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A relação entre a migração e reprodução da tesourinha (*Tyrannus savana*)

Vanesa Fabiola Bejarano Alegre

Dissertação apresentada ao Instituto de Biociências do Campus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Mestre em Ciências Biologia (Zoologia).

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VANESA FABIOLA BEJARANO ALEGRE

A RELAÇÃO ENTRE A MIGRAÇÃO E REPRODUÇÃO DA TESOURINHA (*TYRANNUS SAVANA*)

Orientador: Prof. Dr. Alejandro Edward Jahn
Co-Orientador: Prof. Dr. Milton Cezar Ribeiro

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AUTORA: VANESA FABIOLA BEJARANO ALEGRE
ORIENTADOR: ALEJANDRO EDWARD JAHN
COORIENTADOR: MILTON CEZAR RIBEIRO

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Prof. Dr. MILTON CEZAR RIBEIRO
Departamento de Ecologia / Instituto de Biociências de Rio Claro - SP

Prof. Dr. CESAR CESTARI
Pós-doutorando do Departamento de Zoologia / Instituto de Biociências de Rio Claro/SP

Prof. Dr. KARL STEPHAN MOKROSS
Pós-doutorando do Departamento de Ecologia / Instituto de Biociências de Rio Claro - SP

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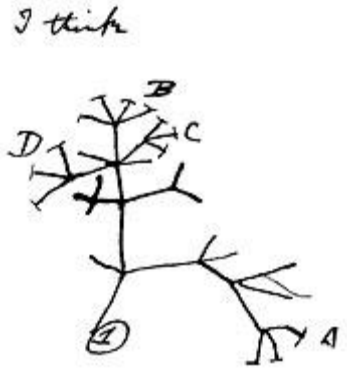

"Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved."

— Charles Darwin, "The Origin of Species"

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Resumo

As aves migratórias devem realizar uma série de atividades-chave, incluindo migração, criação e muda, para sobreviverem e se reproduzirem com sucesso. É essencial que estes eventos ocorram no período adequado, pois possuem um elevado custo energético, podendo afetar a aptidão da ave. A migração pre-reprodutiva é importante para que a reprodução seja bem sucedida, já que chegar cedo na área reprodutiva tem muitos benefícios (p.e., seleção sexual e aquisição do melhor território). Além disso, a reprodução pode acarretar em um custo de energia que varia entre as populações, dependendo da quantidade de investimento reprodutivo. Igualmente, cada local de reprodução pode diferir na quantidade de alimento disponível e na competição por territórios. Portanto, relação entre a data de chegada e o resultado reprodutivo em tesourinhas foi estada em uma área de Cerrado. Adicionalmente, foi descrita a condição corpórea das tesourinhas fêmeas após da postura de ovos. Trabalhamos na Estação Ecológica de Itirapina, no Brasil, anilhando adultos, procurando adultos anilhados e monitorando os ninhos. Os indivíduos que chegaram cedo nas áreas reprodutivas tiveram um sucesso reprodutivo significativamente mais alto que os indivíduos que chegaram mais tarde, o que é similar a resultados de pesquisas no Hemisfério Norte. Os machos chegaram em média 9.8 dias antes que as fêmeas, possivelmente devido à seleção sexual. Além disso, foi encontrada uma interação significativa entre sucesso reprodutivo e a condição energética entre as duas populações. As fêmeas com sucesso reprodutivo na Argentina tiveram condições energéticas significativamente mais elevadas do que as fêmeas que falharam, com uma relação oposta no Brasil. Estes resultados oferecem sugestões para pesquisas futuras sobre os potenciais compromissos fisiológicos que as tesourinhas e outros pássaros enfrentam durante a reprodução.

Palavras chaves: Tesourinhas, Cerrado, Pampas, reprodução, condição corporal

Abstract

Migratory birds must undertake a number of key activities, including migration, breeding and molt, to successfully reproduce and survive. Properly timing these events is key, because each is energetically costly and can result in significant fitness consequences. Spring migration, in particular is important for successful reproduction, because arriving early to the breeding area has many benefits (e.g., sexual selection and acquisition of a better territory). Furthermore, reproduction represents an energetic cost that varies among populations, depending on the amount of reproductive investment. In addition, each breeding site may differ in the amount of food available and in competition for territories. Therefore, I evaluated the relationship between arrival date and the reproductive outcome in Fork-tailed Flycatchers in the Cerrado ecoregion. I also described body condition of female flycatchers after they laid eggs. Colleagues and I worked at the Estação Ecológica de Itirapina, Brazil. We banded flycatchers, searched for banded adults and monitored their nests. I found that individuals that arrived early to the site achieved significantly higher reproductive success than those that arrived later, similar to findings of numerous studies at north-temperate latitudes. Additionally, males arrived on average 9.8 days before females, which may be related to strong sexual selection. I also found a significant interaction between nest success and energetic among the two populations, with successful females in Argentina having a significantly higher body condition than those that failed, with the opposite pattern in Brazil. I offer directions for future research on the potential physiological tradeoffs that flycatchers and other birds face during the breeding season.

Key words: Fork-tailed flycatcher, Cerrado, Pampas, reproduction, body condition

CONTEÚDO

A RELAÇÃO ENTRE A MIGRAÇÃO E REPRODUÇÃO DA TESOURINHA (*TYRANNUS SAVANA*)

INTRODUÇÃO

Dentre as atividades vitais para as aves migratórias estão a migração, reprodução e a muda das penas, realizadas em uma ampla gama de áreas geografias e habitats (Ramenosfsky e Wingfield, 2007; Schmidt-Wellenburg, 2007). Fatores como o clima e a qualidade do habitat nas áreas de invernada ou nas áreas reprodutivas influenciam estes processos (Wikelski *et al.* 2003, Bearhop *et al.* 2004, McKellar *et al.* 2013). Além de isso, podem ser afetadas pela data de chegada à área de reprodução, que está relacionada ao sucesso reprodutivo (Norris *et al.* 2004, Rockwell *et al.* 2012, McKellar *et al.* 2013).

O sucesso reprodutivo tende a diminuir conforme se posterga o início da reprodução, devido à diminuição da disponibilidade de alimentos, aumento dos predadores de ninhos ou mudanças fisiológicas (Verhulst *et al.* 1995, Hansson *et al.* 2000). As aves migratórias tem um tempo limitado para se reproduzirem com sucesso, de modo que a chegada adequada ao local de reprodução é importante para que esta seja bem sucedida (p.ex., Murphy 1986, 1988, Regosin e Pruett-Jones 1995, revisto por Martin 1987). Além de isso, chegar cedo nas áreas de reprodução pode trazer benefícios individuais. Por exemplo, os machos incrementam as suas chances de ter um território ou uma fêmea de alta qualidade, maior fecundidade e sucesso reprodutivo (Møller 1990,1994, Lozano *et al.* 1996, Smith e Moore 2005, Tomotani *et al.* 2017). Já as fêmeas que chegam cedo podem ter maiores chances de aquisição de um macho de alta qualidade física e iniciar a postura de ovos mais cedo (Kokko, 1999, Smith e Moore, 2005, Morbey *et al.* 2012).

Conjuntamente, a reprodução pode significar um custo energético que pode variar entre populações dependendo da quantidade de investimento reprodutivo (ex., tamanho de posta de ovos, Coleman e Whittall, 1988, Moreno e Carlson, 1989). Além disso, cada sítio de reprodução pode diferir na quantidade disponível de alimento e na competição por territórios (Betts *et al.* 2008). A condição energética de um indivíduo é uma métrica útil para entender seu investimento relativo em várias atividades, como migração e reprodução, uma vez que nos fornece uma avaliação entre um organismo e o seu ambiente (Stevenson e Woods, 2006).

