksonen, T., M. Ahola, T. Eeva, R. A. Väisänen, and E. Lehikoinen (2006). Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. Oikos 114:277–290.

Lack, D. (1947). The significance of clutch-size. Ibis 89:302–352.

Lee, J.-Y., J. Marotzke, G. Bala, L. Cao, S. Corti, J. P. Dunne, F. Engelbrecht, E. Fischer, J. C. Fyfe, C. Jones, A. Maycock, et al. (2021). Future Global Climate: Scenario-based Projections and Near-term Information. In Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, et al., Editors). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 553–672.

Liu, M., D. R. Rubenstein, S. A. Cheong, and S. F. Shen (2018). Multitasking and the evolution of optimal clutch size in fluctuating environments. Ecology and Evolution 8:8803–8817.

Lovejoy, T. E., and L. Hannah (2019). Biodiversity and Climate Change: Transforming the Biosphere. Yale University Press, London.

Lundblad, C. G., and C. J. Conway (2021). Ashmole's hypothesis and the latitudinal gradient in clutch size. Biological Reviews 96:1349–1366.

Lv, L., M. van de Pol, H. L. Osmond, Y. Liu, A. Cockburn, and L. E. B. Kruuk (2023). Winter mortality of a passerine bird increases following hotter summers and during winters with higher maximum temperatures. Science Advances 9:eabm0197.

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

Marcelino, J., J. P. Silva, J. Gameiro, A. Silva, F. C. Rego, F. Moreira, and I. Catry (2020). Extreme events are more likely to affect the breeding success of lesser kestrels than average climate change. Scientific Reports 10:7207.

Marini, M. Â., M. Barbet-Massin, L. E. Lopes, and F. Jiguet (2009). Predicted climate-driven bird distribution changes and forecasted conservation conflicts in a neotropical savanna. Conservation Biology 23:1558–1567.

Marini, M. Â., M. Barbet-Massin, J. Martinez, N. P. Prestes, and F. Jiguet (2010). Applying ecological niche modelling to plan conservation actions for the Red-spectacled Amazon (*Amazona pretrei*). Biological Conservation 143:102–112.

Marini, M. Â., L. Hall, J. Bates, F. D. Steinheimer, R. McGowan, L. F. Silveira, D. A. Lijtmaer, P. L. Tubaro, S. Córdoba-Córdoba, A. Gamauf, H. F. Greeney, et al. (2020). The five million bird eggs in the world’s museum collections are an invaluable and underused resource. The Auk 137:1–7.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra (2015). A call for full annual cycle research in animal ecology. Biology Letters 11:20150552.

Marrot, P., D. Garant, and A. Charmantier (2017). Multiple extreme climatic events strengthen selection for earlier breeding in a wild passerine. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160372.

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. (1995). Avian Life History Evolution in Relation to Nest Sites, Nest Predation, and Food. Ecological Monographs 65:101–127.

Martin, T. E. (2008). Egg size variation among tropical and temperate songbirds: an embryonic temperature hypothesis. Proceedings of the National Academy of Sciences of the United States of America 105:9268–9271.

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

Martin, T. E., and J. C. Mouton (2020). Longer-lived tropical songbirds reduce breeding activity as they buffer impacts of drought. Nature Climate Change 10:953–958.

McCleery, R. H., and C. M. Perrins (1998). ...Temperature and egg-laying trends. Nature 391:30–31.

McCleery, R. H., C. M. Perrins, B. C. Sheldon, and A. Charmantier (2008). Age-specific reproduction in a long-lived species: The combined effects of senescence and individual quality. Proceedings of the Royal Society B: Biological Sciences 275:963–970.

Mclean, N., C. R. Lawson, D. I. Leech, and M. van de Pol (2016). Predicting when climate-driven phenotypic change affects population dynamics. Ecology Letters 19:595–608.

McNamara, J. M., Z. Barta, M. Klaassen, and S. Bauer (2011). Cues and the optimal timing of activities under environmental changes. Ecology Letters 14:1183–1190.

Mobley, J. (2020). White-throated Kingbird (*Tyrannus albogularis*). In Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D. Christie and E. de Juana, Editors). Cornell Lab of Ornithology.

Mobley, J., and E. de Juana (2020). Loggerhead Kingbird (*Tyrannus caudifasciatus*). In Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D. Christie and E. de Juana, Editors). Cornell Lab of Ornithology.

Møller, A. P., and W. M. Hochachka (2019). Long-term time series of ornithological data. In Effects of Climate Change on Birds (P. O. Dunn and A. Pape Møller, Editors). Second. Oxford University Press, pp. 37–43.

Moreau, R. E. (1944). Clutch size: a comparative study, with special reference to African birds. Ibis 86:286–347.

Morrissey, J. S., B. Barr, A. E. Austin, L. R. Babcock, and R. Powell (2020). Do latitude, elevation, temperature, and precipitation influence body and clutch sizes of female common five-lined skinks, *Plestiodon fasciatus* (Linnaeus, 1758)? Journal of North American Herpetology 2020:32–41.

Murphy, M. T. (1983a). Ecological aspects of the reproductive biology of Eastern Kingbirds: geographic comparisons. Ecology 64:914–928.

Murphy, M. T. (1983b). Clutch Size in the Eastern Kingbird: Factors Affecting Nestling Survival. The Auk 100:326–334.

Murphy, M. T. (1985). Nestling Eastern Kingbird Growth: Effects of Initial Size and Ambient Temperature. Ecology 66:162–170.

Murphy, M. T. (1996). Survivorship, Breeding Dispersal and Mate Fidelity in Eastern Kingbirds. The Condor 98:82–92.

Nägeli, M., P. Scherler, S. Witczak, B. Catitti, A. Aebischer, V. van Bergen, U. Kormann, and M. U. Grüebler (2022). Weather and food availability additively affect reproductive output in an expanding raptor population. Oecologia 198:125–138.

Nager, R. G., and A. J. Van Noordwijk (1992). Energetic limitation in the egg-laying period of great tits. Proceedings of the Royal Society B: Biological Sciences 249:259–263.

Nakagawa, S., and H. Schielzeth (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Newton, I. (1998a). Population limitation in birds. 1st edition. Elsevier Academic Press, San Diego.

Newton, I. (1998b). Weather. In Population limitation in Birds (I. Newton, Editor). 1st edition. Elsevier Academic Press, San Diego, CA, pp. 287–317.

Norris, D. R., and C. M. Taylor (2006). Predicting the consequences of carry-over effects for migratory populations. Biology Letters 2:148–151.

Ockendon, N., D. Leech, and J. W. Pearce-Higgins (2013). Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. Biology Letters 9:20130669.

O’Donnell, M. S., and D. A. Ignizio (2012). Bioclimatic predictors for supporting ecological applications in the conterminous United States. U.S. Geological Survey Data Series 691:10.

O’Neill, B. C., E. Kriegler, K. Riahi, K. L. Ebi, S. Hallegatte, T. R. Carter, R. Mathur, and D. P. van Vuuren (2014). A new scenario framework for climate change research: The concept of shared socioeconomic pathways. Climatic Change 122:387–400.

Peña, C., and N. Navarro (2023). Giant Kingbird (*Tyrannus cubensis*). In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology.

Perez, D. M., J. L. Gardner, and I. Medina (2020). Climate as an Evolutionary Driver of Nest Morphology in Birds: A Review. Frontiers in Ecology and Evolution 8:1–11.

Phillips, A. R. (1994). A tentative key to the species of kingbirds, with distributional notes. Journal of Field Ornithology 65:295–306.

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

van de Pol, M., and L. D. Bailey (2019). Quantifying the climatic sensitivity of individuals, populations, and species. In Effects of Climate Change on Birds (P. O. Dunn and A. Pape Møller, Editors). Second. Oxford University Press, pp. 44–59.

van de Pol, M., L. D. Bailey, N. McLean, L. Rijsdijk, C. R. Lawson, and L. Brouwer (2016). Identifying the best climatic predictors in ecology and evolution. Methods in Ecology and Evolution 7:1246–1257.

van de Pol, M., and A. Cockburn (2011). Identifying the critical climatic time window that affects trait expression. American Naturalist 177:698–707.

van de Pol, M., B. J. Ens, D. Heg, L. Brouwer, J. Krol, M. Maier, K.-M. Exo, K. Oosterbeek, T. Lok, C. M. Eising, and K. Koffijberg (2010). Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? Journal of Applied Ecology 47:720–730.

Potti, J. (2009). Advanced breeding dates in relation to recent climate warming in a Mediterranean montane population of Blue Tits *Cyanistes caeruleus*. Journal of Ornithology 150:893–901.

Price, T., and L. Liou (1989). Selection on clutch size in birds. American Naturalist 134:950–959.

R Core Team (2022). R: A Language and Environment for Statistical Computing. [Online.] Available at https://www.r-project.org/.

Rahn, H., and A. Ar (1974). The Avian Egg: Incubation Time and Water Loss. The Condor 76:147–152.

