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RESEARCH ARTICLE

Ecological determinants of *Tyrannus* flycatcher nestling growth at north- and south-temperate latitudes

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ABSTRACT

An organism's life history strategy is made up of a suite of physiological, behavioral, and ecological traits, which vary at both the interspecific and intraspecific levels in accordance with selective pressures operating on individuals. For birds, 2 primary ecological factors have been proposed to explain intraspecific and interspecific variation in nestling growth: nest predation and food availability. Individual nestling growth rates have important consequences for overall fitness because growth speed could influence subsequent reproductive performance and survival. We studied the relationship between ecological factors (i.e. precipitation level and predation rate) and nestling growth patterns of 2 New World flycatcher species (Tyrannidae) of the genus *Tyrannus* (Fork-tailed Flycatcher [*T. savana*] and Scissor-tailed Flycatcher [*T. forficatus*]) breeding at south- and north-temperate latitudes. We tested the hypothesis that nestling growth rates are driven by nest predation rates and predicted that nestling growth rates would be higher in species experiencing higher nest predation rates. We also tested the hypothesis that nestling growth rates are related to precipitation levels (a proxy for food abundance) and predicted that nestling growth rates would be higher at sites with higher precipitation levels. Growth rate was not associated with predation rate, but it varied with precipitation level, with faster nestling growth rates during wet years for the Scissor-tailed Flycatcher living at north-temperate latitudes. Among species, similar growth rates were found during wet years. These results indicate that, at least as proximate causes, precipitation explains intraspecific and interspecific growth rate variation in *Tyrannus* species to a larger degree than predation. Additionally, the variation in growth rate we observed between wet and dry years indicates a high level of plasticity in growth rate in this group of insectivorous birds.

Keywords: Argentina, life history, growth rate, Oklahoma, predation, rain, Tyrannidae

Determinantes ecológicos del crecimiento del pichón de Tyrannus flycatcher en latitudes templadas del norte y del sur

RESUMEN

La estrategia de historia de vida de un organismo se compone de un conjunto de caracteres fisiológicos, comportamentales y ecológicos, los cuales varían tanto a nivel intra como inter-especifico de acuerdo a la presión selectiva que opera sobre los individuos. En aves, se han propuesto dos factores ecológicos principales para explicar la variación intra e inter-especifica en el crecimiento de los pichones: la predación de nidos y la disponibilidad de alimento. Las tasas de crecimiento individuales de los pichones tienen importantes consecuencias sobre el éxito reproductivo debido a que la velocidad del crecimiento influye en el posterior rendimiento reproductivo y en la supervivencia. En el presente trabajo, estudiamos la relación entre factores ecológicos (e.g. nivel de precipitaciones y tasa de predación), y los patrones de crecimiento de pichones de dos especies de Atrapamoscas del Nuevo Mundo (Tyrannidae) del género *Tyrannus* (la Tijereta, *T. savana* y la Tijereta rosada, *T. forficatus*) que se reproducen a latitudes temperadas del norte y del sur. Se puso a prueba la hipótesis que la tasa de crecimiento de los pichones está influenciada por la tasa de predación de nidos y predecimos que el crecimiento de los pichones sería más rápido en especies que experimentan altas tasas de predación. También, se puso a prueba la hipótesis que la tasa de crecimiento de los pichones está relacionada con los niveles de precipitaciones (estimador de la abundancia de alimento) y predecimos que la tasa de crecimiento de los pichones sería mayor en sitios con mayores niveles de precipitaciones. La tasa de crecimiento no estuvo asociada con la tasa de predación en ninguna de las especies estudiadas, pero su

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variación estuvo relacionada con los niveles de precipitaciones. La tasa de crecimiento de los pichones fue mayor durante los años húmedos para la Tijereta rosada que vive en latitudes temperadas del norte. La tasa de crecimiento entre especies fue similar durante los años húmedos. Estos resultados indican que, por lo menos en una escala de tiempo ecológica, las precipitaciones explican la variación en la tasa de crecimiento tanto intra como inter-especifica en mayor grado que la predación en estas especies de *Tyrannus*. Finalmente, la variación en la tasa de crecimiento observada entre años secos y húmedos indica una alta plasticidad fenotípica en la tasa de crecimiento en este grupo de aves insectívoras.

