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BREEDING BIOLOGY OF PASSERINES IN THE SUBTROPICAL BRAZILIAN ATLANTIC FOREST

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Resumo. – **Reprodução de passeriformes na Mata Atlântica subtropical brasileira.** – Informações da biologia reprodutiva das aves são fundamentais para o entendimento das histórias de vida e conservação. Apesar de que tais informações estejam finalmente se acumulando para aves neotropicais, o subtrópico sul continua negligenciado. Aqui descrevemos a biologia reprodutiva de aves passeriformes na Mata Atlântica subtropical. Foram monitorados 265 ninhos de 38 espécies na temporada 2012–2013. A reprodução começou em setembro, porém observamos espécies iniciando tardiamente (dezembro). A média de duração do ciclo reprodutivo foi de 64 dias, mas variou bastante entre as espécies. Tamanhos de ninhada médios variaram de dois a cinco ovos entre as espécies. Em geral, a fenologia reprodutiva, tamanhos de ninhada e períodos de incubação e ninhegos foram similares àqueles encontrados em outras duas localidades na Argentina em mesma latitude. Nossos dados corroboram a idéia de que os pequenos tamanhos de ninhada associados a ciclos reprodutivos curtos vistos no subtrópico da América do sul não são corretamente explicados pelo atual paradigma tropical-temperado das histórias de vida das aves.

Abstract. – Information on breeding biology of birds is fundamental for the understanding of life history evolution and conservation. This information is only beginning to accumulate for Neotropical birds but the southern subtropics are still overlooked. Here we describe the breeding biology of passerines in subtropical Brazilian Atlantic Forest. We monitored 265 nests of 38 species during the 2012–2013 breeding season. Breeding began in September, but some species started as late as December. Average breeding season length was 64 days, but varied broadly across species. Average clutch sizes ranged from two to five eggs. The breeding season phenology, clutch sizes, and nesting periods were similar to other two communities at the same latitude in Argentina. Our data contribute to the debate that the combination of small clutch sizes and short breeding seasons seen in subtropical South America challenges the tropical-temperate paradigm of life-history theory.

Key words: Body mass, Brazil, breeding parameters, breeding phenology, breeding strategies, clutch size, egg size, nesting period, passerines, timing of breeding.

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INTRODUCTION

The timing of breeding of many species of birds in North and Central America is well known (Davis 1933, Skutch 1950, Johnston 1964, Snow & Snow 1964), while in South America it is known for few species, mostly in tropical latitudes (2–15°S, Marchant 1959, Oniki & Willis 1983, Sanaiotti & Cintra 2010, Marini *et al.* 2012) and southern temperate latitudes (31–34°S, Mason 1985, Mezquida 2002, 2003, and review in Di Giacomo 2005). In subtropical South America, aside from the limited availability of general data on reproductive biology, information on the timing of breeding is scarce (Roper *et al.* 2010), with the exception of the Argentine Yungas forest (26°S, Auer *et al.* 2007) and the Humid Chaco (25°S, Di Giacomo 2005). For the subtropical Atlantic Forest, information on breeding biology is scattered in the literature, and their phenology remains unstudied at the community level.

Life histories of birds in the southern hemisphere are more complex and variable than expected based on the latitude paradigm of life histories (Martin 1996, 2004). For example, a) the latitudinal increase of clutch size from tropical to temperate regions is smaller or negligible in South America (Yom-Tov 1987, Jetz *et al.* 2008); b) in tropical birds, the response to increased nest predation is not to avoid predation as observed in temperate birds, but to decrease renesting intervals (Roper 2005, Roper *et al.* 2010); c) birds from tropical Brazilian Cerrado and South American subtropics appear to have shorter breeding seasons than expected from the latitudinal gradient (Auer *et al.* 2007, Lima & Roper 2009, Marini *et al.* 2012). In these regions, short breeding cycles (a feature of temperate birds) are combined with small clutches (a feature of tropical birds), an unlikely breeding strategy in the light of life history theory, which predicts high fecundity when the annual time window for breeding is short (Martin 1996).

