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BREEDING BIOLOGY OF BIRDS IN THE CERRADO OF CENTRAL BRAZIL

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Resumo. – Biologia reprodutiva de aves do Cerrado do Brasil central. – Relatamos aspectos da biologia da nidificação de aves do Cerrado (savana, natural e antropizada) do Distrito Federal, Brasil central, com ênfase em ninhos, ovos, períodos de nidificação, placas de incubação, comportamentos reprodutivos e período de atividade de nidificação. Por meio de estudos de 196 ninhos de 42 espécies encontrados entre 2002 e 2009, evidenciamos que a maioria das espécies nidificou entre setembro e novembro/dezembro, no início da estação chuvosa, com grande sobreposição entre espécies. Contrário ao esperado para uma região tropical, a duração do período de nidificação da maioria das espécies foi curto, e durou 3–4 meses. Como esperado para uma região tropical, a maioria das espécies fez posturas de dois ovos, mas o tamanho da ninhada atingiu seis ovos em algumas espécies. A forte sazonalidade no Cerrado, com uma estação chuvosa de 7–8 meses, é aparentemente o fator mais importante que limita a nidificação e outras atividades (ex. muda das penas) nesta região. Poucos estudos como este estão disponíveis para a região Neotropical, mas eles são fundamentais e ainda necessários e úteis para o desenvolvimento da teoria de história de vida. Logo, recomendamos que biologia da nidificação receba muito mais ênfase em pesquisas futuras.

Abstract. – We report the nesting biology of birds in the Cerrado (savanna, both natural and anthropic) of the Federal District of central Brazil, with emphasis on nests, eggs, nesting periods, brood patches, reproductive behavior and period of nesting activity. With 196 nests of 42 species found from 2002 through 2009, we found that most species nested from September to November/December, at the onset of the rainy season, with extensive overlap among species. Contrary to expected for a tropical region, the breeding season period of most species was brief, and lasted 3–4 months. As expected for a tropical

region, most species laid two eggs, but clutch sizes reached a maximum of six eggs in a few species. The strong seasonality of the Cerrado, with a rainy season of 7–8 months, is apparently the most important factor that limits breeding and other activities (ex. molt) in this region. Few studies like this are available for the Neotropical region, yet they are fundamental and are still needed and useful for the development of life history theory. Therefore, we recommend that breeding biology receives much more emphasis in future research than to date. *Accepted 27 September 2012.*

Key words: Eggs, nests, reproduction, savanna, Central Brazil.

INTRODUCTION

Understanding bird reproduction patterns is important not only for ecological, evolutionary, and behavioral studies (Stutchbury & Morton 2001, 2008), but also for systematics, physiology, and conservation (Brown 1987, Bennett & Owens 2002, Begon *et al.* 2006). Many or most of these patterns remain poorly studied in the Neotropics, including Brazil. Patterns of reproduction in many species are simply unknown, and in many others, only simple descriptions of nests, and eggs are available from older studies, which often fail to include the date or place of observation (Euler 1900, Ihering 1900). Detailed studies of reproductive biology of Neotropical birds are increasing recently in Brazil (Carvalho *et al.* 2007, Aguilar *et al.* 2008, Faria *et al.* 2008, Rubio & Pinho 2008, Dias *et al.* 2009, Rodrigues *et al.* 2009, Gomes & Rodrigues 2010, Nóbrega & Pinho 2010, Hoffmann & Rodrigues 2011, Rodrigues & Rodrigues 2011, Johnson *et al.* 2012, Whischhoff *et al.* 2012) and other countries (Robinson *et al.* 2000, Roper 2000, 2003; Greeney *et al.* 2004, 2011; de la Peña 2005, Di Giacomo 2005, Auer *et al.* 2007), but few attempt a theoretical understanding of breeding parameters (Roper *et al.* 2010). This is in stark contrast to studies in Europe and North America (summaries in Baillie 1990 and DeSante & Rosenberg 1998, respectively). As a consequence, little is known about changes in population parameters and dynamics of tropical species, especially in those places with large anthropic influences.

The Cerrado, a Neotropical biome restricted mostly to Brazil, is the largest tropical savanna in the world and the second largest plant formation type in South America (after the Amazon forest, Ratter *et al.* 1997). The Cerrado is also one of the most threatened biomes in the world and, at the same time, is a hotspot for biodiversity (Myers *et al.* 2000, Silva & Bates 2002). By recent estimates, ≤ 50 % of the original formation remains (BRASIL 2007, Brannstrom *et al.* 2008), and that remainder is very fragmented and is rapidly being converted to agriculture (Dias 1990, Klink *et al.* 1993, Ratter *et al.* 1997).

The Cerrado is quite diverse biologically (MMA 1999) with endemic plants comprising 44 % of its 10,000 species (Myers *et al.* 2000) and at least 856 species of birds (Silva 1995, Silva & Santos 2005), about 30 of which are endemic (Silva & Bates 2002) and 48 are threatened (IBAMA 2003, Marini & Garcia 2005, IUCN 2008). As elsewhere in Latin America, little is known of the biology of this wide variety of species. Recently, a new species of flycatcher (Chapada Flycatcher, *Suiriri islerorum*) was described (Zimmer *et al.* 2001). Two other recently rediscovered species were formerly known only from holotypes, both of which are possibly endemic to the Cerrado (Kaempfer's Woodpecker *Celeus obrieni,* Prado 2006, Santos & Vasconcelos 2007, and the Cone-billed Tanager *Conothraupis mesoleuca,* Buzzetti & Carlos 2005). Our research group has been accumulating data on reproductive biology for birds in the Cerrado. Currently, our long-term bird reproduction project,

begun in 2002, is at the Águas Emendadas Ecological Station (ESECAE), in the Distrito Federal in central Brazil. Recently, breeding biology of several species with unique nests or large sample sizes has been reported elsewhere (*Suiriri islerorum* and *Suiriri suiriri,* Lopes & Marini 2005a,b; França & Marini 2009; *Elaenia chiriquensis*, Medeiros & Marini 2007, Paiva & Marini *in press*; *Culicivora caudacuta*, Sousa & Marini 2007; *Charitospiza eucosma*, Borges & Marini 2008; *Melanopareia torquata*, Gressler & Marini 2007; *Elaenia cristata*, Marini *et al.* 2009a; *Tyrannus savana*, Marini *et al.* 2009b; Columbidae, Marini *et al.* 2010; *Cypsnagra hirundinacea*, Santos & Marini 2010; *Neothraupis fasciata*, Duca & Marini 2011; Manica & Marini 2012; *Sicalis citrina*, Gressler & Marini 2011; other spp. in preparation).

Here, to help fill this gap in knowledge, we describe several aspects of the breeding biology of 42 species of birds from the Cerrado region, including descriptions of nests and eggs, incubation and nestling periods, brood patch, breeding behaviors, and period of nesting activity. Many nesting characteristics and parameters have been described in the scientific literature, so our descriptions are brief and mostly add to prior descriptions that were incomplete or different from ours, or obtained in sites far-removed from central Brazil, such as Costa Rica, Colombia or Argentina. By putting these birds in the context of life history theory and current knowledge about their breeding biology, we hope to generate more interest in the study of the reproductive biology of many more Neotropical birds.