Palabras claves: Argentina, historia de vida, tasa de crecimiento, Oklahoma, predación, precipitación, Tyrannidae

INTRODUCTION

Life history traits are shaped by a suite of ecological factors at both ecological and evolutionary time scales. Food availability and predation rate often result in life history trait variation at both interspecific and intraspecific levels (Stearns 1992, Martin 1995). In birds, life history trait variation has been observed in clutch size, offspring number, and growth patterns (Simons and Martin 1990, Yom-Tov et al. 1994, Martin 2004, Auer et al. 2007, Jetz et al. 2008, Mainwaring and Hartley 2012). The evolution of these traits may be influenced by tradeoffs between growth rate and other life history traits (Metcalfe and Monaghan 2003) or by physiological constraints that limit their evolution (West et al. 2001). However, potential factors determining interspecific variation in life history traits in Neotropical bird species remain poorly understood (Martin 2004, Robinson et al. 2010), primarily due to a gap in research on interspecific variation in life history strategies across a wide range of taxa with different diets, breeding strategies, and habitat requirements.

Nestling growth has been shown to be a particularly important component of a bird's life history strategy, since it may have important consequences throughout the life of a bird. Growth rates can be constrained, as occurs when sibling competition is strong (Royle et al. 1999) and can be restricted by physiological limitations (Stearns 1992). Deficient growth during the nestling period may have negative consequences for adult fecundity (Richner 1989, Blount et al. 2006) and fitness (Arendt 1997, Lindström 1999, Metcalfe and Monaghan 2003). Growth in suboptimal conditions may also result in lower juvenile mass (Naef-Daenzer and Keller 1999) and higher juvenile mortality after independence (de Kogel 1997, Bouwhuis et al. 2015, Jones et al. 2016). In contrast, faster nestling growth is associated with a shorter lifespan or lower reproductive performance (Metcalfe and Monaghan 2001, 2003). Nevertheless, growth rates can increase when faster growth results in fitness benefits (Arendt 1997). For these reasons, nestling growth rates are usually the optimum for a given set of conditions and not necessarily the maximum possible (Arendt 1997, Nylin and Gotthard 1998; reviewed by Dmitriew 2011).

Because of the importance of nestling growth on fitness, identifying the drivers that affect it at both evolutionary and ecological timescales has been a subject of intense study for decades. One of the most important factors affecting growth rate among bird species over evolutionary time appears to be predation (Dmitriew 2011, Martin et al. 2011, Mainwaring and Hartley 2012, Martin 2015). Martin et al. (2011) have shown that high nest predation rates are an important evolutionary force, resulting in increased growth rates among avian species. Nestlings of species with fast growth rates are exposed to predation risk for a shorter amount of time because they spend less time in the nest (Ricklefs et al. 1998, Remeš and Martin 2002, Remeš and Matysioková 2016). However, this can result in a lower body mass at fledging (Remeš and Martin 2002, Cheng and Martin 2012, Remeš and Matysioková 2016), which may in turn constrain nestling growth rate because adult size correlates positively with fitness (Roff 1992).

Food availability has also been identified as a key determinant of nestling growth rate (Simons and Martin 1990, Keller and VanNoordwijk 1994, Turner and McCarty 1997, Gebhardt and Richner 1998, Naef-Daenzer and Keller 1999). Both nestling mass (Turner and McCarty 1997) and survival (Simons and Martin 1990) are negatively affected when food availability is low. Birds raised on nutritionally poor diets may have reduced learning performance during adulthood (Fisher et al. 2006) as a result of developmental stress with lasting effects on brain structure (Nowicki et al. 2002), having significantly higher resting metabolic rates (Criscuolo et al. 2008) and reduced exploratory behavior (Krause and Naguib 2011). Seasonality of food availability is also known to be important for nestling growth (Arendt 1997, Martin et al. 2011, Mainwaring and Hartley 2012, Jahn et al. 2014). Given that food availability is often positively related to precipitation (Pinheiro et al. 2002, Jahn et al. 2010), it is not surprising that precipitation correlates positively with growth rate (Konarzewski and Tylor 1989, Mainwaring and Hartley 2016) and thus with the asymptotic or maximum weight that a nestling can reach. Therefore, within-species growth patterns can to a large degree be driven by food abundance, which mainly acts on growth rate at an ecological time scale (Martin et al. 2011).