Understanding the breeding biology of Neotropical birds is fundamental not just in terms of life-history, but also for species conservation (Marini *et al.* 2012). In South America, deforestation is proceeding faster than research, especially in the Atlantic Forest, which today has been reduced to ca. 14% of its original size (Ribeiro *et al.* 2009). Also, the potential of climate change to disrupt breeding patterns implies that we must quickly gather data on basic breeding biology and seasonal patterns in reproduction, thus anticipating and understanding these changes as they occur (Forschhammer *et al.* 1998, Marini *et al.* 2009).

Here, we studied the breeding biology of several species of passerine birds in the Atlantic Forest in subtropical Brazil. We describe dates of initiation of breeding, breeding season length, nest types, incubation and nestling periods, clutch and egg sizes, number of nesting attempts, and nest survival probabilities. We compared some of these reproductive parameters from our study area with those from two other passerine communities located in the subtropical region in South America: in Argentine Yungas forest (hereafter El Rey National Park, Auer *et al.* 2007) and in the Humid Chaco (hereafter El Bagual Reserve, Di Giacomo 2005). Finally, we discuss the results under the light of the life-history paradigm of latitudinal trends.

METHODS

Study sites. We studied breeding birds in four locations near the city of Piraquara, state of Paraná, southern Brazil. The Mananciais da Serra (25º29'S, 48º59'W, 938–1016 m a.s.l.) is transitional Araucaria Forest and Montane Atlantic Rainforest (Reginato & Goldenberg 2007). The Mananciais da Serra plot had 16.4 ha of primary and successional vegetation and some open areas. Two sites are near water reservoirs (13 ha, 25º30'S, 49º01'W, 925 m a.s.l. and 5 ha, 25º30'S, 49º04'W, 900 m a.s.l.), comprising regularly mowed fields, orchards, and marshes, which had 121 nest-boxes installed (details in Wischhoff *et al.* 2015). Another site in a rural area is mostly forested and connects through riparian corridors to other fragments (1 ha, 25º31'S, 49º05'W, 915 m a.s.l.). Hereafter, we refer to our study sites together as Piraquara. Mean annual rainfall is 1427 mm, and monthly minimum and maximum temperature range from 9–20 ºC in July to 17–27 ºC in February (INMET 2014).

Data collection. The four authors and two field assistants were split in two groups to find signs of nesting from June 2012 to April 2013. To identify renesting pairs, birds were captured by mist-netting and in nest-boxes with trap doors. Captured birds and nestlings were uniquely banded with color and numbered metal bands (CEMAVE, National Center of Research for Bird Conservation) and weighed with a spring scale (0.1 g accuracy).

During the spring and summer seasons, we continuously searched for nests in appropriate places in the understory vegetation, and systematically followed adult birds and recorded their behavior for any breeding clue (Martin & Geupel 1993). Nests high above the ground were checked with a camera on a pole and ladder. If the nest was impossible to reach, nesting stage was determined by clues the adults gave while observed (e.g., carrying faecal sac outside). Nests were monitored until no longer in use. The time interval between nest checks was optimized by field work logistics. Near the dates of egg laying and hatching, we checked nests more frequently when possible to estimate the nesting phenology precisely. A nest was considered successful if at least one young fledged. We rechecked nests from as far as possible to minimize disturbance. We report fledging dates from a few unknown nests when we found young birds unable to fly, with fleshy gape flanges, and juvenile plumage.

Here, we refer to clutch initiation date as the date when the first egg was laid in each nest. The initiation of breeding season (hereafter IOB) is defined here as the date of the first clutch initiation of each species. We calculate breeding season length (hereafter BSL) for species using information from clutch initiation dates. We defined the BSL as the time in days elapsed from the first to last clutch initiation. We calculated IOB and BSL only for species with ≥ 5 clutch initiation dates. This cut-off is arbitrary since we have not found any recommendation in the literature. Although low sample sizes may underestimate BSL, we believe this sample size is sufficient since the clutch initiation dates could also be inferred from several other conspicuous cues (e.g., fledglings, see below). Summarizing for all species, we report the average date of IOB and BSL as mean ± SD.

