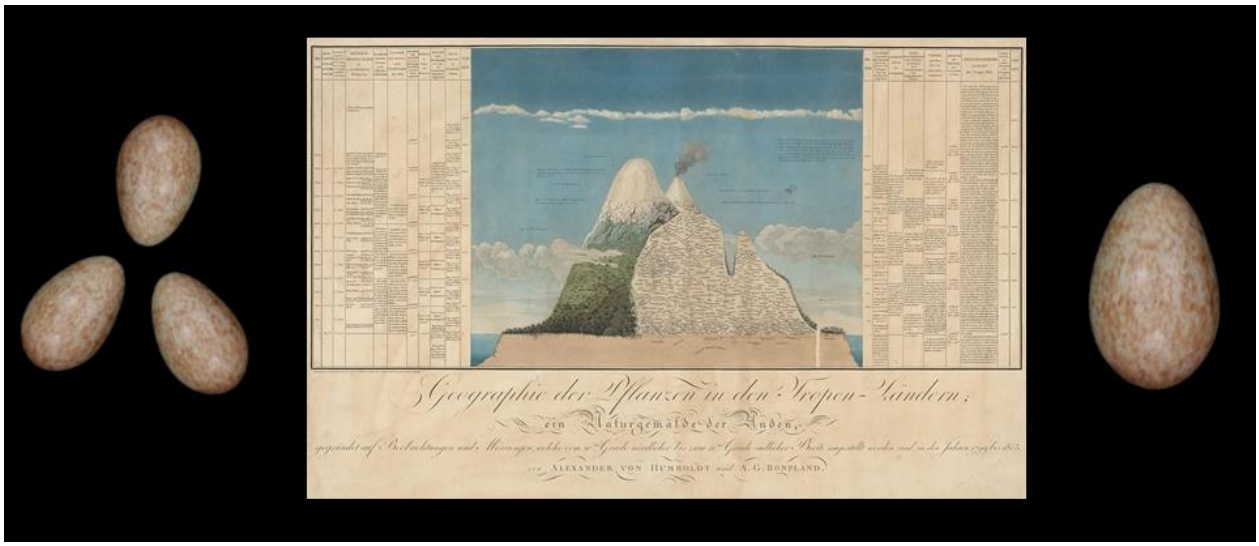
Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Ecologia

LAUREN RUMPEL TEIXEIRA

EXPLORANDO AS COMPLEXIDADES DA BIOLOGIA REPRODUTIVA DE AVES NEOTROPICAIS AO LONGO DE GRADIENTES DE ELEVAÇÃO



Brasília – DF
2024

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EXPLORANDO AS COMPLEXIDADES DA BIOLOGIA REPRODUTIVA DE AVES NEOTROPICAIS AO LONGO DE GRADIENTES DE ELEVAÇÃO

Tese apresentada à Comissão Examinadora de Doutorado do Programa de Pós-Graduação em Ecologia, do Instituto de Ciências Biológicas da Universidade de Brasília para a obtenção do título de Doutora em Ecologia

Orientador: Prof. Dr. Miguel Ângelo Marini

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Imagens da capa:

Esquerda e direita: Ovos de *Turdus grayi* - Museu de Costa Rica – fotografia feita por Lauren Rumpel Teixeira.

Meio: Infográfico “A Naturgemälde” (1807) de Alexander von Humboldt.

.

Dedico este trabalho com todo carinho às minhas sobrinhas

Eu fico com a pureza

Da resposta das crianças

É a vida, é bonita

E é bonita

Viver e não ter a vergonha

De ser feliz

Cantar, e cantar, e cantar

A beleza de ser um eterno aprendiz

O que é, O que é? – Gonzaguinha

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RESUMO GERAL

A pesquisa sobre a história de vida das aves visa compreender as causas e consequências das estratégias reprodutivas das espécies. Nas aves, estratégias reprodutivas, como o tamanho da ninhada, tamanho dos ovos, sucesso reprodutivo e a duração do período reprodutivo, estão intrinsecamente ligadas ao ambiente em que habitam. Os gradientes de elevação oferecem uma perspectiva única para investigar a história de vida, uma vez que fatores abióticos, como temperatura, precipitação e pressão atmosférica, e fatores bióticos, como predação, variam nesses gradientes, impactando as estratégias reprodutivas das aves. Em altitudes maiores, observamos uma redução gradual da temperatura, enquanto a precipitação pode variar significativamente, influenciando a produtividade do ambiente e a disponibilidade de recursos alimentares. Além do mais, as mudanças climáticas podem reorganizar, restringir ou até extinguir espécies em diferentes altitudes. Os três capítulos desta tese exploram os padrões reprodutivos, focando no tamanho da ninhada e no volume do ovo em gradientes de elevação. No primeiro capítulo, investigamos a hipótese de que o tamanho da ninhada é menor em maiores altitudes. O segundo capítulo analisa a variação no volume do ovo em relação a fatores ambientais e ecológicos em gradientes de elevação, considerando, por exemplo, o tipo de ninho. A hipótese é que em temperaturas mais baixas e com maior precipitação o tamanho do ovo aumente. O tipo de ninho também é um fator influente, com ninhos fechados favorecendo um microclima ideal, possivelmente resultando em ovos menores. O terceiro capítulo analisa a influência da temperatura e precipitação nos últimos 120 anos no tamanho da ninhada e volume dos ovos em três faixas altitudinais. A principal hipótese prevê um aumento da temperatura como protagonista na modificação da história de vida das espécies, levando a uma diminuição no tamanho da ninhada e no volume do ovo. Encontramos aumento de 1°C temperatura mínima mensal em 120 anos. Provavelmente foi o principal fator que levou a redução tamanho dos ovos conforme os anos passam e em todos os gradientes altitudinais, mas o tamanho da ninhada não se mostrou significativo. A exploração dos gradientes de elevação tropicais permanece um aspecto crucial a ser investigado, especialmente para compreender os investimentos reprodutivos das aves nessas regiões elevadas. Em síntese, a pesquisa destaca a influência dos gradientes de elevação nas estratégias reprodutivas das aves, evidenciando respostas distintas relacionadas ao tamanho da ninhada e volume do ovo. Observa-se uma adaptação sensível ao ambiente, onde fatores climáticos e ecológicos moldam essas

estratégias. As análises mostraram que com o aumento de 1°C em 120 anos já houve modificações de características reprodutivas. Desta forma, enfatizamos a importância de compreendermos o impacto das mudanças ambientais nas populações de aves, especialmente em regiões tropicais de elevação. Essas novas informações contribuem para uma compreensão mais abrangente da ecologia reprodutiva das aves em gradientes altitudinais da região Neotropical.

Palavras-chave: Passeriformes, altitude, características reprodutivas, tamanho da ninhada, volume do ovo, clima, mudanças climáticas.

ABSTRACT

Research into the life history of birds aims to understand the causes and consequences of species' reproductive strategies. In birds, reproductive strategies such as clutch size, egg size, reproductive success and the length of the reproductive period are intrinsically linked to the environment they inhabit. Elevation gradients offer a unique perspective for investigating life history, since abiotic factors, such as temperature, precipitation and atmospheric pressure, and biotic factors, such as predation, vary across these gradients, impacting the birds' reproductive strategies. At higher altitudes, we see a gradual reduction in temperature, while precipitation can vary significantly, influencing the productivity of the environment and the availability of food resources. Furthermore, climate change can reorganize, restrict or even extinguish species at different altitudes. The three chapters of this thesis explore reproductive patterns, focusing on clutch size and egg volume across elevation gradients. In the first chapter, we investigate the hypothesis that clutch size is smaller at higher altitudes. The second chapter analyzes the variation in egg volume in relation to environmental and ecological factors in elevation gradients, considering, for example, the type of nest. The hypothesis is that at lower temperatures and with more precipitation, egg size increases. The type of nest is also an influential factor, with closed nests favoring an ideal microclimate, possibly resulting in smaller eggs. The third chapter employs a historical analysis to investigate the influence of temperature and rainfall over the last 120 years on clutch size and egg volume across three altitudinal ranges. The primary hypothesis posits that an increase in

temperature plays a pivotal role in influencing the life history of the species, resulting in a reduction in clutch size and egg volume. A 1°C increase in the minimum monthly temperature was observed over the 120-year period. This was likely the primary factor contributing to the observed reduction in egg size over time and across all altitudinal gradients, although clutch size did not show a significant trend. Further investigation into tropical elevation gradients is crucial, particularly to gain insight into the reproductive strategies of birds in these elevated regions. In conclusion, the research demonstrates the impact of elevation gradients on the reproductive strategies of birds, exhibiting divergent responses with regard to clutch size and egg volume. An environmentally sensitive adaptation is observed, whereby climatic and ecological factors shape these strategies. The analyses demonstrated that an increase of 1°C over 120 years has already resulted in changes to reproductive characteristics. Consequently, we emphasize the importance of understanding the impact of environmental changes on bird populations, particularly in tropical regions of elevation. This new information contributes to a more comprehensive understanding of the reproductive ecology of birds across altitudinal gradients in the Neotropical region.

Keywords: Passeriformes, altitude, reproductive effort, clutch size, egg volume, climate, climate change.

INTRODUÇÃO GERAL

Investigações em regiões montanhosas tiveram início com o naturalista Alexander von Humboldt (1769 - 1859), o qual forneceu conhecimento em botânica e geologia e tornou-se um dos primeiros a estudar sistematicamente os efeitos dos fatores físicos, como a altitude e topográfica na distribuição das espécies. Suas ideias influenciaram e guiaram grandes nomes como de Charles Darwin (Helferich 2004). Experimentos naturais usando gradientes altitudinais têm sido empregados para investigar o impacto de diversos fatores ambientais, tais como temperatura, precipitação, pressão atmosférica e radiação solar (Körner 2007) e nos fornecem informações importantes sobre as espécies (Grinnell 1914). Sua influência é grande o suficiente para que indivíduos de uma única população experimentem pressões seletivas diferentes em diferentes altitudes (Lundblad et al. 2020). Assim, a mesma espécie pode ter características reprodutivas singulares em diferentes gradientes de elevação.

Um objetivo crucial na ecologia é compreender os mecanismos que influenciam os processos ecológicos e a composição das comunidades ao longo de gradientes geográficos (MacArthur et al. 1967; Diamond 1975; Hubbell 1979). A pesquisa sobre a história de vida das aves visa discernir as causas e consequências da variação nas estratégias reprodutivas (Martin 1987; Roff 1992; Stearns 1992). Em aves, tais estratégias incluem aspectos como sucesso de nidificação, tamanho de ninhada e duração do ciclo do ninho, sendo estreitamente vinculadas ao habitat (Ricklefs 2000). A plasticidade fenotípica, isto é, a habilidade de indivíduos moldarem suas características em resposta ao ambiente, pode influenciar processos ecológicos, dinâmicas populacionais, e aspectos funcionais de comunidades e ecossistemas (Miner et al. 2005).

Ao longo dos anos, vários pesquisadores exploraram os padrões reprodutivos relacionados ao tamanho de ninhada em gradientes latitudinais. Moreau (1944) propôs que o tamanho de ninhada é maior em regiões temperadas do que tropicais. Lack (1947) sugeriu que em latitudes mais altas, o tamanho de ninhada é maior devido ao maior tempo disponível para forrageamento, resultante de um fotoperíodo prolongado. Skutch (1949) sugeriu que aves nos trópicos têm tamanhos de ninhada reduzidos devido à alta taxa de predação de ninhos. Por fim, Ashmole (1963) defendeu a hipótese da sazonalidade de recursos, sugerindo que em estações com alta mortalidade (inverno), a disponibilidade de recursos na estação reprodutiva aumenta para uma baixa densidade populacional,

resultando em ninhadas maiores. Essas perspectivas ilustram a busca por padrões na variação do tamanho de ninhada em relação à latitude nas últimas décadas, destacando a necessidade de investigações semelhantes em gradientes de elevação.

Nesse contexto, estudos têm explorado as variações nas estratégias de história de vida em populações de aves relacionadas à elevação (Martin 2001). Uma análise da literatura ratificou que o tamanho de ninhada tende a diminuir com o aumento da elevação, destacando a carência de estudos abrangentes em gradientes de elevação na região Neotropical (Hille & Cooper et al. 2015). Uma meta-análise, envolvendo pesquisas sobre reprodução em gradientes de elevação, evidenciou uma diminuição na fecundidade, com tamanhos de ninhada menores e uma elevação na sobrevivência adulta (Boyle et al. 2016). Uma possível explicação para essa redução no tamanho de ninhada é a escassez de recursos alimentares, resultante da diminuição da temperatura e da produtividade primária (Boyle et al. 2016). Apesar da existência de estudos sobre investimento reprodutivo em gradientes de elevação, uma análise mais abrangente em termos geográficos é necessária para discernir padrões reprodutivos altitudinais na região Neotropical.

Espécies que se reproduzem ao longo de gradientes de elevação enfrentam condições ambientais diversas em escalas espaciais relativamente curtas (Bears et al. 2009). Diversos fatores, como pressão atmosférica, temperatura, precipitação, produtividade e taxa de predação de ninhos em gradientes de elevação, impactam a história de vida das espécies (**Figura 1**). A pressão atmosférica e a temperatura diminuem em média 11% e 5,5ºC, respectivamente, a cada 1.000 m de elevação (Barry 1981, Körner 2000), padrão observado também em montanhas tropicais (Forero-Medina et al. 2011; Freeman & Class Freeman 2014). A precipitação pode variar em gradientes de elevação, geralmente sendo mais elevada em altitudes médias (Sanders et al. 2003; Kluge et al. 2006). Em gradientes tropicais de elevação, o regime de chuvas é variável, com máximas próximas ao nível do mar (Lauscher 1976; Barry 2008; Colberg & Anders 2014). As baixas temperaturas afetam a produtividade primária, embora a relação entre produtividade e temperaturas mais baixas possa ser invertida em gradientes de elevação devido à precipitação (Boyle et al. 2016). Além disso, locais tropicais de maior elevação são menos sazonais e não apresentam picos anuais de produtividade (Scholer et al. 2019). No que diz respeito à taxa de predação em ninhos, alguns estudos observaram que ela é menor em altas elevações (Skutch 1985; Boyle 2008, Londoño et al. 2023), embora essa

relação ainda não esteja totalmente esclarecida em toda a região Neotropical (Sandercock et al. 2005). A exploração dessas variáveis oferece uma base mais sólida para uma compreensão aprimorada da história de vida de aves em sistemas tropicais.

Figura 1: Mapa mental dos efeitos esperados da altitude sobre a história de vida de aves em baixa e alta elevação. Flechas azuis = aumento da característica; vermelho = redução e bolas amarelas = variação. Adaptado de Hille & Cooper et al. (2015).

Apesar de ainda ser um tema pouco explorado (Martin et al. 2006), o ovo é um excelente modelo para compreender o investimento energético por estação reprodutiva (Deeming 2007; Deeming & Reynolds 2015). Sendo um sistema fechado, a ave alocará todos os recursos alimentares necessários para o desenvolvimento do embrião, e a taxa de transformação desses recursos para a formação do embrião dependerá da quantidade de calor transferida pelos progenitores durante a incubação (Brua 2002; Deeming 2002). O clima e a disponibilidade de alimento determinarão o quanto o indivíduo poderá investir

por ninhada. Geralmente, ocorre um *trade-off* (conflito) entre o investimento no volume do ovo e o tamanho da ninhada.

O tamanho da ninhada está vinculado à aptidão individual em diferentes épocas e regiões (Ricklefs & Bloom 1977). O aumento no tamanho da ninhada está associado à taxa de ganho de energia proporcionada pelas condições ambientais na área de vida do indivíduo (Bêty et al. 2003). Em elevações mais altas, o tamanho da ninhada frequentemente diminui (Bears et al. 2009) (ex. Järvinen 1989; Badyaev & Ghalambor 2001; Lu et al. 2005; Boyce et al. 2015; Dillon & Conway 2015, Balasubramaniam & Rotenberry, 2016; Johnson et al. 2018; Guo & Lu 2022). No entanto, poucos estudos se concentraram em analisar o tamanho do ovo em gradientes altitudinais na região Neotropical, com a maioria indicando aumento no tamanho do ovo (Lu et al. 2005, 2008a, 2008b, Guo & Lu 2022; Levin et al. 2023; Deckel et al. 2024), e um estudo encontrou ovos menores, explicados pela baixa condição corporal das fêmeas reprodutoras (Johnson et al. 2018).

O tipo de ninho também exerce influência no tamanho da ninhada. Além de servir como local para incubação e criação dos ovos e ninhegos (Heenan, 2013), os ninhos desempenham uma função reguladora de temperatura, umidade e pH para o desenvolvimento da prole (Collias & Collias, 1984) e oferecem proteção contra predadores (Mainwaring et al., 2014). O microclima interno do ninho pode otimizar o desenvolvimento embrionário, resultando em melhor desempenho e sobrevivência dos ninhegos (Durant et al., 2013; Ospina et al., 2018). No entanto, em altitudes mais elevadas, muitas espécies reduzem o tamanho da ninhada e/ou aumentam o investimento parental (Badyaev & Ghalambor, 2001), implicando em maior dispêndio de energia pelos pais (Biebach, 1984; Williams, 1996; Nord & Williams, 2015). A incubação de ninhadas maiores pode acarretar maiores custos, prejudicando a sobrevivência e a reprodução dos pais (Hanssen et al., 2005; de Heij & Tinbergen, 2006). Assim, a diminuição do tamanho da ninhada pode representar uma estratégia para compensar o elevado gasto energético dos pais, especialmente em ninhos abertos.

A compreensão da biologia das aves em gradientes de elevação, quando comparada às espécies de regiões mais baixas, ainda é menos abrangente (Boyle & Martin 2015). Dessa maneira, surge a necessidade de estudos que comparem as histórias de vida dessas aves, levando em consideração latitude, continentalidade e peculiaridades

regionais (Hille & Cooper 2015). Além disso, muitas espécies têm alterado suas distribuições em resposta a mudanças ambientais recentes e perda de habitat. Essa movimentação ocorre geralmente nos polos ou em altas elevações e é relatada em diversos grupos (Parmesan & Yohe 2003; Alexander et al. 2018). Dunn (2004) demonstrou mudanças significativas no tamanho de ninhada ou no sucesso reprodutivo associado às mudanças climáticas. Se houver essa reorganização, espécies de baixas elevações podem ajustar sua distribuição em direção a maiores elevações em busca da temperatura ideal para seu desenvolvimento, podendo, assim, alterar o investimento reprodutivo. Ainda existem questões relevantes a serem respondidas sobre a história de vida das aves em gradientes de elevação tropicais, especialmente em uma escala geográfica mais ampla. Além disso, as mudanças climáticas podem impactar a distribuição e a história de vida das espécies, tanto em áreas de planície quanto em elevações mais altas. Para minimizar os impactos negativos de grandes mudanças em espécies tropicais de maior altitude, será necessário um esforço conjunto (Freeman et al. 2018). Para obter uma resposta em nível continental, análises em larga escala só são viáveis com a compilação de dados disponíveis na literatura e em coleções científicas.

As coleções oológicas globais abrigam aproximadamente 1.9 milhões de ninhadas, sendo que cerca de 313 mil pertencem à região Neotropical (Marini et al. 2020). Essa vasta reserva de dados possibilita abordagens multifacetadas para entender a história de vida das aves. Tantos espécimes quanto ovos e ninhos oferecem riqueza em dados, permitindo investigações temporais, geográficas e filogenéticas. No entanto, apesar da disponibilidade em coleções científicas em todo o mundo, esses dados ainda são subutilizados pelos pesquisadores (Russell et al. 2013). Diante da necessidade contínua de compreender a história de vida das aves, este estudo explora a aliança entre a falta de informações e a relevância da utilização de dados de coleções científicas e bases de dados, visando entender os padrões reprodutivos das aves em gradientes de elevação na região Neotropical e projetar um panorama reprodutivo futuro dessas espécies.