Although there have been previous comparative studies on nestling growth (e.g., open vs. cavity nesters or clutch size; Martin and Li 1992, Remeš and Martin 2002), studies

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about gain in mass or size in passerine nestlings have focused on differences in growth patterns between tropical- and temperate-breeding species. Indeed, decades of research have shown that tropical-breeding songbirds generally grow with a slower maximum growth rate than temperate species (e.g., Ricklefs 1976, Austin-Bythell 2006, Martin 2015), but that the 2 groups have a similar average growth rate (Martin 2015). However, species breeding at north- and south-temperate latitudes also often exhibit substantial differences in other life history strategies. For example, compared to north-temperate breeders, birds at south-temperate latitudes often have a "slow" reproductive strategy, laying smaller clutches (Yom-Tov et al. 1994, Martin et al. 2000, Martin et al. 2006, Auer et al. 2007, Jetz et al. 2008) and producing juveniles that have a long time to independence (Russell et al. 2004). Additionally, birds in each hemisphere are often under different ecological limitations. Because the Southern Hemisphere is primarily covered by water (i.e. oceans), South America's climate is more buffered than North America's, resulting in a generally milder climate (Yom-Tov et al. 1994, Dingle 2008). As a result, compared to the situation in North America, food resources for South American birds are likely to be available for a longer period of time during the breeding season. South-temperate habitats are also characterized by higher variability in net primary production than those at north-temperate latitudes, in part due to the El Niño Southern Oscillation (Goetz et al. 2000). It is therefore likely that nestling growth patterns at north- vs. south-temperate latitudes are under different selective environmental pressures.

We studied the relationship between ecological factors (i.e. predation rate and precipitation level) and nestling growth patterns of 2 New World flycatcher species (Tyrannidae) of the genus *Tyrannus* (*T. savana* and *T. forficatus*) breeding at temperate latitudes of South and North America. First, we tested the hypothesis that interspecific variation in nestling growth rate is driven by nest predation rate. If so, we predicted a positive relationship between nestling growth rate and nest predation rate (i.e. the species with a higher predation rate will show a faster growth rate). Second, we hypothesized that both interspecific and intraspecific variation in nestling growth rate would be affected by food availability. *Tyrannus* species feed primarily on flying insects during the breeding season (Fitzpatrick 1980, Murphy 1983) and multiple studies have shown that abundance of arthropod food is positively related to rainfall (Denlinger 1980, Pinheiro et al. 2002, Amorim et al. 2009, Sofaer et al. 2013b), including abundance of arthropods consumed by *Tyrannus* species (Jahn et al. 2010). Thus, we predicted that nestling growth rates and asymptotic weight will be higher at sites and/or years with higher levels of precipitation.

METHODS

Study Sites and Species

Our south-temperate study site was Reserva Natural El Destino (35°08′S, 57°23′W), near the town of Magdalena, Province of Buenos Aires, Argentina. The study site primarily consists of flat, marshy grasslands mixed with old- and second-growth stands of tala (*Celtis ehrenbergiana*) and coronillo (*Scutia buxifolia*) trees. Fork-tailed Flycatchers (*T. savana*; hereafter FTFL) breed from central to southern South America (Marini et al. 2009, Jahn et al. 2014), migrating to northern South America to overwinter (Jahn et al. 2013b). We studied FTFLs at Reserva Natural El Destino from 2011 to 2014, during their breeding season there (November–January). Average clutch size is 3.5 (3–5) eggs and average brood size is 3.3 nestlings (Jahn et al. 2014). Adult mass at our field site is on average 30.9 ± 0.2 g (n = 102; AEJ and DTT personal observations).

At north-temperate latitudes, we studied Scissor-tailed Flycatchers (*T. forficatus*; hereafter STFL) at Elmer Thomas Park in the town of Lawton (34.38°N, 98.24°W) in southwestern Oklahoma, USA, during May to July, from 2011 to 2013. This site is characterized by mowed grass and scattered trees dominated by elm (*Ulmus* spp.), hackberry (*C. occidentalis*), and oak (*Quercus* spp.). STFLs breed May–August in the central United States, migrating to Central America to overwinter (Fitzpatrick et al. 2004, Jahn et al. 2013a). Average clutch size is 4.7 (3–5) eggs and average brood size is 3.7 nestlings (Regosin and Pruett-Jones 1995). STFL adult mass at our field site is on average 36.3 ± 0.3 g (n = 35; AEJ personal observation). Using data collected during the 3 study years, we found that clutch sizes of the northern temperate species (STFL: 4.46 ± 0.07 eggs, n = 48 nests) were higher than those of the southern species (FTFL: 3.48 ± 0.05 eggs, n = 136 nests; ANOVA: F = 106.5, df = 1 and 182, $P < 0.01$); however, the 2 species had similar brood sizes (STFL: 3.1 ± 0.1 nestlings, n = 40 nests and FTFL: 3.2 ± 0.1 nestlings, n = 87 nests; ANOVA: F = 0.08, df = 1 and 127, P = 0.78).