METHODS

Study site. This study was carried out at the Águas Emendadas Ecological Station (ESECAE, a 10,547 ha reserve, protected since 1988), in the Distrito Federal, Brazil (15°29'–15°36'S, 47°31'–47°41'W; 1040 m a.s.l.). We also collected data in a nearby rural area (Jardim Morumbi). The ESECAE has not suffered major anthropogenic impacts at least in the last ~ 30 years, except for sporadic burns, occasional illegal animal hunting, and use by domestic animals, especially feral dogs. The ESECAE is located within the Cerrado, a Neotropical savanna biome, with vegetation dominated by *cerrado sensu stricto*, which is dense and shrubby with some emergent trees that may reach 15 m. Intermixed within that are patches of other natural phytophysiognomies, such as dense *cerrado* (an even denser *cerrado sensu stricto* with more trees), open *cerrado* (which has few shrubs and no trees > 15 m), *campo sujo* (which is a grassland with scattered shrubs and trees), and *campo limpo* (which is a grassland without shrubs or trees). Other types of phytophysiognomies found in the reserve are, *vereda* (a valley-side marsh), gallery forest (narrow forest strips along streams), and *cerradão* (closed woodland with trees ~ 8–12 m) (Ribeiro & Walter 1998). Within the reserve, some small patches of vegetation are partially disturbed by human use, such as logging, trails, or frequent fire, which we refer to, e.g., disturbed open *cerrado* or disturbed *cerrado sensu stricto.* The rural area (15°30'–15°31'S, 47°37'–47°39'W) just outside of the ESECAE is a mosaic of small properties, disturbed *cerrado* fragments, and dirt roads and houses that were built during the 1980s (details in Borges & Marini 2010), where fire and several kinds of human uses are common.

Climate of the region is rainy tropical with a marked seasonality: a rainy season from October to April and a very strong dry season from May to September (the southern winter) usually with little or no rain. Mean annual rainfall of the Cerrado ranges from 1500–1750 mm, and mean temperature ranges from 20 to 26 ºC (Nimer 1979).

Nests. We searched for nests in undisturbed habitats at the ESECAE from August to December 2002–2009, September–December 2005 along the reserve border, and at the rural area (Jardim Morumbi) in 2006. Because of little or no evidence of breeding of the study species at other times of the year (Piratelli *et al.* 2000, Marini & Durães 2001, Silveira & Marini 2012), these months include most or all of the breeding season. However, this nest search period overlaps little with the breeding season of some birds in the region, such as granivorous species like *Sicalis citrina* (Gressler & Marini 2011) and *Volatinia jacarina* (Carvalho *et al.* 2007, Aguilar *et al.* 2008). We found nests by following adults while they were building nests or feeding young, as well as by the inspection of potential nest sites and by accidental encounters. We checked almost all nests, once found, every 3–4 days until the nest was no longer in use (either due to failure or fledging).

Nest diameter and depth of some nests were measured after use. We weighed eggs prior to the third day after laying with a spring scale (to 0.1 g) and measured (length and width) with calipers (to 0.01 mm). Incubation period was estimated as the number of days between the date the last egg was laid and the last egg hatched (Martin 2002). The nestling period was the number of days from hatching to fledging. Summary statistics are reported as means and standard deviations (mean ± SD). The period of nesting activity was defined from the first evidence of nest building to the last evidence of fledgling. Whenever appropriate, we backdated the incubation period and estimated forward the fledgling period to better estimate the period of nesting activity.

Bird captures. Some birds were captured from July 2002 to December 2009 during a banding program in ESECAE, with 36 mm mesh mist-nets of various lengths, usually between 06:00–13:00 h. We banded all captured birds with a uniquely numbered metal band (CEMAVE/IBAMA), and presence of a brood patch was noted. Bird taxonomy follows Remsen *et al.* (2012).

Bibliographic review. We first compared our data with that presented in the Handbook of the Birds of the World series (del Hoyo *et al.* 1992–2011), which is by far the most comprehensive compilation about the biology of Neotropical birds. In cases where our observations did not differ significantly from the data summarized in del Hoyo *et al.* (1992–2011), no additional comment was presented. In those cases where our observations diverged from, or added new information, we highlighted this fact and scanned the literature for other papers on this theme. It is necessary to remember that the first volumes of the handbook were published two decades ago, and thus some information is now outdated.

RESULTS

We found 196 nests of 42 species of birds (Table 1). Details of each species follow, listed by family.

TINAMIDAE

Crypturellus parvirostris. We found five nests from September to November. The earliest nest was found 29 September 2009 and the latest was initiated during the first week of November 2003 (an interval of approximately 38 days over which egg laying occurred). Nests were found in *cerrado sensu stricto* (n = 2) and open *cerrado* (3). Nests were merely eggs laid on the ground. Clutch sizes were two (n = 2) and three (3), differing from the clutch of 4–5 eggs reported by del Hoyo *et al.* (1992). Eggs were elliptical and chocolate-colored with violet tint and two had small brown dots. Egg mass was 17.2 ± 0.9 g (n = 5), which was about 8% of the adult body mass (220 g, Dunning 2007). Egg dimensions were 39.2 ±

0.7 x 28.3 ± 1.2 mm (n = 10). The incubation period lasted at least 21 days (n = 2), two days more than that observed in captivity (del Hoyo *et al.* 1992). Hatching occurred around October 6, October 31, November 19, and December 3 (n = 4 nests) and hatchlings were downy (n = 2). Egg shells were found at three nests after hatching. Twice we observed an adult defending eggs by feigning a broken wing. The period of nesting activity lasted from mid-September to early December.

ACCIPITRIDAE

Buteogallus meridionalis. The one nest found on 19 September 2003 was a mass of twigs hidden in the tree canopy in the *cerrado sensu stricto* at nearly 8 m high. The day the nest was found, an adult bird was close to the nest and vocalized and the incubating bird left the nest. The single white egg hatched on 6 October. The nest was found empty on 13 October, suggesting predation. The period of nesting activity was estimated to be early September to late October.

NYCTIBIIDAE

Nyctibius griseus. A nest found on 25 October 2003 was merely an egg on a branch of a snag 3 m high in the *cerrado sensu stricto*. The egg hatched between 6–11 November, but since the nest was found with an egg, incubation was longer than the 13 days it was monitored. The nestling stayed in the same place for ~ 35 days when it moved to nearby branches of the same tree. Only one adult bird was ever seen near the nest. This nest was in the same tree in which we were monitoring a *Suiriri suiriri* nest. During our observations of the latter, unaware, we approached quite near the *Nyctibius* nest. Only when about 2 m away from the nest we saw the silent and motionless adult, looking at us with its large yellow eyes. The adult flew away when we saw the egg. The period of nesting activity was estimated to be mid-October to late December.

CAPRIMULGIDAE

The study of the breeding biology of Caprimulgidae requires special attention. First, a nest is never found before egg laying because there is no nest eggs are laid on the ground on whatever substrate happens to be present. Second, the transition from nestling to fledgling is difficult to define (they are semi-precocial) since nestlings will become fledglings upon leaving the nest, but they may move a very short distance. Also, the nestling period is very short. Lastly, nest fate after hatching is imprecise and difficult to estimate by simple observations of the original nest site. With these limitations in mind, we describe the breeding biology of three species.