The clutch initiation dates of nests with incomplete records were inferred by backdating laying dates of subsequent eggs, and occasionally, using the average number of days for the incubation or nestling period based on nests of the same species with complete information. We defined the incubation period as the interval in days between the last egg laid and the first egg hatched, and the nestling period as the number of days from the first hatched egg to the last fledged nestling. When nest checks did not coincide with the hatching day, or when they were more than two days apart at fledging, we used mid-point dates to estimate these transitions between nest stages. We used the resulting less accurate nesting periods only to compute BSL and IOB, and to draw the figure. Thus, these values were not included when reporting nesting periods. Daily survival rates (DSR) of nests were estimated for those species with a number of observed nests > 10, using the program MARK (White

& Burnham 1999) and assuming constant DSR between nesting stages (mean ± SE). Again, this cut-off is arbitrary but should still provide unbiased estimates of DSR if we assume that nests were found randomly.

Nests were classified as open-cup (superior entrance), enclosed (pendular or globular with side entrance), or cavity (built inside natural tree holes, nest-boxes or beneath roofs) following Auer *et al.* 2007. We recorded clutch sizes only for nests that survived through the laying period. Clutch sizes were summarized as mean ± SD by species. Eggs were weighed on a digital scale (0.01 g accuracy) and measured by taking photographs with a ruler for scale and then analyzing the pictures in the software ImageJ (Schneider *et al.* 2012). To summarize mean egg sizes by nest type (mean ± SD) we first calculated the average by clutch and then again by species.

To compare with the literature, sampling units are species. Thus, we used one average measure of clutch size, egg mass, and incubation and nestling period for each species. Egg mass was statistically controlled by female body mass in our study in Piraquara and also for El Rey National Park (Auer *et al.* 2007). For data from El Bagual Reserve (Di Giacomo 2005), when the female body mass was unavailable, we used the adult body mass. To gather breeding information from El Bagual Reserve, we first selected all passerine species with n ≥ 5 nests in the appendix 2 from Di Giacomo (2005). From this subset, IOBs were taken from the text and nest types were classified according to the descriptions. The end of breeding is given as last active nest without reference to the nesting stage, thus BSL could not be estimated. The taxonomic nomenclature follows the IOC World Bird List (Gill & Donsker 2015).

Statistical tests. Analyses were performed using *t*-test or generalized linear models (GLM) in the program R (R Core Team 2015). Using GLM, we visually checked the distribution of the residuals with the R package RT4Bio (Reis *et al.* 2015) to ensure the model was appropriate. In the event of bad residual distribution, we first tried other family distributions prior to transformation. We explicitly stated in the results any non-Gaussian distribution or data transformation. For models with more than one predictor variable, we tested first order interactions and, if significant, retained them in the model, otherwise they were excluded and the simplified model was used. In the case of rejecting null hypothesis in a model with a predictor variable with three levels, we used contrast analysis to determine which level pairs are responsible for the difference (Crawley 2013).

RESULTS

Banding and breeding search effort. We recorded 108 passerine species in the Piraquara. Of these, we banded 78 species (373 adults). Most adults (55%) were banded early in the winter. We spread our effort during 182 field days, from June 2012 to April 2013 (277 calendar days), including capturing, checking nests, and searching for breeding clues (4.4 ± 2.5 field days week^{-1}, median = 5). Systematical behavioral observations of birds were carried out from 7 September 2012 to 21 March 2013 (49.4 ± 35.4 behavioral observations week^{-1}, median = 47 behavioral observations week^{-1}). From the resulting 1631 behavioral observations, 86% revealed no breeding activity. The median frequency of nests checks excluding nest-boxes was 2-day intervals, with 83% of checks in ≤ 3-day intervals.