Dados coletados

Considerando a vasta quantidade de dados armazenados em coleções ornitológicas, realizamos visitas a 37 museus (e acessamos dados da literatura para o capítulo 1) para responder questões relacionadas ao investimento reprodutivo de aves em

gradientes neotropicais. Esses museus acessados estão localizados na Europa, América do Sul, América Central e América do Norte (**Figura 2**). Para a elaboração desta tese, foram analisadas 5.889 ninhadas de 285 espécies de Passeriformes pertencentes a 12 famílias, provenientes de coleções de ovos e dados da literatura.

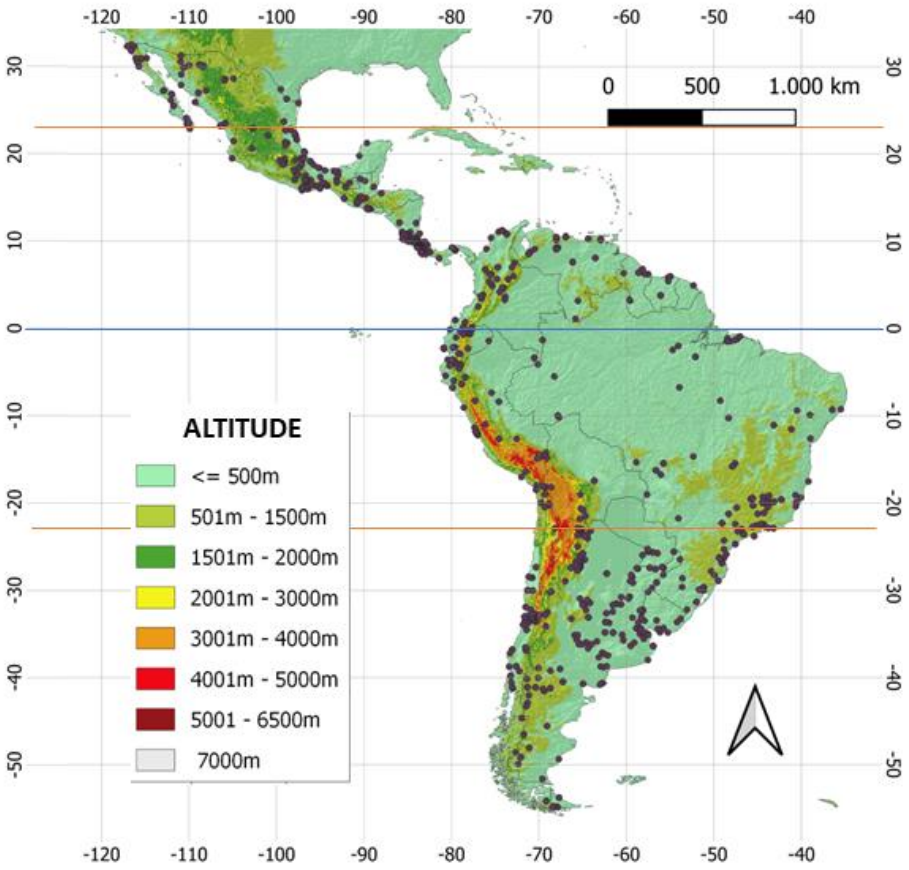


Figura 2: Distribuição geográfica das 5.889 ninhadas (pontos pretos) utilizadas neste estudo. Linha laranja indica trópico de câncer e capricórnio; linha azul indica a linha do equador; (m) metros.

Objetivo geral

Esta tese tem como propósito aprofundar o entendimento dos parâmetros reprodutivos de Passeriformes Neotropicais em gradientes de elevação. Está estruturada nos seguintes capítulos:

Capítulo I – "*Passerine clutch size decreases at higher altitudes in the Neotropics"*

Neste capítulo, o objetivo foi compreender se o tamanho de ninhada varia com o aumento da altitude e se o tipo de ninho, aberto, cúpula e cavidade, exerce influência sobre o tamanho da ninhada em gradientes altitudinais. Também comparamos o tamanho das ninhadas entre as famílias de Passeriformes.

Capítulo II – "*Altitudinal effects of climate and nest type on egg volume of Neotropical Passerines"*

O objetivo deste capítulo foi analisar se há modificações no volume do ovo à medida que a altitude aumenta e identificar quais variáveis climáticas exercem maior influência nesses gradientes. Além disso, propõe-se verificar se o tipo de ninho aberto, cúpula ou cavidade, exerce influência sobre o tamanho do ovo em gradientes altitudinais.

Capítulo III – *"Impact of climate change on Neotropical Passeriformes: A 120-year data of reproductive traits across elevation gradients"*

O objetivo deste capítulo foi analisar dados históricos de 120 anos para investigar como o clima afeta o tamanho do ovo e o tamanho de ninhada de Passeriformes ao longo de gradientes altitudinais.

CAPÍTULO I

Passerine clutch size decreases at higher altitudes in the Neotropics

Lauren Rumpel, Eduardo Guimarães Santos, Neander Marcel Heming and Miguel Ângelo Marini

1. CAPÍTULO I: Passerine clutch size decreases at higher altitudes in the Neotropics

running title: Clutch size changes with altitude

Abstract

Elevation provides important information about the characteristics/adaptations of species, and a single species can experience different selective pressures across an altitudinal gradient. Animals living at higher altitudes have a slower "pace of life" compared to those at lower altitudes. However, most studies on reproduction in altitudinal gradients have been carried out in temperate regions, and most species have shown changes in reproductive investment, such as smaller clutch sizes and shorter reproductive seasons with increasing altitude. Our objective was to identify whether there is a change interspecific and intraspecific in clutch size of Passeriformes across altitudinal gradients in the Neotropical region. We carried out a phylogenetic analysis (PGLMM), where clutch size was used as the response variable and altitude, nest type and taxonomic family as fixed variables, controlling for latitudinal variation and phylogeny. We used 5,889 clutches from 285 species of Passeriformes, comprising 65 genera from 12 families. The results showed that species reduce clutch size as altitude increases, and open nests showed greater reductions in egg numbers.. Of the 18 species analyzed, 16 showed a negative relationship, two a positive one, but only five a significant one. We found a significant negative relationship between clutch size and increasing altitude for only three families (Furnariidae, Icteridae and Parulidae), but when we inserted the interaction (Altitude * Family), no relationship was significant. We conclude that Neotropical Passeriformes are reducing their reproductive effort in relation to clutch size at higher altitudes, but there are major response differences among bird families and in relation to nest type. In addition, it is possible that the birds' physiology for living in low temperatures means that they are constrained to lay a reduced number of eggs per clutch.

Keywords: Reproductive effort, elevation, life history, phylogeny.

Translated abstracts [Portuguese]

A elevação fornece informações importantes sobre as características/adaptações das espécies, e uma única espécie pode experimentar pressões seletivas diferentes em um gradiente altitudinal. Animais que vivem em altitudes maiores apresentam o "ritmo de vida" mais lento em comparação aos de altitudes menores. Entretanto, a maioria dos estudos sobre reprodução em gradientes altitudinais foram feitos em regiões temperadas, e a maioria das espécies apresentaram modificações no investimento reprodutivo, como tamanho de ninhada menor e menor estação reprodutiva com a altitude. Nosso objetivo foi identificar se há mudança interespecifica e intraespecifica no tamanho de ninhada de Passeriformes em gradientes altitudinais na região Neotropical. Fizemos uma análise filogenética (PGLMM), onde o tamanho de ninhada foi utilizado como variável resposta e altitude, tipo de ninho (aberto, fechado e cavidade) e família taxonômica como variáveis fixas, controlando a variação latitudinal e a filogenia. Utilizamos 5.889 ninhadas de 285 espécies de Passeriformes, compreendendo 65 gêneros de 12 famílias. Os resultados mostraram que as espécies reduzem o tamanho de ninhada conforme a altitude aumenta e o ninho aberto mostrou reduzir ainda mais o número de ovos. Das 18 espécies analisadas, 16 mostraram relação negativa, dois positiva, mas apenas cinco significativa. Encontramos relação negativa significativa do tamanho da ninhada conforme a altitude aumenta para apenas três famílias (Furnariidae, Icteridae e Parulidae), mas quando inserimos a interação (Altitude * Família), nenhuma mostrou-se significativa. Concluímos que os Passeriformes Neotropicais estão reduzindo o esforço reprodutivo em relação a tamanho da ninhada em maiores altitudes, mas que existem grandes diferenças entre famílias de aves e em relação ao tipo de ninho. Além disso, é possivelmente que a fisiologia para viver em locais com baixa temperatura faça com que as aves coloquem um número reduzido de ovos por ninhada.

Palavras-chave: Esforço reprodutivo, elevação, história de vida, filogenia.

1.1. Introduction

Diversity in life history strategies is a central theme in evolutionary ecology (Partridge & Harvey, 1988). Variation within species across their geographical distributions is increasingly being observed, which may have important consequences for population responses to environmental changes (Reed et al., 2011). Furthermore, this variation also occurs in relation to elevation gradients, where altitudinal gradients can serve as a proxy for temporal changes induced by climate change (Cody, 1966; Körner, 2007).

In addition to the reproductive characteristics of birds being shaped by environmental conditions, ecological and phylogenetic characteristics also influence the reproductive life history of birds (Stearns, 1992). High elevation environments share similar environmental characteristics to temperate regions, such as: lower temperatures, greater seasonality, greater environmental stochasticity and, consequently, shorter breeding seasons (Martin, 2001; Boyle et al., 2015). There is a 5.5ºC reduction in temperature and an 11% reduction in atmospheric pressure for every 1,000 m increase in elevation (Barry 2008; Körner, 2000). Thus, the environmental changes observed make high elevation environments more demanding for organisms that live in them, especially during the reproductive period. Clutch size, for example, is related to the rate of energy gain by the individual provided by the environmental conditions in its living area (Bêty et al., 2003). To cope with the extreme conditions generated by the higher elevation environment, birds have developed specific behaviors and physiological characteristics (Wilson & Martin, 2011). It is therefore expected that species nesting at high elevations will reduce their clutch size.

Various studies on the reproductive biology of birds and latitudinal geographical gradients have shown that the higher the latitude, the larger the clutch size (Moreau, 1944), and the shorter the reproductive period in temperate regions (Baker 1938). Moreau (1944) argued that the clutch size of birds is larger in temperate zones than in tropical ones. Lack (1947), proposed that at higher latitudes clutch size is larger because there is more time for foraging due to the greater amount of light available per day (photoperiod). Skutch (1949) suggested that birds in the tropics have reduced clutch sizes due to the high rate of nest predation. Ashmole (1963) defended the resource seasonality hypothesis, which suggests that in seasons with a high mortality rate (in

winter), the number of resources in the breeding season becomes high for a low population density, resulting in an increase in clutch size. Finally, Martin (1995) proposed that adult survival decreases as reproduction increases. Therefore, tropical species have greater adult survival, but reproduce less. This shows that a pattern has been sought to understand the variation in clutch size in relation to latitude (Moreau 1944, Lack 1947, 1968, Skutch 1949, Ashmole 1963, Ricklefs 2000), and the same should be investigated in elevation gradients.

The general pattern known between species from tropical and temperate regions, is that tropical species exhibit the slow "pace of life" syndrome (Sandercock et al. 2005; Hille & Cooper 2015; Boyle et al. 2016). This means, for example, reduced clutch size and higher adult survival of tropical than of temperate species (Martin, 1996, 2004, Ricklefs, 2000). Animals living at high elevations also have a slow "pace of life" strategy, with high rates of energy expenditure due to the costs of maintenance and acclimatization to lower temperatures (McKechnie & Swanson, 2010). This can usually cause clutch size to reduce with elevation (e.g. Badyaev & Ghalambor, 2001; Bears et al., 2009; Boyce et al., 2015; Dillon & Conway, 2015, 2018; Johnson et al., 2018; Lu et al., 2009, 2010; Garcia-Navas et al., 2021; Guo & Lu, 2022; Levin et al., 2023). However, there are only a few studies on the life history of birds at higher elevations in the tropical region (Boyce et al. 2015, Boyle et al., 2016; Hille & Cooper 2015; Londoño et al., 2023), with a poor knowledge on the effects on reproduction, including reproductive period, incubation period, clutch size, egg size, and reproductive success. The meta-analysis by Boyle et al. (2016) showed that there is a reduction in clutch size in tropical areas, although not all species show the same pattern. Boyce et al. (2015) studied three tropical areas of low and high elevation, finding a reduction in clutch size and the existence of geographical variation. However, they included island areas and the data showed an even smaller clutch size on islands than on the mainland. The authors also suggest the need for intraspecific analyses. One of the biotic explanations for the low investment in clutch size in tropical regions is the high nest predation rate (Skutch, 1949). Despite the high diversity of nest predators in the Neotropical region (Menezes & Marini, 2017), there are few studies suggesting lower nest predation at higher tropical elevations (Skutch, 1985; Boyle 2008; Londoño et al., 2023). Thus, the lower predation rates at higher elevations suggest larger clutches, contrary to the pattern found in studies involving clutch size and altitudinal gradients. Therefore, another factor may be related

444 to the smaller clutch size at higher elevations, such as high rates of energy expenditure
445 (e.g. low temperatures). Smaller clutches reheat faster, reducing the parents' energy
446 costs during incubation (Biebach, 1981; Conway & Martin, 2000), compensating for the
447 high metabolic cost at low temperatures (Camfield & Martin, 2009). In addition, low
448 temperature reduces net primary productivity, and consequently reduces food
449 availability (Whittaker et al., 1974; Raich et al., 1997; Sundqvist et al., 2013). Although
450 temperature decreases with elevation, rainfall varies greatly depending on the altitudinal
451 region, and this variation in rainfall can maintain or reverse the relationship between
452 elevation and plant productivity (Boyle et al., 2015). Therefore, low food availability
453 can vary among elevations due to variations in rainfall. And this suggests that low food
454 availability at higher elevations can favor smaller broods (Badyaev, 1997). Finally,
455 reductions in clutch size in high-elevation tropical birds may also reflect an adaptive
456 strategy of a slow life history associated with higher adult survival at higher elevations
457 (Martin, 2002, 2004). Despite the emergence of several hypotheses, an analysis on a
458 larger, tropical geographic scale is still needed.

459 The type of nest can also influence the size of the clutch. Besides providing a
460 place/receptacle for the eggs and nestlings (Heenan, 2013), nests have a regulatory
461 function in terms of temperature, humidity and pH for the development of nestlings
462 (Collias & Collias, 1984), as well as provide protection against predators (Mainwaring
463 et al., 2014). The insulating function of the closed nest can be important in altricial
464 Passeriformes, whose nestlings are incapable of thermoregulation (Hansell, 2000), as it
465 reduces the parents' costs of heating the eggs and nestlings (O'Connor, 1975; Haftorn &
466 Reinertsen, 1985). In low-temperature locations, the insulating function of a nest can be
467 important for maintaining a suitable microclimate for eggs, nestlings, and parents, so
468 birds may also select materials with low thermal conductivity (Heenan et al., 2015). The
469 microclimate inside the nest can promote the embryonic development of the eggs,
470 which improves the performance and survival of the nestlings (Durant et al., 2019;
471 Ospina et al., 2018). However, at higher elevations, many species reduce clutch size
472 and/or increase the time spent on parental care (Badyaev & Ghalambor, 2001), requiring
473 greater energy expenditure from the parents (Biebach, 1981; Williams, 1996; Nord &
474 Williams, 2015). Incubating larger broods can have significant costs, reducing parental
475 survival and reproduction (Hanssen et al., 2005; de Heij et al., 2006). In this way,

476 reducing the clutch size can be a way of compensating for the high energy expenditure
477 of the parents, especially in open-cup nesters.

478 Therefore, in this study we aim to better understand how bird reproduction
479 changes with elevation gradients in the Neotropical region. Based on 5,889 clutches of
480 285 species of Neotropical Passeriformes, we tested whether there is a interspecific and
481 intraspecific change in clutch size across elevation gradients and among three types of
482 nests (open,cavity and domed). We also sought to understand whether the same pattern
483 holds among 12 families of Passeriformes to evaluate if there is a phylogenetic effect.
484 Our main hypotheses are that clutch size decreases with increasing elevation, and that
485 closed nests have a smaller decrease in number of eggs than open nests with increasing
486 elevation, a pattern known at lower elevations.

487

488 ## 1.2. Methods

489

490 ### 1.2.1. Database

491

492 We used two complementary data sets in our analyses: (1) historical records of
493 egg sets deposited in scientific collections (**Supplementary materials – S1a, S3a and**
494 **S3a**), and (2) nesting records in the literature. Data from scientific collections was
495 collected from the 37 museums in Europe, South America, Central America and North
496 America. At each museum, egg sets were photographed along with their label/card
497 containing all the available information. We included in our analysis all species from
498 the Neotropical region, from the northern border of Mexico to the southern tip of South
499 America (Parker database in Stotz 1996) that contained information on the species
500 name, clutch size, and collection date and locality.

501 We searched the literature (Google Scholar) for papers related to the
502 reproduction of species, using the keywords: "breeding biology" OR "reproduction"
503 AND "species name". This search was carried out separately for each species of interest
504 and only for species with little data in higher altitude environments **(See**
505 **supplementary materials – S3a**). Only articles with information on clutch size,
506 complete locality and elevation were considered. This literature search made it possible
507 to add 125 clutches from 24 species (Aráoz et al., 2017; Ávalos & Gomes, 2010;

Collins & Ryan, 1994; Costa et al., 2019; Dyrcz & Greeney, 2010; Hapluka & Greeney, 2009; Greeney, 2009; Greeney et al, 2011; Hartert & Venturi, 1909; Alarcón et al., 2023; Martinez, 2019; Morales-Rozo et al., 2009; Valdez et al., 2023; Olaciregui & Botero-Delgadillo, 2012; Peraza, 2009; Pozo-Zamora, 2014; Salaman et al., 1998; Salvador, 1992; Salvador, 2015; Solano-Ugalde et al., 2007).

Nests were classified into three types: open (cup), domed (spheres, domes, pendons) and cavity (nests inside trunks and terrain, according to 'Birds of the World' (Billerman et al., 2022).

1.2.2. Taxonomic resolution

Since egg sets deposited in museums might have outdated taxonomy, we made a taxonomic resolution by checking for synonyms of the species names in the cards/labels, following a temporal sequence of species name catalogs published from 1874 to 1987, depending on the date of egg set collection. A taxonomic update was made using the British Museum of Natural History catalogs (Seebohm, 1881; Sclatter, 1986, 1988; Sharpe, 1888), followed by the catalogs of the Field Museum of Natural History (Cory & Hellmayr, 1924, 1925, 1927; Hellmayr, 1934, 1935, 1936, 1937, 1938) and the Museum of Comparative Zoology (Peters, 1951; Mayr & Paynter, 1964; Paynter, 1967, 1968, 1970; Traylor, 1979). Finally, the scientific name was updated according to Clements et al. (2022).

1.2.3. Clutch selection

To diminish inconsistencies and egg set records with possible conflicting/suspicious information, we were strict and selective when it came to consider an egg set a true clutch and include it in our analysis. First, only clutches from 2 to 6 eggs with a complete location, i.e. with country, state and municipality, were considered. However, for *Troglodytes aedon*, clutches of 2 to 9 eggs were considered, as this species lays more eggs than the other species selected (de la Peña, 2013). One-egg clutches are very rare in tropical passerines (but see Sánchez Martínez & Londoño, 2012), but some were considered as valid when the information in the slip/card stated

that the clutch was complete. The clutch size was checked according to the minimum and maximum number of eggs for each species. Clutch sizes outside the margin for each species were removed from the data base. We excluded clutches with eggs of nest parasites (*Molothrus* spp. and *Tapera naevia*) because they can reduce clutch size by ejecting the eggs (Sick, 1997). We also excluded clutches located outside the breeding range of each species, and clutches from islands. Species that nest on islands have a different reproductive biology than species that nest in the mainland, known as “island syndrome” (Blondel, 1985, Blondel et al., 1992, Covas, 2012), with smaller clutches (Jezierski, 2024).