Nyctidromus albicollis. Two nests were found on 27 September 2006 and 9 October 2009 in *cerrado sensu stricto*, but one of them was near a *vereda*. Both nests were basically eggs laid on the ground on whatever substrate was there. Clutch size was two (one had eggs, the other had nestlings). Nestlings of the first nest hatched between 28 September and 2 October and were apparently depredated by 5 October. Nestlings of the second nest were last seen on 14 October and fledged the nest site by 16 October. Adults defended nestlings first by staying put in the nest, then by jumping and flying 1–3 m away from the nest, then by feigning a broken wing, and lastly by calling when we came very close to the nestlings. The period of nesting activity was estimated to be mid-September to mid-October.

Caprimulgus parvulus. We found 12 nests in September–October of 2003, 2004, 2008, and 2009. Nests were in *cerrado sensu stricto* (n = 8), open *cerrado* (2) or disturbed *cerrado sensu stricto* (1), and near a *vereda* (1). The earliest date a nest was found with eggs was 16 September 2003. Eggs were elliptical and pinkish-cream with reddish-brown scrawls. Clutch size in nests with only eggs was one (n = 1) or

TABLE 1. Details of nesting information for birds at the Águas Emendadas Ecological Station, 2002–2009, including sample size (N), clutch size (if two values, minimum–maximum), nest height (if two values, minimum–maximum), and month of nesting activity (from nest building to fledgling).

Family	Species	N	Clutch size	Nest height (m)	Month											
					Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Tinamidae	*Crypturellus parvirostris*	5	2-3	0									x	x	x	x
Accipitridae	*Buteogallus meridionallis*	1	1	8									x	x		
Nyctibiidae	*Nyctibius griseus*	1	1	3										x	x	x
Caprimulgidae	*Nyctidromus abicollis*	2	2	0									x	x		
	Caprimulgus parvulus	12	1-2	0									x	x		
	Hydropsalis torquata	11	1-2	0									x	x	x	
Trochilidae	*Eupetomena macroura*	9	2	1.69									x	x	x	x
	Amazilia fimbriata	2	2	1-1.9									x	x		
	Heliactin bilophus	1	2	0.5				x	x							
Bucconidae	*Nystalus chacuru*	3	-	0									x	x	x	
Cariamidae	*Cariama cristata*	1	2	2.5									x	x		
Falconidae	*Caracara plancus*	2	1	5.1-11								x	x			
	Falco femoralis	4	3	3.5-5								x	x	x		
Psittacidae	*Aratinga aurea*	11	3-4	1.8							x	x	x	x	x	
	Amazona aestiva	3	3	1.8-2.1								x	x	x		
Furnariidae	*Lepidocolaptes angustirostris*	8	1-3	2								x	x	x	x	x
Tyrannidae	*Elaenia flavogaster*	1	2	3.5										x	x	x
	Elaenia obscura	1	1	2.6										x	x	
	Camptostoma obsoletum	9	2	1.4								x	x	x	x	
	Suiriri suiriri	15	1-3	4.5							x	x	x	x	x	
	Serpophaga subcristata	1	1	5									x	x	x	
	Sublegatus modestus	1	2	1.6										x	x	
	Culicivora caudacuta	1	3	0.38	x	x	x	x						x	x	x
	Xolmis cinereus	3	1-3	0.7-4.3									x	x	x	
	Myiozetetes cayanensis	1	2	2.45										x	x	
	Myiodinastes maculatus	1	1	5										x	x	
	Empidonomus varius	4	2-3	3-3.5										x	x	

TABLE 1. Continuation.

Family	Species	N	Clutch size	Nest height (m)	Month											
					Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Tyrannidae	*Empidonomus aurantiatrocristatus*	11	1-3	4.06									x	x	x	x
	Tyrannus melancholicus	4	3	5									x	x	x	
	Myiarchus swainsoni	9	2-3	1.16									x	x	x	
Vireonidae	*Cyclarhis gujanensis*	8	1-3	2.17	x								x	x	x	x
Corvidae	*Cyanocorax cristatelus*	5	4-6	4.2									x	x	x	x
Hirundinidae	*Tachycineta leucorrhoa*	1	4	-										x	x	
Troglodytidae	*Troglodytes aedon*	1	3	1.8										x	x	
	Cisthotorus platensis	2	1-2	0.2									x	x	x	x
Turdidae	*Turdus leucomelas*	6	2-3	3.17									x	x	x	
	Turdus amaurochalinus	24	1-3	3.51									x	x	x	x
Thraupidae	*Nemosia pileata*	1	-	6										x		
	Thraupis sayaca	4	2-3	0.35-7.5									x	x	x	
	Coereba flaveola	2	-	1.2-1.8								x	x			
Cardinalidae	*Piranga flava*	2	2	2.65-7										x	x	
Fringillidae	*Euphonia chlorotica*	2	2	2.2									x	x		

two (6). Eggs weighed 6.9 and 7.0 g in one nest - nearly 20 % of the adult body mass (35 g, n = 1), and were substantially heavier than the 4.7 and 5.1 g reported by Di Giacomo (2005). Egg dimensions were 26 ± 1.0 x 21 ± 0.5 mm (n = 4). Incubation lasted at least 17 days (n = 2). The nestling period was 14–16 days, however, as previously noted is difficult to define. Nestlings had pinkish-cream plumage. Incubating birds stayed on the nest when approached and flew quietly away when closely approached. Twice, adults defended nestlings by feigning a broken wing or vocalizing aggressively at the nest. Fledglings were also quiet, and either walked or flew away when approached. Egg and clutch sizes are known, while the remainder of this account is apparently new. The period of nesting activity was estimated to be early September to early October.

Hydropsalis torquata. We found a total of 11 nests from September to November in the years of 2006, 2007, 2008, and 2009, the earliest of which had two eggs on 9 September 2009, and the latest in early October. This is earlier than those reported from SE Brazil, which were found from November to January (del Hoyo *et al.* 1999). Nests were in *cerrado sensu stricto* (n = 6), open *cerrado* (2), in a recently (~ 2 months) burned open *cerrado* (1), and at the edge of a *vereda* (2). Nests had one (n = 2) or two (8) eggs or nestlings. Eggs were short-oval, oval, or cylindrical, and were almost translucent cream-colored with brownish spots. Eggs weighed 6.6 ± 0.5 g, which was about 13 % of the adult body mass (51.2 ± 7.5 g, n = 3). Egg dimensions were 27.8 ± 14 x 20.8 ± 4 mm. The incubation period lasted at least 15 days (n = 2) and the nestling period 14–16 days. Nestling period was difficult to estimate as previously noted. Incubating birds stayed quiet, silently flying away when approached. At three nests, they feigned a broken wing when approached. Egg and clutch sizes are known, while the remainder of this account is apparently new. The period of nesting activity was estimated to be early September to early November.

TROCHILIDAE

Heliactin bilophus. We found one nest with two elliptical white eggs on 3 May 2003, one of which hatched by 5 May. The other egg was found on the ground with an underdeveloped embryo. The single nestling fledged on 29 May. The nestling period lasted 24 days. The same nest was reused with the first egg laid prior to 06:30 h of 27 June, followed by the second egg laid before 08:30 h on the same day. Both eggs had very recently hatched by 28 July (as evidenced by the nestlings with closed eyes), so the egg period lasted ~ 30 days if started on 27 June. Nest height was 50 cm in a small herbaceous plant in *campo sujo*. Only the female was observed in or around the nest. The period of nesting activity was estimated to be late April to late May.