Breeding phenologies. A total of 265 nests of 38 species were found, and observations of fledglings provided approximate breeding dates for five additional species (Fig. 1, with scientific names). Nest-boxes were used by White-rumped Swallows, House Wrens, and

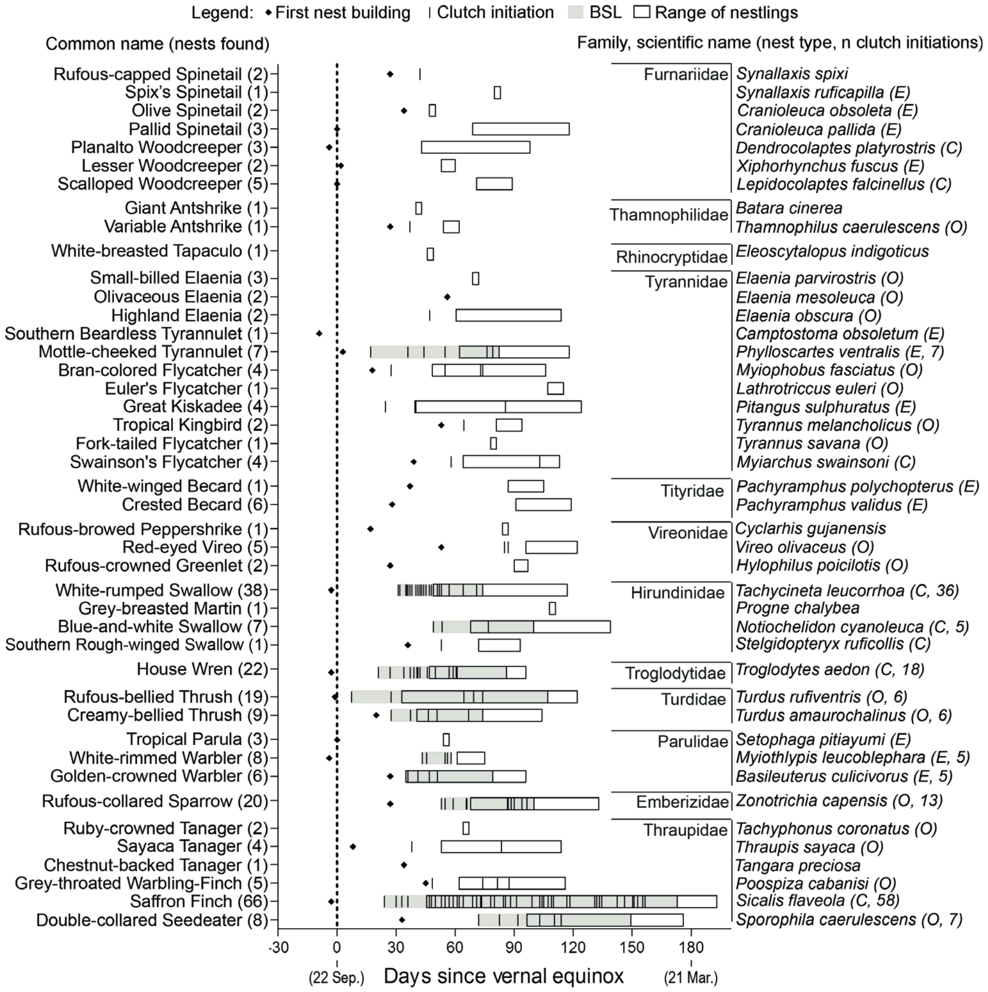

FIG. 1. Breeding timeline of 43 passerines (by family) in the subtropical Atlantic Forest of southern Brazil (Piraquara) in the breeding season of 2012–2013. X axis: days since vernal equinox. Light gray bars show the range of clutch initiations (when n ≥ 5 clutches), which is equivalent to the breeding season length (BSL) and species respective initiation of breeding (IOB) at the left tips of the bars. Number of nests found (in parentheses) includes recently fledged nests. Number of clutch initiation dates (in parentheses in right column, after nest type) are only for those species for which we estimated BSL and IOB. Nest types: open-cup (O), enclosed (E), and cavity (C). Clutch initiation dates were not possible to determine for all nests found.

Saffron Finches. The earliest breeding activity recorded (13 September) was nest building by the Southern Beardless Tyrannulet. We observed nine species building nests prior the onset of the vernal equinox (22 September). The average IOB was 34 days after the equinox (26 October ± 5.5 days, range = 29 September–3 December, n = 11 species). In comparison, at El Rey National Park the average IOB for 17 species was 22 October (± 12 days), and at the El Bagual Reserve it was 12 October (± 24 days) for 75 species. The average IOB was similar among studies ($F_{2,100}$ = 2.85, $P = 0.06$). In Piraquara, BSL averaged 64 ± 35 days (range = 15–149 days, Fig. 1), and was about the same as 50 ± 16 days (range = 28–85 days) recorded in El Rey National Park (gamma distribution, $F_{1,26}$ = 2.18, $P = 0.15$).