1.2.4. Determining elevation and geographical coordinates

We determined the elevation of the clutches recorded using first, information available in the slips/cards, and then, using Google Earth and Neotropical gazetteers (Paynter Jr., 1982, 1988, 1989, 1992, 1993, 1994, 1995, 1997; Paynter & Traylor 1991, Stevens & Traylor Jr., 1983, 1985), where the clutch's collection site was entered, and the elevation and geographical coordinate obtained individually for each clutch. To determine the elevation, only georeferenced records were considered, or records where elevation determination was possible with an error of ± 100 meters.

1.2.5. Data analysis

To control for shared evolutionary history, a phylogenetic generalized linear mixed models (PGLMM) (Ives & Helmus, 2011) was performed using the 'pglmm' function from the 'phyr' package (Li et al., 2020) with the "poisson" family in the R version 4.2.1 program (R Core Team 2023). The phylogenetic signal was also calculated using Pagel's λ value (lambda) using the 'ape' package (Paradis & Schliep, 2019). Pagel's hypothesis was calculated with the 'phylosig' function of the "phytools" package (Revell, 2012). Pagel's λ calculates the phylogenetic signal of the data, where 1 indicates high phylogenetic signal and 0 low phylogenetic signal (Pagel, 1999). Phylogenetic trees were obtained using the website porbirdtree.org (Ericksont All Species; Jetz et al., 2012). We obtained the consensus tree and branch lengths from the ‘ape’ R package (Paradis et al., 2004). Clutch size was used as the response variable and

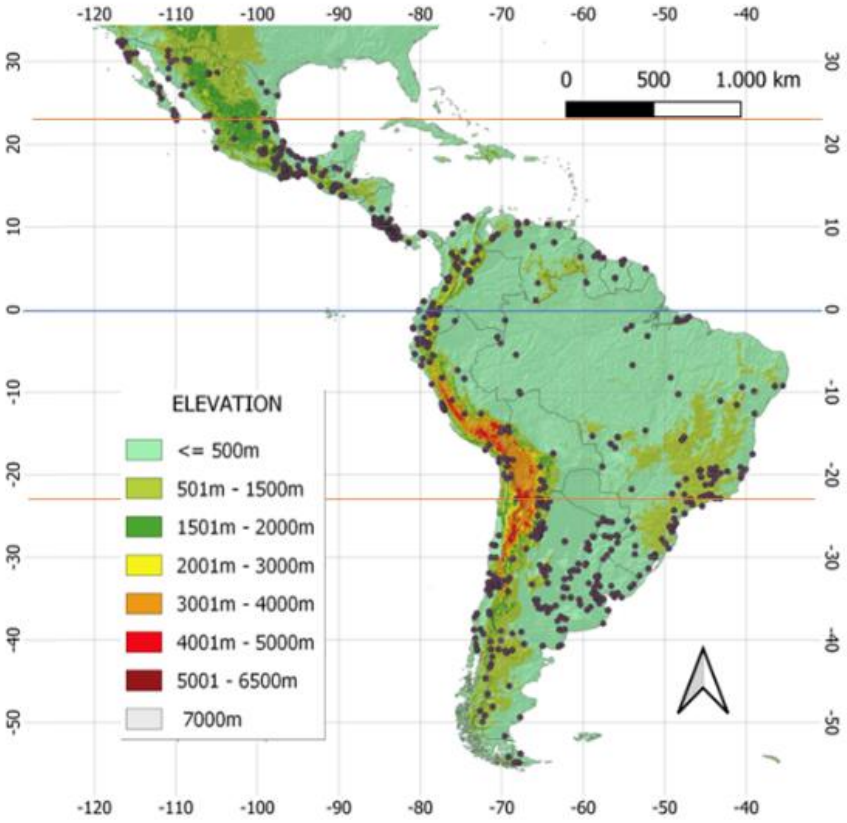
elevation (scale transformation), taxonomy family and nest type as fixed variables. Phylogeny and latitudinal (degree only) effect were controlled for in the analyses. Elevation was used as a continuous variable. We also run separate analyses for 18 species that were distributed along a large altitudinal range (at least 2,000 m) and that we had large sample sizes (40 egg sets).

1.3. Results

We used data from 5,889 clutches of 285 species of Passeriformes, comprising 65 genera from 12 families, collected between 1856 and 2023. We used clutches from 20 countries between 30N to 55S degrees latitude (**Figure 1.1**), and with an altitudinal distribution from 0 to 4,600 meters above sea level. Of the 285 species, 164 have open nests (n =3,638 egg sets), 81 have domed nests (n = 1,462 egg sets), and 40 have cavity nests (n = 789 egg sets). The clutches used in this study come from 12 families: Cotingidae (n = 148), Icteridae (n = 67), Fringillidae (n = 60), Furnariidae (n = 297), Hirundinidae (n = 52), Mimidae (n = 279), Parulidae (n = 177), Passerellidae (n = 438), Thraupidae (n = 1,354), Troglodytidae (n = 522), Turdidae (n = 955), Tyrannidae (n = 1,510).

The phylogenetic signal for the "clutch size" trait was close to 1 (Pagel's λ = 0.86; C.I = 95%, 0,75-0,93), i.e. it has a phylogenetic signal. The PGLMM showed a negative relationship with clutch size as elevation increased (PGLMM Z score = -3.31, p = 0.0009) (**Figure 1.2**), with an average clutch size of 3.1 eggs at sea level and 2.4 eggs at 4,000 m elevation, so for every 1.000 m increase in elevation, there is a decrease of 0.18 eggs per clutch.

Clutch sizes of all three types of nest decreased as elevation increased (**Figure 1.3**), this relation was stronger for open nests (Z score = -4.93, $p < 0.001$). Of the 18 species analyzed (**Supplementary materials – S2a**), 16 showed a negative relationship, two a positive one, but only five a significant one. Of the 12 families analyzed, Furnariidae, Icteridae, Parulidae had a significant negative relationship between clutch size and increasing elevation (**Table 1-1**).



604

605 **Figure 1.1:** Geographic distribution of the 5,889 clutches (black dots) used in this
606 study. Orange line indicates Tropic of Cancer and Capricorn; blue line indicates the
607 equator; (m) meters.

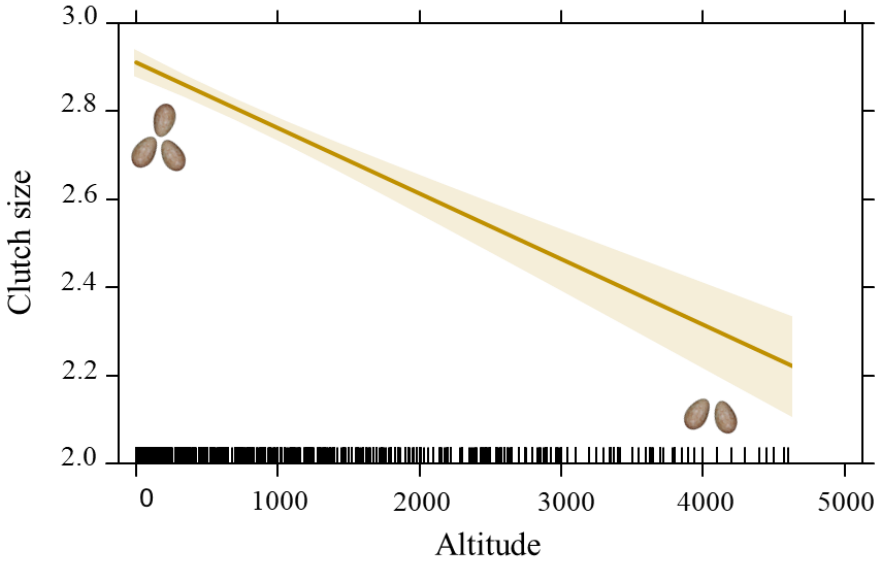
608

609 **Table 1-1:** Parameter estimates and tests from phylogenetic generalized linear mixed
610 models (PGLMM) of clutch size, nest and families.

	Estimate	**SE**	**Z score**	**P value**
Intercept	1.23	0.06	18.5	< 0.001
Altitude	-0.32	0.00	-3.31	**< 0.001**
Nest - Dome	-0.06	0.03	-2.04	**0.04**
Nest - Open	-0.20	0.04	-4.93	**< 0.001**
Icteridae	0.29	0.09	-2.932	**0.003**
Furnariidae	0.26	0.07	-3.77	**< 0.001**
Parulidae	-0.14	0.07	-2.05	**0.03**
Troglodytidae	0.10	0.06	1.67	0.09
Passerellidae	-0.09	0.05	-1.695	0.09
Fringillidae	0.06	0.08	0.74	0.4

Mimidae	0.04	0.06	0.675	0.5
Thraupidae	-0.03	0.05	-0.718	0.5
Turdidae	-0.20	0.05	-0.506	0.6
Tyrannidae	-0.02	0.05	-0.37	0.7
Hirundinidae	0.01	0.10	0.177	0.8
R-squared value = 0.3033				

611



612

613 **Figure 1.2:** Clutch size of Neotropical birds in relation to elevation (m). Black
614 markings indicate the density of clutches. The yellow shading corresponds to the 95%
615 confidence interval**.**

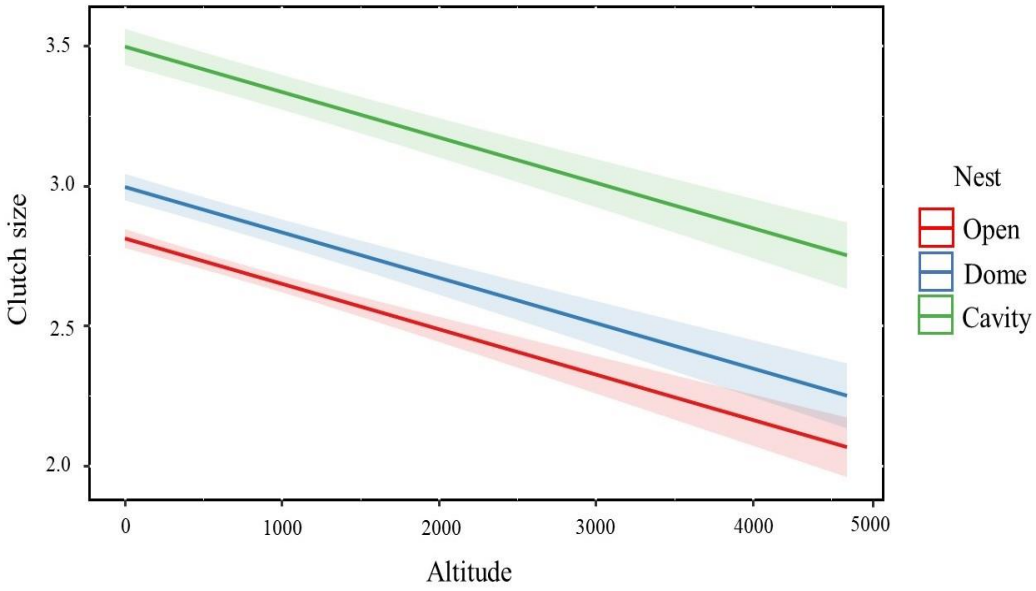


Figure 1.3: Clutch size of Neotropical birds with open (red), cavity (green), and domed (blue) nests in relation to elevation (m). Shaded areas around trend lines correspond to the 95% confidence interval.

When we analyze the 18 most abundant species in relation to the number of clutches (**Supplementary materials - S1b and S5a**), we found that 16 species showed a negative relationship, and two a positive relationship. Of the 16 species with a negative relationship, only five were significant.

1.4. Discussion

We demonstrated a significant effect of elevation on bird clutch size. This is the first study to analyze clutch size in relation to elevation on a broad geographic scale in the Neotropics, encompassing 12 families and 285 species. We found a phylogenetic effect, showing the relative influence of evolution on current ecology (Pagel, 1999).

The results obtained showed that clutch size decreased as elevation increased. This finding is consistent with other studies carried out in tropical (Skutch, 1985; Boyce et al., 2015; Boyle et al., 2016; Hille & Cooper, 2015; Balasubramaniam & Rotenberry, 2016; Levin et al., 2023; Londoño et al. 2023) and other (Badyaev, 1997; Badyaev & Ghalambor, 2001; Johnson et al., 2018; Garcia-Navas et al., 2021; Guo & Lu; 2022; Li

et al., 2012, 2022; Liu et al., 2023) regions. One of the largest studies in the tropics was conducted by Boyce et al. (2015), the study in question examined passerine species in three tropical areas-Venezuela, Borneo, and New Guinea-and found a significant negative relationship in clutch size, clarifying much of the pattern observed for clutch size at tropical altitudes. In our study, we analyzed 20 countries in the continental Neotropical region, excluding data from islands to avoid the "island syndrome" (Blondel, 1985; Blondel et al., 1992; Covas, 2012). Thus, our data indicate a reduction in reproductive investment related to clutch size at higher altitudes in the Neotropics.

Our results showed that for every 1.000 m of increase in elevation, there is a decrease of 0.18 eggs per clutch, meaning that tropical species, besides reducing clutch size with latitude, reduce their clutch size even more at higher elevations (Boyce et al., 2015). However, in a study carried out in Colombia with *Zonotrichia capensis*, no difference was found in clutch size in relation to elevation (Cardona-Salazar et al., 2021), a result that agrees with our lack of relationship for Passerellidae, but not when we evaluate only *Zonotrichia capensis* from our database. The authors argue that evolutionary time may have been too short to have altered clutch size. However, perhaps the altitudinal range of the area sampled is too narrow within higher elevations (1,800-3,800 meters) for the species to change its clutch size. Therefore, our study corroborates the majority of studies carried out to date, with a consistent reduction in reproductive investment in relation to elevation.

Explanations for the smaller clutch sizes of tropical than temperate species include short foraging time (photoperiod) (Lack, 1947), the high predation rate (Skutch, 1949) or the seasonality of resources (Ashmole, 1963), and higher adult survival (Martin, 1995, 2004). Photoperiod does not seem to be a plausible explanation for our results, given that photoperiod does not vary among elevations at the same latitude. Regarding nest predation rate, some studies have observed that it is lower as elevation increases (Skutch, 1985; Boyle, 2008; Londoño et al., 2023), but this pattern is not yet fully understood (Sandercock et al., 2005), and this hypothesis needs to be tested in more areas of the altitudinal gradient in the Neotropical region. Foraging time per breeding season at higher elevations is reduced compared to low elevations (Hille & Cooper, 2015), favoring smaller clutches. Finally, the species' strategy of reducing clutch size is associated with high adult survival (Martin, 1995, 2004). Although we

669 don't have specific studies on adult survival at higher altitudes, we can suggest that
670 species are decreasing reproduction and increasing adult survival.

671 Food availability may be one explanation for the reduction in clutch size.
672 Primary productivity and temperature at higher elevations are lower than at lower
673 elevations, so food availability is lower (Sundqvist et al., 2013; Balasubramaniam &
674 Rotenberry, 2016; Boyle et al., 2016). However, it is still necessary to quantify food
675 resources at different elevations to relate them to clutch size (Ruffino et al., 2014).
676 Productivity is also linked to rainfall, and it may be necessary to quantify this type of
677 factor in each region sampled. Despite this, in view of the consistency of our findings,
678 we consider that the food resource may be a consistent explanation to the reduction in
679 reproductive investment, expressed here in the reduced number of eggs per clutch.

680 The type of nest is a relevant variable that should be considered in studies, as it
681 is directly related to reproductive investment, given the control of the microclimate. In
682 fact, for birds, nest microclimate influences the survival of embryos and the growth of
683 nestlings (Lundy, 1969). It was expected that the closed nest, by maintaining a suitable
684 microclimate, would maintain the number of eggs as elevation increased. However, our
685 results were partially contrary, as we found that clutch size decreased with altitude for
686 all three types of nests. When the parent leaves the nest, the temperature of the eggs is
687 determined by precipitation, ambient temperature, solar radiation and wind (Haftorn,
688 1978; Webb & King, 1983; Carey, 2002). The fact that the nest is more exposed to these
689 climatic factors can lead to a smaller clutch, precisely because the smaller the clutch, the
690 less energy the parents spend on heating the clutch (O'Connor, 1975; Haftorn &
691 Reinertsen, 1985). However, clutch reduction can also work to minimize the costs of
692 lower food availability while dealing with higher metabolic costs and colder
693 temperatures (Camfield & Martin, 2009).

694 Predation is a relevant factor and should be considered when we seek to
695 understand the influences related to the reproductive investment of birds. Some studies
696 suggest that predation at higher elevations is reduced (Skutch, 1985; Boyle, 2008;
697 Londoño et al., 2023). This is contrary to the hypothesis that the high rate of predation
698 in the tropics promotes a decrease in clutch size (Skutch, 1949). Londoño et al. (2023),
699 evaluated predation between closed and open nests across altitudinal gradients in
700 Colombia and recorded a small reduction in the predation rate in closed nests, but found

no statistically significant difference between nest types. We therefore suggest that smaller clutch sizes at higher elevations occur at colder temperatures due to the constrain for thermoregulation of the eggs and nestlings (Hansell, 2000), thus reducing the parents' costs of heating the eggs and nestlings (O'Connor, 1975; Haftorn & Reinertsen, 1985).

Therefore, differences in clutch size may be due to short seasonal foraging activity and unfavorable weather conditions that negatively influence the available resources allocated to breeding (Cody, 1966; Fitch, 1985; Meiri et al., 2013), reducing clutch size. This leads us to understand that bird species nesting at higher elevations tend to adopt slower pace of life history strategies (Sandercock et al., 2005; Hille & Cooper, 2015; Boyle et al., 2016). The selection imposed by higher elevation tropical locations is strong enough to further drive the reduction in clutch size of bird species (Boyce et al., 2015).

The high variation of clutch size along altitudinal changes among families showed that there is a strong phylogenetic component in the response. Most of the 12 families analyzed showed no significant effect of clutch size and elevation. However, seven of the 12 families had a negative relationship of clutch size with elevation, with a significant relationship for three families (Furnariidae, Parulidae, Icteridae). Four families had a positive relationship of clutch size and elevation. Boyle et al. (2015) carried out a meta-analysis involving 101 species from tropical and temperate regions at low and high elevations, and although they found lower clutch size and greater offspring development, they did not find all the characteristics of the "slow pace of life" strategy. It is possible that different taxa have solved the same set of evolutionary challenges in different ways (Boyle et al., 2015). Alternatively, part of the non-significant results could be explained by the low number of families sampled or the distribution of data over altitude. Thus, reproductive biology at high elevations is still not entirely clear, and there seems to be multiple factors affecting birds from different families in various ways.

One of the families that showed a positive relationship was Troglodytidae. This family is widely distributed. Levin et al. (2023) analyzed the reproductive biology of *Troglodytes aedon* in altitudinal gradients in the southwestern United States (temperate region) and Costa Rica (tropical) and concluded that there is a reduction in clutch size in

both regions, especially in the tropical one. With the species *Troglodytes pacificus* in a study area in Canada, they found no reduction in clutch size (Evans-Ogden et al., 2012). Furthermore, among the families analyzed, this is the one with the greatest variation in the number of eggs per clutch.

Although this study has a wide geographical scale, studies involving life history and altitude of Neotropical birds are still scarce (Hille & Cooper, 2015; Boyce et al., 2015; Boyle et al., 2016; Londoño et al., 2023), and basic information is still needed for many species, such as clutch size and reproductive period. Future studies could analyze climatic variables such as temperature, precipitation, wind speed and humidity to try to determine what is altering clutch size across altitudinal gradients, because although temperature and other abiotic factors often change with elevation, they need not vary with elevation in a similar way across different elevation gradients, regionally or globally (Sundqvist et al., 2013). The Neotropical region lacks attention and research to better understand the life history of birds.

Our main hypothesis was supported for the as one explanation of the reduction in clutch size as elevation increases. However, we demonstrated that the nest type affects this relationship even more, with open and domed nesters having a greater reduction in clutch size that cavity nesters. It seems that the lower temperature at higher altitudes, is acting on clutch size, thus causing species to modify their life history in high elevation environments. Also, the large differences among bird families demonstrates a strong phylogenetic component and raises the question that the elevation effect on birds breeding traits may not be widespread and considered a rule.