No entanto, a maioria dos estudos que tentam explicar estes mecanismos foram focados em aves de regiões temperadas e com longas migrações (Jahn e Cueto 2012), regiões onde as mudanças sazonais são fortemente marcadas. Consequentemente, a migração tem diferentes estágios vitais nas quais podem enfrentar diversos fatores que podem ajudar ou prejudicar o sucesso da migração (Newton, 2006). Foram realizados poucos estudos em aves de migração intra-tropical, onde os efeitos sazonais sobre a migração são poucos marcados, e diferenciados em época seca e chuvosa (Jahn e Cueto 2012), além de ter uma migração relativamente curta onde as escalas são raras ou inexistente.

Este projeto objetivou compreender: 1) a relação entre a data de chegada e o sucesso reprodutivo de aves que migram em América do Sul, e 2) os compromissos físicos envolvidos para que essas aves tenham diferentes níveis de investimento reprodutivo, como a quantidades de ovos no ninho. Explorando a relação entre a condição energética, e o sucesso reprodutivo.

A tesourinha (*Tyrannus s. savana*) é uma espécie migratória amplamente distribuída pela América do Sul (Chesser, 1995; Jahn *et al*. 2006.), tendo áreas de reprodução no centro e no sul, e áreas de invernada no norte (Chesser, 1997; Marini *et al.* 2009). Apresentam diferentes tamanhos de posturas de ovos em diferentes latitudes (Jahn *et al.* 2014). As fêmeas apresentam um comportamento muito característico durante a construção dos ninhos; o que torna mais fácil encontrar os ninhos. Finalmente, é uma ótima espécie para modelos descritivos sobre a reprodução. Com o presente trabalho se espera obter dados de interesse biológico que ajudem no entendimento e na conservação das espécies migratórias nas áreas tropicais.

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Chapter 1. The relationship between timing of spring migration and reproductive success: Is there a benefit to early arrival for an intra-tropical migratory bird?

Introduction

Every year, migratory birds must undertake a number of key activities, including migration, breeding and molt, to successfully reproduce and survive. Properly timing these events is key, because each is energetically costly and can result in significant fitness consequences. Thus, these activities must be properly timed so as to take advantage of temporally and spatially ephemeral food resources, while simultaneously avoiding negative effects, such as competition for breeding territories, inclement weather and predation (Kokko 1999, Betts *et al.* 2008).

Properly timing spring migration in particular has been shown to be important across numerous bird species. Due to a steep decline in avian reproductive success as the breeding season progresses, caused by timing relative to phenology of other organism of which it feeds or by other physiological preparation, to start another cycle unrelated to reproduction (Verhulst *et al.* 1995, Hansson *et al*. 2000). Therefore, migratory birds have a limited window of time available in which to successfully reproduce, (e.g., Murphy 1986a, 1988, Regosin and Pruett-Jones 1995, reviewed by Martin 1987), such that properly timing arrival on the breeding grounds is very important to successful reproduction (Lack 1968, Møller and Gregersen 1994a, Kokko 1999, Smith and Moore 2005, Visser *et al*. 2006).

Early arrival to the breeding site often results in higher breeding success (Verboven and Visser 1998, Verhulst and Nilsson, 2008, Williams, 2012); this is attributed to several factors such as environmental benefits, greater food availability, and nest predator avoidance (Verhulst *et al.* 1995, Van Noordwijk *et al.*1995). Nest success is often higher at the beginning of the breeding season; therefore, clutch sizes typically decrease as the breeding season progresses (e.g., Rowe *et al*. 1994). For males, early arrival increases chances of acquisition of territories (Smith and Moore 2005), mates (Møller 1990, Møller and Gregersen 1994a, Lozano *et al.* 1996, Smith and Moore 2005), more extra-pair young (Langefors *et al.* 1998), higher fecundity (Tomotani *et al*. 2017) and reproductive success (Møller 1994b). Benefits of early

arrival for females may be in acquiring a high quality mate (Kokko 1999, Morbey *et al.* 2012) and in an earlier egg laying date (Smith and Moore 2005). Another benefit of early arrival is more time to physiologically recover from migration before initiating reproduction (Ramenofsky and Wingfield 2007) (see figure 1). However, an early spring arrival may incur a high physiological cost, such as encountering inclement weather (Møller 1994b, Gordo *et al.* 2005, Jonzén *et al.* 2007, Rockwell *et al.* 2012) or low food availability (Newton, 2006, Preston and Rotenberry, 2006, Dunn *et al.* 2011) at the breeding site. Additionally, rapid spring migration may require high energy expenditure (Low *et al.* 2015), which can translate into reproductive costs, for example leading females to lay smaller clutches (Murphy 1986b), abandoning nests (Bleeker *et al.* 2005) and having lower reproductive success (Hansson *et al.* 2000). As a result, the spring migration strategy a bird uses can incur positive or negative consequences that 'carry over' into the breeding season and ultimately influence individual fitness (see Fig.1).

To date, most research on migration timing has focused on birds that breed at north-temperate latitudes, such that little is known about migratory strategies (e.g., timing of migration) and their consequences for birds that breed and migrate at tropical latitudes (Jahn and Cueto 2012). Research on intra-tropical bird migration, in which birds migrate wholly within the tropics, promises new insights into the consequences of adopting a given migratory strategy because tropical birds are characterized by an overall 'slower' pace of life compared to temperate breeding birds (Wingfield 2005, Wiersma *et al.* 2007, Robinson *et al*. 2010, Johnson *et al*. 2012). For example, tropical breeding birds tend to have lower basal metabolic rates (Wiersma *et al.* 2007) and smaller clutch sizes (Jetz *et al.* 2008) than those breeding at north-temperate. Furthermore, intra-tropical migratory birds are predicted to be under less selective pressure to rapidly migrate to the breeding site, as compared to counterparts breeding at temperate latitudes (Jahn and Cueto 2012). Additionally, because seasonality at tropical latitudes is largely defined by variation in rainfall throughout the year (Jahn *et al.* 2010), the availability of food resources that tropical birds track is likely to be very different than at north-temperate latitudes, where seasonality is largely temperature-based (Dingle 2008). As a result, these intrinsic and extrinsic factors may lead to different migration strategies at tropical vs. temperate latitudes.