Eupetomena macroura. Nine nests were found September–December. The earliest was found with two eggs in mid-September 2006 and the latest began on 5 December (a nest found with one egg that had two the next day). Nests were in open *cerrado* (n = 6), and *cerrado sensu stricto* (3). Nest height varied from 80–240 cm, averaging 169 ± 6 cm. Nests were in *Kielmeyera* sp. (n = 2), *K. coriacea* (3), *K. speciosa* (2), and *Miconia* sp. (1). Clutch size was two, and eggs were 14.8 ± 0.1 x 9.75 ± 0.2 mm. Incubation lasted a minimum of 14 days (n = 1), and the nestling period lasted 24–25 days (n = 1). The period of nesting activity was estimated to be mid-September to late December.

Amazilia fimbriata. We found two nests, the earliest of which had two nestlings on 7 October 2005 (and so nest initiation was esti-

mated to be in early September). The second nest had two eggs on 10 October 2007 that hatched by 18 October (hence the nest was likely initiated three weeks earlier, in late September). One nest was in a *Miconia* sp. in *cerrado sensu stricto* and the other in *campo limpo*. Nests were tightly woven on small stems and difficult to remove, as is common for hummingbirds. Nest height was 100 and 190 cm, respectively. The period of nesting activity was estimated to be early/mid-September to late October.

BUCCONIDAE

Nystalus chacuru. We found three nests, in October 2005 and 2007, respectively, and in September 2009. One nest remained active until early November 2005. We captured a total of 64 birds, of which three had brood patches in October, and eight had brood patches that were in early stages of development in August (n = 1), September (6), and October (1). Immature birds were caught in all months except July to September, including nine of a total of 31 birds captured in December. Nests were below ground, at the end of a tunnel $\geq$ 120 cm in length, so exact dates, clutch size, and reproductive success could not be monitored. Nest entrances faced east and southeast. Two nests were found in dense *cerrado*, and the other in open *cerrado*. Considering all evidences of breeding, the apparent period of nesting activity was estimated to be September to early November.

CARIAMIDAE

Cariama cristata. A nest found on 20 October 2003 was 2.5 m high in a *Stryphnodendron adstringens* in the *cerrado sensu stricto*. The nest was a large pile of twigs with dirt on top, forming a stable flat platform. Del Hoyo *et al.* (1996) describe nests as "lined with leaves and clay or cattle dung." As no cattle are found less than 1.5 km from the nest, cattle dung would be unlikely and not a natural behavior. One egg and one nestling were in the nest when it was found. By 31 October, the nestling perched ~ 70 cm from the nest, and by 4 November it had fledged. The egg remained in the nest and was found predated some days later. The period of nesting activity was estimated to be September to late October.

FALCONIDAE

Caracara plancus. We found two nests on 27 August 2008, and 23 September 2009 in *cerrado sensu stricto*. Nests were 5 m and around 11 m in height, both in *Vochysia thyrsoidea*. One nest was built with small sticks on a branch fork and was a high cup nest. The one nest that we were able to check had one egg on 27 August through 5 September. This nest was found tilted and empty on 8 September, with egg shells on the ground. Nesting activity occurred from late August to late September.

Falco femoralis. We found all four nests in August in 2003, 2007, 2008, and 2009. The earliest record for an active nest was on 15 August 2007 and the latest was in mid-October 2007. Nests were 3.5 m (n = 1), 4.0 (n = 1), and ~ 5 m (n = 2) high. One was in a dry tree snag in the open *cerrado*, and three others were in *Sclerolobium paniculatum*, *Vochysia thyrsoidea*, and *Qualea grandiflora* in the *cerrado sensu stricto*. All nests were shallow open cups made of thick sticks and three were on top of abandoned nests of *Phacellodomus rufifrons*. Clutch size was always three. Eggs were beige-orange with small dark orange spots. Incubation lasted at least 17 days, but as we did not follow all nests from the beginning, it should have lasted 31–32 days (del Hoyo *et al.* 1994). Nestling period lasted between 27 and 31 days, in agreement with del Hoyo *et al.* (1994). Fledglings from two nests remained in the nest tree, where they were fed by the adults, for at least 20 days after leaving the nest. During incubation or nestling periods, one or two adults defended the nest, vocalizing and

attacking observers. The period of nesting activity was estimated to be early August to mid-October.

PSITTACIDAE

Aratinga aurea. Of the 11 nests found, the earliest was on 13 July 2009 and had two nestlings, and the latest on 9 November 2004. Del Hoyo *et al.* (1997), and Antas *et al.* (2009) report nests from September to December in central Brazil. Measured nests were from 1.3–3.0 m in height (1.8 ± 0.5 m, n = 10), always in an arboreal termite nest in *cerrado sensu stricto*. Nests were in a snag (n = 2) and one in each of the following tree species: *Annona crassiflora*, *Aspidosperma tomentosum*, *Hymenaea stigonocarpa*, *Bowdichia virgilioides*, *Qualea parviflora*, and *Qualea* sp.. Nest entrance was from below with an egg chamber above. Clutch sizes were three (n = 4) and four (1). Eggs were white and apparently hatched synchronously because all the nestlings were of the same size. This suggests that incubation began when the last egg was laid. One nest that was only occasionally monitored was used twice in one season. It had nestlings on 13 July, was empty on 28 July and again had two nestlings on 4 September 2009. The nestling period in one nest was at least 24 days, considerably less than the 48 days recorded in captivity (del Hoyo *et al.* 1997). In one case, nestlings were infested with mites. Nestlings were aggressive while being monitored including attacking the observer. The typical peach forecrown was evident on the fledglings. Both adults perched high in a nearby tree and vocalized while nests were checked. The period of nesting activity was estimated to be early July to late November.

Amazona aestiva. We found three nests in 2003, the earliest of which was found with three eggs on 29 August. We estimate that the latest date of nest activity was in October. One nest was in a terrestrial termite mound in *campo limpo* and two in holes in tree trunks in open *cerrado*, and were on the ground, 1.8 and 2.1 m in height, respectively. Arboreal nests were in *Dalbergia miscolobium*, and *Vochysia thyrsoidea*. One arboreal nest entrance was 150 mm diameter and was 20 cm deep in a *Vochysia thyrsoidea* tree of 40 cm DBH. Clutch size was always three, one nest had three eggs, one had two eggs and one nestling, and one had three nestlings when found. The nestlings of one nest were taken by poachers. The period of nesting activity was estimated to be late August to late October, much earlier than October to March as in del Hoyo *et al.* (1997).

FURNARIIDAE

Lepidocolaptes angustirostris. We found eight nests September–November, the earliest found with three nestlings on 25 September 2008. We estimate that the latest nest initiation was in early October. Captured birds had brood patches in August (n = 1), September (4), and October (3). The cavity nest (80 and 120 cm deep) was in a hollow tree lined with small pieces of bark. Nest entrance was 119–250 cm in height, averaging 200 ± 40 cm high (n = 8). Nests were in snags (n = 6), *Dalbergia miscolobium*, and *Byrsonima* sp.. Nests had one (1), two (5), or three (1) eggs or nestlings. Another nest had at least one nestling that could not be monitored. Eggs were white. Eggs in one nest were 25 x 18 mm, and 25 x 18.5 mm. The nestling period lasted around 22 days in one nest. Nestlings had botflies in three nests. All nests were in the *cerrado sensu stricto*. The period of nesting activity was estimated to be late August/early September to early November.

TYRANNIDAE

Elaenia flavogaster. One nest had two nestlings with well-developed plumage on 27 October 2008. It was in a *vereda*, in a 3.5 m tall tree (Melastomataceae). The nestlings fledged approximately 1 November. Another indivi-

dual was captured in December with a brood patch. The period of nesting activity was estimated to be early October to December.