1.5. References

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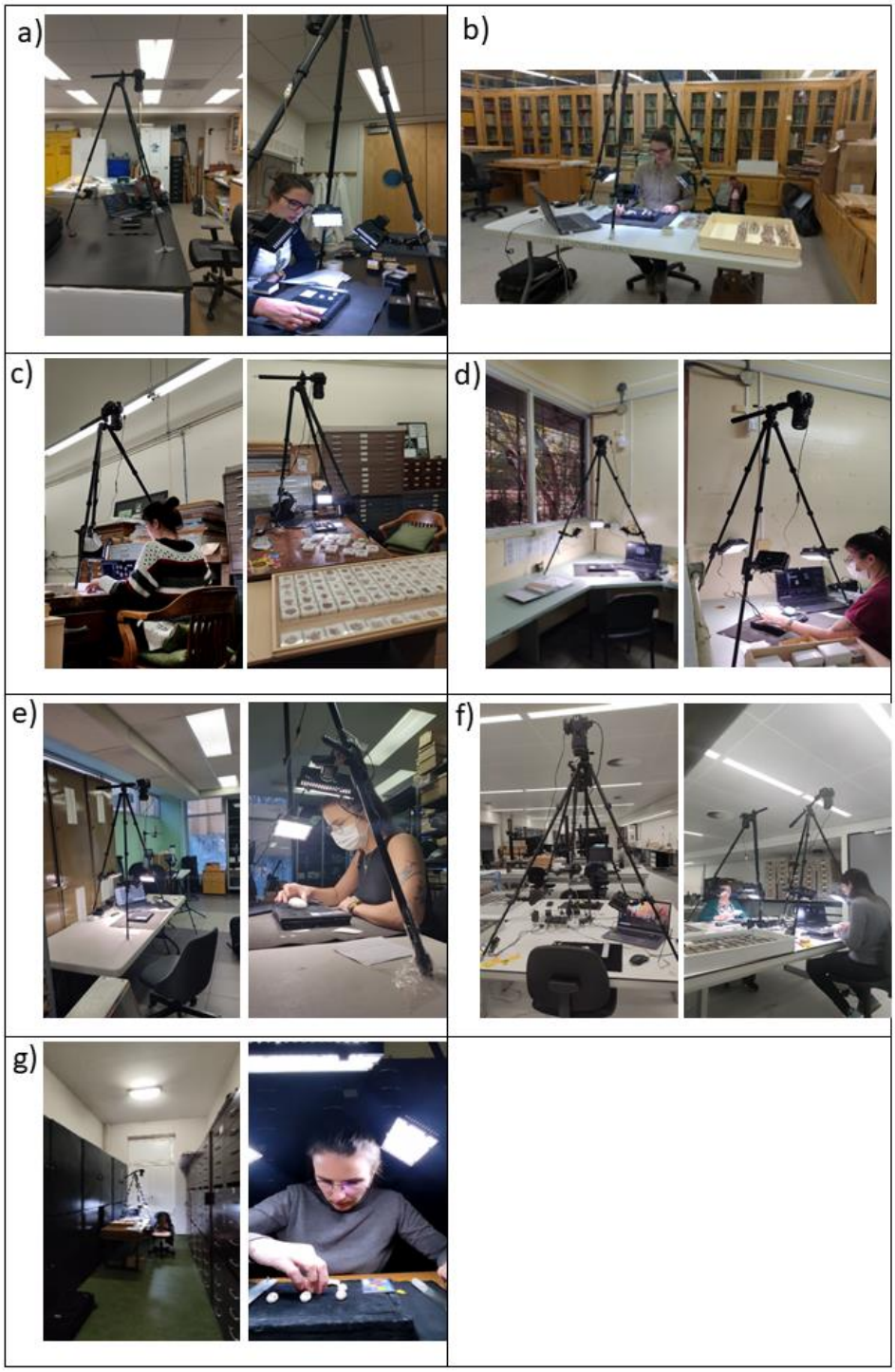
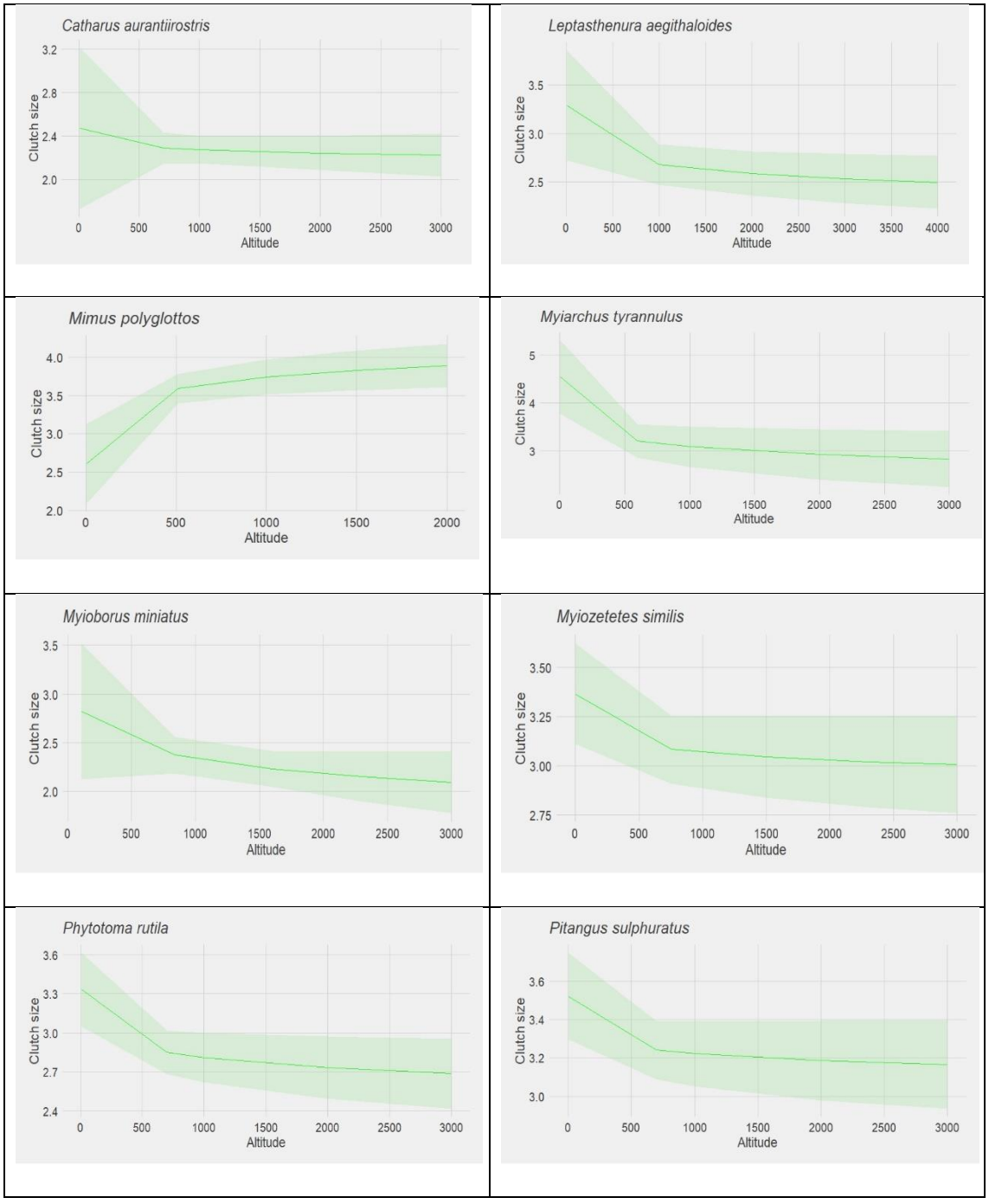
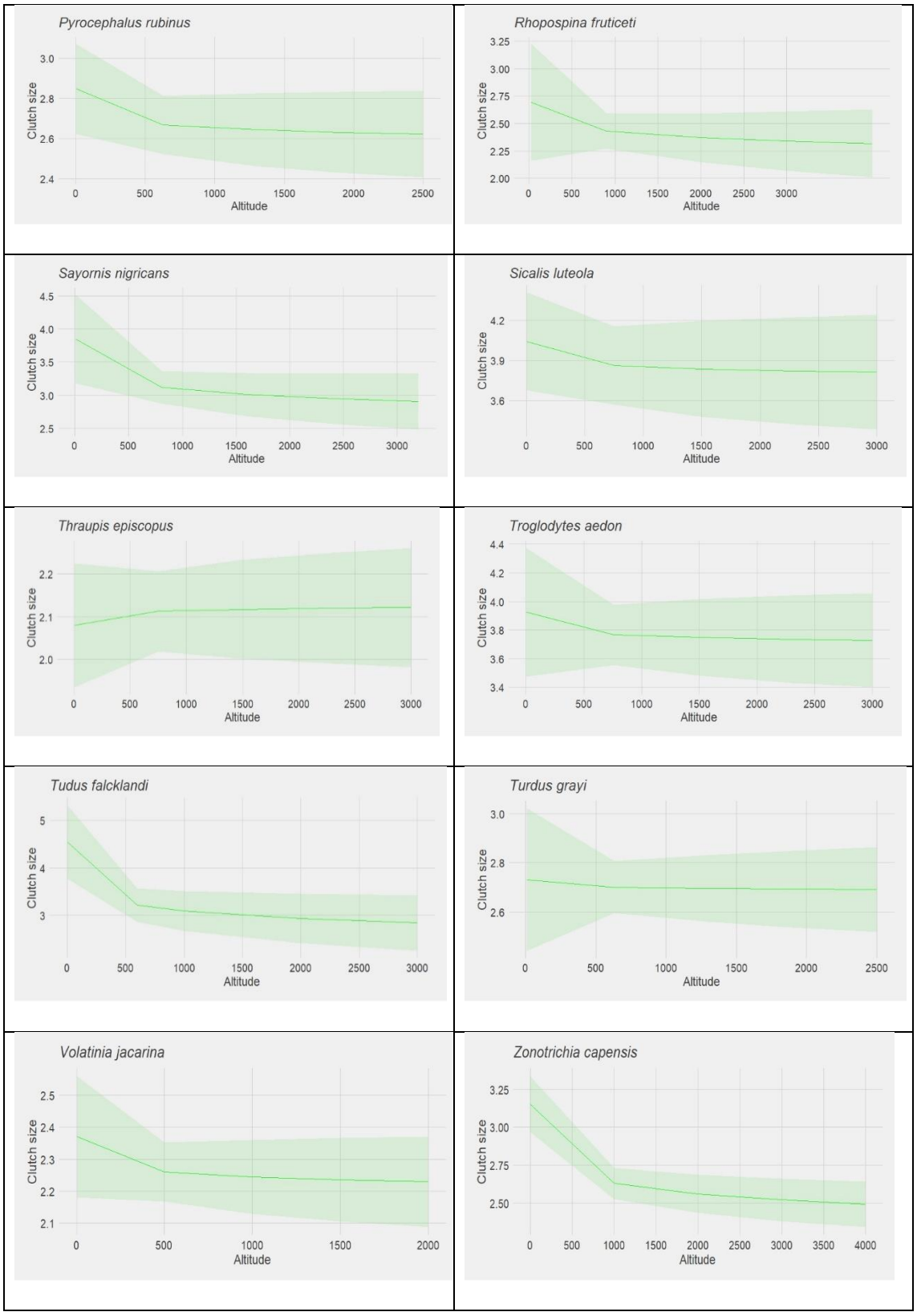
1.6. Supplementary materials



S1a: Collecting data in ornithological collections. a) California Academy of Sciences in San Francisco (CAS – San Francisco, EUA); b) San Bernardino County Museum (SBCM - San Bernadino, EUA); c) Western Foundation of Vertebrate Zoology (WFVZ – Camarillo, EUA); Universidad de Costa Rica (UCR – San José, Costa Rica); e) Museo

Nacional de Costa Rica (MNCR – San José, Costa Rica); f, Naturalis Biodiversity Center (NBCN – Leiden, Holanda) and g) Țării Crișurilor Museum (CRRP – Oradea, România).





S2a: Simple linear regression analysis for the 18 species analyzed. Plots are in alphabetical order.

1200 **S3a:** Total number of clutches collected in relation to museums and literature data.

1201

Museum/literature	Clutches	Literature	Clutches
AMNH - New York	191	de la Peña (2005)	332
CAS - San Francisco	6	de la Peña (2013)	10
COMB - Brasília	91	Di Giacomo (1992)	1
CRRP - Oradea	37	Dyrcz & Greeney (2010)	4
DMNH - Wilmington	181	Fraga & Narosky (1985)	16
FLMNH - Gainesville	1	Grant (1911)	1
FML - San Miguel de Tucumán	62	Greeney (2009)	2
FMNH - Chicago	5	Greeney (2010)	2
FZB - Porto Alegre	4	Greeney (2011)	3
IAvH - Villa de Leyva	45	Halupka & Greeney (2009)	23
MACN - Buenos Aires	199	Hartert & Venturi (1909)	2
MCZ - Cambridge	15	Hartert & Venturi (1906)	1
MHNG - Genebra	14	Hoy (1975)	1
MLP - La Plata	52	Hoy (1980)	2
MLUH - Halle	110	Alarcón et al. (2023)	4
MN - Rio de Janeiro	121	Ewert (1975)	2
MNCR - San José	70	Martinez (2019)	24
MNHN - Paris	2	Morales-Rozo et al. (2009)	3
MPEG - Belém	38	Narosky (1975)	1
MVZ - Berkeley	74	Narosky & Salvador (1998)	39
MZS - Strasbourg	1	Narosky et al. (1983)	11
MZUSP - São Paulo	159	Ocallez et al. (2023)	1
NBCN - Leiden	799	Olaciregui & Botero-Delgadillo (2012)	3
NHM - Tring	518	Partridge (MACN)	3
NMBE - Berna	77	Peraza (2009)	1
NMS - Edinburgh	66	Pereyra (1938)	1
NMW - Viena	15	Pozo-Zamora (2014)	1
PUCRS - Porto Alegre	4	Runnacles (MLP)	5
SBCM - San Bernardino	144	Salaman et al. (1998)	1
SNMB - Braunschweig	3	Salvador (1992)	1
UCR - San José	36	Salvador (1993)	1
UFRRJ - Seropédica	19	Salvador & Salvador (1984)	21
USNM - Washington	190	Salvador (2005)	28
WFVZ - Camarillo	1910	Salvador (2015)	40
ZMB - Berlin	18	Smyth (1928)	4
Literature		Solano-Ugalde et al. (2007)	2

Aráoz et al. (2017)	15
Avalos & Gomez (2010)	1
Barrows (1883)	1
Collins & Ryan (1994)	5
Costa et al. (2019)	3
	Clutches = 5,889

1202

1203 **S4a:** Scientific collection and localization. (*) data collected from the scientific

1204 collection database.

Acronym	Museum	Location
AMNH	American Museum of Natural History	New York, USA
CAS	California Academy of Science	San Francisco, USA
COMB	Coleção Ornitológica Marcelo Bagno	Brasília, Brazil
CRRM	Țării Crișurilor Museum	Oradia, Romania
DMNH	Delaware Museum of Natural History	Willmington, USA
FLMNH	Field Museum of Natural History	Chicago, USA*
FML	Fundación Miguel Lillo	Tucuman, Argentina
FMNH	Florida Museum of Natural History	Gainesville, USA
FZB	Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul	Porto Alegre, Brazil
IAvH	Instituto de Investigación de Recursos Biológicos Alexander von Humboldt	Villa de Leiva, Colombia
IBGE	Coleção do Instituto Brasileiro de Geografia e Estatística	Brasília, Brazil
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”	Buenos Aires, Argentina
MCZ	Museum of Comparative Zoology, Harvard University	Cambridge, USA
MHNG	Museum d’Histoire Naturelle de Genève	Genebra, Switzeland
MLP	Museu de La Plata	La Plata, Argentina
MLUH	Zentralmagazin Naturwissenschaftlicher Sammlungen, Martin Luther University Halle-Wittenberg	Halle, Germany
MN	Museu Nacional	Rio de Janeiro, Brazil

MNCR	Museo Nacional de Costa Rica	San José, Costa Rica
MNHN	Muséum National d'Histoire Naturelle	Paris, France
MPEG	Museu Paraense Emilio Goeldi	Belém, Brazil
MVZ	Museum of Vertebrate Zoology	Berkeley - USA*
MZS	Musée zoologique de l'Université Louis Pasteur et de la Ville de Strasbourg	Strasbourg, France
MZUC	Museo de Zoología de la Universidad de Concepción	Concepcion, Chile
MZUSP	Museu de Zoologia da Universidade de São Paulo	São Paulo, Brazil
NBCN	Nationaal Natuurhistorisch Museum	Leinden, Netherlands
NHM	Natural History Museum	Tring, Egland
NMBE	Naturhistorisches Museum Bern	Bern, Switzeland
NMS	National Museums of Scotland	Edinburgh, Scotland
NMW	Naturhistoriches Museum	Vienna, Austria
PUCRS	Museu de Ciências e Tecnologia da PUCRS	Porto Alegre, Brazil
SBCM	San Bernardino County Museum	San Bernadino, USA
SNMB	National Museum of Natural History	Braunschweig, Germany
UCR	Universidad de Costa Rica	San José, Costa Rica
UFRRJ	Universidade Rural do Rio de Janeiro	Rio de Janeiro, Brazil
USNM	Natural History Museum - Smithsonian Institution	Washington, USA
WFVZ	Western Foundation of Vertebrate Zoology	Camarillo, USA
ZMB	Museum für Naturkunde	Berlin, Germany

S5a: Results of the simple linear regression analysis of the 18 species. Values in bold are significant.

Species	Estimate	SE	T value	P value	Clutches
Zonotrichia capensis	-0.09	0.02	-4.36	< **0.001**	312
Mimus polyglottos	0.22	0.05	3.73	< **0.001**	40
Myiarchus tyrannulus	-0.23	0.08	-2.7	**0.008**	65
Phytotoma rutila	-0.11	0.04	-2.57	**0.01**	120
Leptasthenura aegithaloides	-0.13	0.05	-2.25	**0.03**	46

Sayornis nigricans	-0.15	0.08	-1.86	0.06	78
Pitangus sulphuratus	-0.05	0.03	-1.66	0.09	504
Myiozetetes similis	-0.05	0.03	-1.63	0.1	155
Myioborus miniatus	-0.22	0.14	-1.55	0.1	40
Pyrocephalus rubinus	-0.03	0.03	-1.10	0.3	172
Volatinia jacarina	-0.02	0.02	-0.94	0.3	143
Rhopospina fruticeti	-0.07	0.07	-0.98	0.3	47
Troglodytes aedon	-0.02	0.05	-0.52	0.6	378
Sicalis luteola	-0.03	0.07	-0.51	0.6	113
Catharus aurantiirostris	-0.04	0.07	-0.55	0.6	52
Thraupis episcopus	0.00	0.01	0.32	0.7	128
Turdus grayi	-0.00	0.03	-0.19	0.8	122
Turdus falcklandii	-0.01	0.05	-0.23	0.8	49

S6a: Total number of species used in this study, respective number of clutches and minimum and maximum record of the altitude of the collection site for each clutch. Taxonomy according to Clements (2022).