Ricklefs, R. E. (1980). Geographical variation in clutch size among passerine birds: Ashmole’s hypothesis. The Auk 97:38–49.

Ricklefs, R. E. (2000). Lack, Skutch, and Moreau: The early development of life-history thinking. The Condor 102:3–8.

Riddell, E. A., K. J. Iknayan, L. Hargrove, S. Tremor, J. L. Patton, R. Ramirez, B. O. Wolf, and S. R. Beissinger (2021). Exposure to climate change drives stability or collapse of desert mammal and bird communities. Science 371:633–638.

Roberts, S. G., D. P. Thoma, D. W. Perkins, E. L. Tymkiw, Z. S. Ladin, and W. G. Shriver (2021). A habitat-based approach to determining the effects of drought on aridland bird communities. Ornithology 138:1–13.

Roff, D. A., and D. J. Fairbairn (2007). The evolution of trade-offs: Where are we? Journal of Evolutionary Biology 20:433–447.

Rosenzweig, M. L. (1968). Net Primary Productivity of Terrestrial Communities: Prediction from Climatological Data. The American Naturalist 102:67–74.

Rubel, F., K. Brugger, K. Haslinger, and I. Auer (2017). The climate of the European Alps: Shift of very high resolution Köppen-Geiger climate zones 1800–2100. Meteorologische Zeitschrift 26:115–125.

Runge, M. C., and P. P. Marra (2005). Modeling Seasonal Interactions in the Population Dynamics of Migratory Birds. In Birds of two worlds: the ecology and evolution of migration (R. G. P. P. Marra, Editor). JHU Press, pp. 375–390.

Sakai, O. (2021). One or two eggs: what underlies clutch size variation within a gecko species? Zoology (Jena, Germany) 146:125911.

Sauve, D., V. L. Friesen, and A. Charmantier (2021). The Effects of Weather on Avian Growth and Implications for Adaptation to Climate Change. Frontiers in Ecology and Evolution 9:1–20.

Schaper, S. V., A. Dawson, P. J. Sharp, P. Gienapp, S. P. Caro, and M. E. Visser (2012). Increasing Temperature, Not Mean Temperature, Is a Cue for Avian Timing of Reproduction. The American Naturalist 179:E55–E69.

Schifferli, L., M. U. Grüebler, H. A. J. J. Meijer, G. H. Visser, and B. Naef-Daenzer (2014). Barn Swallow Hirundo rustica parents work harder when foraging conditions are good. Ibis 156:777–787.

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

Schöll, E. M., M. P. Aparisi, and S. M. Hille (2020). Diurnal patterns of ambient temperature but not precipitation influence incubation behavior in Great Tits. Journal of Ornithology 161:529–538.

Schulenberg, T. S., and T. Johnson (2020). Snowy-throated Kingbird (*Tyrannus niveigularis*). In Birds of the World (T. S. Schulenberg, Editor). Cornell Lab of Ornithology.

Schultz, P. A., and M. S. Halpert (1993). Global correlation of temperature, NDVI and precipitation. Advances in Space Research 13:277–280.

Schwartz, M. D., and L. Liang (2019). Finding and analysing long-term climate data. In Effects of Climate Change on Birds (P. O. Dunn and A. P. Møller, Editors). Second. Oxford University Press, Oxford, pp. 29–36.

Sclater, P. L. (Editor) (1888). Volume 14 - Tyrannidae. In Catalogue of the birds in the British Museum. British Museum, London.

Selonen, V., S. Helle, T. Laaksonen, M. P. Ahola, E. Lehikoinen, and T. Eeva (2021). Identifying the paths of climate effects on population dynamics: dynamic and multilevel structural equation model around the annual cycle. Oecologia 195:525–538.

Seneviratne, S. I., X. Zhang, M. Adnan, W. Badi, C. Dereczynski, A. Di Luca, S. Ghosh, I. Iskandar, J. Kossin, S. Lewis, F. Otto, et al. (2021). Weather and Climate Extreme Events in a Changing Climate. In Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, et al., Editors). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1513–1766.

Shave, A., C. J. Garroway, J. Siegrist, and K. C. Fraser (2019). Timing to temperature: Egg-laying dates respond to temperature and are under stronger selection at northern latitudes. Ecosphere 10.

Sheader, M. (1996). Factors influencing egg size in the gammarid amphipod Gammarus insensibilis. Marine Biology 124:519–526.

Simmons, R. E., P. Barnard, W. Dean, G. F. Midgley, W. Thuiller, and G. Hughes (2004). Climate change and birds: perspectives and prospects from southern Africa. Ostrich 75:295–308.

Smith, C. C., and S. D. Fretwell (1974). The optimal balance between size and number of offspring. The American Naturalist 108:499–506.

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

Stępniewski, J., L. Halupka, and B. Czyż (2021). Eggs of little bitterns show high variation and their size increases with latitude. The European Zoological Journal 88:891–899.

Stevens, G. C. (1989). The Latitudinal Gradient in Geographical Range: How so Many Species Coexist in the Tropics. The American Naturalist 133:240–256.

Stevenson, I. R., and D. M. Bryant (2000). Climate change and constraints on breeding. Nature 406:366–367.

Stillwell, R. C. (2010). Are latitudinal clines in body size adaptive? Oikos 119:1387–1390.

Stoddard, M. C., E. H. Yong, D. Akkaynak, C. Sheard, J. A. Tobias, and L. Mahadevan (2017). Avian egg shape: Form, function, and evolution. Science 356:1249–1254.

Stouffer, R. J., V. Eyring, G. A. Meehl, S. Bony, C. Senior, B. Stevens, and K. E. Taylor (2017). CMIP5 scientific gaps and recommendations for CMIP6. Bulletin of the American Meteorological Society 98:95–105.

Stutchbury, B. J. M., and E. S. Morton (2001). Behavioral ecology of tropical birds. 1st edition. Academic Press, San Diego.

Therrien, J.-F., N. Lecomte, T. Zgirski, M. Jaffré, A. Beardsell, L. J. Goodrich, J. Bêty, A. Franke, E. Zlonis, and K. L. Bildstein (2017). Long-term phenological shifts in migration and breeding-area residency in eastern North American raptors. The Auk 134:871–881.

Thompson, R. M., J. Beardall, J. Beringer, M. Grace, and P. Sardina (2013). Means and extremes: building variability into community-level climate change experiments. Ecology Letters 16:799–806.

Thomson, C. E., and J. D. Hadfield (2017). Prenatal maternal effects appear to be insensitive to experimental or natural environmental variation. Functional Ecology 31:2008–2020.

Tidon, R. (2006). Relationships between drosophilids (Diptera, Drosophilidae) and the environment in two contrasting tropical vegetations. Biological Journal of the Linnean Society 87:233–247.

Tökölyi, J., J. M. McNamara, A. I. Houston, and Z. Barta (2012). Timing of avian reproduction in unpredictable environments. Evolutionary Ecology 26:25–42.

Töpfer, T. (2018). Morphological Variation in Birds: Plasticity, Adaptation, and Speciation. In Bird Species: How They Arise, Modify and Vanish (D. T. Tietze, Editor). Springer International Publishing, Cham, pp. 63–74.

Trautmann, S. (2018). Climate Change Impacts on Bird Species. In Bird Species: How They Arise, Modify and Vanish (D. T. Tietze, Editor). 1st edition. Springer International Publishing, Cham, pp. 217–234.

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

Tryjanowski, P., T. H. Sparks, L. Kuczyński, and S. Kuźuniak (2004). Should avian egg size increase as a result of global warming? A case study using the red-backed shrike (Lanius collurio). Journal of Ornithology 145:264–268.

Tweit, R. C., and J. C. Tweit (2020). Cassin’s Kingbird (*Tyrannus vociferans*). In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology.

Vera, C., G. Silvestri, B. Liebmann, and P. González (2006). Climate change scenarios for seasonal precipitation in South America from IPCC-AR4 models. Geophysical Research Letters 33:2–5.

Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences 275:649–659.

Visser, M. E., C. Both, and M. M. Lambrechts (2004). Global Climate Change Leads to Mistimed Avian Reproduction. In Advances in Ecological Research. pp. 89–110.

Volodin, E., E. Mortikov, A. Gritsun, V. Lykossov, V. Galin, N. Diansky, A. Gusev, S. Kostrykin, N. Iakovlev, A. Shestakova, and S. Emelina (2019). INM INM-CM5-0 model output prepared for CMIP6 ScenarioMIP. [Online.] Available at https://doi.org/10.22033/ESGF/CMIP6.12322.

Wallace, A. R. (1876). The geographical distribution of animals: with a study of the relations of living and extinct faunas as elucidating the past changes of the earth’s surface. Harper and Brothers, New York.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein (2002). Ecological responses to recent climate change. Nature 416:389–395.

Wellmann, R. (2023). Selection index theory for populations under directional and stabilizing selection. Genetics Selection Evolution 55:1–17.

Welty, J. C. (1982). The Life of Birds. 3rd edition. Saunders College Publishing, New York.