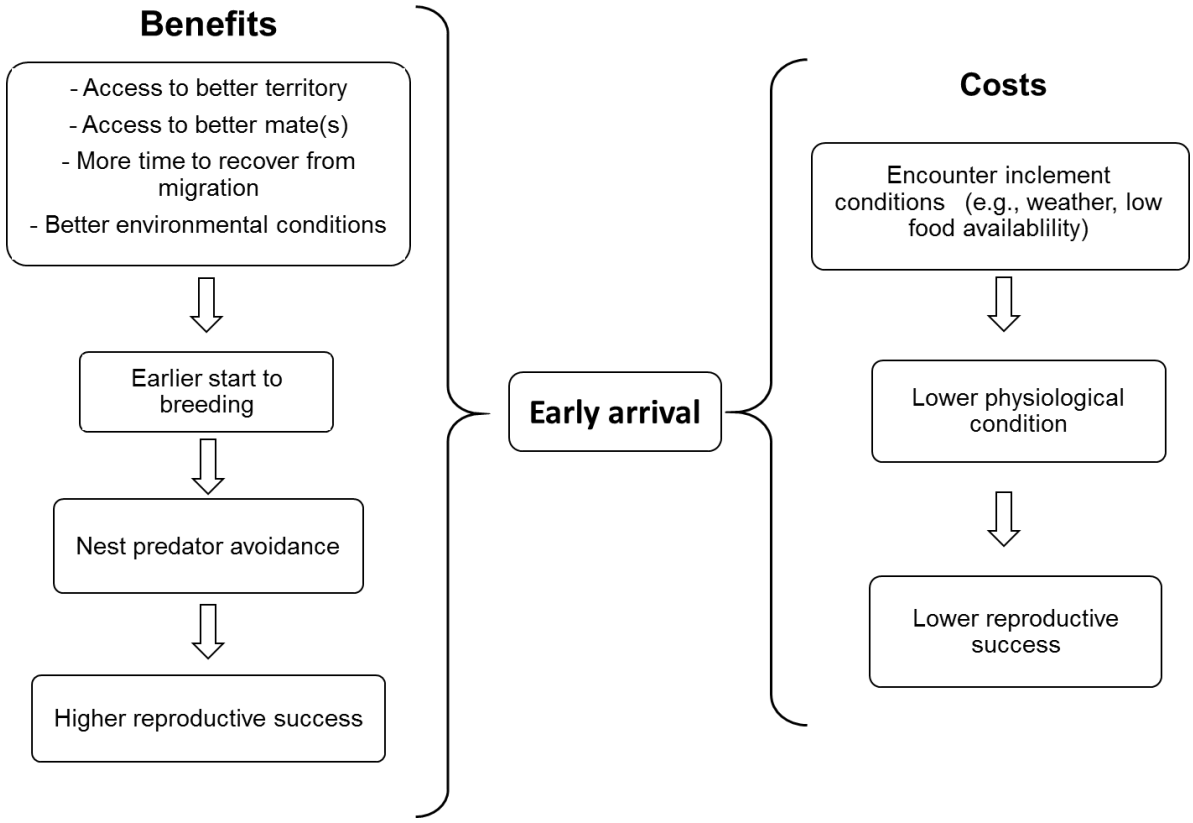

Figure 1. Illustrative model of the potential costs and benefits of early arrival to the breeding site.

With >230 migratory bird species that migrate wholly within the continent, South America holds the third-largest bird migration system on the planet (Chesser 1994). The most common family in this system is the New World flycatchers (Tyrannidae; Chesser 1994). The Fork-tailed Flycatcher (*Tyrannus savana*) is one of the most common and widespread migratory species in this family, breeding across a wide range of habitats and regions, making it an ideal model within which to study the effects of migration timing on reproduction (Fitzpatrick *et al*. 2004). In Brazil, Fork-tailed flycatchers breed in a variety of habitats, including forest edge, secondary vegetation, pastures, residential areas, lawns, and Cerrado vegetation (Mobley 2004, Jahn and Tuero 2013). The incubation period lasts an average of 13.6 days and the nestling period 15.0 days (Marini *et al.* 2009). Little about the parental care of this flycatcher is documented, but see Salvador (2013). I observed the female building the nest and incubating the eggs, whereas other breeding activities such as feeding nestlings and nest guarding were shared with the male. Additionally, few studies have evaluated the relationship between migration and other life-history activities throughout the annual

cycle, or how one activity (e.g., migration) might influence the timing and performance of other activities (e.g., reproduction; Bauer and Klassen 2013).

I aimed to understand whether timing of arrival on the breeding site influences the timing of reproduction and reproductive success of intra-tropical Fork-tailed flycatchers (hereafter, “flycatchers”) in South America. I had two objectives: 1) to describe the timing of arrival of male and female flycatchers at a tropical breeding site, and 2) to test the hypothesis that reproductive success is related to date of arrival on the breeding site. If so, I predicted that flycatchers that arrived earlier to the breeding site have higher reproductive success than those that arrive later. To investigate whether this relationship is mediated by the timing of the initiation of breeding, I also predicted that flycatchers that arrive earlier to the breeding site initiate breeding earlier, compared to those that arrive later

Study sites and methods

Study sites: Fork-tailed Flycatchers were studied at Estação Ecológica de Itirapina (EEI), São Paulo State, Brazil (22.3° S, 47.9° W) (see Fig. 2). ‘Campos sujos’, ‘campos cerrados’ and ‘campos limpos’ predominate in the EEI landscape, as well as smaller portions of Cerrado *sensu stricto*, gallery forest and marshes. These areas represent one of the last areas of natural field and Cerrado vegetation remnants of the state of São Paulo (Gianotti, 1988).

Nest monitoring: Just prior to and during each of three breeding seasons (October-January), from 2014 to 2015, colleagues and I searched for nests six days per week, beginning when the first evidence of reproductive behavior of Fork-tailed Flycatchers (e.g., collection of material for nesting building) was recorded in each season. I monitored flycatcher nests at each site from construction until failure or fledging of nestlings. I visited the nests three or four times per week. I recorded the number of eggs and/or nestlings, following Ralph *et al.* (1993) and Martin and Geupel (1993), to determine clutch size and whether the nest attempt was successful (i.e., fledged at least one nestling) or had failed (i.e., in which eggs disappeared between nest checks or nestlings disappeared before the date they were ready to fledge). I attempted to search for and monitor nests at each site until no active nests were found. I defined

the initiation of the breeding season as the date on which we encountered the first egg in a nest.

Capture and banding: We captured adult flycatchers between 5:00 and 8:00 am, six days a week, using one or two 3x12 or 3x18 m polyester or nylon mist nets (38 mm mesh size) during the breeding season (October-January), from 2013 to 2015. Nets were placed 2-4 m from an active flycatcher nest (i.e., containing eggs or nestlings), along with a predator model (e.g., Savannah Hawk, *Buteogallus meridionalis*) or a speaker that emitted a conspecific call, within two meters of the net. Flycatchers were first held in a cotton bag, banded with an individually-numbered metal band and with up to three Darvic color bands, so that each individual had a unique color band combination, which allowed for individual recognition.

Area searches: I conducted area searches for color-banded flycatchers on established areas, beginning just prior to the arrival of flycatchers (typically, late August), from 2014 to 2016, to record the first date on which each color-banded individual was observed in each season, as a proxy for arrival date. To do so, I divided the study area into 12 sample areas, slowly walking along the periphery and when possible, through each plot. There were usually two people conducting the area searches on separate plots. Because the habitat at the site is relatively open, we were regularly able to see banded flycatchers up to 100 m away. These area searches were conducted in different directions and randomly across different plots on different days, to avoid bias between plots and observers (Fig. 2). Area searches were conducted between dawn and 12:00 pm, from every day to every three days, until the reproductive seasonal was start, which happened around the end of October. At times, we aided our detection ability by using a playback speaker emitting the conspecific song of a flycatcher, which often attracted birds closer to the observer, so as to better see the color band combinations. Upon sighting a color-banded flycatcher, the location was georeferenced, noting the date, time and color band combination of the flycatcher.