Nest Monitoring and Nestling Mass

We searched for and monitored nests throughout the breeding season at each site. We followed 151 and 34 nests of FTFL and STFL, respectively. Most nests were found during construction or with eggs. Nestlings were individually identified by marking their tarsi with 1–4 short lines, using waterproof ink. We weighed nestlings every 1–2 days to the nearest 0.1 g using a hand-held portable electronic scale (Ohaus, Parsippany, New Jersey, USA). We weighed nestlings during the morning from the first day they hatched (or, if found post-hatching, we estimated their hatch date based on the number of days elapsed between 2 consecutives nest checks or on the date when incubation

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started) until day 13–16 after hatching, to avoid premature fledging.

Ecological Measurements

We modeled daily nest survival rates (DSR) using program MARK v8.1 (White and Burnham 1999) to explore the influence of 2 covariates: species and year. We used a data set of 128 nests (34 STFL nests and 92 FTFL nests), followed until they were either successful (i.e. at least one nestling fledged), abandoned, or depredated. To carry out this analysis, we used failed nests (i.e. all eggs or nestlings disappeared between 2 consecutives visits) due to predation, and those nests for which laying date of the first egg was known. Since this is a multi-year study, we also evaluated whether DSR differed among years. An assumption to estimate DSR in MARK is that nest fates are independent (Dinsmore et al. 2002). For this reason, we excluded renesting attempts from the analysis. We evaluated models using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002), and present beta estimates with standard errors (SE) and confidence intervals (CI). We also calculated the nest survival of each species using the DSR obtained and the period of time from egg laying until the first nestling fledged. This period of time was 27.5 and 31 days for FTFL and STFL, respectively.

We obtained precipitation data from the Argentinean National Meteorology Service (SMN) for the south-temperate site and the Oklahoma Climatological Survey (Mesonet) weather station dataset for the north-temperate site. At both study sites, we calculated precipitation levels using cumulative rainfall during the 3 mo prior to the breeding season, and for the 3 mo corresponding to the breeding season. Precipitation levels were defined as "dry," "intermediate," or "wet" using precipitation data from 6 yr prior to the study period (i.e. 2005–2010) as a reference. A year was classified as "dry" if cumulative precipitation during the year was in the 0–25% percentile range, "intermediate" if it was in the 26–75% range, and "wet" if it was in the 76–100% range.

Nestling Growth

To evaluate nestling growth, we fitted growth curves for the dataset as a whole to a Richards model, which is a generalization of the logistic, Gompertz, and von Bertalanffy models (Tjørve and Tjørve 2010), primarily used to describe avian growth curves (Ricklefs 1967, Tjørve and Tjørve 2010). Richards family models include a shape parameter d, associated with the inflection point of the curve, t_i (Tjørve and Tjørve 2010). Depending on the value of d, it is possible to fit the better known models mentioned above. The advantage of using a Richards model is that it does not require the assumption of a particular growth shape, such as for logistic, Gompertz, and von Bertalanffy models. Thus, when Richards models are used, no particular growth model is assumed, as mentioned above. This is recommended for species for which no particular model has been previously found as the best to fit their growth pattern, such as in the *Tyrannus* species we studied. We therefore fitted growth data of nestlings that fledged to a Richards model using the parameterization proposed by Tjørve and Tjørve (2010).

The fitted body mass (W) reached at time t is:

$$W_t = A^*\left(1 + (d-1)^* e^{\left(-K\left(t - ti/d\wedge\left(d/(1-d)\right)\right)\right)}\right)\wedge\left(1/(1-d)\right),$$

see Tjørve and Tjørve (2010), where A is the asymptote of the growth curve, K is the maximum relative growth rate, and t_i is the inflection point or age of maximum growth. K determines how sigmoid the curve is (Tjørve and Tjørve 2010) and is the exponential rate, whose units are 1/time, of approach from hatching to asymptotic weight (Austin et al. 2011). Also, we calculated the maximum absolute growth rate g_{max} as AK (Tjørve and Tjørve 2010). Maximum absolute growth rate is defined as the growth rate at inflection point t_i or the maximum growth rate reached during the growing period (Tjørve and Tjørve 2010).