Egg-laying frequencies. Only Scalloped Woodcreeper (one nest), Variable Antshrike (one nest), and Mottle-cheeked Tyrannulet (two nests) laid eggs on alternate days. The Bran-colored Flycatcher (two nests), Swainson's Flycatcher (one nest), White-rumped Swallow (16 nests), House Wren (six nests), White-rimmed Warbler (two nests), Golden-crowned Warbler (two nests), Rufous-collared Sparrow (three nests), and Saffron Finch (eight nests), all laid eggs on consecutive days. For the remaining species in Fig. 1, the laying frequency is unknown.

Clutch sizes. We recorded clutch sizes for 25 species (Table 1). The modal clutch sizes were two (n = 10 species) and three eggs (n = 10 species), ranging from two to five eggs. Clutch sizes in open-cup nests ranged from one to three eggs (2.4 ± 0.4, n = 13 species). Enclosed nests had two or three eggs (2.5 ± 0.4, n = 4 species). Cavity nests had two to six eggs (4.0 ± 0.8, n = 8 species). Clutch sizes for species nesting in open-cup nests were marginally different between studies ($F_{2,54}$ = 3.33, $P = 0.04$, El Rey National Park: 2.4 ± 0.4, n = 9 species, El Bagual Reserve: 2.7 ± 0.5, n = 35 species). However, the contrast analysis revealed that none of the pairwise comparisons between sites reached significance (all $P > 0.1$). Species with enclosed nests had similar clutch sizes between studies ($F_{2,29}$ = 2.28, $P = 0.12$, El Rey National Park: 2.7 ± 0.1, n = 6 species, El Bagual Reserve: 3.0 ± 0.5, n = 22 species). For cavity species, the ones in Piraquara had the same clutch sizes than El Bagual Reserve ($F_{1,12}$ = 2.09, P = 0.17, in that study: 3.4 ± 0.7, n = 6 species), but comparisons with El Rey National Park were not possible because of the low sample size (n = 2 species) at this site. For species that are shared between Piraquara and El Rey National Park, the cavity-nesting House Wren had on average a larger clutch size in Piraquara (t_{23} = 3.10, $P = 0.004$, El Rey National Park: 3.5 ± 0.8 eggs, n = 8 clutches), whereas the clutch size of the open-cup nesting Rufous-bellied Thrush was similar (t_{38} = 1.1, P = 0.27, El Rey National Park: 2.7 ± 0.5 eggs, n = 28 clutches). The lack of measures of dispersion in El Bagual Reserve prevented the comparison of clutch sizes within species.

Egg sizes. Mean egg mass was 2.87 ± 1.45 g (n = 18 species, Table 1). When controlling for adult body mass, two outliers with extremely large body sizes and small eggs were removed from El Bagual Reserve dataset to fit a linear model: Purplish Jay (*Cyanocorax cyanomelas*) and Solitary Cacique (*Cacicus solitarius*). Egg mass correlated positively with adult body mass and differed between studies (GLM model with natural logarithm transformed mass, adult body mass: $F_{1,76}$ = 889, $P < 0.001$; study region: $F_{1,74}$ = 3.75, $P = 0.03$). Contrast analysis revealed that this difference occurs between Piraquara and El Rey National Park, and a 20 g female would have eggs 12% smaller in Piraquara ($P = 0.048$). Eggs had a similar average size in Piraquara and El Bagual Reserve ($P = 0.72$).