Species	**Clutches**	**Altitude (m)**	
		Smaller	Bigger
Acanthidops bairdi	20	1388	3100
Agriornis lividus	9	20	599
Agriornis micropterus	6	25	950
Agriornis montanus	15	116	4500
Aimophila rufescens	22	297	3973
Anairetes flavirostris	2	3245	3245
Anairetes parulus	56	10	2965
Arremon aurantiirostris	18	15	1400
Arremon basilicus	1		1200
Arremon brunneinucha	60	245	3048
Arremon castaneiceps	4	1075	1388
Arremon costaricensis	6	609	711
Arremon crassirostris	4	1111	1329
Arremon dorbignii	17	380	650
Arremon flavirostris	13	51	800
Arremon semitorquatus	4	10	730
Arremon taciturnus	9	20	360
Arremon torquatus	7	650	1950
Arremon virenticeps	8	2468	2468
Asthenes baeri	32	42	300
Asthenes dorbignyi	13	2041	3900
Asthenes fuliginosa	2	3000	3000

Asthenes hudsoni	41	3	128
Asthenes modesta	91	53	3720
Asthenes pyrrholeuca	36	26	2500
Asthenes sclateri	10	1806	4000
Asthenes steinbachi	6	2000	2954
Asthenes wyatti	3	3900	3900
Atlapetes albinucha	21	1100	1468
Atlapetes citrinellus	28	650	1650
Atlapetes fulviceps	5	1900	2500
Atlapetes latinuchus	6	1468	2500
Atlapetes leucopis	1		2200
Atlapetes melanocephalus	6	2100	2580
Atlapetes pallidinucha	1		2800
Atlapetes pileatus	11	1828	3048
Atlapetes schistaceus	2	1400	1400
Basileuterus culicivorus	21	23	650
Basileuterus culicivorus	3	75	75
Basileuterus lachrymosus	8	245	245
Basileuterus melanotis	2	1400	1400
Basileuterus rufifrons	14	102	1500
Basileuterus tristriatus	4	1825	3316
Campylorhynchus griseus	30	50	355
Campylorhynchus jocosus	15	914	1676
Campylorhynchus rufinucha	121	15	1219
Campylorhynchus turdinus	7	156	357
Cantorchilus longirostris	13	10	880
Cantorchilus modestus	22	15	1550
Cantorchilus nigricapillus	18	3	1900
Cantorchilus superciliaris	7	5	45
Cantorchilus thoracicus	9	55	650
Cardellina rubra	9	2225	3505
Catamenia inornata	14	3350	3600
Catharus aurantiirostris	118	10	2895
Catharus dryas	4	1920	1920
Catharus frantzii	22	1867	3048
Catharus fuscater	8	1000	1100
Catharus gracilirostris	20	2550	3100
Catharus mexicanus	28	50	1676
Catharus occidentalis	59	1828	2895
Chlorophonia cyanea	18	30	1200
Chlorophonia cyanocephala	3	2450	2450
Chlorophonia elegantissima	3	1700	1700
Chlorophonia occipitalis	3	1371	1371
Chlorospingus flavopectus	19	1100	2545
Chlorospingus pileatus	2	3100	3100
Cinclodes albiventris	2	3000	3000

Cinclodes antarcticus	11	2080	4500
Cinclodes comechingonus	4	2080	2080
Cinclodes excelsior	2	3400	3400
Cinclodes fuscus	44	25	4500
Cinclodes nigrofumosus	5	20	116
Cinclodes oustaleti	6	2080	2100
Cinclodes pabsti	14	1100	1300
Cinclodes patagonicus	19	10	1500
Cinclodes taczanowskii	4	3	3
Cistothorus platensis	125	10	3600
Contopus cinereus	29	50	1300
Contopus fumigatus	16	60	2600
Contopus pertinax	33	6	2600
Contopus sordidulus	16	165	1828
Diglossa albilatera	2	2500	2500
Diglossa caerulescens	2	2545	2545
Diglossa cyanea	4	2545	2545
Diglossa gloriosa	2	3800	3800
Diglossa humeralis	4	2800	2800
Diglossa lafresnayii	6	3350	3350
Diglossa plumbea	4	370	3100
Geositta cunicularia	83	1	4000
Geositta peruviana	90	25	450
Geositta poeciloptera	5	980	980
Geositta rufipennis	19	1350	4500
Geositta tenuirostris	4	2850	3000
Geospizopsis plebejus	32	736	4000
Geospizopsis unicolor	38	900	4572
Geothlypis beldingi	35	30	522
Geothlypis poliocephala	10	458	650
Geothlypis semiflava	8	50	1127
Geothlypis trichas	13	40	40
Geothlypis velata	78	10	1330
Henicorhina leucophrys	8	10	1500
Henicorhina leucosticta	19	609	1524
Knipolegus aterrimus	25	650	2500
Knipolegus cabanisi	41	337	1200
Knipolegus cyanirostris	12	18	165
Knipolegus lophotes	16	713	900
Knipolegus striaticeps	14	138	800
Leptasthenura aegithaloides	124	10	4200
Leptasthenura andicola	2	3800	3800
Leptasthenura fuliginiceps	4	2800	3600
Leptasthenura platensis	45	1	673
Lessonia oreas	9	3340	4500
Lessonia rufa	126	10	1021

Melanotis caerulescens	48	250	2743
Melanotis hypoleucus	2	1500	1500
Mimus dorsalis	6	2350	3700
Mimus gilvus	51	5	1468
Mimus longicaudatus	138	45	300
Mimus patagonicus	34	25	1200
Mimus polyglottos	140	6	2009
Mimus saturninus	316	21	1200
Mimus thenca	66	10	900
Mimus triurus	63	5	380
Muscisaxicola albifrons	2	4500	4500
Muscisaxicola albilora	7	2300	2800
Muscisaxicola alpinus	4	3500	4100
Muscisaxicola capistratus	14	10	2080
Muscisaxicola cinereus	2	3000	3000
Muscisaxicola flavinucha	10	500	2800
Muscisaxicola juninensis	2	4400	4400
Muscisaxicola maclovianus	2	20	20
Muscisaxicola maculirostris	30	40	2000
Myadestes melanops	22	1200	1853
Myadestes occidentalis	49	10	2743
Myadestes ralloides	2	1020	1020
Myiarchus ferox	81	20	900
Myiarchus nuttingi	10	10	1193
Myiarchus panamensis	10	4	355
Myiarchus phaeocephalus	4	500	500
Myiarchus semirufus	3	20	20
Myiarchus swainsoni	28	2	906
Myiarchus tuberculifer	83	3	2600
Myiarchus tyrannulus	231	2	2545
Myioborus brunniceps	28	358	3800
Myioborus flavivertex	25	950	2500
Myioborus melanocephalus	11	2500	2500
Myioborus miniatus	87	107	3048
Myioborus ornatus	6	1388	2545
Myioborus pictus	3	1500	1500
Myioborus torquatus	4	1853	2100
Myiodynastes chrysocephalus	3	2150	2150
Myiothlypis bivittata	6	500	500
Myiothlypis conspicillata	6	1200	1300
Myiothlypis coronata	4	1900	2545
Myiothlypis flaveola	5	800	800
Myiothlypis fulvicauda	12	20	1100
Myiothlypis leucoblephara	16	53	793
Myiothlypis luteoviridis	3	420	420
Myiothlypis nigrocristata	4	1400	2545

Myiothlypis rivularis	7	10	880
Myiozetetes cayanensis	471	4	1468
Myiozetetes granadensis	112	15	1100
Myiozetetes similis	493	5	3000
Ochetorhynchus andaecola	4	3600	4000
Ochetorhynchus melanurus	23	480	3413
Ochetorhynchus phoenicurus	17	500	750
Ochetorhynchus ruficaudus	4	2800	3573
Ochthoeca cinnamomeiventris	2	2545	2545
Ochthoeca fumicolor	8	10	3800
Ochthoeca leucophrys	2	3000	3000
Ochthoeca salvini	3	89	89
Oreothlypis gutturalis	2	2636	2636
Oreothlypis superciliosa	9	2225	2895
Orochelidon murina	24	2549	3800
Pheugopedius felix	14	250	1828
Pheugopedius genibarbis	10	20	380
Pheugopedius maculipectus	8	650	1524
Pheugopedius rutilus	6	10	762
Phrygilus atriceps	57	2954	4447
Phrygilus gayi	74	10	4300
Phrygilus patagonicus	9	796	1100
Phytotoma rara	86	10	2150
Phytotoma rutila	360	10	2954
Pitangus sulphuratus	1686	3	2600
Progne chalybea	11	57	138
Psarocolius angustifrons	14	1388	3100
Psarocolius decumanus	46	6	800
Psarocolius guatimozinus	2	726	726
Psarocolius montezuma	77	6	500
Psarocolius viridis	4	150	150
Psarocolius wagleri	12	20	726
Pygochelidon cyanoleuca	137	2	3340
Pygochelidon melanoleuca	3	125	125
Pyrocephalus rubinus	470	3	2500
Rauenia bonariensis	43	2	3500
Rhopospina alaudina	55	23	1920
Rhopospina fruticeti	115	27	3600
Rhynchocyclus brevirostris	26	15	1524
Rhynchocyclus fulvipectus	2	1388	1388
Rhynchocyclus olivaceus	2	2647	2647
Saltator atriceps	23	10	1230
Saltator aurantiirostris	87	23	2970
Saltator coerulescens	79	23	1330
Saltator fuliginosus	7	713	750
Saltator grandis	24	30	1600

Saltator maximus	202	12	1800
Saltator olivascens	88	5	150
Saltator orenocensis	2	50	50
Saltator similis	91	53	880
Saltator striatipectus	67	10	1468
Sayornis nigricans	254	7	3200
Sicalis citrina	34	880	1200
Sicalis columbiana	22	50	50
Sicalis flaveola	396	5	1568
Sicalis lebruni	13	90	900
Sicalis lutea	60	25	3700
Sicalis luteola	445	5	3000
Sicalis olivascens	11	3000	3400
Sicalis uropygialis	4	2294	2294
Spinus atratus	7	3573	4600
Spinus barbatus	41	10	700
Spinus crassirostris	6	3371	3573
Spinus lawrencei	5	40	40
Spinus magellanicus	51	10	4000
Spinus notatus	5	1828	1829
Spinus psaltria	43	30	2300
Spinus tristis	4	9	9
Sporophila caerulescens	95	20	42
Sporophila collaris	5	20	23
Sporophila corvina	51	15	1299
Sporophila funerea	5	28	800
Sporophila hypoxantha	11	42	900
Sporophila intermedia	14	10	1400
Sporophila minuta	22	4	1468
Sporophila morelleti	59	10	2600
Sporophila nigricollis	41	10	1800
Sporophila nuttingi	2	40	40
Sporophila palustris	2	30	30
Sporophila peruviana	56	25	2650
Sporophila ruficollis	6	42	42
Sporophila telasco	86	5	1800
Sporophila torqueola	37	230	3000
Thraupis abbas	9	165	1500
Thraupis cyanoptera	12	10	750
Thraupis episcopus	269	4	3000
Thraupis ornata	9	10	750
Thraupis palmarum	77	5	750
Thraupis sayaca	144	2	880
Thryophilus pleurostictus	98	15	1066
Thryophilus rufalbus	22	20	1676
Thryorchilus browni	2	3000	3000

Tiaris olivaceus	91	40	2364
Troglodytes aedon	1440	2	3048
Troglodytes solstitialis	9	650	3000
Turdus albicollis	121	4	1200
Turdus amaurochalinus	105	12	930
Turdus assimilis	197	607	1829
Turdus chiguanco	33	10	3800
Turdus falcklandii	106	10	1900
Turdus flavipes	20	10	2457
Turdus fumigatus	18	20	900
Turdus fuscater	17	1400	3400
Turdus grayi	330	9	2500
Turdus hauxwelli	2	157	157
Turdus infuscatus	4	1645	2895
Turdus leucomelas	346	6	1100
Turdus leucops	50	1400	2000
Turdus migratorius	45	27	2895
Turdus nigrescens	8	1200	3100
Turdus nigriceps	50	650	1300
Turdus nudigenis	312	6	411
Turdus olivater	6	1200	1200
Turdus plebejus	3	1330	1330
Turdus reevei	2	500	500
Turdus rufiventris	329	5	1600
Turdus rufopalliatus	7	731	975
Turdus serranus	5	380	1020
Upucerthia albigula	2	3550	3550
Upucerthia dumetaria	27	116	2800
Upucerthia validirostris	4	3573	3573
Uropsila leucogastra	16	14	14
Volarinia jacarina	327	4	2000
Xenotriccus mexicanus	17	1480	2030
Zonotrichia capensis	868	5	4100
Total = 285 species			

CAPÍTULO II

Effects of elevation and nest type on egg volume of Neotropical Passerines

Lauren Rumpel, Neander Marcel Heming and Miguel Ângelo Marini

2. CAPÍTULO II: Effects of elevation and nest type on egg volume of Neotropical Passerines

Abstract

The elevation gradient provides a wide field for answering questions involving the reproductive investment of birds, since biotic and abiotic factors change with altitude and influence the reproductive investments of individuals. Egg volume is a field of research that remains relatively unexplored, but it can have a significant influence on adult fitness and the timing of laying. We photographed Passerine clutches from 34 ornithological collections in South and Central America, USA and Europe, and measured egg volumes. We used the average egg volume of 2,313 clutches from 182 species of Neotropical birds to assess whether there is a change in egg volume in relation to nest type and climatic variables across elevation gradients. The aim of this study was to test whether temperature and precipitation influence egg volume in altitudinal gradients; and understand whether the type of nest influences the egg volume. The database covers 120 years (1901-2021), and altitude distribution from 0 to 4,500 meters. We found that the average clutch egg volume of each clutch increased as altitude increased; the lower the temperature and precipitation, the lower the egg volume; egg volume was biggest in domed nests. Thus, Neotropical Passeriformes are increasing egg size with increasing altitude, possibly as a response to colder temperatures.

Keywords: Altitude, climate, egg volume, life history, breeding biology, temperature precipitation.

Resumo [Portuguese]

O gradiente de elevação oferece um amplo campo para responder a perguntas que envolvem o investimento reprodutivo das aves, uma vez que os fatores bióticos e abióticos mudam com a altitude e influenciam os investimentos reprodutivos dos indivíduos. O volume dos ovos é um campo de pesquisa que permanece relativamente inexplorado, mas pode ter uma influência significativa sobre a aptidão dos adultos e o momento da postura. Fotografamos ninhadas de Passeriformes de 34 coleções ornitológicas nas Américas do Sul, Central e do Norte, nos EUA e na Europa, e

medimos o volume dos ovos. Usamos o volume médio de ovos de 2.313 ninhadas de 182 espécies de aves neotropicais para avaliar se há uma mudança no volume de ovos em relação ao tipo de ninho e às variáveis climáticas em gradientes de elevação. O objetivo deste estudo foi testar se a temperatura e a precipitação influenciam o volume dos ovos em gradientes altitudinais e entender se o tipo de ninho influencia o volume dos ovos. O banco de dados abrange 120 anos (1901-2021) e uma distribuição de altitude de 0 a 4.500 metros. Descobrimos que o volume médio de ovos de cada ninhada aumentou com o aumento da altitude; quanto menor a temperatura e a precipitação, menor o volume de ovos; o volume de ovos foi maior em ninhos de cúpula. Assim, os Passeriformes neotropicais estão aumentando o tamanho dos ovos com o aumento da altitude, possivelmente como uma resposta às temperaturas mais frias.

Palavras-chave: Altitude, clima, volume dos ovos, história de vida, biologia reprodutiva, temperatura, precipitação.

2.1. Introduction

Life history is defined by a series of events over the course of an individual's life, in which it invests time and energy (Cody 1966). One of the main objectives of life history studies is to understand how biotic factors (e.g. predation) and abiotic factors (e.g. temperature, precipitation and atmospheric pressure) influence survival and reproductive effort of individuals (Reznick and Endler 1982; Stearns 1992; Roff *et al*. 2002). Climate, as an abiotic factor, affects organisms largely through precipitation and temperature (Pörtner and Farrell 2008). Altitudinal gradients show major changes in abiotic factors, and thus, provide many opportunities to test theories related to offspring size and number (Körner 2007).

The distribution of temperature and rainfall can determine the occurrence and abundance of insects (Wolda 1978) and prey availability (Price *et al*. 2011), for example. Most food resources come from plant sources or ectothermic prey, and these are very sensitive to changes in climate (Dillon *et al*. 2010; Pau *et al*. 2013). Temperature decreases as altitude increases, with a reduction of 5.5°C for every 1,000 meters of increase in altitude (Barry 2008). Precipitation increases with altitude in most

arid and temperate mountains, while in tropical and semi-tropical mountains, precipitation can be unimodal, bimodal and decrease or increase with altitude, depending on local climatic and geographical characteristics (Barry 2008). However, a study covering four areas of the tropical region showed that generally rainfall decreases as altitude increases (Anders and Nesbitt 2015). Thus, these changes in temperature and rainfall have cascading effects on abundance and distribution of life forms, such as altering food resources (i.e. fruits, seeds, and arthropods) for larger organisms.

Environmental conditions can determine birds' reproductive investment. In this way, the egg can be a good model to understand energy investment per reproductive attempt (Deeming 2007; Deeming and Reynolds 2015), although reproductive investment in wild birds has not yet been well investigated (Martin *et al*. 2006). Because the egg is a closed system, the individual birds allocate all the food resources necessary for the development of the embryo to the eggs. Relative egg volume can have a major influence on the fitness of organisms, so that larger eggs contain more energy, resulting in good quality growth and survival of the young (Krist 2011). Birds in the Neotropics already lay few eggs, usually two or three, so the size of the clutch may not offer much alternative to adjust investment, what can be achieved by investing in egg volume.

The rate at which egg resources are transformed to form the embryo depends on the amount of heat transferred by the parents during incubation (Brua 2002; Deeming 2002). When energy for reproductive investment is limited, the mass of each egg is expected to decrease with increased effort in clutch size within species (Roff 1992; Stearns 1992). There is an energy cost to the parents during incubation (Biebach 1981; Conway and Martin 2000). When the parent leaves the nest, the eggs lose energy as time progresses, being affected by rainfall, temperature, solar radiation and wind (Haftorn 1978; Webb and King 1983; Carey 2002) (**Figure 2.1a**). Thus, the smaller the egg, the faster its temperature loss. If the egg is larger at higher altitudes, there is less chance of a greater reduction in temperature. However, if the egg needs to be completely reheated and is larger, it will require more time and energy from the incubating parents than a smaller egg (**Figure 2.1b**). Larger eggs survive better in extreme conditions (Williams 1994; Christians 2002). Considering that the environmental conditions of higher locations are harsh, it is expected that egg volume will be larger. Similarly, one hypothesis proposed that egg volume is larger in locations

with reduced temperatures (Martin 2008). In addition, a reduction in atmospheric pressure, causes the egg to lose water, what is compensated by increasing its volume (Rahn and Ar 1974). Both these climatic characteristics (lower air temperature and atmospheric pressure) are present at higher altitudes.

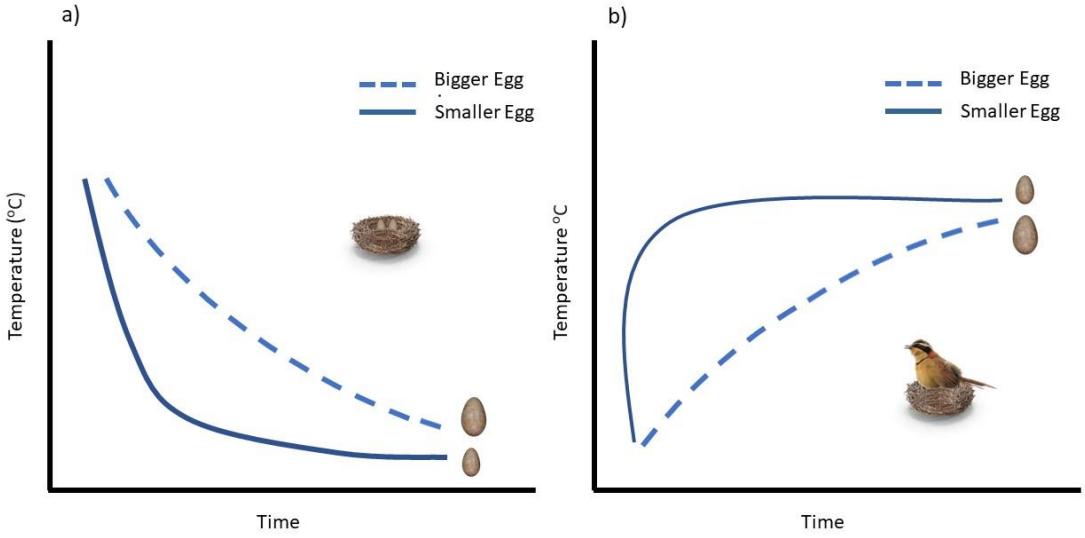


Figure 2.1: Relationships between the cooling and heating of eggs. a) Relationship between the time the parent leaves the nest and the cooling of the eggs; b) Relationship between the time the parent returns to the nest and the heating of the eggs. Small eggs lose heat more quickly than large eggs and small eggs gain heat more quickly than large eggs.