Statistical Analysis

To study variation in growth trajectories between species, we used a nonlinear mixed model (NLMM; Pinheiro and Bates 2000, Sofaer et al. 2013a). This model allowed fitting our data to the Richards curve to estimate the growth parameters (A, K, t_i, and d) of each nestling, while taking into account the lack of statistical independence among data due mainly to data from nestlings that were from the same nests and data obtained from repeated measurements on the same nestling (Pinheiro and Bates 2000, Sofaer et al. 2013a). We used nestling identity and nest as random factors to estimate curve parameters (A, K, and t_i) when fitting weight data to a Richards model using a NLMM (Pinheiro and Bates 2000, Sofaer et al. 2013a). This model also allows simultaneously testing the effects of explanatory variables on curve parameters, such that differences in growth patterns between species and potential effects of ecological variables on growth can be evaluated. To do this, we introduced species and year as explanatory variables in the model. All random or fixed factors that did not affect the curve parameters were removed from the model. We used a Gaussian family distribution for NLMM models. Brood size effects over g_{max} and A were analyzed using a linear mixed model (LMM) with a Gaussian family distribution. Nestlings were introduced as a random factor to the model. All analyses were done in R version 3.0.1 (R Core Team 2013) using the lme and nlme packages (Pinheiro et al. 2016) to conduct

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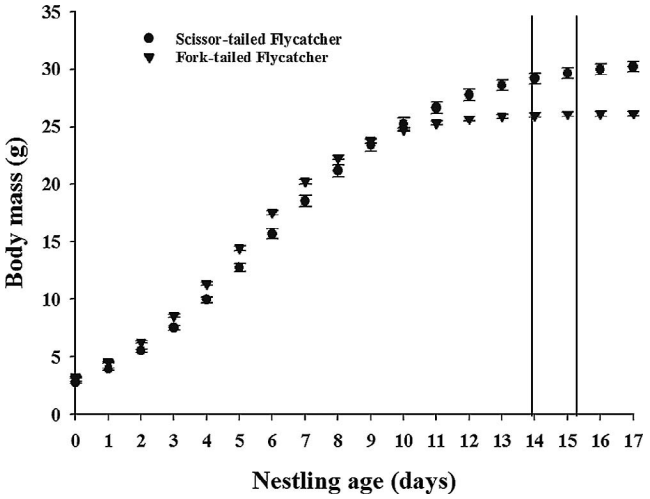


FIGURE 1. Body mass as a function of nestling age (days after hatching) during the breeding season for 2 flycatchers in the genus *Tyrannus*. The left and right vertical lines represent the fledging day of Fork-tailed Flycatcher and Scissor-tailed Flycatcher, respectively.

the LMM and NLMM analyses, respectively. We report results as mean ± SE.

RESULTS

Growth Patterns Across Years

FTFL nestlings grew with a maximum absolute growth rate (g_{max}) of 3.27 ± 0.03 g day^{-1}, their maximum relative growth rate (K) was 0.125 ± 0.001 1 day^{-1}, reaching an asymptotic weight of 26.2 ± 0.2 g; STFL nestlings gained mass with a maximum absolute growth rate (g_{max}) of 3.01 ± 0.09 g day^{-1}, the maximum relative growth rate (K) was 0.100 ± 0.003 g day^{-1}, reaching an asymptotic weight of 30.8 ± 0.4 g (Figure 1).

Maximum absolute growth rate (g_{max}) varied significantly with the interaction between species and year (LMM: $F = 11.49$, df = 2 and 98, $P < 0.001$; Tables 1 and 2). Also, we found significant variation during the 3 yr studied (LMM: $F = 12.92$, df = 2 and 98, $P < 0.001$; Tables 1 and 2) and among species (LMM: $F = 20.72$, df = 1 and 43, $P < 0.001$; Tables 1 and 2). For FTFL, the maximum absolute growth rate was similar during the entire study period (LMM: $F = 0.60$, df = 2 and 74, $P = 0.29$; Table 1). However, maximum absolute growth rate of STFL during 2013 reached the highest value in comparison to both 2011 (LMM: $t_9 = 6.40$, $P < 0.001$; Table 1) and 2012 (LMM: $t_9 = 3.98$, $P < 0.001$; Table 1). When we compared growth rate within year and among species during 2011, nestlings of the south-temperate species (FTFL) grew significantly faster, showing a higher maximum absolute growth rate, compared to that of the north-temperate species (LMM; STFL: $t_{16} = 4.33$, $P < 0.001$; Table 1). During 2012, FTFL also grew faster than STFL (LMM: $t_{14} = 2.70$, $P = 0.01$; Table 1). But, during 2013 FTFL and STFL showed similar maximum absolute growth rates (LMM: $t_{14} = 2.01$, $P = 0.07$; Table 1).