Nesting periods. Mean incubation period was 14.8 ± 1.9 days, (range = 11–18 days, n = 11 species), and mean nestling period was 17.3 ± 4.6 days (range = 11–24 days, n = 8 species, Table 2). Incubation periods ($F_{2,82}$ = 1.91, P = 0.15, El Rey National Park: 15.6 ± 1.9, n = 17 species, El Bagual Reserve: 14.7 ± 1.6, n = 57

TABLE 1. Clutch, egg, and female sizes of passerine species in the subtropical Atlantic Forest of southern Brazil (Piraquara). Each row in clutch size indicates the number of nests with known clutch sizes. Egg sizes were first averaged by clutch, thus SD shows variation between nests, and n is the number of clutches. Females measured are breeding adults with monitored nests.

Species	Clutch size						Egg sizes (SD)				Female size (SD)	
	1	2	3	4	5	6	Mass (g)	Length (mm)	Width (mm)	n	Body mass (g)	n
Rufous-capped Spinetail		1										
Planalto Woodcreeper				1								
Lesser Woodcreeper			1									
Scalloped Woodcreeper			3	1								
Variable Antshrike			1				2.93	21.02	15.44	1		
Small-billed Elaenia		1										
Highland Elaenia		1										
Mottle-cheeked Tyrannulet		2	1				1.6 (0.01)	17.74 (0.58)	13.35 (0.28)	3		
Bran-colored Flycatcher		2	2				1.57	18.01	12.82	1	10.5	1
Tropical Kingbird		1					4.44	26.59	17.37	1	44.3	1
Swainson's Flycatcher			1	2			3.05 (0.08)	21.26 (0.96)	16.81 (0.66)	2	28.5	1
Red-eyed Vireo		2	1				2.27 (0.04)	20.32 (0.82)	14.65 (0.13)	2		
White-rumped Swallow			2	4	23	2	2.06 (0.13)	19.75 (0.71)	13.9 (0.41)	37	22.0 (1.3)	32
Southern Rough-winged Swallow					1							
House Wren			2	4	10	1	1.74 (0.11)	17.75 (0.7)	13.54 (0.41)	15	13.2 (1.5)	5
Rufous-bellied Thrush		6	6				6.58 (0.43)	31.7 (0.4)	21.23 (0.31)	2	76.9	1
Creamy-bellied Thrush		1	4				5.87 (0.48)	27.26 (1.29)	20.57 (0.08)	2		
White-rimmed Warbler			5				2.62 (0.14)	20.02 (0.69)	15.35 (0.42)	5	15.6 (0.7)	5
Golden-crowned Warbler		1	3				1.73 (0.12)	17.25 (0.95)	13.46 (0.4)	4	10.5 (2.1)	2
Rufous-collared Sparrow			5				2.38 (0.22)	19.12 (0.88)	14.69 (0.87)	8	21.7 (2.3)	4
Ruby-crowned Tanager		1					3.73	22.58	17.09	1	29.0	1
Sayaca Tanager		1	1				2.98	22.48	16.31	1		
Grey-throated Warbling-Finch		1	1				2.53 (0.03)	19.84 (0.38)	14.98 (0.15)	2	21.0	1
Saffron Finch		4	24	22	2		2.15 (0.18)	19.67 (0.79)	14.37 (0.45)	58	19.0 (1.6)	16
Double-collared Seedeater	1	3					1.43 (0.16)	16.5 (1.58)	12.71 (0.55)	4	11.0 (0.5)	2

TABLE 2. Length of the nesting periods of 14 passerine species in the subtropical Atlantic Forest of southern Brazil (Piraquara). Incubation period is the time from laying of the last egg until hatching of the first egg. Nestling period ranges from hatching of the first egg to fledging of the last young. Included are only data with 1-day precision at hatching and at least 2-days precision at fledging. Values are presented as mean and standard deviation (n ≥ 3) or individually.

Species	Nesting period in days (SD)			
	Incubation	n	Nestling	n
Mottle-cheeked Tyrannulet	16	1		
Bran-colored Flycatcher	17, 17	2	14	1
Red-eyed Vireo	14	1	11	1
White-rumped Swallow	15.2 (1.1)	25	24.1 (2.2)	8
Blue-and-white Swallow			20	1
Southern Rough-winged Swallow	15	1	21	1
House Wren	14.7 (0.8)	7		
Rufous-bellied Thrush	11	1		
White-rimmed Warbler	17, 19	2		
Golden-crowned Warbler	14	1		
Rufous-collared Sparrow	15	1		
Sayaca Tanager			19	1
Saffron Finch	13.2 (0.3)	12	17 (2.7)	6
Double-collared Seedeater			12	1

species) and nestling periods ($F_{2,\,82}$ = 1.71, P = 0.19, El Rey National Park: 14.7 ± 3.0, n = 17 species, El Bagual Reserve: 14.9 ± 3.5, n = 60 species) were similar between the three studies.