White, E. R., and A. Hastings (2020). Seasonality in ecology: Progress and prospects in theory. Ecological Complexity 44:100867.

Whitfield, M. C., B. Smit, A. E. McKechnie, and B. O. Wolf (2015). Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. Journal of Experimental Biology 218:1705–1714.

Williams, T. D., and T. G. G. Groothuis (2015). Egg quality, embryonic development, and post-hatching phenotype: an integrated perspective. In Nests, eggs, & incubation (D. C. Deeming and S. J. Reynolds, Editors). 1st edition. Oxford University Press, Oxford, pp. 113–126.

Winkler, D. W., S. M. Billerman, and I. J. Lovette (2020). Tyrant Flycatchers (Tyrannidae). In Birds of the World (S. M. Billerman, B. K. Keeney, P. G. Rodewald and T. S. Schulenberg, Editors). Cornell Lab of Ornithology.

Winkler, D. W., P. O. Dunn, and C. E. McCulloch (2002). Predicting the effects of climate change on avian life-history traits. Proceedings of the National Academy of Sciences of the United States of America 99:13595–13599.

Wolda, H. (1978). Seasonal fluctuations in rainfall, food and abundance of tropical insects. The Journal of Animal Ecology 47:369–381.

Wolda, H. (1988). Insect seasonality: why? Annual review of ecology and systematics. Vol. 19:1–18.

Wolfe, J. D., C. J. Ralph, and P. Elizondo (2015). Changes in the apparent survival of a tropical bird in response to the El Niño Southern Oscillation in mature and young forest in Costa Rica. Oecologia 178:715–21.

Xiao, H., Y. Hu, Z. Lang, B. Fang, W. Guo, Q. Zhang, X. Pan, and X. Lu (2017). How much do we know about the breeding biology of bird species in the world? Journal of Avian Biology 48:513–518.

Young, B. E. (1994). Geographic and seasonal patterns of clutch-size variation in house wrens. The Auk 111:545–555.

Yue, Y., D. Yan, Q. Yue, G. Ji, and Z. Wang (2021). Future changes in precipitation and temperature over the Yangtze River Basin in China based on CMIP6 GCMs. Atmospheric Research 264:105828.

Yukimoto, S., T. Koshiro, H. Kawai, N. Oshima, K. Yoshida, S. Urakawa, H. Tsujino, M. Deushi, T. Tanaka, M. Hosaka, H. Yoshimura, et al. (2019). MRI MRI-ESM2.0 model output prepared for CMIP6 CMIP. [Online.] Available at https://doi.org/10.22033/ESGF/CMIP6.621.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith (2009). Mixed Effects Models and Extensions in Ecology with R. In Statistics for biology and health. Springer Science, pp. 1–10.

MATERIAL SUPLEMENTAR (FIGURAS)

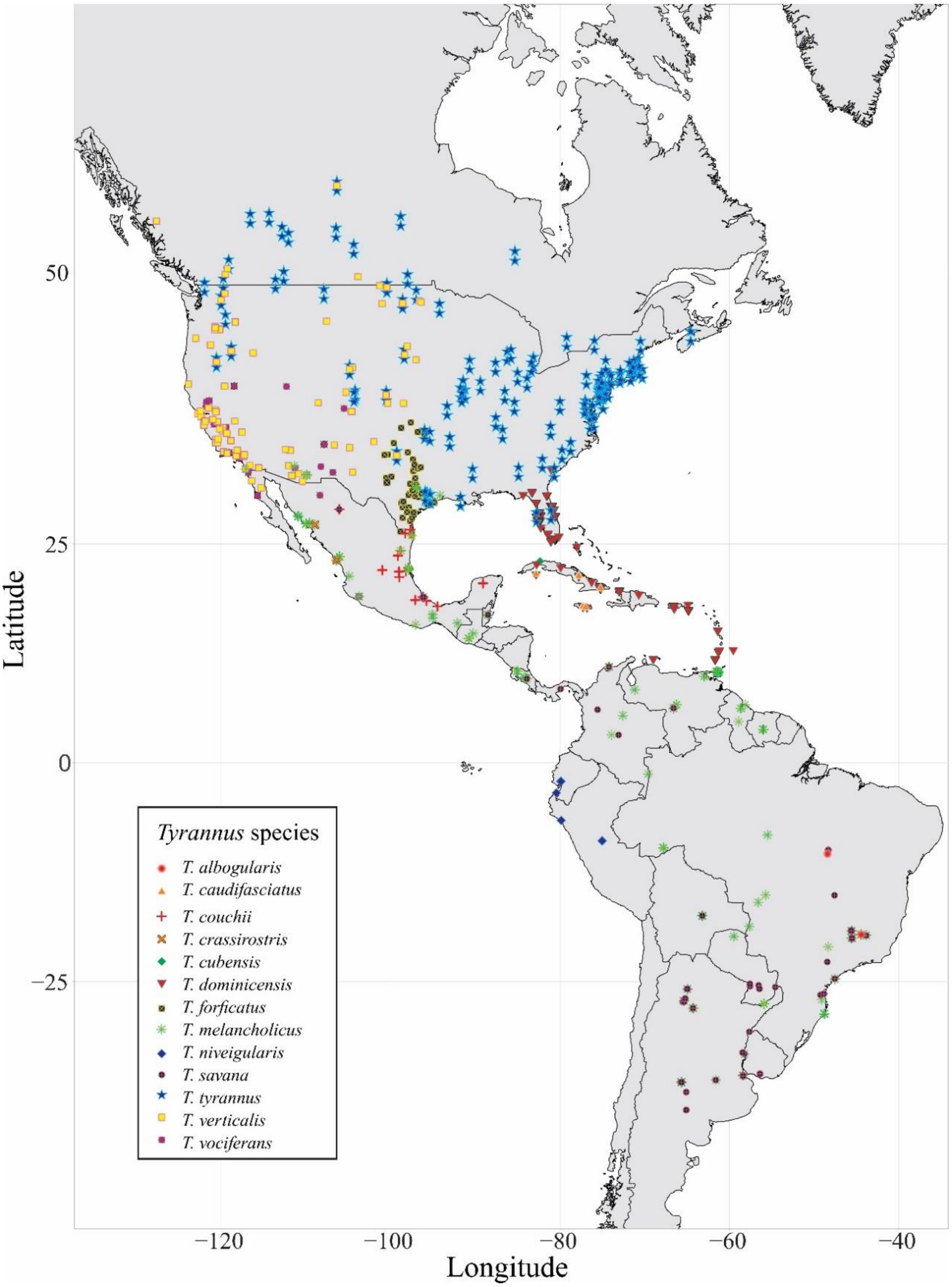


Figura S1 - Distribuição dos registros de reprodução coletados de 13 espécies do gênero ***Tyrannus*** *(****T. albogularis; T. caudifasciatus; T. couchii; T. crassirostris; T. cubensis; T. dominicensis; T. forficatus; T. melancholicus; T. niveigularis; T. savana; T. tyrannus; T. verticalis; e T. vociferans****). Com cores e formas diferentes por espécie, os pontos mostram os locais onde as ninhadas foram coletadas.*