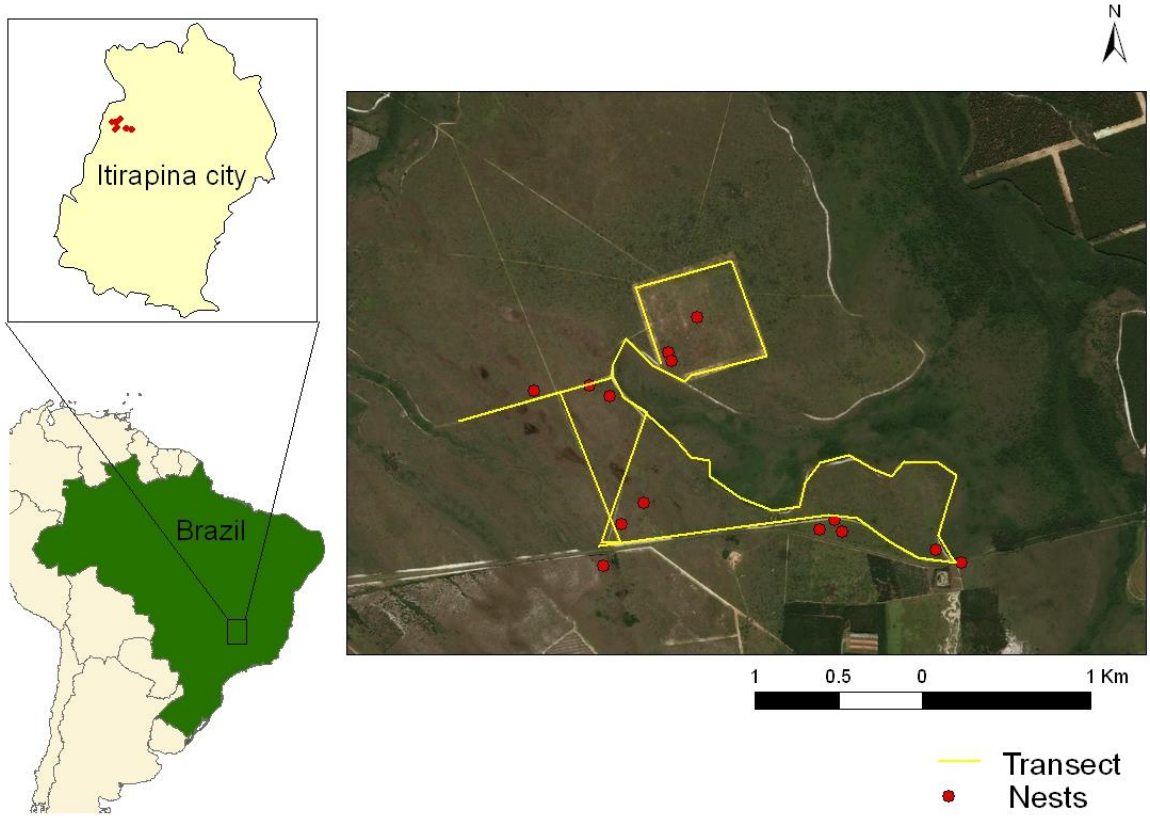

Figure 2. Map of Estação Ecológica de Itirapina, showing paths of transect (in yellow) and the distribution of nest (point red) where Fork-tailed flycatchers nested.

Statistical analysis: I analyzed nest survival rate in program MARK (White and Burnham, 1999). To evaluate the variation in arrival time at the breeding site between sexes, I ran Monte Carlo Simulation to test the null hypothesis of differences between these groups and a *P*-value was generated from 1000 simulated distributions. I calculated arrival date as a function of Julian date, with a beginning date of 19 August (since no flycatchers were ever seen at the study site prior to that date). I conducted a Spearman Rank Correlation to evaluate the relationship between arrival date and the date on which the first egg was laid in each nest (i.e., as a proxy for the initiation of the breeding season for the owners of each nest), in program SigmaPlot 11 (Systat Software Inc., San Jose, CA). Using logistic regression, I evaluated the relationship between arrival date and nest success, as well as between egg laying date and nest success, and used Chi Squared Test to evaluate the independence between variables. These tests were done in program R (R Core Team 2016).

Results

During area searches, I recorded a total of 43 color-banded flycatchers (25 males and 18 females), and I considered each individual as the owner of a single nest. In many cases, females and males were the owners of the same nest. The total number of independent nests was 22. Overall, the fraction of color-banded flycatchers re-observed in a subsequent season ranged from a high of 52.6% to 13.5% (Table 1). The proportion of re-observed flycatchers of each sex decreased as the study progressed (Table 1). The probability of a nest surviving was 0.06 (±0.040 SE), which is a 6% annual survival rate of flycatcher nests at the study site.

Table 1. Number of Fork-tailed flycatchers that were color-banded in each year of the study, and then re-observed in following years. Percent of flycatchers re-observed in a given year represents the total number of flycatchers of each sex observed in a given year divided by the total number of flycatchers of that sex that had been color-banded during previous years. Finally, the effort of the hour search by individual followed by the total hours per year.

No. banded			**No. re-observed**				**Sample effort**	
Year	**Females**	**Males**	**Females**	**Males**	**% Females re-observed**	**% Males re-observed**	**Indiv./ Hrs**	**Total hours / years**
2013	12	19	-	-	-	-		
2014	17	14	4	10	33.3	52.63	0.099	141:07
2015	8	8	9	8	31.03	24.24	0.069	245:33
2016	-	-	5	7	13.51	17.07	0.255	47:03
Total	37	41	18	25	-	-		433:43

Arrival date, initiation of breeding and reproductive success: Males tended to arrive significantly earlier to the breeding site than females (Dif_{obs}= 9.8 days, P = 0.029). There was also a significantly positive relationship between arrival date and the date on which the first egg was laid ($r_{s\ (n=22)}$ = 0.746; P < 0.0001; Fig. 3), as well as a significantly positive relationship between the date on which the first egg was laid and reproductive success (OR = 0.69; P = 0.017; X^2= 11.156; P = < 0.001; Fig. 4). Overall,

there was a significantly positive relationship between arrival date and reproductive success, with earlier arriving individuals exhibiting higher reproductive success (OR = 0.86; P = 0.030; X^2= 9.756; P= 0.002; Fig. 5).

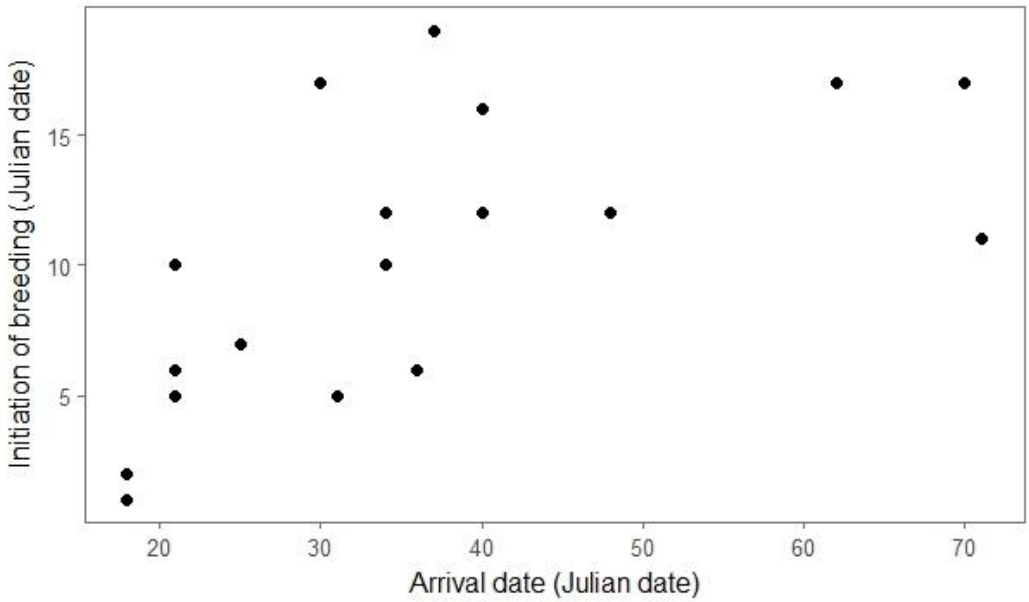

Figure 3. Initiation of breeding (date the first egg was laid in each nest) as a function of arrival date on the breeding site, for female and male Fork-tailed flycatchers.