Number of nesting attempts. The first attempt of a Mottle-cheeked Tyrannulet was preyed on during laying (10 October), and was followed by a second nest 93 m from the first, two weeks later (24 October). That three-egg clutch also failed due to predation (3–6 November). This pair then resumed the construction on an incomplete nest (8 November) that we found a month earlier (when it was laying in the first nest). This two-egg nest was preyed on during the nestling stage (11–14 December). Three pairs of the White-rumped Swallow renested after abandonment (possibly due to handling), of which two nests successfully fledged (6 and 17 January). One pair of the House Wren abandoned a nest during incubation (15 November) and seven days later laid in another nest-box, and that nest was successful. Saffron Finches often renested (62% with two and 19% with three nest attempts, Table 3). Three pairs of Saffron Finch had two successes in three attempts each. Another three pairs had two successes in two nest attempts. Five pairs had one success in two nest attempts. One pair succeeded with just one attempt. Two pairs with two attempts and two with one attempt had no success in the breeding season. Two pairs of the White-rimmed Warbler had two unsuccessful attempts (Table 3).

Nest survival. In the White-rumped Swallow, nests had DSR of 0.990 ± 0.003 (mean ± SE, n = 37 nests), in the House Wren of 0.998 ± 0.005 (n = 16), in the Rufous-collared Sparrow of 0.901 ± 0.027 (n = 13), and in the Saffron Finch of 0.981 ± 0.004 (n = 59). Of 41 nests (not in nest-boxes) of known fate,

TABLE 3. Number of nesting attempts per banded pair during the 2012–2013 breeding season in the subtropical Atlantic Forest of southern Brazil (Piraquara) Number of banded pairs with at least one success is in parenthesis.

Species	Nest attempts		
	One	Two	Three
Scalloped Woodcreeper		1 (1)	
Mottle-cheeked Tyrannulet	2 (0)		1 (0)
Bran-colored Flycatcher	2 (1)	1 (1)	
Swainson's Flycatcher	1 (0)	2 (0)	
White-rumped Swallow	31 (24)	3 (2)	
House Wren	8 (5)	1 (1)	
Rufous-bellied Thrush	2 (0)	2 (0)	
White-rimmed Warbler	4 (1)	2 (0)	
Golden-crowned Warbler	6 (1)		
Rufous-collared Sparrow	3 (0)	3 (1)	
Saffron Finch	3 (1)	10 (8)	3 (3)
Double-collared Seedeater	1 (1)	1 (0)	

which were discovered before the laying period, 14 (34%) were successful.

DISCUSSION

The paradigm of latitudinal trends in breeding parameters of birds is old (Lack 1947, Moreau 1944) but still prevailing (Martin, 2004). This idea implies convergence in the reproductive strategy of many species in a region, possibly due to climatic or ecological factors which in turn causes the latitudinal patterns observed (Jetz *et al.* 2008, Roper *et al.* 2010). Our comparisons indicate that the passerine communities in three different regions (Piraquara, El Rey National Park and El Bagual Reserve) at roughly the same latitude in South America have similar breeding phenologies, clutch sizes, and nesting periods. In this sense, these communities fit well to the idea of latitudinal convergence in breeding parameters. However, as previously pointed out (Auer *et al.* 2007, Marini *et al.* 2012), the combination of small clutches and short breeding seasons in these mid-latitudes in South America is not concordant with the latitudinal life-history paradigm based on northern hemisphere birds. This observation also applies to our study in subtropical Atlantic Forest (Piraquara) and to the study with Humid Chaco passerines (El Bagual Reserve, Di Giacomo 2005). The only major difference between the studies analyzed was that eggs sizes were smaller in Piraquara than El Rey National Park. This difference speaks against the latitudinal convergence in breeding strategies, and could indicate either intrinsic ecological variation caused by distinct species compositions or, more importantly, that geographical variation at the same latitude (e.g., altitude) may influence climate and consequently breeding ecologies.