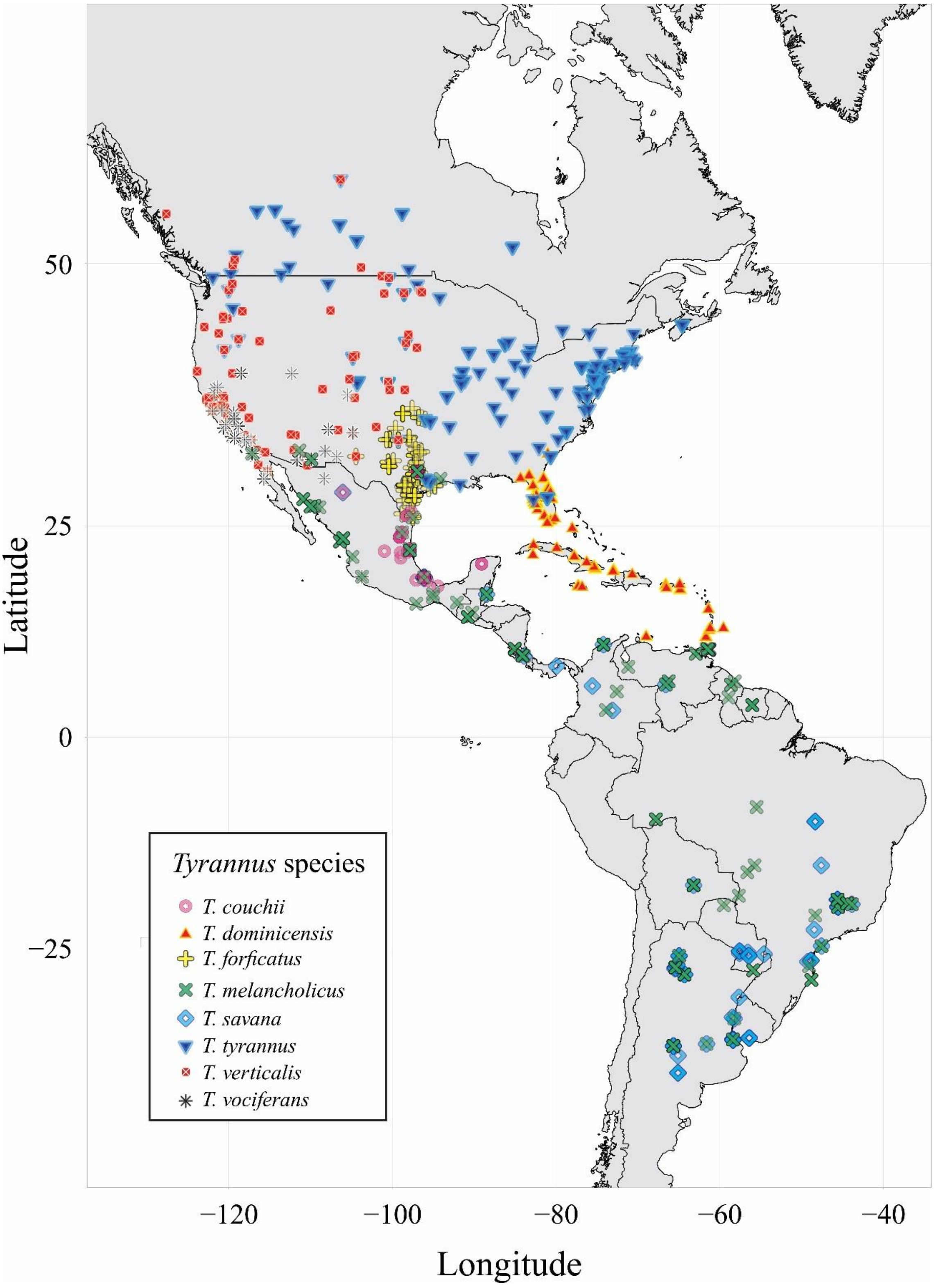


Figura S2 - Distribuição dos registros de reprodução coletados de oito espécies do gênero ***Tyrannus*** *analisados no capítulo 1 (****T. couchii; T. dominicensis; T. forficatus; T. melancholicus; T. savana; T. tyrannus; T. verticalis; e T. vociferans****). Com cores e formas diferentes por espécie, os pontos mostram os locais onde as ninhadas foram coletadas.*

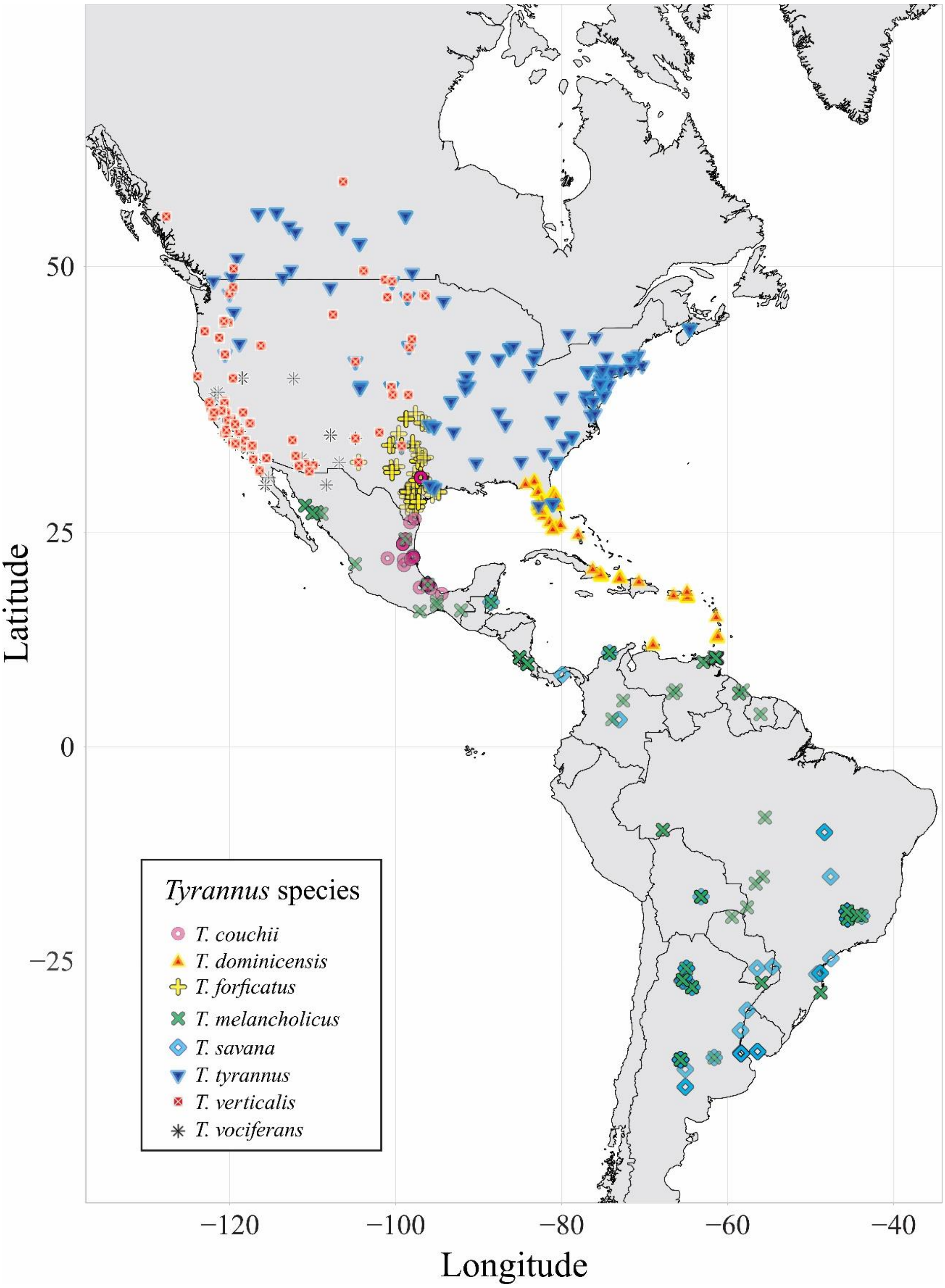
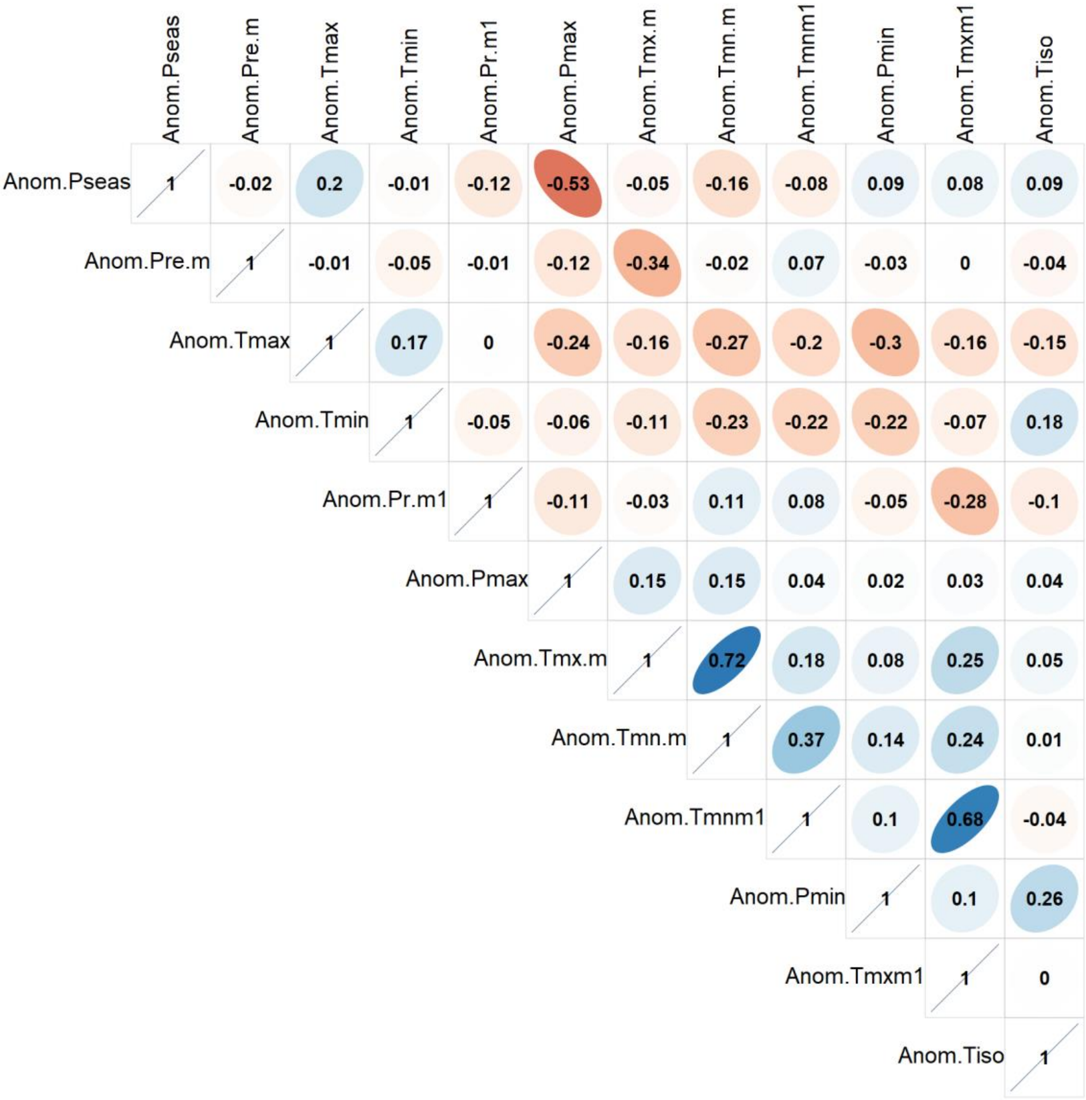