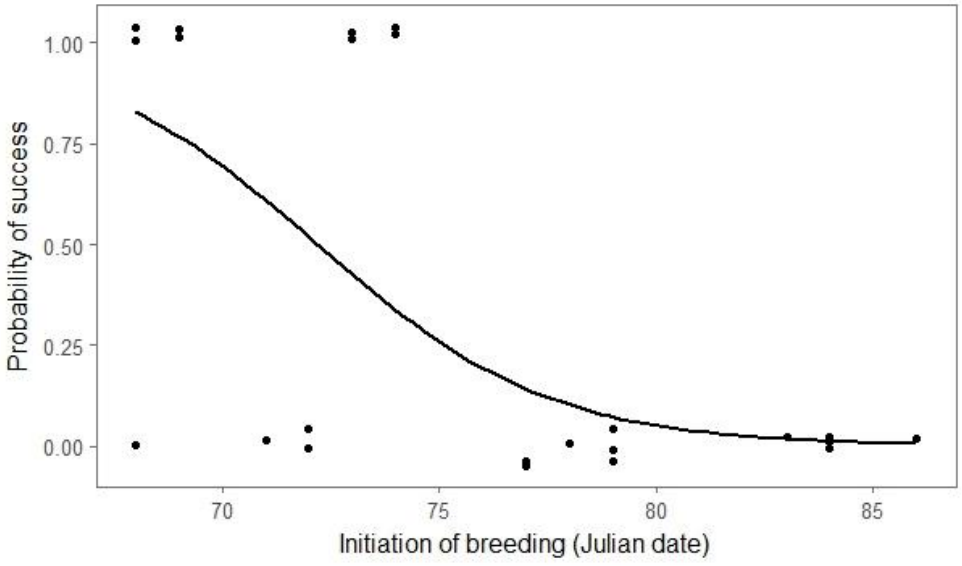

Figure 4. Probability of reproductive success (i.e., producing at least one fledgling) as a function of initiation of breeding (date the first egg was laid in each nest), for female and male Fork-tailed flycatchers.

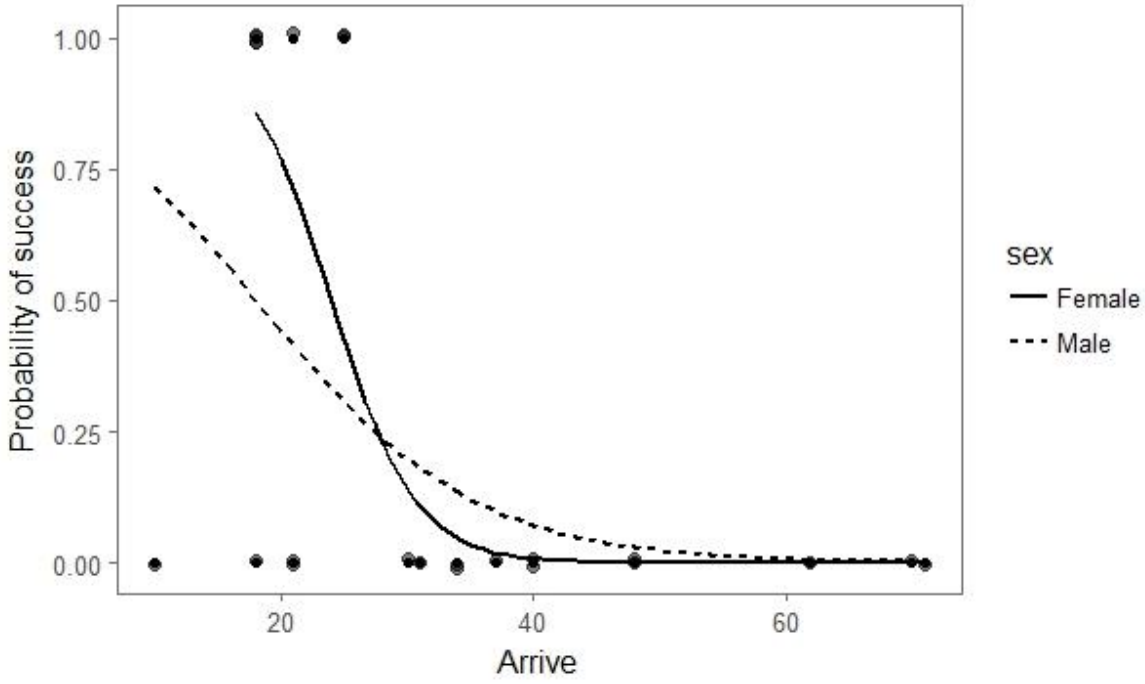

Figure 5. Probability of reproductive success (i.e., producing at least one fledgling) as a function of arrival date on the breeding site, for female and male Fork-tailed flycatchers.

Discussion

I found that flycatchers that arrived early to a tropical breeding site in South America have significantly higher reproductive success than those that arrive later. This relationship may be mediated by the timing of the initiation of breeding, since there was a significantly positive relationship between their arrival date and the date on which they laid the first egg, and between the initiation of breeding and breeding success. Overall, these results support the hypothesis that reproductive success of intra-tropical migrant flycatchers is related to their date of arrival on the breeding site. Finally, I found that male Fork-tailed Flycatchers arrived at the breeding site earlier than females, which to the best of my knowledge is the first documented evidence of protandry in an intra-tropical migratory passerine.

These results suggest that timing of arrival after spring migration plays a role in determining fitness of intra-tropical migratory Fork-tailed flycatchers. Substantial evidence from research on other migratory systems has suggested that arrival date is a key determinant of reproductive timing and success. For example, Tarka *et al.* (2015)

found that Great Reed warblers (*Acrocephalus arundinaceus*) are under selection favoring earlier spring arrival that acts through reproductive success, and that arrival date is heritable. Tomotani *et al.* (2017) found that, in European pied flycatchers (*Ficedula hypoleuca*) early-arriving males were paired with earlier laying females.

Although protandry (i.e., the earlier arrival of males vs. females to a breeding site) has been well-documented in songbirds that breed in North America and Europe (reviewed by Morbey and Ydenberg 2001, Tøttrup and Thorup 2008), virtually nothing is known about how common it is in intra-tropical migratory birds. That male Fork-tailed flycatchers tend to arriver earlier than females is also true of congeneric Eastern Kingbirds (*Tyrannus tyrannus*), which arrive a few days earlier than females in spring (Cooper *et al.* 2009). Those authors found that protandry in that species is not related to differences in body condition or to the ability of early-arriving males to acquire territories of higher quality. Instead, they suggest that protandry in Eastern Kingbirds is due to enhanced opportunities for early arriving males to engage in extra-pair mating. Indeed, evidence from European songbird migrants suggests that extra-pair mating opportunities may strongly influence male arrival date (Coppack *et al.* 2006), and in some shorebirds first access to mates may drive early arrival (Reynolds *et al.* 1986). Future research on protandry in flycatchers could test existing hypotheses for the existence of protandry, such as the 'rank advantage hypothesis', which posits that competition among males for breeding territories selects for earlier arrival in males than females, or the 'mate opportunity hypothesis', which states that early arrival improves the chances for mate acquisition more for males than for females (reviewed by Kokko *et al.* 2006, Saino *et al.* 2010).