The IOB was more or less subsequent to the onset of spring and spread over almost two months in Piraquara (Fig. 1). BSL was also quite variable, from less than one to five months. Thus, latitudinal convergence in breeding phenologies is either weak or nonexistent at local level. Since our study covers one location and a single year, any variation observed in breeding phenology between species, instead of being caused by climatic variation in space and time, might be due to ecological differences and/or phylogenetic distances among species.

BSL tends to be shorter in migratory birds, probably due to time constraints (Jahn & Cueto 2012). However, in Piraquara, BSL is independent of migratory status. House Wren, Grey-throated Warbling finch, White-browed, and Golden-crowned Warblers – all residents – had surprisingly short breeding seasons that were similar to the migrant White-rumped Swallow. IOB also varied widely among migrants, with the Southern Beardless Tyrannulet being the earliest to build the nest, before the vernal equinox, whereas the Red-eyed Vireo was the last, beginning in mid-December (FMS unpub. data of residence status). Variability in breeding phenologies among sympatric species in either El Rey National Park or El Bagual Reserve is difficult to evaluate due to temporal effects, since these data were merged from several years.

The extensive gathering of breeding information is essential to outline dynamics in breeding activity over space and time (as illustrated by Young 1994). However, particularly for breeding phenologies, much of this effort is lost when the information is pooled across years and habitats for the sake of sample sizes (Wolfe *et al.* 2009, Sanaioti & Cintra 2010, Marini *et al.* 2012). Also, information is often gathered only in the nesting season, or opportunistically during other studies, resulting in fragmented compendia that lack a spatio-temporal context. On the other hand, intensive, focused, and local surveys of breeding activity can better assess the variation between species, because this can help to reduce the impact of spatio-temporal confounding factors.

We believe that the breeding phenology of birds in Piraquara indicates true patterns for two reasons: 1) The monitoring of banded and unbanded pairs was intensive and lasted from winter throughout fall, and not just in the expected nesting season. This method aided in determining absent – rather than overlooked – breeding activity. 2) The monitoring yielded a relatively high density of nests found. We have found 7.5 nests ha^{-1} (4.5 nests ha^{-1} excluding the nest-boxes), while at El Rey National Park (Auer *et al.* 2007) average nest density was 1.4 nests ha^{-1} per season.

In Piraquara, IOB and nest success of House Wrens using nest-boxes were similar to that reported at El Rey National Park in natural cavities, even though the mean clutch size was one egg larger and BSL was 85% longer in Piraquara. This species may lay eggs earlier, and produce larger clutches, when nesting in boxes (Purcell *et al.* 1997), but no differences have been reported on breeding season length.

The Saffron Finch had a long BSL (5 months) relatively to the rest of the studied species. Surprisingly, this finch combines frequent renesting, typical of tropical breeders (Roper 2005, Roper *et al.* 2010), with the temperate traits of relatively large clutch sizes and high nest success (Martin 2004). By the end of the breeding season, 37% of females had reared two broods successfully. Although the high average success might be partly due to the use of nest-boxes (Robertson & Rendell 1990), the wide variation within the population in clutch size, egg size, number of nest attempts, and nest success suggests other influencing factors. This variation can arise from inter-individual variability in quality (Roper 2005) or adaptative phenotypic plasticity (Husby *et al.* 2010). In any case, individuals may invest differently in reproduction, and a single population may show a broad range of strategies similar to that in the temperate-tropical life-histories continuum.

Here, we described breeding parameters for various passerine birds in the subtropical Brazilian Atlantic Forest, which showed remarkable similarities with other two biomes in Argentina at the same latitude (Di Giacomo 2005, Auer *et al.* 2007). Taken together, these studies and our data from birds in Piraquara add to the debate and reinforce that the life histories of passerines in subtropical South America are not easily classified as tropical or temperate (slow or fast pace of life, Martin 1996) and do not easily fit the dogma of tropical-temperate life-history patterns.

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