Figura S3 - Distribuição dos registros de reprodução coletados de oito espécies do gênero ***Tyrannus*** *analisados nos capítulos 2 e 3 (**T. couchii; T. dominicensis; T. forficatus; T. melancholicus; T. savana; T. tyrannus; T. verticalis; e T. vociferans**). Com cores e formas diferentes por espécie, os pontos mostram os locais onde as ninhadas foram coletadas.*



	Anom.Pseas	Anom.Pre.m	Anom.Tmax	Anom.Tmin	Anom.Pr.m1	Anom.Pmax	Anom.Tmx.m	Anom.Tmn.m	Anom.Tmnm1	Anom.Pmin	Anom.Tmxm1	Anom.Tiso
Anom.Pseas	1	-0.02	0.2	-0.01	-0.12	-0.53	-0.05	-0.16	-0.08	0.09	0.08	0.09
Anom.Pre.m		1	-0.01	-0.05	-0.01	-0.12	-0.34	-0.02	0.07	-0.03	0	-0.04
Anom.Tmax			1	0.17	0	-0.24	-0.16	-0.27	-0.2	-0.3	-0.16	-0.15
Anom.Tmin				1	-0.05	-0.06	-0.11	-0.23	-0.22	-0.22	-0.07	0.18
Anom.Pr.m1					1	-0.11	-0.03	0.11	0.08	-0.05	-0.28	-0.1
Anom.Pmax						1	0.15	0.15	0.04	0.02	0.03	0.04
Anom.Tmx.m							1	0.72	0.18	0.08	0.25	0.05
Anom.Tmn.m								1	0.37	0.14	0.24	0.01
Anom.Tmnm1									1	0.1	0.68	-0.04
Anom.Pmin										1	0.1	0.26
Anom.Tmxm1											1	0
Anom.Tiso												1

Figura S4 - Análises de correlação (-1, 1) entre anomalias de variáveis meteorológicas.

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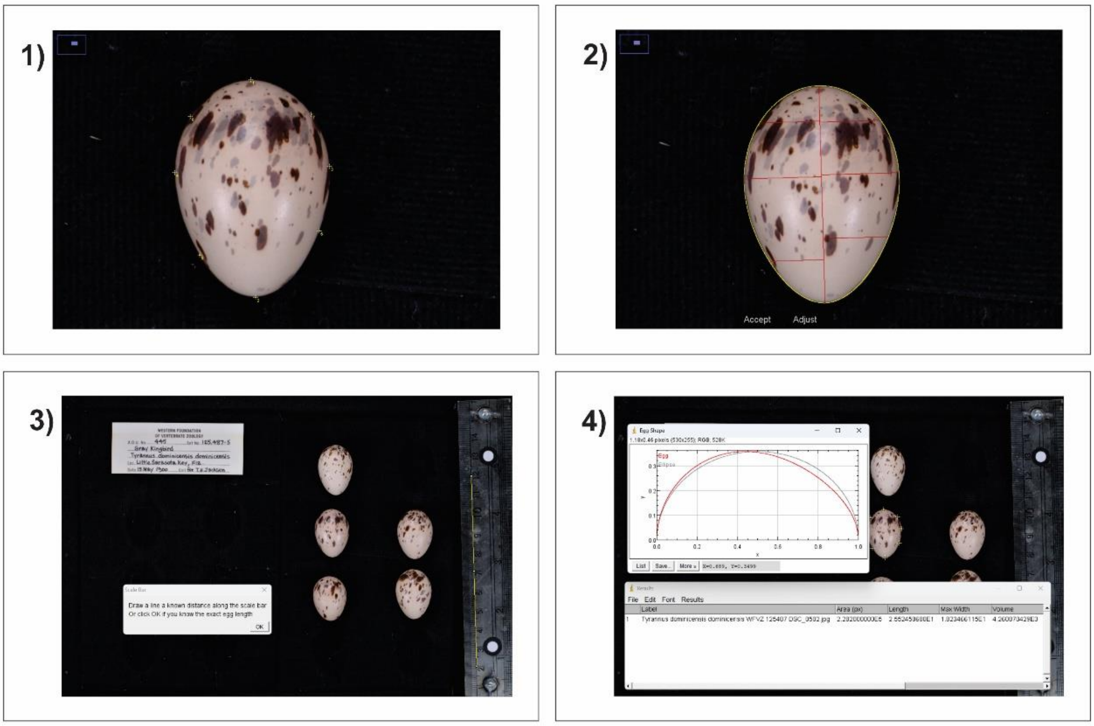
Figura S5 - Processo de obtenção de registros fotográficos de ninhadas de aves em coleções de ovos. A) Smithsonian National Museum of Natural History (Washington DC/EUA); B) American Museum of Natural History (Nova Iorque/EUA); C) Harvard Museum of Comparative Zoology (Cambridge/EUA); D) Museo Argentino de Ciencias Naturales (Buenos Aires/Argentina); E) Western Foundation of Vertebrate Zoology (Camarillo/EUA); F) Natural History Museum (Tring/Inglaterra); e G) Museum d'Histoire naturelle (Genebra/Suíça).



Draw a line a known distance along the scale bar
Or click OK if you know the exact egg length

	Label	Area (px)	Length	Max Width	Volume
1	Tyrannus dominicensis dominicensis WFVZ 125487 DSC_0502.jpg	2.282000000E5	2.552459680E1	1.823466115E1	4.260070429E3

Figura S6 – Processo de extração digital das medidas dos ovos utilizando o software ImageJ, seguindo a metodologia de Troscianko (2014): 1) Definição de pontos nas extremidades principais; 2) Visualização e reajuste da circunferência do ovo gerado; 3) Ajuste da escala; e 4) Dimensões calculadas.