Maximum relative growth rate (K) was significantly different, with an interaction between species and years (NLMM: $F = 3.34$, $P = 0.03$; Tables 1 and 2). Also, species (NLMM: $F = 21.44$, df = 1 and 1,214, $P < 0.001$; Tables 1 and 2) and year (NLMM: $F = 4.84$, df = 2 and 1,214, $P < 0.01$; Tables 1 and 2) significantly affected maximum relative growth rate. Pairwise comparisons showed that nestlings of the south-temperate species (FTFL) reached a significantly higher maximum relative growth rate (K) compared to that of STFL during 2011 and 2012 (2011: $t_{440} = 2.55$, $P = 0.01$ and 2012: $t_{420} = 4.45$, $P < 0.01$; Table 1), with no significant difference in growth rate between the 2 species during 2013 ($t_{346} = 0.47$, $P = 0.63$; Table 1). FTFL nestlings had the same maximum relative growth (K) rate during the 3 yr analyzed

TABLE 1. Asymptotic weight (g), maximum growth rate (g day^{-1}), and maximum relative growth rate (1 day^{-1}) during the breeding seasons 2011–2013 of Fork-tailed Flycatcher at Buenos Aires, Argentina, and Scissor-tailed Flycatcher at Oklahoma, USA.

Year		Fork-tailed Flycatcher	Scissor-tailed Flycatcher
2011	Asymptotic weight	26.4 ± 0.3	29.9 ± 0.7
	Maximum growth rate (g_{max})	3.24 ± 0.05	2.50 ± 0.10
	Maximum relative growth rate (K)	0.120 ± 0.002	0.080 ± 0.002
	t_i	5.1 ± 0.1	6.61 ± 0.08
	n	41 nestlings (13 nests)	12 nestlings (5 nests)
2012	Asymptotic weight	26.3 ± 0.3	29.6 ± 0.7
	Maximum growth rate (g_{max})	3.34 ± 0.05	2.79 ± 0.05
	Maximum relative growth rate (K)	0.130 ± 0.002	0.090 ± 0.002
	t_i	5.4 ± 0.1	5.9 ± 0.2
	n	41 nestlings (13 nests)	10 nestlings (3 nests)
2013	Asymptotic weight	25.5 ± 0.5	31.9 ± 0.7
	Maximum growth rate (g_{max})	3.24 ± 0.08	3.62 ± 0.05
	Maximum relative growth rate (K)	0.130 ± 0.003	0.110 ± 0.002
	t_i	4.76 ± 0.07	5.4 ± 0.1
	n	29 nestlings (11 nests)	14 nestlings (4 nests)

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TABLE 2. Final Richards's growth model of 2 species of flycatchers in the genus *Tyrannus*. In the initial model, Species (STFL = Scissor-tailed Flycatcher, FTFL = Fork-tailed Flycatcher) and Year (2011, 2012, 2013) are used as predictor variables, modeling *A* (asymptotic mass), *K* (maximum relative growth rate), and t_i (age at the inflection point) growth parameters; *d* is a shape parameter that was only modeled using Species as a predictor variable. Only significant predictor variables that remained in the final model are shown. STFL and 2011 are included in the intercept. Models were fitted as nonlinear mixed models.

Parameter	Predictor variable	Estimate ± SE	t_{1214}	*P*
A	Intercept	30.8 ± 0.8	37.39	*< 0.001*
	Species (FTFL)	−4.6 ± 0.9	−5	*< 0.001*
K	Intercept	0.080 ± 0.007	10.48	*< 0.001*
	Species (FTFL)	0.042 ± 0.009	4.63	*< 0.001*
	Year (2012)	0.01 ± 0.01	1.08	0.27
	Year (2013)	0.03 ± 0.01	3.1	*0.001*
	Species (FTFL):Year (2012)	−0.007 ± 0.01	−0.53	0.59
	Species (FTFL): Year (2013)	−0.03 ± 0.01	−2.51	0.01
t_i	Intercept	6.2 ± 0.3	22.74	*< 0.001*
	Species (FTFL)	−0.9 ± 0.3	−3.5	*< 0.001*
	Year (2012)	−0.1 ± 0.2	−0.47	0.63
	Year (2013)	−0.6 ± 0.2	−2.44	*0.01*
d	Intercept	1.9 ± 0.1	12.77	*< 0.001*
	Species (FTFL)	0.8 ± 0.2	3.91	*< 0.001*

(NLMM: $F = 0.28$, df = 2 and 909, $P = 0.76$; Table 1). However, STFL nestlings had significantly lower maximum relative growth rates in 2011 and 2012 (NLMM: $t_{300} = 5.94$, $P < 0.01$ and $t_{300} = 3.13$, $P < 0.01$, respectively; Table 1). Also, inflection point or age of maximum growth (t_i) was significantly different among species (NLMM: $F = 12.26$, df = 2 and 1,214, $P < 0.001$; Tables 1 and 2) and years (NLMM: $F = 3.29$, df = 2 and 1,214, $P = 0.04$; Tables 1 and 2), with a nonsignificant interaction between these variables (NLMM: $F = 2.90$, df = 2 and 1,212, $P = 0.06$; Tables 1 and 2). FTFL reached the maximum growth rate at 5.11 days of age and STFL at 5.96 days of age.