Elaenia obscura. We found a nest with a single nestling on 30 October 2009 in a *vereda* in an unidentified plant (Family Melastomataceae) with a nest height of 2.6 m. The half to almost full grown nestling was eaten by a 40 cm long snake (*Erythrolamprus aesculapii*) within 10 days. The snake was observed for 80 min while it was eating the nestling, and the adults were nearby and agitated. Other bird species, including *Phacellodomus ruber*, were also agitated by the snake. The period of nesting activity was estimated to be mid-October to mid-November.

Camptostoma obsoletum. Of the nine nests found between August and October, the earliest was found during construction on 31 August 2006. Two eggs were laid by 11 September. By back-dating, we estimated that the earliest date of egg laying was on ~ 6 September and the last on ~ 22 September. One captured bird had the beginnings of a brood patch on 20 August and a second had a full patch on 1 October. We found six nests in the rural area, two in open *cerrado*, and one in dense *cerrado.* Nest height varied 110–175 cm, averaging 140 ± 19 cm high. Nests were in *Mimosa claussenii* (n = 5), *Connarus* sp. (2), *Connarus suberosus* (1), and *Ouratea hexasperma* (1). Eight nests had two eggs or nestlings (one nest was never in use while being observed). The incubation period and the nestling period in one nest both lasted 18 days, longer than that (14–15 days) reported by del Hoyo *et al.* (2004). The period of nesting activity was estimated to be late August/early September to mid-November.

Suiriri suiriri. We found 15 nests August–October 2004–2008 in addition to the 29 nests described in Lopes & Marini (2005a). The earliest active nest was under construction in early July, and one had eggs on 23 August 2005 (egg laying was estimated to be around 10 August). The latest nest initiation was mid-October. Of 122 individuals captured from 2004–2009, 10 had brood patches (3 in August, 6 in September, and 1 in October). Nests were in *cerrado sensu stricto* (n = 11), open *cerrado* (2), and two were near roads. Nest height varied from 2.2–8.0 m, averaging 4.5 ± 1.6 m. Nests were in *Qualea* sp. (n = 3), and one each on *Q. grandiflora, Vochysia* sp., *Vochysia thyrsoidea, Piptocarpha rotundifolia*, and *Sclerolobium paniculatum*. Clutch size was one (n = 1), two (12) or three (1). Incubation period in one nest was ~ 17 days and the nestling period in two nests lasted 19 and 20 days. With nests described in Lopes & Marini (2005a) and the breeding evidence reported here, the period of nesting activity was estimated to be early July to late November.

Serpophaga subcristata. We found a nest lined outside with lichens and bark, and lichens in the interior under construction by both adults on 29 September 2009. Nest height was ~ 5 m in a fork in *Connarus* sp. One egg was laid ~ 15 October and hatched ~ 31 October. Fledging occurred around 16 November. The period of nesting activity was estimated to be late September to mid-November.

Sublegatus modestus. One nest had two nestlings on 29 October 2003. Nest height was 1.6 m, in *Qualea* sp., in the *cerrado sensu stricto.* These nestlings were heavily infested by botfly larvae and died some days later. Botfly larvae left the corpse of the nestlings and buried in the nest, were the pupae usually develop. We collected this nest to await fly emergence; 110 flies emerged. The period of nesting activity was estimated to be October to mid-November.

Culicivora caudacuta. In addition to the three nests described in Sousa & Marini (2007), we

found a nest on 4 October 2009 in a *campo sujo* in a shrub about 38 cm above the ground. Three long, oval and spotless eggs weighed 0.85 ± 0.05 g, were 14.4 ± 0.5 mm x 10.7 ± 0.2 mm. Eggs hatched around 17 October and nestlings were preyed on about eight days later. A bird was captured with a brood patch in December 2009. Considering the breeding evidence described by Souza & Marini (2007) and that reported here, the period of nesting activity was estimated to be early October to April.

Xolmis cinereus. Three nests were found in September and October, the earliest of which was in construction 19 September 2006, much earlier than reported for central Brazil (January, in del Hoyo *et al.* 2004). The first egg was laid by 25 September and all three by 28 September. The latest nest began in early October. Two nests were in open *cerrado* and one in *campo sujo.* Nest height was 0.7, 3.0, and 4.3 m, in *Davilla eliptica*, *Stryphnodendron adstringens*, and another unidentified plant. Nests had two (n = 1) or three eggs or nestlings. Eggs were light cream-colored. Egg dimensions in one nest were 28.5, 29.7, and 29.9 mm by 19.3, 19.6, and 19.5 mm, respectively, and weighed 5.8, 5.6, and 6.2 g. Egg mass was ~ 11% of adult body mass (53.1 g, Marini *et al.* 1997). Fledglings were seen out of their nests on 7 November. The period of nesting activity was estimated to be mid-September to mid-November.

Myiozetetes cayanensis. We found a closed nest on 30 October 2009 in a *vereda* at 2.45 m high with two nestlings. The nest was oval with a side entrance under a roof made of fine grasses. The nest was 165 mm high, 180 mm wide, and had a frontal roof of 150 mm. The elliptical nest entrance was 65 x 40 mm. The period of nesting activity was estimated to be October to November.

Myiodynastes maculatus. One nest had an egg and a nestling on 24 October 2006. The nest was near a dirt road and houses, small plantations, and small patches of disturbed *cerrado.* Nest height was 5 m in a partially destroyed and abandoned *Furnarius rufus* nest. The single nestling fledged between 6 and 9 November. The period of nesting activity was estimated to be early October to early November.

Empidonomus varius. We found four nests in October in yards of houses. Nests are cups in a horizontal fork in braches in *Aspidosperma tomentosum*, *Annona crassiflora*, or *Miconia* sp. Nest initiation was in mid-October (n = 3), and in late October (n = 1). Nest height was 3.0–3.5 m, with one exception. A nest in 2009 was > 7 m high in a horizontal fork with large, interlaced twigs and a finely lined interior. Nests had two or three (n = 2 each) eggs. Eggs were oval-shaped, and the blunt end was spotted. Hatching occurred in late October in one nest and early November in another. Incubation period was 12–15 days (n = 2) and the nestling period ~ 16 days (n = 1). The period of nesting activity was estimated to be early October to mid-November.

Empidonomus aurantioatrocristatus. The earliest of 11 nests found from September–November was under construction 26 September 2006, and by 29 September it contained had two eggs. The latest date of nest initiation was 2 November. Nest construction took at least six days (n = 1). Nests were in the rural area, close to houses and dirt roads. Nest height varied 2.1–6.0 m, averaging 4.1 ± 1.2 m. Nests were in *Annona crassiflora*, *Eriotheca pubescens*, *Qualea parviflora*, *Sclerolobium paniculatum*, and *Erythroxylum* sp. Nests had one (n = 1), two (8) or three (2) eggs or nestlings. Eggs were short and pyriform in shape, averaging 20.0 ± 0.1 mm x 14.7 ± 0.4 mm and 2.03 ± 0.16 g. The incubation period of three nests was 15, 17, and 18 days and the nestling

period 13–17 days, averaging 15.0 ± 1.6 days (n = 4). The period of nesting activity was estimated to be late September to early December.