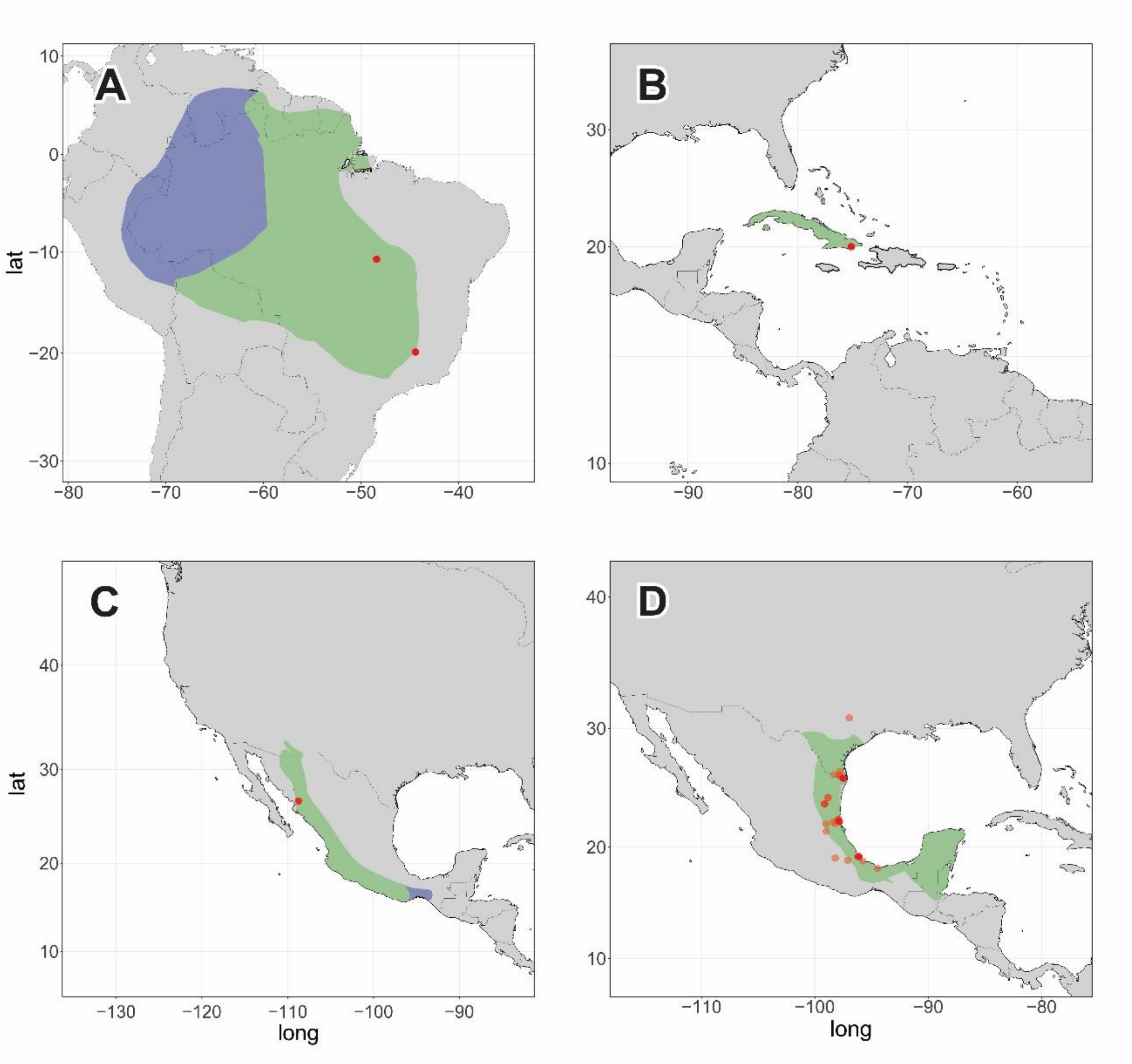


Figura S7 - *Distribuição das espécies do gênero* ***Tyrannus*** *e seus registros reprodutivos obtidos em coleções de museus. Região em azul representa sua área de invernada e a região em verde sua área reprodutiva. Pontos vermelhos mostram as localizações dos dados reprodutivos obtidos. A)* ***T. albogularis****; B)* ***T. caudifasciatus****; C)* ***T. crassirostris****; D)* ***T. couchii****.*

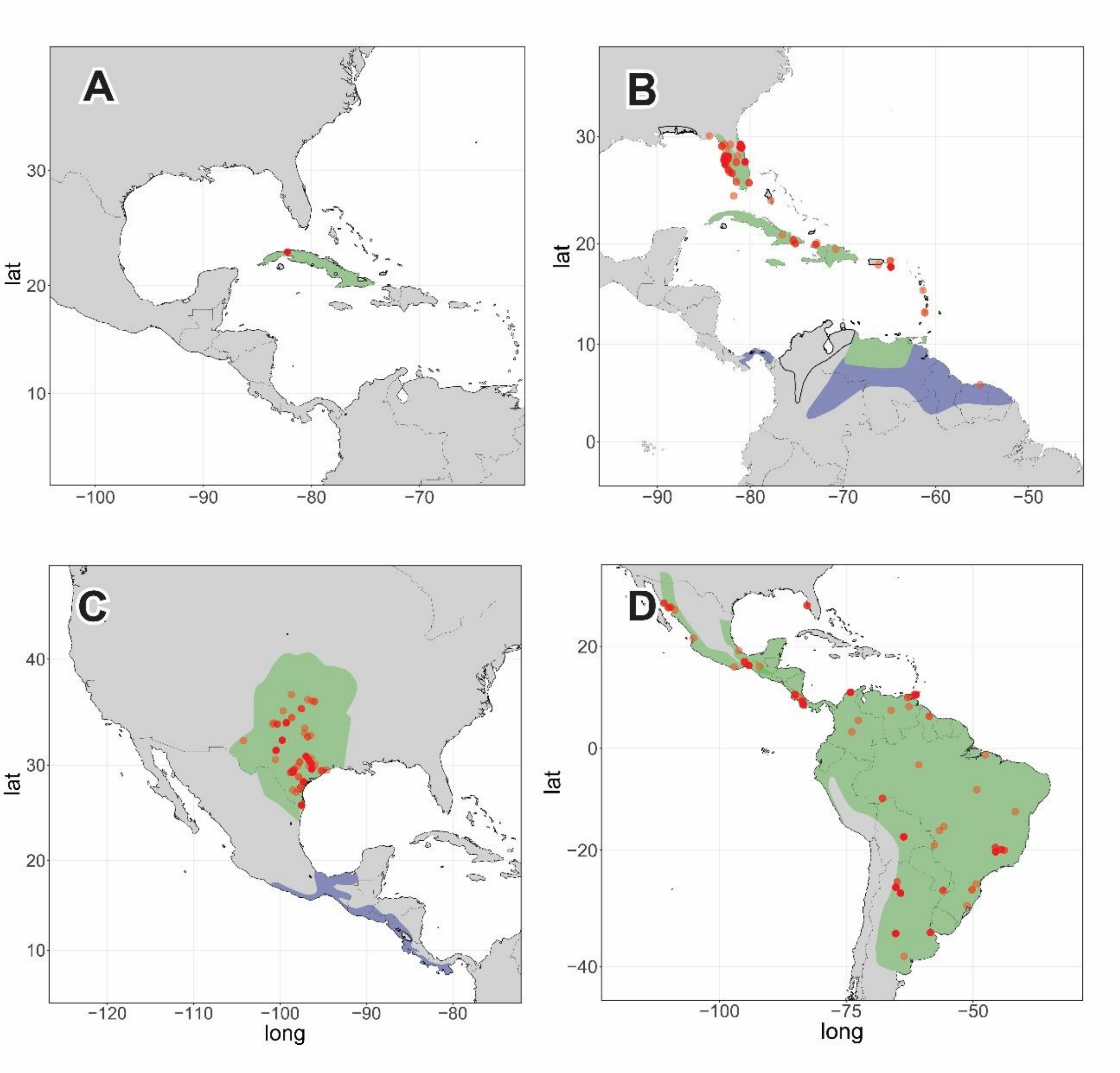


Figura S8 – Distribuição das espécies do gênero **Tyrannus** *e seus registros reprodutivos obtidos em coleções de museus. Região em azul representa sua área de invernada e a região em verde sua área reprodutiva. Pontos vermelhos mostram as localizações dos dados reprodutivos obtidos. A)* ***T. cubensis****; B****) T. dominicensis****; C)* ***T. forficatus****; D)* ***T. melancholicus.***