Additionally, understanding the strategies birds use to arrive on the breeding site earlier than others is of interest, since it elucidates the proximate mechanisms involved in timing migration. For example, Schmaljohann *et al.* (2015) found that male Northern wheatears (*Oenanthe oenanthe*) in Europe are able to arrive earlier than females not because they overwinter closer to the breeding sites or migrate faster than females, but because they initiate spring migration earlier than females. Likewise, Savannah sparrows (*Passerculus sandwichensis*) breeding in North America are able to arrive earlier because the overwinter closer to the breeding grounds, reducing spring migration distance (Woodworth *et al.* 2016).

Understanding how timing of flycatcher migration is related to their reproductive success would benefit from research on the variation in spring migration timing among different populations, as well as variation in timing between years for the same individual. Vardanis *et al*. (2011) found that timing of migration varied much less between repeated journeys of the same individual Marsh Harrier (*Circus aeruginosus*) than between different individuals, a pattern which is not yet been studied in intra-tropical migrants, but which offers key insights into how flexible individual birds are in their timing of migration. Another potentially fruitful line of research could involve comparing the fitness consequences of timing fall vs. spring migration. Spring migration is often faster and shorter than fall migration, in terms of flight speeds (airspeed, ground speed, daily travel speed), stopover duration, and total speed and duration of migration (McKinnon *et al.* 2013, Nilsson *et al.* 2013). Does spring migration strategy (e.g., timing of departure and arrival, speed and number of stopovers) more accurately predict breeding success or adult survival than fall migration strategy? Understanding whether such a pattern exists, as well as underlying mechanisms driving such a pattern, could shed new light on the various selective pressures exerted on migratory birds throughout their annual cycle (e.g., Marra *et al.* 2015).

Understanding how capable different migratory bird populations are able to adapt to current and future climate change across the planet is a major challenge for migratory bird conservation (e.g., Both *et al.* 2009). What is apparent is that arrival timing is flexible to a degree and varies by species with different life history strategies. For example, advancement of arrival dates of migratory birds has been found to be greater in species with more general diets, shorter migration distances, and which lay more broods per year (Végvári *et al.* 2010). Given our lack of information on what determines arrival timing, or whether variation in arrival date has a genetic component (Both *et al.* 2010), future research on migration timing, arrival timing and its consequences for migratory bird populations should be highly multi-disciplinary, incorporating ecological, physiological and molecular components to understand the proximate and ultimate mechanisms underlying such patterns.

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Chapter 2. The relationship between reproductive investment, body condition and reproductive success in a Neotropical grassland bird, the Fork-tailed Flycatcher (*Tyrannus savana*)

Introduction

For songbirds, breeding is an energetically costly activity, since egg production and incubation require a substantial input of calories and nutrients (Williams 2005, Nord and Williams 2015). Both males and females often share in defending the territory and feeding nestlings, such that tradeoffs may exist for both sexes between investing in reproduction and other activities during the breeding season, such as feather molt (e.g., Rohwer *et al.* 2011; Echeverry-Galvis and Hau 2013). However, the cost of reproduction can vary between populations, depending on their level of investment in reproduction, such as the number of eggs they lay per clutch. Larger clutches can be more energetically costly to produce (e.g., Coleman and Whittall 1988; Moreno and Carlson 1989), potentially leaving less energy for other activities, such as molt. Additionally, some sites may be characterized by higher food availability during the breeding season, which can depend on the level of competition for those resources.

An ability to quantify the body condition of an individual is a useful metric for understanding its relative investment in a number of activities, such as migration and reproduction (Stevenson and Wood 2006). Body condition provides an evaluation of the interaction between an organism and its environment (Boersma 1998, Barbraud *et al.* 2003, Lovvorn *et al*. 2003). Although there is much on which estimate of body condition is most appropriate (Speakman 2001, Labocha and Hayes 2012, Jacobs *et al.* 2012, Labocha *et al.* 2014), non-destructive indices of body condition are commonly used, since they do not require sacrificing the animal (Stevenson and Wood 2006, Hayes and Shonkwiler 2001).

Much research has focused on temperate-tropical comparisons among breeding birds (Ricklefs, 1969; Nolan and Ketterson, 1983; Stutchbury and Morton, 2001). Birds that breed at tropical latitudes tend to have lower resting metabolic rates (Wiersma *et al.* 2007), slower or more protracted molts (Helm and Gwinner 1999, Ryder and Wolfe 2009), and laying fewer eggs per clutch (e.g., Young 1994, Martin *et al.* 2000, Jetz *et al.* 2008, Jahn *et al*. 2013). As a result, tropical breeding birds may save more energy than those breeding at temperate latitudes (Foster 1974, Moreno

2004, Johnson *et al.* 2012). However, most research on life history strategies have focused on forest birds, such that little information on the potential tradeoffs associated with adopting a given life history strategy are little understood for grassland species (Robinson *et al.* 2010).

With the aim of evaluating the physiological tradeoffs involved in having different levels of annual reproductive investment for an insectivorous, grassland bird in South America, I explored the relationship between body condition, reproductive investment and reproductive success in the nominate subspecies of the Fork-tailed Flycatcher (*Tyrannus savana*). This species is an ideal system with which to investigate the physiological costs of reproduction because it is composed of populations that breed across a wide geographic range (Fitzpatrick *et al.* 2004), and which are characterized by different levels of annual investment in reproduction (Jahn *et al.* 2013). Populations breeding at south-temperate latitudes, in Argentina, lay on average more eggs than those at tropical latitudes (Jahn *et al*. 2013), as seen in various species of birds globally (Jetz *et al.* 2008). Based on these results, I offer directions for future research on the potential physiological tradeoffs that flycatchers and other birds face during the breeding season.

Study sites and methods

Fork-tailed Flycatchers were studied at Estação Ecológica de Itirapina, São Paulo State, Brazil (22.3° S, 47.9° W). This site is composed of low campo and cerrado grassland. Flycatchers were also studied at Reserva Natural El Destino, Buenos Aires Province, Argentina (35.1° S, 57.4° W). The main habitats at this site are grasslands and marshes where cattle graze, intersected by woodland tracts dominated by *Celtis ehrenbergiana* and *Scutia buxifolia*.

Nest monitoring: Colleagues and I searched for nests on established areas beginning when flycatchers were seen carrying nesting material or defending a territory during each breeding season (October-January), from 2013 to 2015. We searched for and monitored flycatcher nests at each site from construction until failure or fledging of nestlings. Because clutch size could be affected strongly by laying date (Stutchbury and Roberston 1988; Winkler and Allen 1996), we monitored nests throughout the breeding season at each site. When a nest was found, it was geo-referenced and

monitored following standard protocols (Ralph *et al.* 1993). On each visit to a nest, I recorded the number of eggs and/or nestlings, following Ralph *et al.* (1993) and Martin and Geupel (1993), to determine clutch size and whether the nest attempt was successful (i.e., fledged at least one nestling) or had failed (i.e., in which eggs disappeared between nest checks or nestlings disappeared before the date they were ready to fledge). I attempted to search for and monitor nests at each site until no active nests were found. I define the initiation of the breeding season as the date on which we encountered the first egg in a nest.