We found a highly significant difference in asymptotic weight between species (NLMM: $F = 25.09$, df = 1 and 1,214, $P < 0.001$; Table 2). Nestlings of STFL were heavier than FTFL during the 3 yr analyzed (Table 2). Both FTFL and STFL nestlings exhibited similar asymptotic weights during the 3 yr analyzed (NLMM: $F = 0.30$, df = 2 and 1,210, $P = 0.73$; Table 2). Additionally, the interaction between species and year was not significant ($F = 1.25$, df = 2 and 1,208, $P = 0.29$; Table 2). FTFL and STFL fledglings leave the nest with 84% and 80% of adult mass, respectively.

Brood size did not affect maximum absolute growth rate (g_{max}) of nestlings (LMM: $t_{115} = -0.26$, $P = 0.79$), but negatively affected the asymptotic weight of nestlings (LMM: $t_{101} = -3.02$, $P < 0.01$).

Ecological Variables

There was substantial variation in precipitation levels within and between years, as well as between sites. During the breeding season, the Argentinian study site had consistently higher levels of precipitation than the Oklahoma study site (Table 3). However, during the pre-breeding period, both sites showed substantial variation in precipitation levels among years (Table 3). In Oklahoma, 2011 was an exceptionally dry year during both breeding and pre-breeding periods.

The DSR was similar for the 3 species throughout the study period. The best-fitting model was the null model of constant DSR (Table 4). The second and third models included the effect of species and year, respectively, but they were not better than the null model (Table 4). These models were only 0.28 and 1.6 AIC_c units higher than the best model. Indeed, there was weak evidence of a relationship between species and nest survival, being that

TABLE 3. Precipitation levels (in mm) at 2 study sites (Argentina and Oklahoma) during the years of the study (2011–2013) and for 6 yr prior to the study (2005–2010). "Breeding": the 3 mo that correspond to the breeding season at each study site; "Pre-breeding": the 3 mo previous to the breeding season at each site; "dry": cumulative precipitation during the year was in the 0–25% percentile range; "intermediate": 26–75% range; "wet": 76–100% range, using precipitation data of the 6 yr previous to the present study.

Total	Breeding				Pre-breeding			
Year	2011	2012	2013	2005–2010	2011	2012	2013	2005–2010
Argentina	371.1	287.2	391.5	229.4	105.1	552.6	219.7	250.4
Type	Wet	Wet	Wet		Dry	Wet	Intermediate	
Oklahoma	124.7	126.5	329.4	317	25.1	192.0	310.1	158.9
Type	Dry	Dry	Wet		Dry	Wet	Wet	

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TABLE 4. Support for candidate models evaluating the relationship between flycatcher daily survival rates (DSR) and covariates (year of study and species). Models are ranked according to second-order Akaike's Information Criterion corrected for small sample size (AIC_c); K is the number of parameters in the model, ΔAIC_c is the difference between the AIC_c value for the current model and the model with the lowest AIC_c, and w_i is the model Akaike weight, a measure of each model's relative support within the set of candidate models. S(.) is the general model that assumes a constant DSR among nests and over time.

Model	K	AIC_c	ΔAIC_c	w_i
S(.)	1	493	0	0.33
S(Species)	2	493.3	0.28	0.29
S(Year)	2	494.6	1.64	0.14
S(Species + Year)	3	495.08	2.07	0.12
S(Species*Year)	4	495.09	2.08	0.11

the 95% CIs for this effect included zero (Beta coefficient: 0.25 ± 0.15, Inf.: −0.03, Sup.: 0.54). The DSR for FTFL and STFL was 0.97 and 0.98, respectively, and the nest survival probability of FTFL and STFL was 42.9% and 50.2%, respectively.