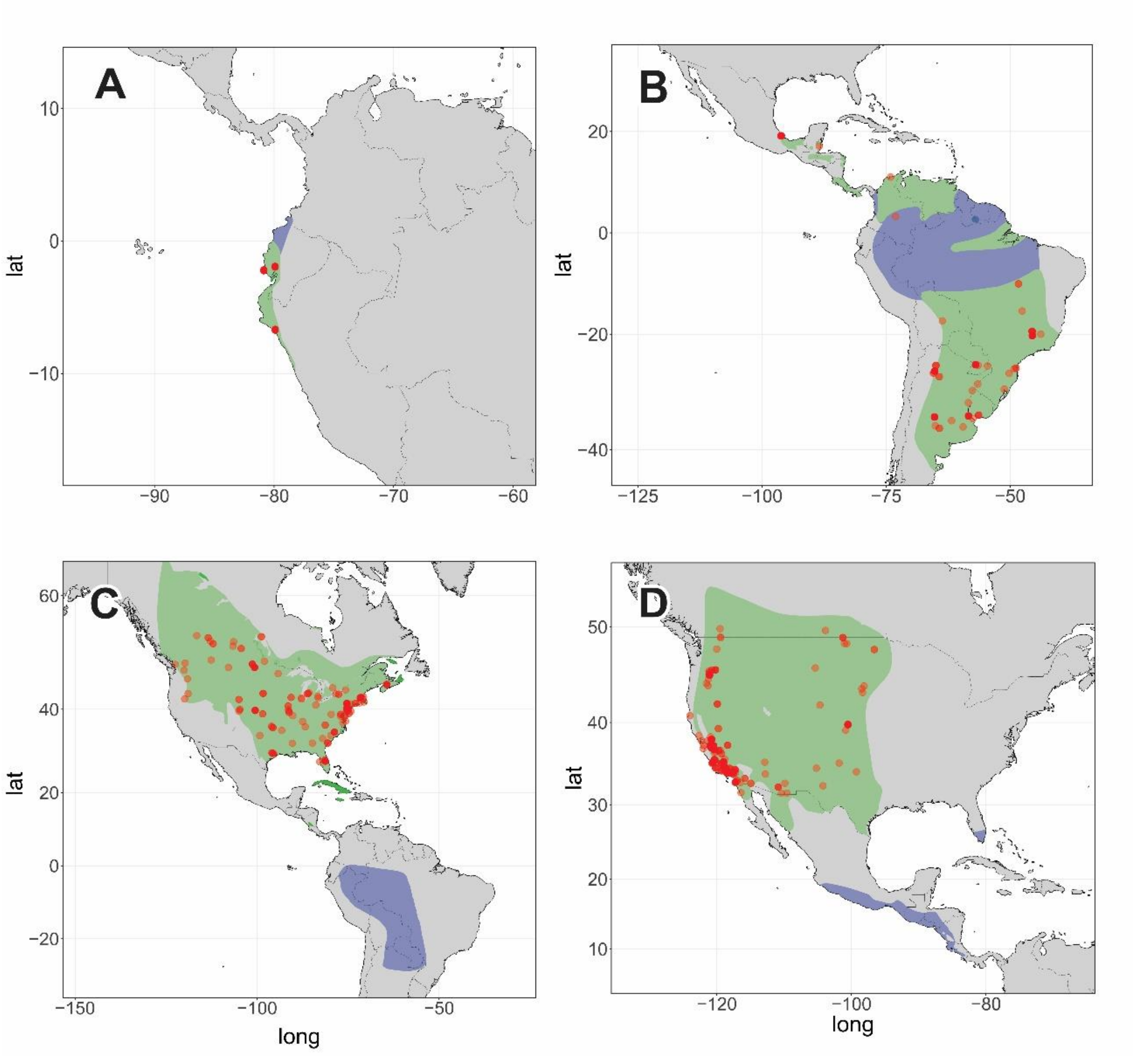


Figura S9 – Distribuição das espécies do gênero ***Tyrannus*** *e seus registros reprodutivos obtidos em coleções de museus. Região em azul representa sua área de invernada e a região em verde sua área reprodutiva. Pontos vermelhos mostram as localizações dos dados reprodutivos obtidos. A)* ***T. niveigula****ris; B)* ***T. savana****; C)* ***T. tyrannus*** *e D)* ***T. verticalis****.*

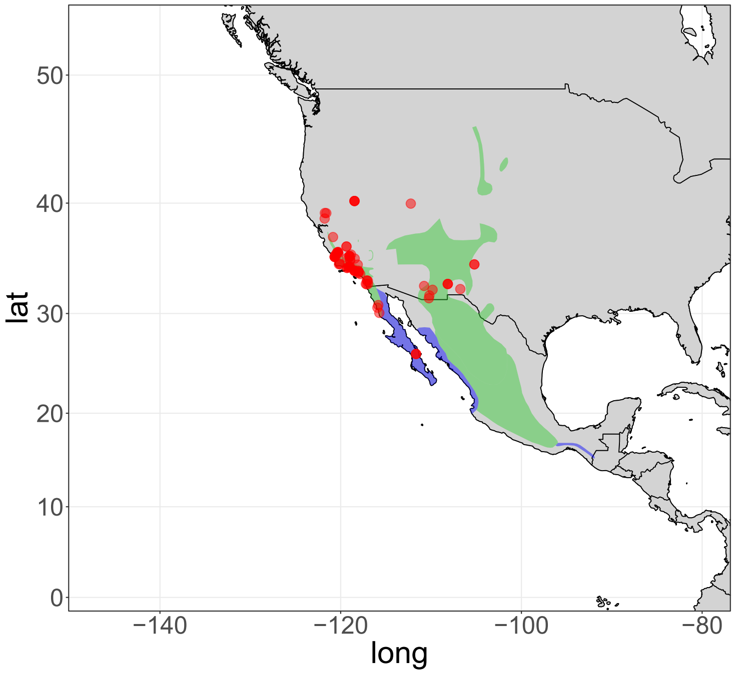


*Figura S10 - Distribuição das espécies do gênero **Tyrannus** e seus registros reprodutivos obtidos em coleções de museus. Região em azul representa sua área de invernada e a região em verde sua área reprodutiva. Pontos vermelhos mostram as localizações dos dados reprodutivos de **T. vociferans**.*

MATERIAL SUPLEMENTAR (TABELAS)

Tabela S1 – Conjunto de dados de ninhadas e ovos de 13 espécies de do gênero ***Tyrannus****. As ninhadas foram fotografadas em 23 coleções de ovos na América do Sul, nos EUA e na Europa. O número fora dos parênteses refere-se às ninhadas, enquanto o valor dentro dos parênteses refere-se ao número de ovos.*

	Tyrannus verticalis	*Tyrannus dominicensis*	*Tyrannus vociferans*	*Tyrannus melancholicus*	*Tyrannus forficatus*	*Tyrannus tyrannus*	*Tyrannus couchii*	*Tyrannus savana*	*Tyrannus albogularis*	*Tyrannus caudifasciatus*	*Tyrannus niveigularis*	*Tyrannus crassirostris*	*Tyrannus cubensis*	Total by collection
AMNH - New York	12 (41)	34 (109)	5 (21)	4 (11)				3 (10)						58 (192)
CAS - San Francisco				1 (4)				1 (3)						2 (7)
COMB - Brasília				17 (28)				13 (25)	2 (4)					32 (57)
DMNH - Delaware	20 (78)	46 (138)		23 (64)				27 (86)						116 (366)
IAvH - Villa de Leyva	3 (9)	1 (4)	1 (5)	2 (4)	1 (5)	7 (28)		1 (3)						16 (58)
MACN - Buenos Aires				2 (6)		1 (4)		8 (25)						11 (35)
MCZ - Harvard	12 (49)	7 (20)	1 (4)	1 (2)		8 (27)		2 (8)		1 (2)				32 (112)
MLP - La Plata				1 (2)				3 (9)						4 (11)
MLUH - Halle		4 (8)		8 (22)				4 (10)			1 (1)			17 (41)
MN - Rio de Janeiro				8 (23)	1 (5)	1 (3)		12 (36)						22 (67)
MPEG - Belém				1 (1)										1 (1)
MVZ - Berkeley			1 (1)	2 (2)				2 (5)						5 (8)
MZUSP - São Paulo	1 (4)			4 (14)		1 (3)		1 (3)						7 (24)
NBCN - Leiden		3 (7)		5 (15)										8 (22)
NHM - Tring	7 (24)	7 (14)	2 (7)	33 (79)	4 (16)	14 (46)		12 (40)		2 (8)	2 (3)	1 (2)		84 (239)

NMBE - Berna				6 (16)										6 (16)
NMS - Edinburgh		1 (3)		2 (5)				6 (16)						9 (24)
NMW - Viena			1 (3)	1 (4)	1 (5)	2 (6)		1 (3)						6 (21)
SBCM - San Bernardino		1 (2)		20 (53)			1 (4)							22 (59)
UFRRJ - Rio de Janeiro				1 (3)				1 (3)						2 (6)
USNM - Washington	19 (68)	26 (72)	16 (53)	11 (36)	2 (10)	4 (15)		4 (12)		3 (9)				85 (275)
WFVZ - Camarillo	186 (787)	109 (361)	90 (366)	39 (118)	125 (561)	147 (532)	60 (218)	36 (112)			3 (9)	4 (17)	1 (2)	800 (3083)
ZMB - Berlin		5 (10)		1 (2)				1 (1)		3 (7)	2 (4)	1 (2)		13 (26)
Total by species	260 (1060)	244 (748)	117 (460)	193 (514)	134 (602)	185 (664)	61 (222)	138 (410)	2 (4)	9 (26)	8 (17)	6 (21)	1 (2)	1358 (4750)

Tabela S2 - Descrição das características de reprodução das 13 espécies de ***Tyrannus****. A tabela mostra o tamanho médio da ninhada e do ovo, o desvio padrão, o intervalo e o número da amostra entre parênteses.*

Species	Clutch size	Clutch size range	Egg size	Egg size range (mm^3)
T. albogularis	2	2 (2)	3522.5 ± 435.77	3140-3980, (4)
T. caudifasciatus	4	4 (1)	4631.14 ± 185.12	4356.55-4760.02, (4)
T. couchii	3.58 ± 0.6	3-5 (55)	4186.37 ± 355.38	3227.2-5281.53, (196)
T. crassirostris	4.25 ± 0.96	3-5 (4)	4545.88 ± 403.51	3514.43-5260, (17)
T. cubensis	3	3 (1)	5565 ± 21.21	5550-5580, (2)
T. dominicensis	3.17 ± 0.62	2-5 (212)	4470.08 ± 358.12	3413.45-5711.94, (665)
T. forficatus	4.59 ± 0.69	2-6 (123)	3337.61 ± 292.82	2434.46-4472.76, (554)
T. melancholicus	2.65 ± 0.65	2-4 (158)	3874.83 ± 387.74	2770-5199.03, (398)
T. niveigularis	3 ± 1	2-4 (3)	3733.33 ± 164.16	3490-3940, (9)
T. savana	3.13 ± 0.71	2-5 (129)	2933.71 ± 288.05	2233.46-3827.19, (393)
T. tyrannus	3.68 ± 0.69	2-6 (159)	3853.3 ± 377.41	2245.13-5140, (573)
T. verticalis	4.27 ± 0.71	2-6 (215)	3703.83 ± 322.52	2465.92-4925.18, (902)
T. vociferans	4.07 ± 0.74	3-6 (94)	3699.06 ± 319.38	2891.56-4823.67, (380)

Tabela S3 – Climas de acordo com Köppen-Geiger e suas descrições de temperatura e precipitação para os quais as respectivas espécies de ***Tyrannus*** *foram registradas. O tamanho da amostra de ninhadas e ovos é mostrado para cada clima principal e subclima para cada espécie. Fonte: Adaptado de* Kottek et al. (2006).