Capture and banding: Flycatchers were captured between from 5:00 to 08:00 am using one or two 3x12 or 3x18 m polyester or nylon mist nets (38 mm mesh size) during the breeding season, from 2013 to 2015. Nets were placed 2-4 m from an active flycatcher nest (i.e., containing eggs or nestlings), along with a predator model (e.g., Savannah Hawk) or a speaker that emitted a conspecific call, within two meters of the net. Flycatchers were first held in a cotton bag, banded with an individually-numbered metal band and up to three Darvic color bands so that each individual had a unique color band combination, which allowed for individual recognition. Flycatchers were aged using the primary feather notch, present only in flycatchers that are >1 year old (Pyle 1997) and sexed flycatchers based on the shape of the primary notch (Pyle 1997). Unflattened wing chord was measured to the nearest mm using a wing ruler, and measured tarsus and bill length (from the front of the nare to bill tip) using plastic dial calipers (to the nearest 0.1 mm), and measured body mass (to the nearest 0.1 g) using an Ohaus ABS hand-held portable electronic scale.

Data analysis: I excluded from the analysis re-nesting attempts by the same birds within the same season and define the beginning of the breeding season as the date in which the first egg was found at the study site during a given season. Additionally, I did not include in the analysis individuals for which it was not clear whether they were parents of any nest at the site. For example, at some nests there was often more than one female near the nest, such that which female had laid the eggs was not clear. Additionally, I did not analyze data from females captured during the beginning of the egg laying period. Nest survival rate was calculated in program MARK which analyzes the probability of nest survival through reproductive duration on Julian days (White and Burnham, 1999), using data on nests for which we had data on Scaled Mass Index

(SMI) for females, in order to relate their nest success to their body condition (Peig and Green 2009, 2010).

I estimated body condition of female using the Scaled Mass Index (SMI), which accounts for the scaling relationship between body length and mass at different body sizes. To calculate SMI, I first estimated the scaling exponent between body mass and size by performing a standardized major axis regression on the natural log of body mass by the natural log of wing chord (Peig and Green 2009). I used a two-way ANOVA to evaluate the relationship between body condition and reproductive success, using the SMI value as a response variable and reproductive success and site as independent predictor variables. I used a Tuckey's test to evaluate differences among groups. All analyses were conducted in program R 3.3.1 (R Core Team 2016).

Results

Colleagues and I captured 25 female flycatchers (12 in Argentina and 13 in Brazil) at the end of the egg laying period. The mean clutch size at the site in Argentina was 3.4 (± 0.004) and was 3.0 (±0.002) at the site in Brazil . Percentages of nest success was 66.6% in females from Argentina and 30.76% in Brazil (Fig. 1). The nest survival probability in Argentina was 37.8%, whereas only 18.6% of nests were successful at the site in Brazil (Table 1).

Table 1. Nest surivival probability of female from Argentina and Brazil, calculated in program MARK for two study sites.

Estimates of Derived Parameters Survival Estimates of {B0}

Site	Probability of survival	Standard Error	95% Confidence Interval	
			Lower	Upper
Argentina	0.351	0.164	0.116	0.690
Brazil	0.107	0.080	0.023	0.381

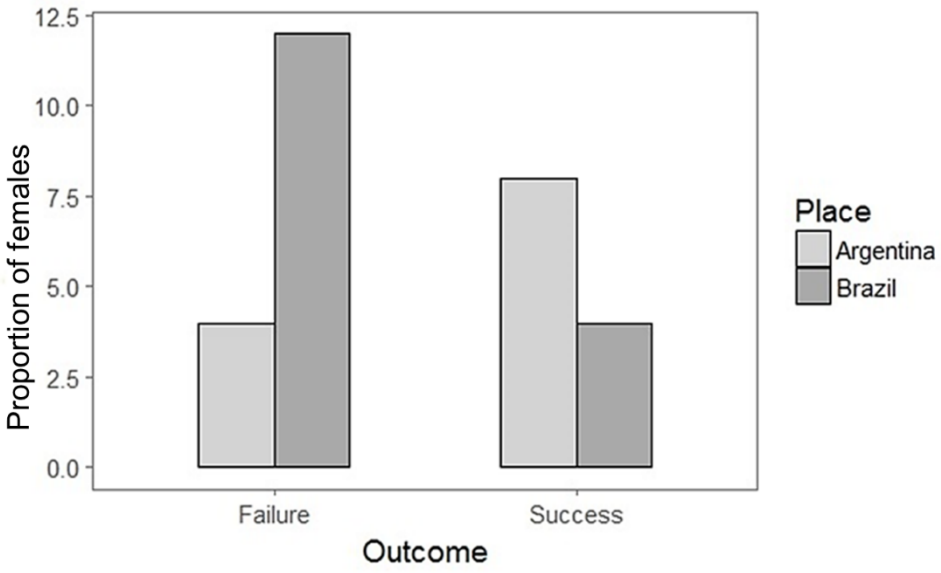

Figure 1. Poportion of Fork-tailed Flycatcher females with different reproductive outcomes at two study sites.

Body condition and reproductive success: I found a significant interaction between nest success and SMI among the two populations ($F_{1,24} = 7.98$, $P < 0.009$), with successful females in Argentina having a higher SMI than those that failed, with the opposite pattern in Brazil, although the effect within each population was not significant (Figure 2 and Table 2). I found a similar interactive effect between nest success and body mass among the two populations ($F_{1,24} = 17.35$, $P < 0.0003$), although site was also a significant factor, with females in Argentina being overall heavier than those in Brazil (Figure 3; Table 2).

Table 2. Results of a two-way ANOVA, on body mass and Scaled Mass Index (SMI).

SMI	**DF**	**Sum. Sq.**	**Mean Sq.**	**F value**	***P***
Outcome	1	0.073	0.073	0.0095	0.923044
Place	1	10.282	10.282	1.3396	0.258487
Outcome : Place	1	61.259	61.259	7.9815	0.009365
Residuals	24	184.203	7.675		
Body mass					
Outcome	1	0.002	0.002	0.0009	0.9761358
Place	1	25.518	25.518	9.6715	0.0047727
Outcome : Place	1	45.801	45.801	17.3591	0.0003457
Residuals	24	63.323	2.638		

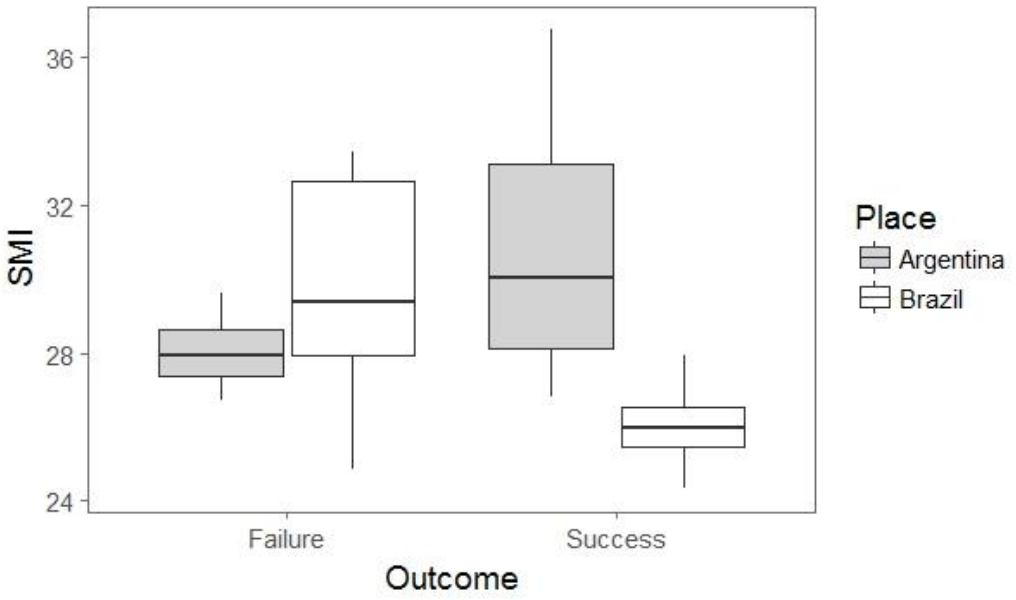

Figure 2. Fork-tailed Flycatcher body condition (as measured by Scaled Mass Index, SMI) as a function of reproductive outcome at two study sites.