The type of nest can also influence egg size due to eggs' exposure to climatic factors (Perez et al. 2020). The insulating function of the closed nest may be important in altricial Passeriformes, whose nestlings are incapable of thermoregulation (Hansell 2000) and reduces the parents' costs of heating the eggs and nestlings (O'Connor 1975; Haftorn and Reinertsen 1985). For example, a study carried out at high elevation revealed that nests were built in the highest treetops, probably to receive more solar energy, and had denser walls, probably to improve thermal insulation (Mainwaring *et al.* 2014). The nest wall can prevent the loss of water from the eggs, as it raises the humidity of the environment, thus contributing to the survival of the embryo (Deeming

et al. 2020 Therefore, closed nests reduce the exposure of eggs to climatic factors (Perez et al. 2020).

By studying variations in egg size in relation to geographical and ecological gradients can improve understanding how female reproductive investment is subject to ecological and environmental factors (Martin *et al*. 2006; Heming and Marini 2015). From these perspectives, we sought to understand whether climatic and ecological factors are influencing egg volume of Neotropical Passerines across elevation gradients. The aim of this study was to test whether temperature and precipitation influence egg volume in altitudinal gradients. We also tested whether the type of nest (open, cavity or domed) influences egg volume in elevation gradients. We predicted that: 1) the lower the temperature, the greater the egg volume; 2) the higher the precipitation, the larger the egg volume;3) and in relation to nest type, that egg volume is larger in open nests than in cavity or domed nests at higher altitudes than in lower areas.

2.2. Methods

2.2.1. Database

We collected data of passerine clutches from 34 scientific collections in Europe, South America, Central America and North America (**Supplemental material – S1b**). We took a digital photograph of each clutch containing the eggs and the information available on the cards, such as clutch size, species name, location, and date. To enable us to use the actual clutch size of the specific clutches sampled and not the average of each species, we trimmed clutch size data as follows. To exclude dubious records of clutch sizes too small or too large for a given species, we selected clutches according to the range of number of eggs per clutch known for each species following Birds of the World (Billerman et al. 2022). Along this line, we removed clutches with eggs of nest parasites (Cowbird - *Molothrus* spp. and Striped Cuckoo - *Tapera naevia*), as they can eject host eggs (Sick 1997). In addition, we did not use data of clutches outside the known breeding range and of clutches from islands. Species that nest on islands have a different reproductive investment than species that nest in the mainland, known as "island syndrome" (Blondel, 1985, Blondel et al., 1992, Covas, 2012), with smaller clutches (Jezierski, 2024).

We made a taxonomic resolution of each clutch according to catalogs published between 1874 and 1987. We used the British Museum of Natural History catalogs (Seebohm 1881; Sclater 1986, 1988; Sharpe 1888), followed by the catalogs of the Field Museum of Natural History (Cory and Hellmayr 1924, 1925, 1927; Hellmayr 1934, 1935, 1936, 1937, 1938) and the Museum of Comparative Zoology (Peters 1951, 1960; Mayr and Painter 1968; Painter 1970; Deignan *et al*. 1964; Amadon *et al*. 1979). The scientific name was updated according to Clements *et al*. (2022).

We classified nests in three types: open cup, cavity (cavities in trees, soil or dirt bank) and domed (spheres, domes, cracks in rocks, pensile) nests following Birds of the World (Billerman et al. 2022). Allometric effects can influence egg size (Sæther 1987). For this reason, the average body mass of the females of each species was incorporated into the analyses. Body mass was obtained mainly from Dunning (2008), supplemented by Birds of the World (Billerman et al. 2022).

2.2.2. Egg volume

Egg volume was measured from high-resolution digital photographs of the clutches taken *in situ* at egg collections with their respective collection labels/cards. Each egg set was arranged on a black base with a ruler scale (in mm) and photographed with a macro lens. Each egg was carefully leveled horizontally. At the lab, each egg was measured (egg volume, mm^3) (**Supplemental material – S2b**) in the *ImageJ* software (https://imagej.nih.gov/ij/), using the "Egg Tools" plugin (details in Troscianko 2014, and http://www.jolyon.co.uk/research/eggs/). To achieve so, we opened the digital photo on ImageJ, and for each egg we placed eight points around the egg, one on the tip, one in the base, and three extra points on each side of the egg. Then we opened the Egg Tools plugin and extracted the measurements. Then, we estimated average egg volume of each clutch (“average egg volume” herein) to test the hypotheses. We used the average number of eggs per clutch to avoid pseudoreplication.

2.2.3. Climatic variables

We collected the climate data for each point (geographic coordinate) of each clutch from the Center for Environmental Data Analysis (CEDA) Archive ([https://catalogue.ceda.ac.uk/uuid/715abce1604a42f396f81db83aeb2a4b/]) (Harris *et al*. 2020). We extracted the following climatic variables for the month/year of laying of each clutch: Tmn = "Near-surface temperature minimum"; Tmx = "Near-surface temperature maximum" and Pre = "Precipitation". Climatic variables were extracted for the laying months and years of 2,313 clutches collected between 1901-2021.

2.2.4. Statistics

We performed a phylogenetic generalized linear mixed model (PGLMM) (Ives and Helmus 2011), using the "pglmm" function from the "phyr" package (Li *et al*. 2020). The phylogenetic signal was also calculated using Pagel's λ value (lambda) using the 'ape' package (Paradis and Schliep 2019). We obtained the phylogeny from the website “birdtree.org” (Ericson All Species; Jetz *et al*. 2012). We made a consensus tree and measured branch lengths using the ape R package (Paradis *et al*. 2004). All analyses were performed in the R version 4.2.1 program (R Core Team 2023). The average egg volume was used as the response variable and altitude (scale transformation) and nest type (open, domed or cavity), maximum monthly temperature, minimum monthly temperature, and precipitation were used as fixed effects. We also put the interaction of maximum monthly temperature (Tmx) and elevation into the model, as well as making a separate model for nest type. The latitudinal effect, average female body mass, clutch size and year were controlled for in the analyses. Altitude was used as a continuous variable. Reproductive investment is known to change with latitude (Stearns 1992). With regard to weight, there is an allometric effect, i.e. egg volume is related to the female's body size (Blackburn 1991). As for clutch size, there is a balance between the number of eggs and the egg volume of the clutch (Roff, 2002). In addition, we controlled the year in the analysis, since the database covers 120 years (1901-2020).

2.3. Results

We analyzed a total of 6,387 eggs from 2,313 clutches, comprising 182 species from 11 families. The database covers 120 years (1901-2021), and altitude distribution

from 0 to 4,500 meters. The average minimum monthly temperature of the months analyzed ranged from -6.6 to 25.2°C, the average maximum monthly temperature ranged from 5.2 to 32.9°C, the monthly precipitation ranged from 0 to 663 mm^3 (**Figure 2.2**). Of the 182 species analyzed, 26 have cavity nests, 44 domed and 112 open nests. The average egg volume ranged from 1,039 to 10,860 mm^3.

The phylogenetic signal for the "volume" trait was close to 1 (Pagel's $\lambda = 0.86$, C.l. = 95%: 0.74 a 0.95) i.e. much of the variation is due to phylogeny. The average egg volume increased as altitude increased (coefficient = 418.48; $p < 0.001$) (**Figure 2.3**).

About climatic variables (Tmn/Tmx/Prec) (see distribution in **Figure 2.2**), average clutch egg volume reduced with a decrease in average maximum monthly temperature and month precipitation, but increased with minimum monthly temperature (**Table 2-1**). The results of the PGLMM model indicate a significant interaction between elevation and maximum temperature (Tmx) on average clutch egg volume (coefficient = -13.758, P-value < 0.001). This negative coefficient suggests that the positive effect of elevation on average clutch egg volume decreases as maximum temperature increases.

The volume of eggs increases with elevation at lower maximum temperatures; however, this effect is less pronounced at higher maximum temperatures. These results suggest that the influence of elevation and maximum temperature on egg volume is a complex, interactive process, potentially reflecting ecological adaptations to varying environmental conditions at different altitudes.

With respect to the type of nest, the data indicate that all nest types exhibited an increase in egg volume when the interaction with altitude was incorporated into the

model (**Figure 2.4**). Nevertheless, only open nests were found to be statistically significant.

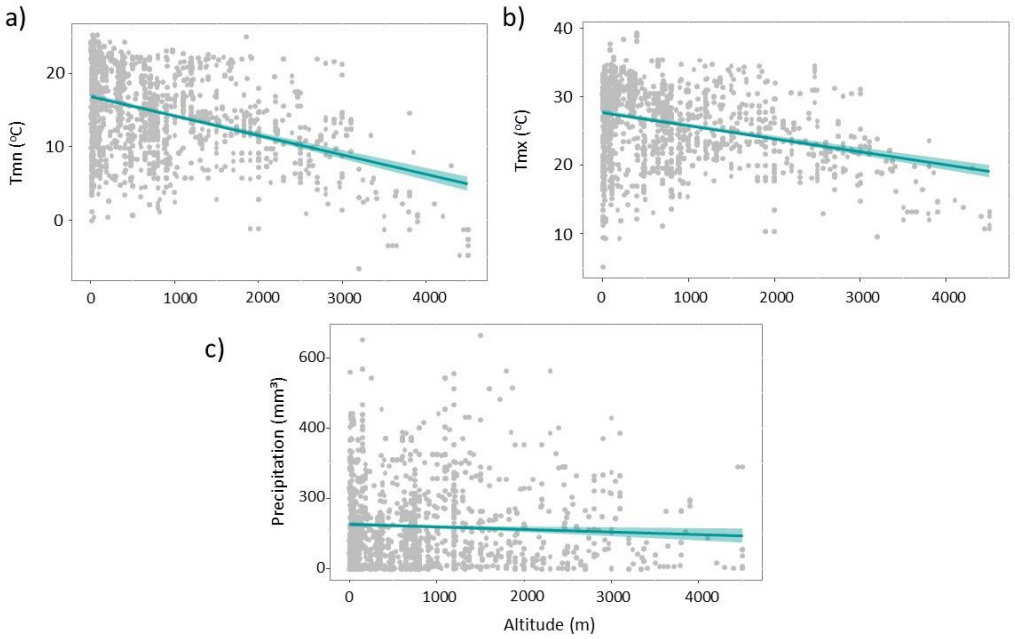


Figure 2.2: Relationship between climatic variables and altitude: a) "Tmn" = average minimum monthly temperature (°C); b) "Tmx" = average maximum monthly temperature (°C); c) monthly precipitation (mm³). Climatic variables were extracted for the laying months and years of 2,313 clutches collected between 1901-2021.

Table 2-1: PGLMM of the average egg volume of Passerine clutches in relation to altitude, type of nest and climatic variables; "Tmn" = average minimum monthly temperature; "Tmx" = average maximum monthly temperature; "Prec" = monthly precipitation; ":" interaction between altitude and Tmx. Climatic variables during the laying month of the clutch.

	Estimate	**SE**	**Z-score**	**P-valor**
Intercept	11551	1257200	0.0092	0.99267
Altitude	418.48	55.255	7.5736	< **0.001**
Tmn	38.497	7.4030	5.2002	< **0.001**
Tmx	-35.122	7.0017	-5.0162	< **0.001**
Prec	-0.010006	0.13298	-0.0752	0.94002
Nest - Dome	180.05	88.308	2.0389	**0.04146**
Nest - Open	-11.988	75.441	-0.1589	0.87374
Altitude:Tmx	-13.758	2.2982	-5.9864	< **0.001**
			R-squared value: 0.503	

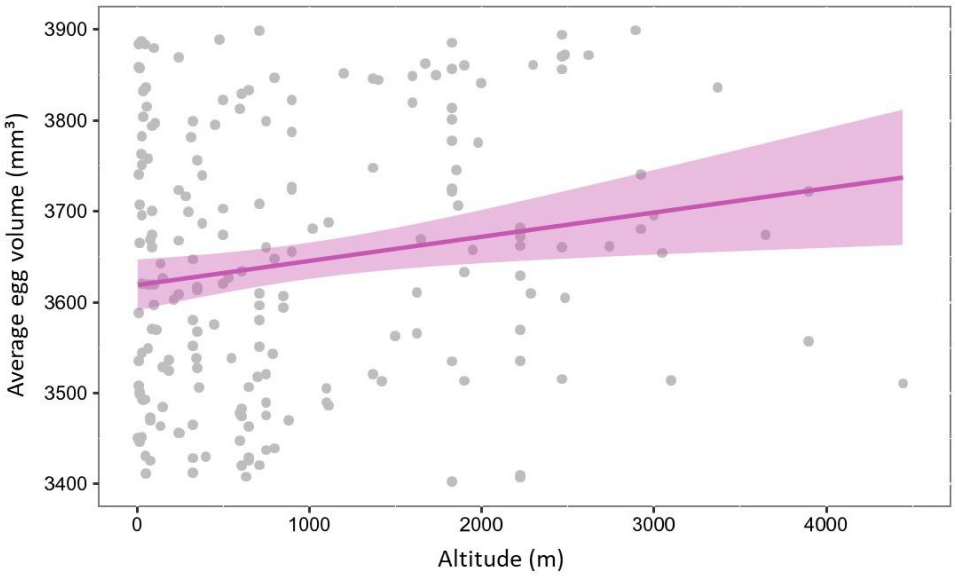


Figure 2.3: Average clutch egg volume (mm^3) of 182 Neotropical passerine species in relation to altitude (m). Shaded area in pink corresponds to the 95% confidence interval.

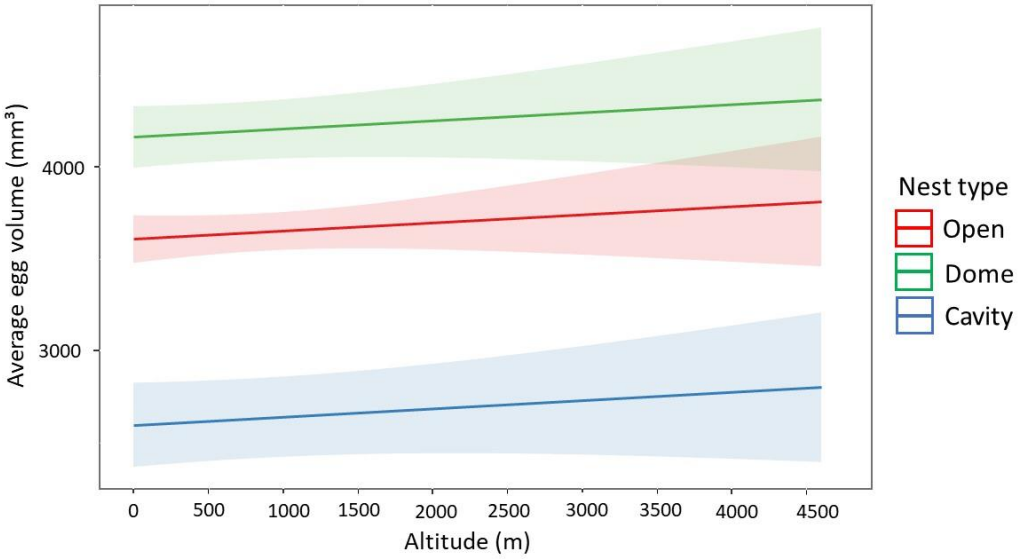


Figure 2.4: Average egg volume (mm^3) of Neotropical birds with open, domed and cavity nests in relation to altitude (m). Shaded areas in green, red and blue correspond to 95% confidence intervals.

2.4. Discussion

Average egg volume was positively correlated with increasing altitude, when controlled for latitudinal effect, average female body mass and clutch size, corroborating our initial hypothesis. This means that species are producing larger eggs as altitude increases. The few studies that evaluated this relationship also recorded an increase in egg volume within species (Lu *et al*. 2005, 2008a, 2008b, Levin *et al*. 2023; Deckel *et al*. 2024) and within and across species (Guo and Lu 2022). A single exception isa study with Tree Swallows (*Tachycineta bicolor*) that found smaller eggs at higher altitude, what was explained by the poor body condition of the breeding females (Johnson *et al*. 2018). However, body mass was not incorporated as a control in their analysis. We also found a reduction in clutch size across and within species as altitude increased, although it was not our main objective. There is a trade-off between clutch size and egg volume, such that larger eggs may be associated with smaller clutches (Roff 1992).

One way that organisms cope with lower temperatures is by increasing body size according to Bergmann's Rule (Winkler 2016), however, at study with four tropical elevational gradients lacked to find a pattern of larger body masses of birds at higher elevations (Freeman 2017). Birds need mechanisms to cope with low temperatures, but the mechanisms that confer cold tolerance to tropical bird species are still not well understood (Londoño *et al*. 2017). In addition, birds can thermoregulate through a combination of feather insulation and increased basal metabolic rate (Swanson and Liknes 2006). Therefore, it is possible that birds living at high altitudes in the tropics may be using one of these mechanisms to cope with the low temperatures.

We showed that average egg volume reduced with increased maximum temperature. Environmental temperature is a significant abiotic constraint for birds (Swanson and Liknes 2006). Larger eggs result in increased nutrient reserves available to the nestling (Martin 1987; Pelayo and Clark 2003). Larger eggs can also cope better with heat loss through the egg's surface-area ratio (Meiri 2011). Colder and windier weather not only increases thermoregulatory costs for females, but also reduces the availability of flying insects (Nooker *et al.* 2005, Winkler *et al*. 2013). In this way, it may be more important to increase egg volume, even with fewer food resources, as a larger egg provides a greater chance of survival (Krist 2011). Birds thermoregulate through a combination of feather insulation and an increase in basal metabolic rate (Swanson and Liknes 2006). This feather variation has been seen in birds across

altitudinal gradients (Barve and Cedena, 2022), but Londoño et al. (2015) did not find a strong relationship with increased basal metabolic rate in a tropical high-altitude region maybe because they had better feather insulation.

We also showed that increased precipitation was correlated with reduced average egg volume. However, precipitation trends are not linear in relation to latitude, altitude and seasonality. Climate models that predict changes in precipitation are highly sensitive (Christensen *et al*. 2007; Barry 2008), even though precipitation is considered very difficult to model, evaluate and measure (McCain and Colwell 2011).This has been seen in several studies in the Neotropics (e.g. Forero-Medina *et al*. 2011; Rosselli *et al*. 2017; Freeman *et al*. 2018; Pepin *et al.* 2022). Nevertheless, generally, the annual amount of precipitation decreases with altitude (Anders and Nesbitt 2015). Usually, the greater the rainfall, the greater the investment in egg volume, because rainfall can increase the abundance of insects (Wolda 1978). Rainfall is an important factor in primary productivity and increasing invertebrate populations (Pinheiro *et al*. 2002). The abundance of invertebrates is crucial for many of the species analyzed in this study. All this leads one to think that the greater the amount of rain, the greater the egg volume. Despite this, our data revealed larger eggs at higher altitudes. Another important issue is that increased rainfall at higher altitudes, i.e. colder weather, can lead to greater cooling of the eggs and chicks and can influence thermoregulatory costs. It is difficult to visualize an altitudinal rainfall trend, there is no clear rule (Körner 2007). Therefore, it seems that rainfall is not directly influencing egg volume, and it may not be as important as other biotic.