Tyrannus melancholicus. We found four nests September–October, the earliest of which had two nestling in 29 September. The last initiation date was in mid-October. All nests were in the rural area, two near roads, and two in small farms. Nest height was 3.7 to ~ 8 m, averaging 5.0 ± 1.7 m (n = 4). Nests were in *Caryocar brasilienses* (n = 1), and *Eriotheca pubescens* (1). Clutch size was three. Incubation lasted around 14 days in one nest. One nestling had botflies. The period of nesting activity was estimated to be early September to early November.

Myiarchus swainsoni. Nine nests found September–November, the earliest of which was empty 16 September 2005 and had three eggs 3 October. The latest nest initiation was 16–20 October. Captured birds had brood patches in October and November (n = 2). One bird in August and another in September had early stages of a brood patch. Nest construction lasted at least six days. Nests were in tree cavities (snags, one in *Qualea* sp.) and lined with plant fibers, with plastic in one nest. Five nests were in open *cerrado* and four in *cerrado sensu stricto*. Nest height was 0.7–2.2 m, averaging 1.2 ± 0.6 m. Nests had two (n = 2) or three (6) eggs or nestlings. Eggs were ovoid and yellowish-cream colored with brownish-red spots and scrawls concentrated at the blunt end. Eggs in one nest were 20.3 x 15.7 and 22.4 x 16.6 mm and weighed 2.2 and 2.95 g (~ 11 % of the adult body mass, 22.5 ± 1.7 g, n = 76). One nest had two nestlings that fledged when the nest was found. Incubation and nestling periods lasted 15–16 days. The period of nesting activity was estimated to be late September to late November.

VIREONIDAE

Cyclarhis gujanensis. Eight nests in September (n = 1) and October (n = 7), with the earliest nest estimated to begin the first week in September 2009. A bird captured in October and another in January had brood patches. Cup nests are in a horizontal fork in branches. Nests were in open *cerrado*, and three in the edge of a *vereda*. Nest height ranged from 1.6 to 3.0 m, averaging 2.2 ± 0.6 m. Nests had an external diameter of 89 mm, an internal diameter of 63 mm, a thickness of 68 mm, and a depth of 53 mm. Clutch size was one (n = 2), two (5), or three (1) eggs or nestlings. Long oval eggs were white with brown-cinnamon speckles. Eggs were 22.66 ± 1.48 x 15.78 ± 0.82 mm, and weighed 2.94 ± 0.56 g. Incubation and nestling periods were estimated to be 14 and 16 days. Fledglings were outside of one nest on 23 April. The period of nesting activity was estimated to be early September to January.

CORVIDAE

Cyanocorax cristatellus. Five nests found September–November, the earliest of which had three eggs on 27 September 2007. The latest nest began in early November. One captured bird had a brood patch in September. Nests are open-cups of thick twigs with a finer layer lining the interior. Nests were 30 cm in external diameter and 15 cm thick. All nests were in *cerrado sensu stricto*. Nest height was 2.2–5.7 m, averaging 4.2 ± 1.2 m. Nests were in *Vochysea* sp. (n = 2), *Caryocar brasiliensis* (n = 1), and *Kielmeyera* sp. (n = 1). Nests had four (n = 3) or six (n = 1) elliptical, ovoid or pyriform eggs. Eggs were bluish-green with grayish-brown dots, more concentrated at the blunt end. Eggs were 34.1 ± 1.0 mm x 24.3 ± 0.4 mm (n = 4). Incubation lasted around 22 days and nestlings stayed in the nest about 17 days. Incubating bird vocalized when flushed. The period of nesting activity was estimated to be late September to mid-December.

HIRUNDINIDAE

Tachycineta leucorrhoa. One nest that was being built on 28 October 2003 had four eggs by 4 November. Two captured birds had brood patches in November. The nest was lined with feathers and was in open *cerrado*, in a cavity of *Dalbergia miscolobium*. The period of nesting activity was estimated to be late October to late November.

TROGLODYTIDAE

Troglodytes aedon. One nest found with three eggs 28 October 2003 had nestlings by 4 November. One captured bird had a brood patch in October. The nest was in *cerrado sensu stricto*, in a snag (dead tree) at 1.8 m high. Nestling period lasted at least 14 days. The period of nesting activity was estimated to be mid-October to late November.

Cistothorus platensis. We found two nests in October–November, the earliest of which had two older nestlings and one translucent egg on 30 October 2006. We estimate that this nest began in mid-September. The second nest was found with two translucent eggs on 14 November 2006. Clutch size was much smaller than the 4–8 eggs for the North American subspecies, *C. p. stellaris* (del Hoyo *et al.* 2005). Both nests were in *campo limpo* with mounds of *cerrado*. Nest height was 20 cm for both nests. Nests were an oval ball of fine grass with a side entrance. Eggs were ovoid and cream-colored, and measured in one nest 15.8 x 11.7 and 16.1 x 12.2 mm. Two eggs weighed 1.2 and 1.3 g in one nest, approximately 15 % of the adult body mass (8.3 ± 0.7 g, n = 5 individuals for adult body mass). The period of nesting activity was estimated to be mid-September to early December.

TURDIDAE

Turdus leucomelas. We found six nests September–November 2006, the earliest of which had two eggs on 16 September. The latest was during incubation with three eggs on 5 November. Nests were in the rural area, five close to a dirt road. Nest height was 2.2–5.0 m, averaging 3.2 ± 1.6 m (n = 4). One nest had plastic fibers in its structure. Two nests were in mango trees, one in *Ouratea hexasperma*, another in *Eriotheca pubescens*, and one in *Pinus* sp. The nest is a typical thrush type nest, made of mud covered with fine roots. Nests had two (n = 3) or three (3) eggs or nestlings. Eggs were oval, bluish, and spotted. Eggs weighed 6.97 ± 0.06 g (n = 3) and were 28.4 ± 0.4 mm x 21.5 ± 0.2 mm (n = 3). Nesting activity was estimated to be early September to late November.

Turdus amaurochalinus. Of 24 nests found from September–November 2006, the earliest had three eggs on 19 September. The latest nest initiation began with egg laying on 20 November. Nest construction lasted at least four days, and one nest was empty for at least 12 days after construction before the first egg was laid. Eight nests were lined with plastic (n = 5), paper (n = 2), or synthetic (nylon) straws (n = 1). Twenty nests were in the rural area close to houses and dirt roads, and four in *veredas* in 2009. Nests were from 1.6 to 7.0 m high, averaging 3.51 ± 1.64 m (n = 24), in mango trees (n = 5), *Piptocarpha rotundifolia* (n = 4), and one each in *Stryphnodendron adstringens*, *Dalbergia miscolobium, Kielmeyera* sp., *Bowdichia virgilioides*, *Sclerolobium paniculatum*, *Pterodon* sp., a lime tree, and a jackfruit tree (*Artocarpus heterophyllus*). Nests had one (n = 2), two (8), or three (10) eggs or nestlings (the others were not determined). One nest was parasitized by the Shiny Cowbird *Molothrus bonariensis* on 29 September (1 egg). Incubation lasted 11–15 days (n = 3) and the nestling period 11–14 days (n = 3). Eggs in two nests in 2009 were 25.4 ± 1.3 mm x 19.7 ± 1.1 mm (n = 3) and weighed 4.93 ± 1.01 g (n = 3). Eggs were oval, bluish, and spotted. Nesting activity was

estimated to be mid-September to mid-December.

THRAUPIDAE

Nemosia pileata. We found a single nest on 13 October 2006. The cup nest was built of fine plant fibers and was 6 m high in a *Persea americana* tree in a small altered *cerrado sensu stricto* patch within a landscape with houses and small plantations. A female was incubating when the nest was found.