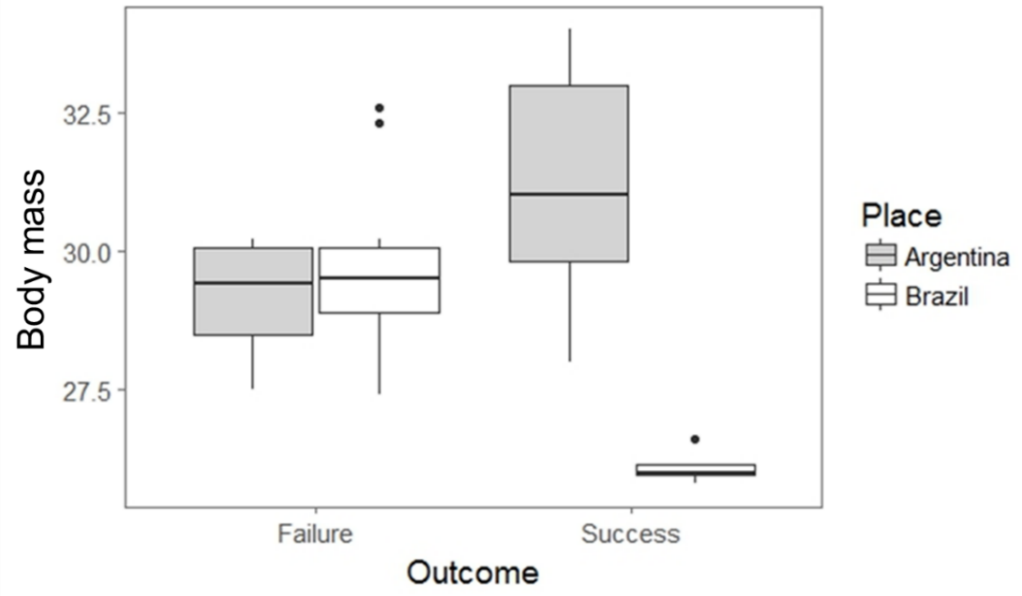

Figure 3. Fork-tailed Flycatcher body mass as a function of reproductive outcome at two study sites.

Discussion

Similar to previous studies, I found that flycatchers breeding in Argentina had a larger clutch size and higher nest survival than those breeding at tropical latitudes. I also found an interaction in body condition relative to reproductive success between my two study sites. Successful females in Argentina had a higher body condition and body mass than those that failed, whereas the opposite was true in Brazil. The patterns I observed in flycatchers between the two study sites offer insights into directions for future research. I therefore offer the following questions as a guide for future studies:

What are the physiological mechanisms underlying the observed interaction between reproductive success and body condition in Argentina vs. Brazil?

That successful females in Argentina had a higher body condition than those that failed, whereas the opposite was true in Brazil, may be because females with a higher body condition may be better able to rapidly raise nestlings and therefore increasing their chance of reproductive success (Wendeln and Becker 1999). This is similar to what is found in Brown thrashers (*Toxostoma rufum*), which are heavier due to fat content, and are also more successful (Hass 1998). However, other studies have shown that body condition alone does not influence success, but that year may also be a factor (Robinson *et al*. 2005). Additionally, an energy model proposed by Downhawer (1976) predicts that smaller individuals have a lower basal metabolic cost in comparison to larger individuals. Such smaller females may spend less time meeting their lower energetic requirements, such that they can dedicate more of resources to reproduction (Murphy 1986).

Future research on the cost of reproduction in these and other birds should take into account various factors, both extrinsic (e.g., food availability, climate) and intrinsic (e.g., body size, daily energy expenditure, metabolic rate), including migratory behavior, since Fork-tailed flycatchers that breed and migrate in Argentina must migrate further than those that breed in Brazil (Jahn *et al*. 2013, 2016). Comparing the consequences of migrating different distances, investing in different levels of annual reproduction, and having a different morphology (e.g., body size) promises key insights into how birds across the planet have adapted to a given set of environmental conditions.

What are the long-term survival and sub-lethal costs to adults when they adopt a given reproductive strategy?

Reproductive investment can affect adult survival by 25% (Linden and Møller 1989). Nevertheless, it is presently unclear whether flycatcher body condition is related to survival, although studies on other, non-reproductive processes have shown that physical condition is positively correlated to survival (Bryant 1988). The highest rates of Fork-tailed Flycatcher nest success were at a south-temperate study site in Argentina, compared to that of a tropical study site in Brazil, which is similar to previous studies showing higher rates of nest predation at tropical vs. temperate latitudes (Robinson *et al.* 2000; Stutchbury and Morton, 2001). Potentially, in tropical regions, females may prefer to abandon a costly reproductive attempt in order to ensure their future survival or future reproductive success (e.g., Hodges *et al.* 2015). Additionally, although previous research comparing reproductive success in this species has not shown significant differences between latitudes (Argentina vs. Bolivia; Jahn *et al.* 2014), other factors could explain why results of the present study are different. For example, the study site in Brazil is surrounded by non-native habitat (e.g., Eucalyptus plantations), such that the natural resource base in this ecosystem may be altered.

Future studies using other measures of energetic condition (see Wilder *et al.* 2015 for a review) may provide further insights in understanding of the tradeoffs incurred in adopting a given life history strategy (e.g., clutch size). Additional research on the physiological tradeoffs involved with different levels of reproductive investment, including avian reproductive biology at tropical latitudes, not only promises further insights into tropical bird biology, it also provides new perspectives into how birds are adapted to reproduce and survive across a rapidly changing planet.

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CONCLUSÃO

- A antecipação da chegada nas áreas de reprodução

O sucesso reprodutivo das tesourinhas está positivamente relacionado com a chegada antecipada nas áreas de reprodução, e que pode ser relacionado com a forte seleção sexual entre os casais (p.ex. Machos que chegam primeiro obtém fêmeas com desempenho reprodutivo mais rápido).

Os machos chegam mais cedo nas áreas reprodutivas que as fêmeas. Isto pode ocorrer devido as estratégias de seleção sexual e de escolha de territórios. O estudo da protandria poderia nós dar novos focos na áreas de seleção sexual, comportamento e ecologia da migração de aves.

- *Condição física*

Existe uma relação entre a condição física e o sucesso reprodutivo em diferentes populações de tesourinhas, indicando a necessidade de novas pesquisas relacionadando fatores extrínsecos (p.ex. disponibilidade de alimentos e clima), e intrínsecos (p. ex. a taxa metabólica e o gasto energético diário) que podem explicar as causas destas interações. Além disso, é possível utilizar outras medidas de condição energética no estudo das consequências de se adotar determinada estratégia de história de vida (p. ex. tamanho da postura de ovos).