As has already been pointed out, temperature and rainfall regulate/determine the amount of food resources, which might alter the investment in eggs. Food resources influence reproductive investment, so too little food available limits the resources provided during the development of the egg and afterwards for the nestling. Vegetation cover and biomass in high-elevation regions (above the tree line) are generally lower compared to tree-covered systems at lower elevations (Loranty and Goetz 2012). There is a decrease trend in overall environmental productivity (McCain 2009) and food availability (insect and fruit abundance) along the altitudinal gradient (e.g. Janzen et al. 1976; Loiselle and Blake 1991). Low food availability in high-altitude areas may force females to extend their foraging time or increase the number of nest off-bouts to obtain sufficient food (Chalfoun *et al*. 2007). Many species of the Thraupidae family from

higher altitudes in the Andes supplement their diet with insects, fruit or nectar (Remsen 1985).

The open nest type had smaller eggs compared to the closed nests. This is opposite to our expectation, since eggs in open nests are more exposed to the cold external environment, which would result in greater heat loss from the eggs and hatchlings. Although closed nests provide a more suitable microclimate for embryonic development and improve nestling performance and survival (DuRant *et al*. 2013; Ospina *et al*. 2018), we lacked to obtain significant results in relation to the closed nest. One possible explanation is that some species modify the material used to build the nest (Kern and Van Riper 1984), ensuring better insulation at higher altitudes. Both open and closed nests can perform the same thermal regulation of the eggs. Feathers help with thermal insulation in dry environments (Windsor *et al*. 2013), but the relationship can be reversed in humid conditions (Hilton *et al.* 2004). Since there is a difference in climatic conditions in higher elevation environments, the way in which the type of nest is related to egg volume needs to be thoroughly evaluated.

Part of our analysis was hampered by the fewer clutches available for higher altitudes. In addition, it is challenging to make comparisons across orographic precipitation gradients, as there is a general lack of observations at higher altitudes (Pepin *et al.* 2022). There is a need to increase the climate monitoring program in high altitude regions with a greater number of climatic variables (Dimri *et al.* 2022), in order to be able to measure meteorological, hydrological and ecological processes. Future analyses of altitudinal and climatic effects on biodiversity depend on more biological and climatic data being collected at higher altitudes. This will also be important to better understand how mountain organisms will cope with climate change.

There are mechanisms we do not yet understand that influence reproductive investment at higher altitudes. We need finer data on climate, especially precipitation, so that we can satisfactorily model climatic variables and life history data of organisms at altitude. In addition, as there is a short reproductive period for birds nesting at higher altitudes (Boyle *et al*. 2016), it is probably better to invest in a reproductive attempt where the chance of success of the offspring is greater than to invest in an offspring of smaller size and lower survivorship. Furthermore, there is a need to know how species

at higher altitudes in the tropical region are breeding, as there is a chance that many species will reduce reproductive investment in relation to future changes in climate.

2.5. Conclusions

We showed that the analyzed species of Neotropical Passerines that breed at higher altitudes tend to increase the volume of their eggs, possibly due to lower environmental temperatures. The lower temperatures at higher altitudes are probably favoring larger eggs, as larger eggs generate offspring with greater fitness and quality (Krist 2011), which can cope better with more adverse environmental conditions.

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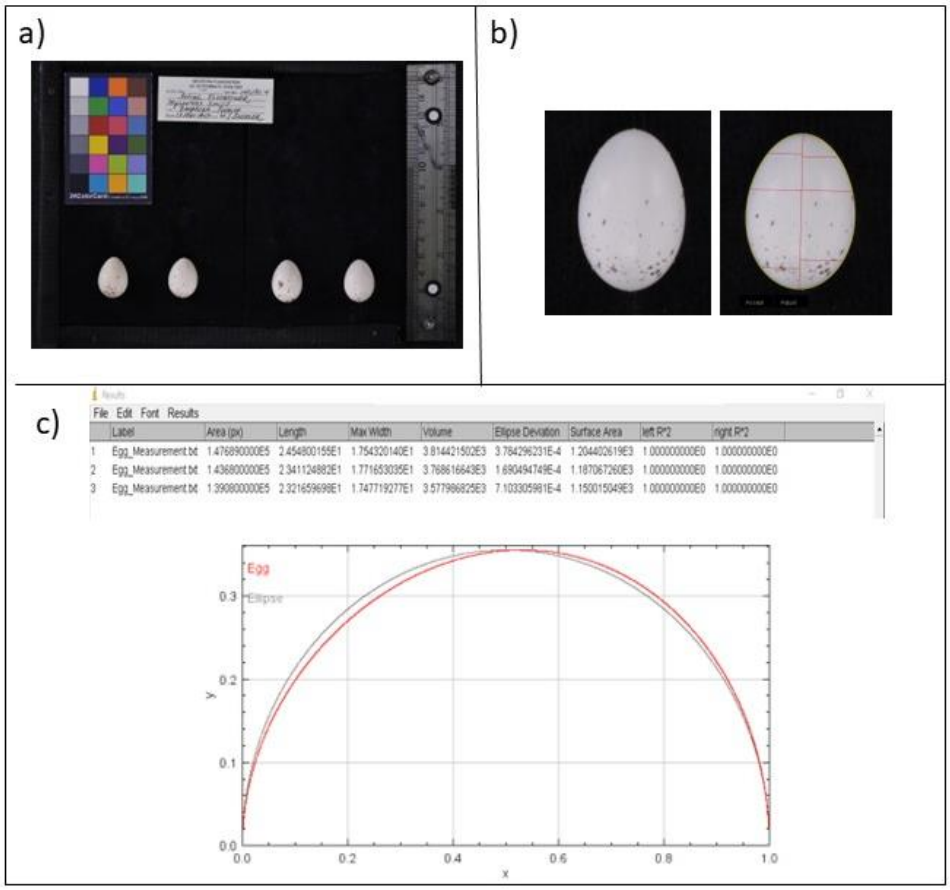
2.7. Supplementary materials

S1b: Total number of clutches collected in each museum and the location of the scientific collection. (*) data collected from the scientific collection database.

Acronym	Museum	Location	Clutches
AMNH	American Museum of Natural History	New York, USA	83
CAS	California Academy of Science	San Francisco, USA	4
COMB	Coleção Ornitológica Marcelo Bagno	Brasília, Brazil	54
CRRM	Țării Crișurilor Museum	Oradia, Romania	12
DMNH	Delaware Museum of Natural History	Willmington, USA	99
FLMNH	Field Museum of Natural History	Chicago, USA*	1
FML	Fundación Miguel Lillo	Tucuman, Argentina	8
FZB	Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul	Porto Alegre, Brazil	3
IAvH	Instituto de Investigación de Recursos Biológicos Alexander von Humboldt	Villa de Leiva, Colombia	37
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”	Buenos Aires, Argentina	95
MCZ	Museum of Comparative Zoology, Harvard University	Cambridge, USA	3
MHNG	Museum d’Histoire Naturelle de Genève	Genebra, Switzeland	6
MLP	Museu de La Plata	La Plata, Argentina	29
MLUH	Zentralmagazin Naturwissenschaftlicher Sammlungen, Martin Luther University Halle-Wittenberg	Halle, Germany	43
MN	Museu Nacional	Rio de Janeiro, Brazil	92
MNCR	Museo Nacional de Costa Rica	San José, Costa Rica	53
MPEG	Museu Paraense Emilio Goeldi	Belém, Brazil	21
MVZ	Museum of Vertebrate Zoology	Berkeley - USA*	40
MZS	Musée zoologique de l’Université Louis Pasteur et de la Ville de Strasbourg	Strasbourg, France	1
MZUSP	Museu de Zoologia da Universidade de São Paulo	São Paulo, Brazil	41
NBCN	Nationaal Natuurhistorisch Museum	Leinden, Netherlands	42
NHM	Natural History Museum	Tring, Egland	176
NMBE	Naturhistorisches Museum Bern	Bern, Switzeland	24
NMS	National Museums of Scotland	Edinburgh, Scotland	24
NMW	Naturhistoriches Museum	Vienna, Austria	1
PUCRS	Museu de Ciências e Tecnologia da PUCRS	Porto Alegre, Brazil	3
SBCM	San Bernardino County Museum	San Bernadino, USA	85
UCR	Universidad de Costa Rica	San José, Costa Rica	23
USNM	Natural History Museum - Smithsonian Institution	Washington, USA	86
WFVZ	Western Foundation of Vertebrate Zoology	Camarillo, USA	1122

ZMB	Museum für Naturkunde	Berlin, Germany	2



S2b: Digital extraction of egg volume using the Image J program. a) Image of the complete clutch; b) insertion of dots at the ends of the egg; c) 'output' with egg data.

CAPÍTULO III

Impact of climate change on Neotropical Passeriformes: A 120-year data of reproductive traits across elevation gradients

Lauren Rumpel, Marcelo A. de Assis Silva, Neander M. Heming, Miguel Â Marini

3. CAPÍTULO III: Impact of climate change on Neotropical Passeriformes: A 120-year data of reproductive traits across elevation gradients

Abstract

Climate change not only influences species distribution across different altitudes but also has the potential to modify the life history of these species. Studies indicate that altitudinal variations can affect clutch size and egg volume of birds. Our objective was to assess whether these reproductive traits varied with changes in temperature and precipitation over the last 120 years across elevation gradients in the Neotropical region. We used data on clutches from scientific collections from 182 species of Passeriformes collected over 120 years (1901-2021). Our results indicate an increase in minimum and maximum temperatures, as well as precipitation, across all altitudinal ranges over the years. We observed a decrease in clutch size and egg volume at all altitudes, with only the reduction in egg volume being statistically significant. This study highlights the importance of ornithological collections for understanding the reproduction of birds, especially in the Neotropical region. The findings have significant implications for conservation and may influence policies aimed at mitigating the negative impacts of climate change on bird populations from tropical and high-altitude.

Keywords: Altitude, climate change, clutch size, egg volume, temperature, precipitation, bird collections.

Resumo [Portuguese]

A mudança climática não só influencia a distribuição de espécies em diferentes altitudes, mas também tem o potencial de modificar a história de vida dessas espécies. Estudos indicam que variações altitudinais podem afetar o tamanho da ninhada e o volume dos ovos. Nosso objetivo foi avaliar se características reprodutivas variam com as mudanças de temperatura e a precipitação ao longo dos últimos 120 anos em gradientes de elevação na região Neotropical. Utilizamos dados de ninhadas de coleções científicas de 182 espécies de Passeriformes coletados ao longo de 120 anos (1901-2021). Nossos resultados indicam um aumento nas temperaturas mínima e máxima, bem como na precipitação, em todas as faixas altitudinais ao longo dos anos. Observamos uma diminuição no tamanho da ninhada e no volume dos ovos em todas as altitudes, sendo que apenas a redução do

volume dos ovos foi estatisticamente significativa. Este estudo destaca a importância das coleções ornitológicas para a compreensão da reprodução de muitas espécies de aves, especialmente na região Neotropical. As descobertas têm implicações significativas para a conservação, podendo influenciar políticas destinadas a mitigar os impactos negativos das mudanças climáticas sobre as populações de espécies tropicais e de alta altitude.

Palavras-chave: Altitude, mudanças climáticas, tamanho da ninhada, volume do ovo, temperatura, precipitação, coleções de aves.

3.1. Introduction

Average global temperature exceeded 1ºC of the pre-industrial era (World Meteorological Organization 2016) and is predicted to increase by an average of up to 4.4 ºC by 2100 in the most extreme scenario (IPCC 2021). The geographical distribution of species is changing in response to temperature changes, which can result in the reorganization of communities (Root et al. 2003). When birds are establishing their breeding territories, they look for suitable climatic conditions to start nesting (Martin & Wiebe 2004). The temperature increase in high mountain regions is greater than in other areas of the globe (Pepin et al. 2015). Species are expected to adjust their altitudinal ranges to higher elevations (Chen et al. 2011), which can influence crucial life history events such as reproductive biology (Parmesan & Yohe 2003; Halupka & Halupka 2017). Birds rely on climate-related environmental cues to adjust their reproductive phenology (MacNamara et al. 2011; Visser et al. 2010). Therefore, we need to understand how changes in climate affect birds' reproductive investment and effort in the past to prevent future.

If reorganization of organisms occurs, species from lower elevations may change their distribution towards higher elevations. Just as some species may contract their range due to the loss of climatically suitable areas (Neate-Clegg et al. 2023). Species that live at higher elevations become more vulnerable to climate change due to their adaptations to naturally adverse environmental conditions and short breeding periods (Lenoir et al. 2019). It is essential to understand reproductive dynamics at higher

altitudes. A review conducted by Dunn (2004) demonstrated significant changes in clutch size and reproductive success associated with climate change. Halupka et al. (2023) found a reduction in the number of descendants, but this varied according to the population studied. Rising temperatures force many mountain species to migrate to higher altitudes, reducing their territories, in some cases completely (Shoo et al. 2005). Changes have already been observed in the reproductive investment of species that breed at higher elevations (Hille & Cooper et al. 2015; Boyle et al. 2016). Species that nest at higher altitudes already have a unique reproductive investment and, with climate change, this behavior could change even more.

Climate change is very likely to have a strong impact on the hydrological cycle, which is predicted to alter rainfall patterns and intensity, as well as the frequency of extreme precipitation (Luitel et al. 2020). In response to the increase in temperature (0.05°C/year) compared to lower areas (0.02°C/year) (Gao et al. 2018; Pepin et al. 2015; Luitel et al. 2020) and rainfall regime, vegetation may also expand or contract (Mayle, 2004; Bush, 2005). Due to climate change and its indirect impacts, several ecological processes are at risk, including the dynamics of vegetation succession in high-altitude areas (Ahmadi et al. 2024). This means that it can affect the availability of resources for high-altitude species (Shumm et al. 2020). Therefore, it can affect the population size of species and their life history.

Many of the questions raised can be answered when you have a comprehensive database on a given trait. In this way, a lot of information remains scarce, partly because such evaluations require long-term data that is difficult to collect and analyze (Wauchope et al. 2021). Despite the fact that basic data on many species is still unknown for the Neotropical region, data from ornithological collections can go some way to fulfilling many of our data requirements in relation to the reproductive biology of bird species (Marini et al. 2020), such as understanding the reproductive investment of migratory species (Sousa et al. 2024), analyzing changes in populations and communities over time (Collar et al. 2003) or in birds' investment and reproductive effort. The aim of this study was therefore to assess whether there have been changes in clutch size and egg volume in Passeriformes over the last 120 years in Neotropical altitude gradients. Our hypothesis is that with the increase in temperature over the years, eggs and clutches will decrease in size in all altitudinal ranges.

3.2. Methods

3.2.1. Database

We collected Passerine clutch data from ornithological collections in Europe, South America, Central America and the USA. We captured a digital image of each clutch, documenting the eggs and the information provided on the cards/labels, such as clutch size, species, location and date. We excluded data from clutches outside the known breeding range and from islands. To ensure the accuracy of the records, we selected the clutches based on known clutch size of each species and eliminated those with nest parasites, such as *Molothrus* spp. and *Tapera naevia*, since these parasites are known to eject host eggs and can alter clutch sizes (Sick 1997). We assessed any taxonomy-related discrepancies in the label data from published catalogs and updated the scientific name according to Clements et al. (2022). From the photographs, we extracted the volume of the eggs (egg volume, mm^3) using the ImageJ program (https://imagej.nih.gov/ij/) with the "EggTool" plug-in (http://www.jolyon.co.uk/research/eggs/) (Troscianko 2014). We used the average number of eggs per clutch to avoid pseudoreplication. In this way, we estimated the average egg volume of each clutch to test the hypotheses.

We selected the climatic variables related to the month and year of each nest's laying period, including “Tmn” = Near-surface temperature minimum, “Tmx” = Near-surface temperature maximum, and “Pre” = precipitation. These variables were extracted for 2,313 nests recorded between 1901 and 2021. The climatic data for each nest, corresponding to its specific geographical coordinates, were obtained from the Center for Environmental Data Analysis (CEDA) Archive (Harris et al. 2020) through the link ([https://catalogue.ceda.ac.uk/uuid/715abce1604a42f396f81db83aeb2a4b/]).

3.2.2. Data analysis

We ran a Phylogenetic Generalized Linear Mixed Model (PGLMM) using the "pglmm" function from the "phyr" package (Li et al. 2020) with the "Gaussian" family for egg volume and the "Poisson" family for clutch size in the R program version 4.2.1 (R Core Team 2022). We used monthly minimum temperature (Tmn), monthly

maximum temperature (Tmx) and monthly precipitation (Prec) as exploratory variables. For the egg volume analysis we controlled (as fixed variables) for female weight, latitude (degree) and clutch size. For the clutch size analysis we controlled for latitude (degree). The phylogenetic trees were obtained using the website porbirdtree.org (Ericson All Species; Jetz et al. 2012). We obtained the consensus tree and branch lengths from the R "ape" package (Paradis et al. 2004). We used temperature in degrees Celsius (°C), and precipitation in cubic millimeters (mm^3). We divided the altitude into three zones: 0-1000 meters (m) as "low", 1001-2000 m as "medium" and 2001 to 4500 m as "high". Zones were created to separate environments above and below the tree line (Körner 1998).

3.3. Results

We analyzed a total of 6,387 eggs from 2,313 clutches, comprising 182 species from 11 families. The database covers 120 years (1901-2021) and an altitudinal range from 0 to 4,500 meters. We observed an increase in minimum and maximum temperatures (**Figure 3.1 and Figure 3.2**), as well as an increase in precipitation at all elevations over the years (**Figure 3.3**).

The PGLMM revealed significant results in the interactions between the categorized elevation, climate and year variables in relation to average egg volume (**Figure 3.4**) (**Table 3-1**). Interactions between high, medium and low elevation and year showed significant decreases in egg volume ($p < 0.05$ for all elevation categories). In addition, the interactions between minimum temperature (Tmn) and maximum temperature (Tmx) and year, were also significant (coefficient = 0.03, $p = 0.001$ and coefficient = - 0.03, $p = 0.002$, respectively), showing that annual increases in minimum and maximum temperature are associated with an increase and decrease in egg volume, respectively. On the other hand, the interaction between precipitation (Prec) and year was not significant (coefficient = - 0.0003 $p = 0.200$), indicating that precipitation does not have a significant effect on egg volume over time.

We observed that clutch size tended to decrease(**Figure 3.5**) as the years went by and in all altitudinal ranges, but the analyses were not significant (**Table 3-2**). All the

interactions were negative, except for Tmx, where the interaction between year and Tmx was shown to increase clutch size.

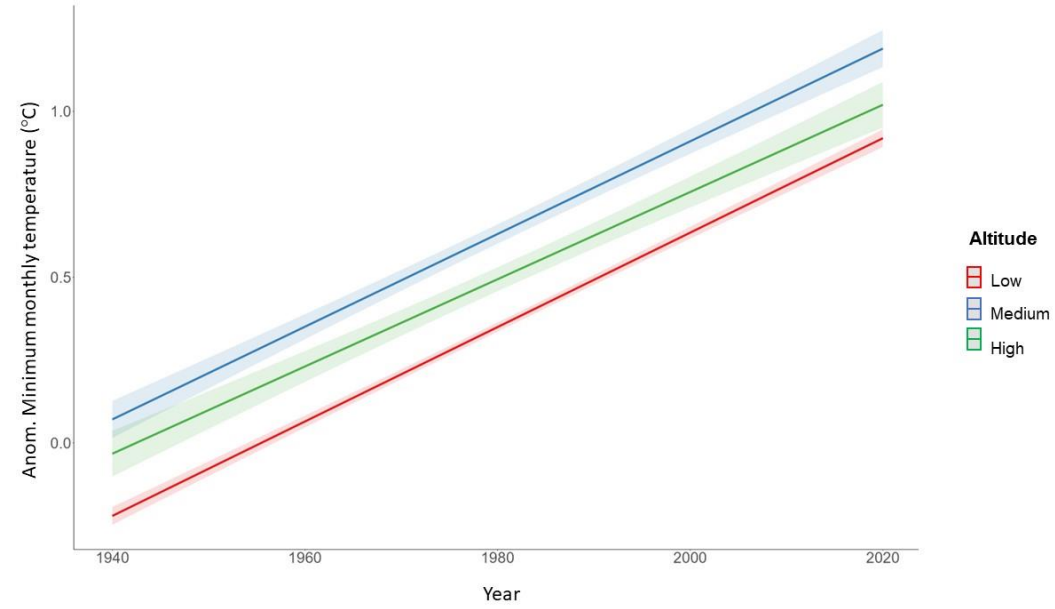


Figure 3.1: Anomaly of the minimum monthly temperature of the month of laying the clutch in relation to time (1901 - 2021) and altitude (0-1000 m as "low", 1001-2000 m as "medium", and 2001-4500 m as "high").