Thraupis sayaca. We found four nests in October 2006–2009. First eggs were laid from mid-September to mid-October. Fledglings were near one nest 26 October. Three nests were in the rural area and one in the open *cerrado*. Nest heights were 0.35, 3.5, 4.0, and 7.5 m. Nests were in *Eriotheca pubescens*, *Cecropia* sp., and *Stryphnodendron adstringens*, and had two (n = 3) or three (n = 1) eggs. One nest was parasitized by the Shiny Cowbird (*Molothrus bonariensis*) on 6 October (with one egg). A nestling in one nest had botfly larvae. The period of nesting activity was estimated to be mid-September to mid-November.

Coereba flaveola. Two nests had one and two nestlings each when found in September 2006. Nests were estimated to begin in late August/early September. Both nests were in the rural area and close to dirt roads. Nest height was 1.2 and 1.8 m, respectively. Nesting activity was estimated to be late August to late September as a minimum.

CARDINALIDAE

Piranga flava. Two nests were found in October 2006, the earliest of which had eggs on 5 October. Nesting apparently begins in late September through October. Nests were in disturbed *cerrado sensu stricto* near small plantations close to dirt roads. Nest height was 2.6 and 7.0 m in *Enterolobium gummiferum* and *Dalbergia miscolobium*. Both nests had two eggs and were parasitized by five and seven Shiny Cowbird eggs, respectively. The period of nesting activity was estimated to be early October to late November.

FRINGILLIDAE

Euphonia chlorotica. Two nests were found during construction on 6 September 2006, the earliest had two eggs by 14 September and the other by 9 October. One nest was in a shrub in the backyard of a house. The other one was in *Conarus* sp.. Nest height in the latter was 2.2 m. Eggs were white with light creamy spots and were pyriform. One egg was 18.5 x 11.5 mm and weighed 1.1 g. The period of nesting activity was estimated to be early September to late October.

DISCUSSION

The breeding season in the cerrado in central Brazil is much shorter than either the rainy or dry seasons, and for most species of birds it is very restricted, from September to November or December. The length of the breeding season varies substantially across the Neotropics, but similar breeding seasons are typical of several additional species at our study site (Lopes & Marini 2005a, b; Gressler & Marini 2007, Medeiros & Marini 2007, Sousa & Marini 2007, Borges & Marini 2008, França & Marini 2009; Marini *et al.* 2009a, 2009b, 2010; Santos & Marini 2010, Duca & Marini 2011, Manica & Marini 2012, Paiva & Marini *in press*). The duration of the breeding season varies between and within sites depending on the species. In the Brazilian Amazon, for instance, some species reproduce throughout the year and many species may reproduce for more than six months (Johnson *et al.* 2012). In Venezuela, reproduction varies among species from 2–7 months (Cruz & Andrews 1989). On the other hand, in a dry area of Ecuador the breeding season lasts for 5–6 months, being related to the rainy season for most

species, also with a large variation (from 2–5 months) among species (Marchant 1959). In southeastern Brazil and in Argentina, breeding seasons can vary among species from 2–6 months (de la Peña 2005, Gomes & Rodrigues 2010, Hoffman & Rodrigues 2011, Repenning & Fontana 2011). In our cerrado study site, the duration of the breeding season is much more similar to that of temperate birds (Snow & Snow 1964, Ricklefs 1969a, Skutch 1985, Roper *et al.* 2010).

Despite the short breeding season, clutch sizes in the Cerrado are in the range typical of tropical birds (Ricklefs 1969b, Skutch 1985). Despite the great diversity of birds in the Neotropics, clutch sizes are surprisingly small, with one to four eggs and a mode of two for most species (Skutch 1985; Argentina, Yom-Tov *et al.* 1994, de la Peña 2005, Auer *et al.* 2007; Brazil, Oniki & Willis 1983a, b, c; Belton 1984, 1985; Ecuador, Marchant 1960, Greeney *et al.* 2004, 2011; Panama, Willis & Eisenmann 1979; Venezuela, Cruz & Andrews 1989). Theory argues that a longer breeding season favors a smaller clutch size; but at that time, breeding season length was poorly known and thought to be consistently longer than for temperate birds. Now we see that the extremely variable breeding season lengths among species and locations suggest that theory is ready for revision, and emphasize that studies of breeding biology are essential for such a revision.

The extremely seasonal climate of the Cerrado, with 7–8 months of rain and 4–5 months of dry is probably the most important factor that limits and concentrates the breeding season to September–November, for most species. This period is the start of the rainy season which lasts until April. For many species, these 7–8 months of more benign climate are used for breeding first, then for molting (Marini & Durães 2001, Silveira & Marini 2012). Breeding occurs during a period of greater arthropod and fruit abundance at the study site, followed by molt, when resource abundance is declining (Pereira 2011).

The large overlap among a wide variety of species in the timing of breeding is a surprising pattern of short and fairly synchronous nesting periods (similar to temperate birds) with small clutch sizes (typical of tropical birds). Thus, these data suggest new patterns that will help generate new hypotheses and avenues for further study. For example, while many species are fairly synchronous, why are many other species not? Also, why are some species able to nest for extended time intervals (e.g., *Culicivora caudacuta*), while other, similar species are restricted to shorter nesting periods? And why are there exceptions, such as some Columbidae, that nests all year round (Marini *et al.* 2010)? Additional studies are required to provide both data and theory to explain these patterns.

Typical discussions of temperate-tropical differences, beginning decades ago with Snow & Snow (1964), assume that the tropics have long potential breeding seasons and little seasonality in climate (Skutch 1985). However, discussions on this topic have ignored seasonally dry regions (e.g., Marchant 1959), that are common throughout Latin America and include the Pantanal, Cerrado, Caatinga, Chaco, coastal Pacific deserts, and dry forests of Central and South America (Janzen 1986). These, in sum, comprise a very large part of Latin America. Indeed, many other species of birds have relatively short breeding seasons in the Cerrado region (Marini 1992, Lopes & Marini 2005a, Medeiros & Marini 2007, Marini *et al.* 2009a, b; Duca & Marini 2011) and some southern subtropical birds also have short seasons (Lima & Roper 2009). Evidence is accumulating to suggest that we need to better understand the entire picture of breeding seasonality in the tropics rather than just the extremes, that are somewhat entrenched in the temperate-tropical

paradigm today (Roper & Goldstein 1997, Roper *et al.* 2010).

To that end, we feel that the data we provide here, though in many ways anecdotal, help to point out a broader picture for understanding the population biology of birds in the Neotropics. We find a conundrum in the dogma in that variation in breeding parameters among species within this single location is as large as that over a wide range in latitudes, even though most species have similar parameters. Because of this variation, we suggest that the time is ripe for studies of nesting biology, especially breeding season lengths and nesting success, as well as other life history parameters in Neotropical birds.

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REFERENCES

Aguilar, T. M., R. I. Dias, A. C. Oliveira, & R. H. Macedo. 2008. Nest-site selection by Blue-black Grassquits in a Neotropical savanna: do choices influence nest success? J. Field Ornithol. 79: 24–31.

Antas, P. T. Z., R. B. Cavalcanti, & M. C. V. Cruz. 2009. Aves comuns do Planalto Central. Editora Univ. Brasília, Brasília, DF, Brazil.