Main climate	Main climate sample	Sub-climate	Sub-climate sample	Species
A Equatorial climates (Tmin ≥+18 ◦C)	309 (838)	Af Rainforest, fully humid Pmin ≥ 60 mm	31 (74)	*Tyrannus dominicensis* (12[27]), *Tyrannus melancholicus* (12[30]), *Tyrannus niveigularis* (3[5]), *Tyrannus savana* (4[12])
		Am Monsoon Pann ≥ 25(100−Pmin)	48 (129)	*Tyrannus caudifasciatus* (4[12]), *Tyrannus couchii* (4[14]), *Tyrannus cubensis* (1[2]), *Tyrannus dominicensis* (8[23]), *Tyrannus melancholicus* (29[71]), *Tyrannus savana* (2[7])
		As Savannah, with dry summer Pmin < 60 mm in summer	9 (31)	*Tyrannus crassirostris* (2[4]), *Tyrannus melancholicus* (7[27])
		Aw Savannah, with dry winter Pmin < 60 mm in winter	221 (604)	*Tyrannus albogularis* (2[4]), *Tyrannus caudifasciatus* (5[14]), *Tyrannus couchii* (30[106]), *Tyrannus dominicensis* (42[105]), *Tyrannus forficatus* (1[5]), *Tyrannus melancholicus* (71[181]), *Tyrannus niveigularis* (4[9]), *Tyrannus savana* (66[180])
B Arid climates (Pann < 10 Pth)	246 (945)	BSh Steppe climate Pann > 5 Pth Hot Tann ≥+18 ◦C	79 (291)	*Tyrannus couchii* (9[35]), *Tyrannus crassirostris* (2[8]), *Tyrannus melancholicus* (13[33]), *Tyrannus savana* (3[8]), *Tyrannus verticalis* (32[128]), *Tyrannus vociferans* (20[79])
		BSk Steppe climate Pann > 5 Pth Cold Tann <+18 ◦C	144 (568)	*Tyrannus crassirostris* (1[5]), *Tyrannus forficatus* (5[23]), *Tyrannus melancholicus* (4[16]), *Tyrannus savana* (2[5]), *Tyrannus tyrannus* (10[36]), *Tyrannus verticalis* (77[303]), *Tyrannus vociferans* (45[180])
		BWh Desert climate Pann ≤ 5 Pth Hot Tann ≥+18 ◦C	14 (53)	*Tyrannus melancholicus* (7[22]), *Tyrannus niveigularis* (1[3]), *Tyrannus verticalis* (5[24]), *Tyrannus vociferans* (1[4])
		BWk Desert climate Pann ≤ 5 Pth Cold Tann <+18 ◦C	9 (33)	*Tyrannus verticalis* (4[16]), *Tyrannus vociferans* (5[17])

C Warm temperate climate (-3 ◦C < Tmin <+18 ◦C)	717 (2649)	Cfa Fully humid neither Cs nor Cw Hot summer Tmax ≥+22 ◦C	518 (1882)	*Tyrannus couchii* (15[56]), *Tyrannus dominicensis* (182[593]), *Tyrannus forficatus* (128[574]), *Tyrannus melancholicus* (34[89]), *Tyrannus savana* (44[144]), *Tyrannus tyrannus* (100[356]), *Tyrannus verticalis* (14[65]), *Tyrannus vociferans* (1[5])
		Cfb Fully humid neither Cs nor Cw Warm summer not (a) and at least 4 Tmon ≥+10 ◦C	10 (32)	*Tyrannus melancholicus* (2[5]), *Tyrannus savana* (1[2]), *Tyrannus tyrannus* (5[18]), *Tyrannus verticalis* (1[3]), *Tyrannus vociferans* (1[4])
		Csa Dry summer Psmin < Pwmin, Pwmax > 3 Psmin and Psmin < 40 mm Hot summer Tmax ≥+22 ◦C	75 (306)	*Tyrannus crassirostris* (1[4]), *Tyrannus verticalis* (58[241]), *Tyrannus vociferans* (16[61])
		Csb Dry summer Psmin < Pwmin, Pwmax > 3 Psmin and Psmin < 40 mm Warm summer not (a) and at least 4 Tmon ≥+10 ◦C	82 (329)	*Tyrannus tyrannus* (1[4]), *Tyrannus verticalis* (53[215]), *Tyrannus vociferans* (28[110])
		Cwa Dry winter Pwmin < Psmin and Psmax > 10 Pwmin Hot summer Tmax ≥+22 ◦C	29 (89)	*Tyrannus couchii* (3[11]), *Tyrannus melancholicus* (12[33]), *Tyrannus savana* (14[45])
		Cwb Dry winter Pwmin < Psmin and Psmax > 10 Pwmin Warm summer not (a) and at least 4 Tmon ≥+10 ◦C	3 (11)	*Tyrannus melancholicus* (2[7]), *Tyrannus verticalis* (1[4])
D Snow climates (Tmin ≤-3 ◦C)	84 (311)	Dfa Fully humid Neither Ds (Psmin < Pwmin, Pwmax > 3 Psmin and Psmin < 40 mm) nor Dw (Pwmin < Psmin and Psmax > 10 Pwmin) Hot summer Tmax ≥+22 ◦C	21 (71)	*Tyrannus tyrannus* (18[62]), *Tyrannus verticalis* (3[9])
		Dfb Fully humid	57 (219)	*Tyrannus tyrannus* (48[178]), *Tyrannus verticalis* (9[41])

	Neither Ds (Psmin < Pwmin, Pwmax > 3 Psmin and Psmin < 40 mm) nor Dw (Pwmin < Psmin and Psmax > 10 Pwmin) Warm summer not (a) and at least 4 Tmon ≥+10 °C		
	Dfc Fully humid Neither Ds (Psmin < Pwmin, Pwmax > 3 Psmin and Psmin < 40 mm) nor Dw (Pwmin < Psmin and Psmax > 10 Pwmin) Cool summer and cold winter not (b) and Tmin >−38 °C	6 (21)	*Tyrannus tyrannus* (3[10]), *Tyrannus verticalis* (3[11])

Tabela S4 - Descrição das variáveis do local de reprodução usadas como preditores para analisar a relação entre as características reprodutivas (tamanho dos ovos e da ninhada) de espécies de aves do gênero ***Tyrannus*** *com condições climáticas de longo e curto prazo.*

	Variável	**Descrição**	**Justificativa**
Janela de longo prazo	Anom.Tmax	Temperatura máxima do mês mais quente (ºC)	A temperatura média máxima extrema registrada para o local de reprodução no mês mais quente determina o quanto as temperaturas aumentaram.
	Anom.Tmin	Temperatura mínima do mês mais frio (ºC)	A temperatura mínima média registrada para o local de reprodução no mês mais frio determina a severidade das condições de inverno.
	Anom.Tiso	Isotermalidade (média da temperatura mensal/intervalo anual de temperatura) *100)	Grau de variação da temperatura durante o ano anterior à data de postura. Quanto maior a isotermalidade, menor a variação de temperatura.
	Anom.Pseas	Sazonalidade da precipitação	Quanta chuva foi distribuída um ano antes da data de postura. Quanto maior for a sazonalidade da precipitação, maior será a probabilidade de períodos de seca e de chuvas concentradas nos períodos.
	Anom.Pmin	Precipitação do mês mais seco (mm^3)	Precipitação acumulada registrada para o mês mais seco do ano antes da postura.
	Anom.Pmax	Precipitação do mês mais úmido	Precipitação acumulada que foi registrada no mês mais chuvoso do ano anterior à postura.
Janela de curto prazo	Anom.Tmxm1	Temperatura máxima do mês anterior à postura (ºC)	A média das temperaturas mais altas registradas pelos indivíduos no mês anterior à postura.
	Anom.Tmx.m	Temperatura máxima do mês de postura (ºC)	A média das temperaturas mais altas que os indivíduos experimentaram no mês de postura.
	Anom.Tmnm1	A temperatura mínima do mês anterior à postura (ºC)	A média das temperaturas mais baixas que os indivíduos experimentaram no mês anterior à postura.
	Anom.Tmn.m	A temperatura mínima do mês de postura (ºC)	A média das temperaturas mais baixas assistida pelos indivíduos no mês de postura.
	Anom.Pr.m1	Precipitação do mês anterior à postura (mm^3)	Precipitação acumulada assistida pelos indivíduos no mês anterior à postura.
	Anom.Pre.m	Precipitação do mês de postura (mm^3)	Precipitação acumulada assistida pelos indivíduos no mês de postura.