DISCUSSION

We found that growth rates (maximum absolute and relative growth rate) of the north-temperate species, Scissor-tailed Flycatcher, were higher during the year with the highest rainfall (2013), supporting the hypothesis that precipitation levels, a proxy of food availability, affect nestling growth rate in *Tyrannus* species. However, the asymptotic weight of Scissor-tailed Flycatcher was similar in dry vs. wet years, which does not support the prediction that nestling asymptotic weights should be higher in years with higher precipitation levels. Maximum (absolute and relative) growth rates of STFL were associated with rainfall level during each year, supporting the prediction that nestling growth rates should be higher at sites and years with higher precipitation levels. At the south-temperate site, precipitation levels were similar during the 3 yr studied, such that it was not possible to assess the effects of rainfall on growth rate in Fork-tailed Flycatchers. Additionally, our results showed similar maximum growth rate (absolute and relative) among species during a specific year (2013), indicating similar growth pattern in these species. The asymptotic weight of Fork-tailed Flycatcher was similar in dry and wet years, not supporting the prediction that nestling asymptotic weights should be higher in years with higher precipitation levels. Although further studies are needed to evaluate the generality of these results, our data suggest that mass gain in flycatchers is highly plastic between seasons for a given population, as well as between species, and that food availability is an important proximate factor driving growth rates in flycatchers. This is to the best of our knowledge the first study demonstrating these patterns between north- and south-temperate breeding passerines.

Although DSR was similar among species and during the 3 yr analyzed, there were differences in growth patterns among species, providing no support for the prediction that nest predation affects nestling growth rates. These results differ from those of most previous studies on the effects of predation on avian growth rates (e.g., Martin et al. 2011). However, the effects of nest predation can be expressed not only via phenotypic plasticity, but also through evolved responses. Given that the effects of predation on growth could be more relevant across longer time periods, further comparative research on a large number of nests across longer periods of time could shed important insights on the selective pressures molding nestling growth rates.

The association between nestling growth rates and rainfall in our study is similar to that found previously for Western Kingbirds (*T. verticalis*), which exhibit a positive relationship between nestling growth rates and rainfall during the winter previous to the breeding season, and with insect food abundance during the breeding season (Blancher and Robertson 1987). Variation in prey abundance greatly impacts the foraging behavior of *Tyrannus* species (Foreman 1978, Blancher and Robertson 1987, Murphy 1987) and at least in some years may be positively related to clutch size in Fork-tailed Flycatchers (Jahn et al. 2014). Thus, arthropod abundance as mediated by climate appears to play an important role in driving productivity in *Tyrannus*, although its effects may be highly variable between years.

Although not detected in our study, too much precipitation or a combination of low temperatures and precipitation during the nesting period can be detrimental. For example, nestling feeding rates of Eastern Kingbirds (*T. tyrannus*) drop during cool, wet weather, likely due to lower adult foraging efficiency (Murphy 1983, Rosa and Murphy 1994), although high temperatures can also result in a slower mass gain in this species (Murphy 1985). Similarly, in Pied Flycatchers (*Ficedula hypoleuca*), nestling growth rates are positively related with temperature and negatively associated with precipitation, likely due to reduced insect food availability during rain (Sanz 1995).

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Likewise, tits (*Parus* spp.) exhibit slower nestling growth rates during rainy weather (Keller and van Noordwijk 1994). How weather impacts food availability for birds with different diets and environments (e.g., north- vs. south-temperate latitudes) is still poorly understood. Given that rainfall likely impacts the availability of different types of food resources in different ways, the varying effect of precipitation on the growth of *Tyrannus* vs. tit nestlings may in large part be as a result of dietary differences (i.e. tits feed primarily on caterpillars [Naef-Daenzer and Keller 1999], whereas *Tyrannus* species primarily feed on aerial arthropods [Fitzpatrick 1980]).

There still exist large gaps in our understanding of the relationship between growth rates, environmental pressures, and fitness, and therefore in our knowledge of life history evolution and diversification (Dmitriew 2011). Future studies should attempt to understand the specific mechanisms underpinning the relationship between an individual bird's growth as a nestling (including the growth of different body components, such as wings and feathers) and its fitness later in life. Further research on the mechanisms underpinning nestling growth rates, as well as the fitness consequences of employing a given growth strategy under different selective pressures, is timely in terms of developing a comprehensive understanding of avian life history evolution across the planet.

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Author contributions: D.T.T. and A.E.J. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). D.T.T., A.E.J., M.S.H., D.V.R., D.A.M., F.P., T.J.M., A.Q., and J.Q.V. performed the experiments (collected data, conducted the research). D.T.T., A.E.J., M.S.H., D.V.R., and J.C.R. wrote the paper. 4. D.T.T. and A.E.J. developed or designed the methods. D.T.T. and M.D. analyzed the data. D.T.T., A.E.J., M.S.H., D.V.R., and J.C.R. contributed substantial materials, resources, or funding.

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