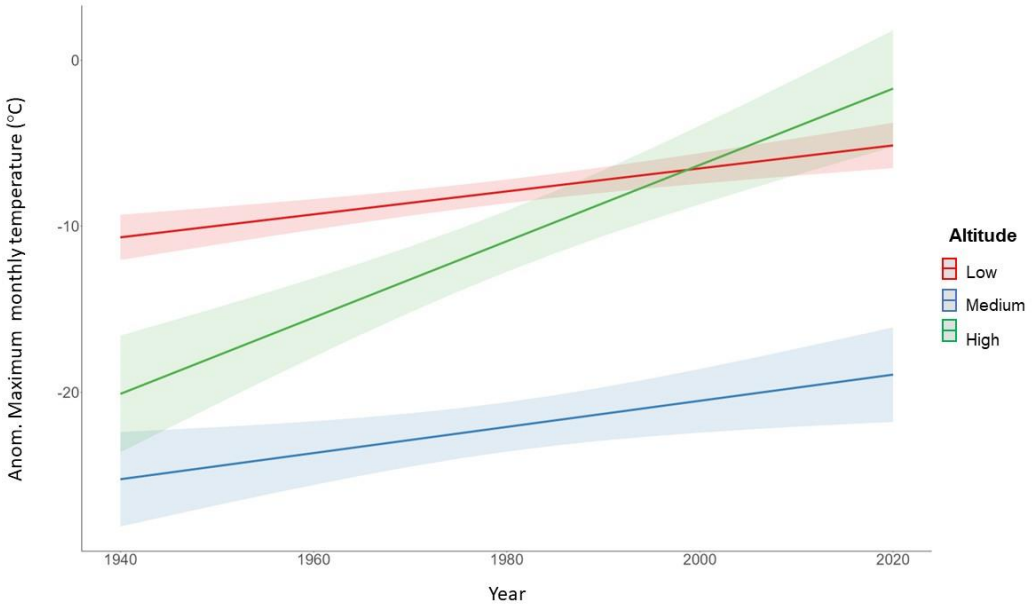


Figure 3.2: Anomaly of the maximum monthly temperature of the month of laying the clutch in relation to time (1901 - 2021) and altitude (0-1000 m as "low", 1001-2000 m as "medium", and 2001-4500 m as "high").

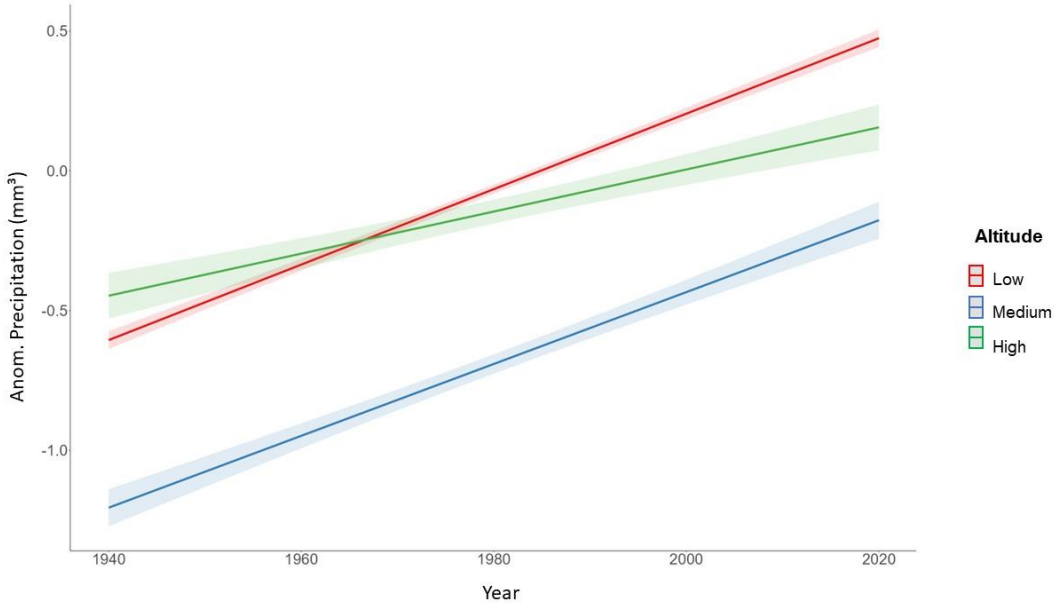


Figure 3.3: Anomaly of the monthly precipitation of the month of laying the clutch in relation to time (1901 - 2021) and altitude (0-1000 m as "low", 1001-2000 m as "medium", and 2001-4500 m as "high").

Table 3-1: PGLMM of the average egg volume of Passerine clutches in relation to altitude (low, medium and high) and climatic variables; "Tmn" = average minimum monthly temperature; "Tmx" = average maximum monthly temperature; "Prec" = monthly precipitation; ":" interaction between variables and year. Statistically significant values in bold.

Average egg volume				
	Valor	SE	Z-Score	P-Valor
Intercept	12237	3076.9	3.977	6.975e-05
Year:Alt.Low	-4.159	1.595	-2.608	**0.009**
Year:Alt.Medium	-4.111	1.583	-2.597	**0.009**
Year:Alt.High	-4.153	1.586	-2.618	**0.009**
Year:Tmn	0.0367	0.0115	3.189	**0.001**
Year:Tmx	-0.0351	0.0114	-3.069	**0.002**
Year:Prec	-0.0003	0.0002	-1.194	0.233

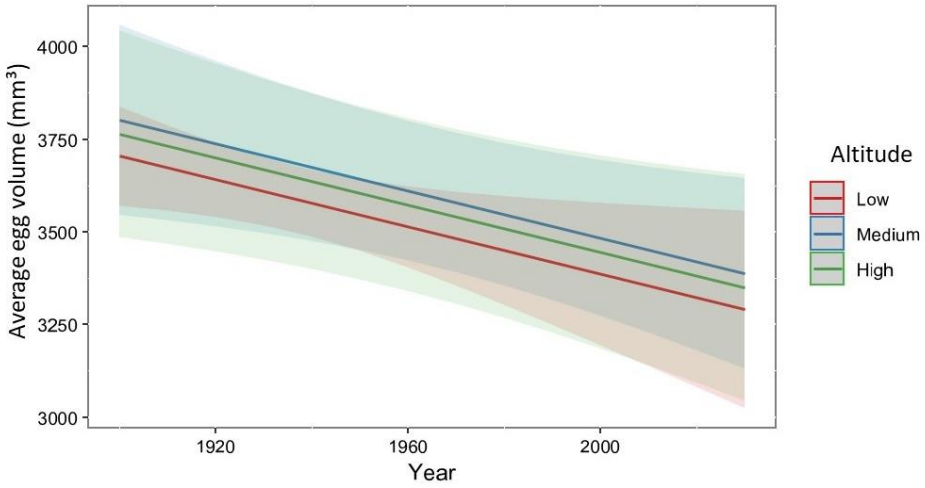
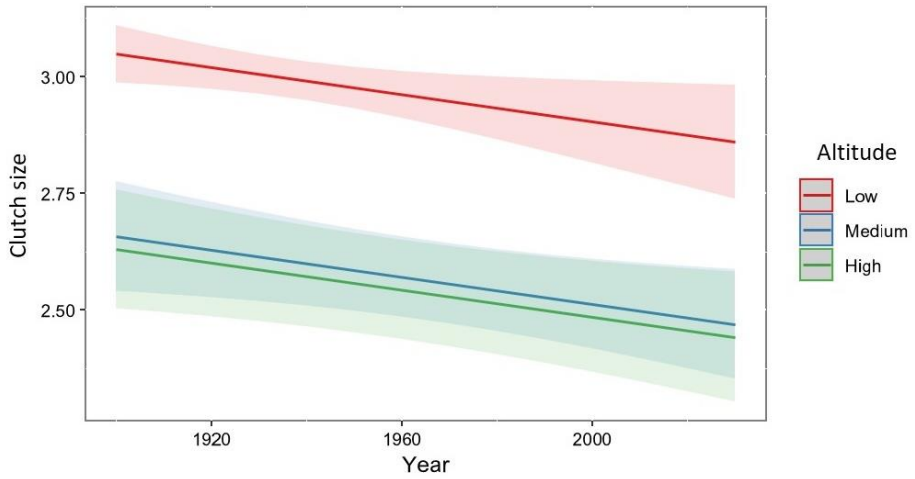


Figure 3.4: Average clutch egg size in relation to time (1901 to 2021) and altitude (0-1000 m as "low", 1001-2000 m as "medium", and 2001-4500 m as "high").

Table 3-2: PGLMM of the clutch size of Passerine clutches in relation to altitude (low, medium and high) and climatic variables; "Tmn" = average minimum monthly temperature; "Tmx" = average maximum monthly temperature; "Prec" = monthly precipitation; ":" interaction between variables and year.

Clutch size				
	Valor	SE	Z-Score	P-Valor
Intercept	1.291	0.919	1.405	0.1600
Year:Alt.Low	-0.0001	0.0005	-0.277	0.7822
Year:Alt.Medium	-0.0002	0.0005	-0.422	0.6728
Year:Alt.High	-0.0002	0.0005	-0.490	0.6243
Year:Tmn	-0.00001	0.000003	-1.732	0.0832
Year:Tmx	0.00001	0.000003	1.524	0.1276
Year:Prec	-0.0000001	0.0000001	-1.533	0.1253



2179

2180 **Figure 3.5:** Clutch size in relation to time (1901- 2021) and altitude (0-1000 m as
2181 "low", 1001-2000 m as "medium", and 2001-4500 m as "high").

2182

2183 ### 3.4. Discussion
2184

2185 Irrespective of the altitudinal range, all of analyses showed a reduction in egg
2186 volume and clutch size over time. It is already known that species at higher altitudes
2187 change their egg size – lager (e.g Lu et al. 2005, 2008a, 2008b, Levin et al. 2023;
2188 Deckel et al. 2024) and clutch size - smaller (e.g Boyce et al., 2015; Boyle et al., 2016;
2189 Hille & Cooper, 2015; Londoño et al. 2023) in relation to the lowlands. Therefore, there
2190 is still variation due to climate change.

2191 A 1°C increase in minimum temperature was observed across all altitudinal
2192 ranges. Since birds changed egg size with altitude, this indicates that a 1°C increase was
2193 sufficient for species to alter their life histories in terms of reproductive investment and
2194 effort.

2195 The results demonstrate the significance of climatic variables (Tmx, Tmn and
2196 Prec) and elevation in the observed variation in average egg volume over time.
2197 However, the influence of rainfall appears to be relatively limited. Nord & Nilsson
2198 (2021) demonstrated that an increase in ambient temperature of 1.5 °C during the
2199 incubation period can facilitate embryonic development. It is well known that larger
2200 eggs give rise to more fit individuals, especially in colder environments, where the
2201 chance of the clutch surviving is increased (Krist 2011). Adverse meteorological

conditions result in a more rapid cooling of the eggs subsequent to the departure of the adult from the nest (Reid et al., 2000). Consequently, elevated temperatures could prove advantageous for species at higher altitudes, as the cost of maintaining egg temperature would be reduced. Nevertheless, the exposure to ever-increasing temperatures can also increase the risk of hatchling mortality due to the inability to regulate egg temperature and energy demands, resulting in heat stress (Bourne et al. 2020; Carroll et al. 2018; Oswald et al. 2021). In this way, there is likely to be a reduction in egg volume. The majority of studies that have evaluated egg size at higher altitudes have demonstrated that the egg is larger (Lu et al. 2005, 2008a, 2008b; Levin et al. 2023; Deckel et al. 2024), probably due to the adult birds' ability to regulate the heat of the eggs more effectively, provide parental care, feed the young, and produce offspring better adapted to the adverse conditions prevailing at higher altitudes.

Halupka & Halupka (2017) reported a reduction in the number of offspring related to changes in climate in populations of several species over the last 50 years. Our results demonstrated a decline in clutch size with increasing years across the three altitudinal ranges, although this trend was not statistically significant. Clutches from higher elevations exhibited a tendency to be smaller than those from lower regions. It is probable that the reduction in clutch size at higher elevations is further exacerbated by climate change. It can be posited that elevated temperatures may favor a greater number of chicks. This raises the question of whether rising temperatures could result in an increase in clutches at higher elevations. While this may be the case, it is crucial to consider that tropical species in these gradients are considered particularly vulnerable to rising temperatures (Freeman et al. 2018). Additionally, climate change can result in alterations to seasonal rainfall patterns (Trenberth 2011), which are crucial for the prevalence and abundance of food sources, such as insects (Wolda 1978). However, elevated temperatures can impede the emergence of insects (Cooper 2022) and diminish the food resources of insectivorous birds. In addition, elevated temperatures may induce hyperthermia in larger clutches (Van Balen & Cavé 1969).

The necessity for a larger clutch size is reflected in the increased time required for foraging and the availability of food. Even in the context of elevated temperatures at higher altitudes, it is crucial for females to maintain an optimal clutch size in order to facilitate adaptation to climatic changes (Pendlebury & Bryant 2005). This approach ensures the avoidance of potential risks.

Despite the higher incidence of rainfall over the years, no significant correlation was observed between rainfall and clutch size or egg volume. Generally, precipitation can vary along elevation gradients. Precipitation is generally higher at medium altitudes (Sanders et al. 2003; Kluge et al. 2006) or near sea level (Lauscher 1976; Barry 2008; Colberg & Anders 2014). In the mountains, for example, precipitation depends on many factors, such as topography, the strength of the moisture-carrying winds and the orientation of the mountain ranges in relation to the direction of the winds (Luitel et al. 2020). The data indicated an increase in precipitation over time, which could suggest a greater availability of food resources and, consequently, a higher probability of larger clutches. Furthermore, Grudinskaya et al. (2022) posited that increased rainfall could lead to an expansion in clutch size due to a reduction in predator activity and enhanced nest concealment resulting from augmented vegetation following precipitation events (Grudinskaya et al., 2022). In contrast, numerous studies have demonstrated that the Americas experience greater precipitation, with an increasing prevalence of extreme rainfall events (Carvalho, 2020). This is also an unfavorable condition for egg and chick development, leading to an elevated frequency of reproductive failures (Moreno & Møller, 2011).

It is also known that birds can change their altitudinal ranges in search of the ideal temperature for their development or reproduction. A study in the Peruvian Andes showed that species changed their elevation distributions in response to recent temperature increases (Freeman et al. 2018). Another well-known study on the adaptations of tropical birds to climatic variations showed that species switch from breeding in the wet season in the lowlands to breeding in the dry season in the highlands (Tye 1992). Higher temperatures permit females to attain a physical condition that enables them to commence breeding at an earlier stage of their life cycle (Slagsvold 1976; García-Navas et al. 2008). This is advantageous, as it allows for the earliest possible breeding (Herényi et al. 2014). In the case of species from higher altitudes, this can be advantageous, as they have a shorter reproductive window than at lower altitudes.

Species specializing in high latitude or altitude habitats face a particularly high risk of population decline (Pimm et al. 2006) and are expected to show low resilience in the face of rapid temperature increases (Martin & Wiebe 2004). The study revealed that birds inhabiting higher altitudes are more susceptible to the adverse effects of climate

change, resulting in a decline in their population Harris et al. (2014). It is possible that these species will face drastic reductions in their populations due to the impact of climate change on their reproductive patterns. However, it is also possible that some species will benefit from warmer breeding seasons and generate larger inividuals (Halupka et al. 2021), especially species with high adaptability to climate change. However, also suggest that the climate at higher altitudes could warm three times faster than the global average (Nogués-Bravo et al. 2007). Although some species have limited dispersal, others could potentially benefit from colonizing new habitats that offer suitable climatic conditions (Brambilla et al. 2022). In addition, species that live higher up do not have higher altitude habitats to accommodate them and may reduce their populations or disappear altogether as climate change leads to an "escalator to extinction" (Sekercioglu et al. 2008; Lawrence et al. 2011). A collaborative effort by society will be needed to reduce the adverse effects caused by significant changes on tropical species that inhabit higher altitude areas (Freeman et al. 2018). Furthermore, there is an urgent need for detailed studies of life history variation in tropical birds living at higher altitudes (Boyle et al. 2015).

We emphasize that we have integrated data from several species over an extensive area in the Neotropics for 120 years. We emphasize the importance of data archived in museums and the answers we can get to the biology and ecology of birds (Marini et al. 2020; Bates et al. 2022). In addition, we highlight the importance of conserving high-altitude areas and implementing public policies aimed at climate change.

3.5. Conclusion

Our analysis revealed a consistent reduction in egg volume and clutch size over time, regardless of altitudinal range. A 1°C increase in minimum temperature across all elevations was significant enough to alter reproductive investment in Passeriformes, indicating the strong influence of climate change on life history traits. While temperature changes notably impacted egg volume, the effect of precipitation was limited. Larger eggs, more common in higher altitudes, are better suited for colder environments, enhancing offspring survival. However, rising temperatures pose risks of heat stress and hyperthermia, potentially reducing egg volume and increasing hatchling

mortality. Despite the complexity of climatic effects, our study underscores the need for conservation efforts and public policies addressing climate change impacts on Neotropical bird populations.

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CONCLUSÃO GERAL DA TESE

Nesta tese examinamos a possibilidade de variações no investimento reprodutivo de Passeriformes na região Neotropical em gradientes altitudinais. Coletamos dados provenientes de 5.889 ninhadas de 285 espécies, originárias de 37 coleções científicas, das quais medimos 6.387 ovos de 2.313 ninhadas de 182 espécies. Além disso, utilizamos dados de 634 tamanho de ninhada de 92 espécies de 27 fontes literárias para espécies com poucos registros e principalmente dados de maiores altitudes.

No primeiro capítulo, investigamos se o tamanho da ninhada é alterado com o aumento da altitude, considerando também a influência do tipo de ninho. Observamos uma redução no tamanho da ninhada à medida que a altitude aumenta. Os ninhos abertos e fechados (cúpula e cavidade) reduzem o volume do ovo, sendo que os ninhos abertos exercem uma influência ainda maior na redução do tamanho da ninhada. Ao analisarmos por família, apenas três famílias demonstraram resultados significativos, indicando possíveis diferenças estratégias reprodutivas em relação aos gradientes de elevação.

No segundo capítulo, exploramos as variáveis climáticas que afetam o volume dos ovos de Passeriformes em gradientes altitudinais. Registramos que o volume do ovo aumenta com a altitude e que temperaturas mais baixas e maior precipitação estão associadas a um aumento no volume dos ovos. Além disso, observamos uma redução no volume dos ovos em ninhos abertos. Essas descobertas sugerem que as espécies de aves analisadas investem mais em ovos volumosos para enfrentar condições climáticas mais frias.

No terceiro capítulo, investigamos como o clima influenciou no esforço e investimento reprodutivo nos últimos 120 anos. Verificamos um aumento na temperatura mínima em todas as faixas altitudinais ao longo dos anos. Desta forma, observamos menor tamanho do ovo e ninhada, mas não significativa no tamanho da ninhada. Em 120 anos o aumento da temperatura mostrou agir negativamente no investimento reprodutivo. Possivelmente ocasionará em reduções drásticas nas populações nesses ambientes no futuro.

Assim, ampliamos o entendimento sobre o esforço/investimento reprodutivo de Passeriformes em gradientes de elevação na região tropical, proporcionando evidencias valiosas sobre os impactos potenciais das mudanças climáticas nesses ambientes. Essas descobertas podem contribuir para o desenvolvimento de estratégias futuras de conservação, particularmente para espécies que podem enfrentar desafios devido às alterações projetadas nas temperaturas e precipitações.

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