Auer, S. K., R. D. Bassar, T. E. Martin, & J. J. Fontaine. 2007. Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. Condor 109: 321–333.

Baillie, S. R. 1990. Integrated population monitoring of breeding birds in Britain & Ireland. Ibis 132: 151–166.

Begon, M., C. R. Townsend, & J. L. Haper. 2006. Ecology: from individuals to ecosystems. Blackwell Publishing, Malden, Massachusetts, USA.

Belton, W. 1984. Birds of Rio Grande do Sul, Brazil. Part 1. Rheidae through Furnariidae. Bull. Am. Mus. Nat. Hist. 178: 371–631.

Belton, W. 1985. Birds of Rio Grande do Sul, Brazil. Part 2. Formicariidae through Corvidae. Bull. Amer. Mus. Nat. Hist. 180: 12–42.

Bennett, P. M., & I. P. F. Owens. 2002. Evolutionary ecology of birds: life histories, mating systems, and extinction. Oxford Univ. Press, Oxford, UK.

Borges, F. J. A., & M. Â. Marini. 2008. Primeira descrição do ninho do mineirinho (*Charitospiza eucosma*) no cerrado do Brasil central. Rev. Bras. Ornitol. 16: 38–39.

Borges, F. J. A., & M. Â. Marini. 2010. Birds nesting survival in disturbed and protected Neotropical savannas. Biodivers. Conserv. 19: 223–236.

Brannstrom, C., W. Jepson, A. M. Filippi, D. Redo, Z. Xu, & S. Ganesh. 2008. Land change in the Brazilian savanna (Cerrado), 1986–2002: comparative analysis and land-use policy implications. Land Use Pol. 25: 579–595.

BRASIL. 2007. Mapas de cobertura vegetal dos biomas brasileiros. Downloaded on 13 February 2009 from http://www.mma.gov.br.

Brown, J. L. 1987. Helping and communal breeding in birds. Princeton Univ. Press, Princeton, New Jersey, USA.

Buzzetti, D., & B. A. Carlos. 2005. A redescoberta do tiê-bicudo *Conothraupis mesoleuca* (Berlioz, 1939). Atual. Ornitol. 127: 4–5.

Carvalho, C. B., R. H. F. Macedo, & J. Graves. 2007. Reproduction of Blue-black Grassquits in central Brazil. Braz. J. Biol. 67: 275–281.

Cruz, A., & R. W. Andrews. 1989. Observations on the breeding biology of passerines in a seasonally flooded savanna in Venezuela. Wilson Bull. 101: 62–76.

De la Peña, M. R. 2005. Reproducción de las aves argentinas (con descripción de pichones). L.O.L.A., Buenos Aires, Argentina.

del Hoyo, J., A. Elliott, & J. Sargatal (eds). 1992. Handbook of the birds of the world. Volume 1: Ostrich to ducks. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & J. Sargatal (eds). 1994. Handbook of the birds of the world. Volume 2: New World vultures to guineafowl. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & J. Sargatal (eds). 1996. Handbook of the birds of the world. Volume 3: Hoatzin to auks. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & J. Sargatal (eds). 1997. Handbook of the birds of the world. Volume 4: Sandgrouse to cuckoos. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & J. Sargatal (eds). 1999. Handbook of the birds of the world. Volume 5: Barn-owls to hummingbirds. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & J. Sargatal (eds). 2002. Handbook of the birds of the world. Volume 7: Jacamars to woodpeckers. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., J. Sargatal, & A. Elliott (eds). 2003. Handbook of the birds of the world. Volume 8: Broadbills to tapaculos. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & D. A. Christie (eds). 2004. Handbook of the birds of the world. Volume 9: Cotingas to pipits and wagtails. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & D. A. Christie (eds). 2005. Handbook of the birds of the world. Volume 10: Cuckoo-shrikes to thrushes. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & D. A. Christie (eds). 2009. Handbook of the birds of the world. Volume 14: Bush-shrikes to Old World sparrows. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & D. A. Christie (eds). 2010. Handbook of the birds of the world. Volume 15: Weavers to New World warblers. Lynx Edicions, Barcelona, Spain.

del Hoyo, J., A. Elliott, & D. A. Christie (eds). 2011. Handbook of the birds of the world. Volume 16: Tanagers to New World blackbirds. Lynx Edicions, Barcelona, Spain.

DeSante, D. F., & D. K. Rosenberg. 1998. What do we need to monitor in order to manage landbirds? Pp. 93–110 *in* Marzluff, J. M., & R. Sallabanks (eds). Avian conservation: research and management. Island Press, Washington, D.C., USA.

Di Giacomo, A. G. 2005. Aves de la Reserva El Bagual. Pp. 201–465 *in* Di Giacomo, A. G., & S. F. Krapovickas (eds). Historia natural y paisaje de la Reserva El Bagual, Provincia de Formosa, Argentina. Inventario de la fauna de vertebrados y de la flora vascular de un área protegida del Chaco Húmedo. Temas de Naturaleza y Conservación 4. Aves Argentinas/Asociación Ornitológica del Plata, Buenos Aires, Argentina.

Dias, B. F. S. 1990. Conservação da natureza no cerrado brasileiro. Pp. 583–640 *in* Pinto, M. N. (ed.). Cerrado: caracterização, ocupação e perspectivas. Editora Univ. de Brasília, Brasília, Brazil.

Dias, R. I., E. S. A. Santos, & R. H. Macedo. 2009. Mating system and sexual conflict in the Blue-black Grassquit (*Volatinia jacarina*: Emberizidae): extra-pair mating behavior sets the scene. Oecol. Bras. 13: 183–191.

Duca, C., & M. Â. Marini. 2011. Variation in breeding of the Shrike-like Tanager in central Brazil. Wilson J. Ornithol. 123: 259–266.

Dunning, J. B. 2007. CRC handbook of avian body masses. 2nd ed. CRC Press, Boca Raton, Florida, USA.

Euler, C. 1900. Descripção de ninhos e ovos das aves do Brasil. Rev. Mus. Paulista 4: 9–148.

Faria, L. C. P., L. A. Carrara, & M. Rodrigues. 2008. Biologia reprodutiva do fura-barreira *Hylocryptus rectirostris* (Aves: Furnariidae). Rev. Bras. Zool. 25: 172–181.

França, L. F., & M. Â. Marini. 2009. Low and variable reproductive success of a Neotropical flycatcher (*Suiriri islerorum*). EMU 109: 265–269.

Gomes, H. B., & M. Rodrigues. 2010. The nest of the Cipó Canastero (*Asthenes luizae*), an endemic furnariid from the Espinhaço Range, southeastern Brazil. Wilson J. Ornithol. 122: 600–603.

Greeney, H. F., P. R. Martin, R. A. Gelis, A. Solano-Ugalde, F. Bonier, B. Freeman, & E. T. Miller. 2011. Notes on the breeding of high-Andean birds in northern Ecuador. Bull. Br. Ornithol. Club 131: 24–31.

Greeney, H. F., R. A. Gelis, & R. White. 2004. Notes on breeding birds from an Ecuadorian lowland forest. Bull. Br. Ornithol. Club 124: 28–37.

Gressler, D. T., & M. Â. Marini. 2007. Nest, eggs and nestling of the Collared Crescentchest *Melanopareia torquata* in the Cerrado region, Brazil. Rev. Bras. Ornitol. 15: 598–600.

Gressler, D. T., & M. Â. Marini. 2011. Breeding biology of the Stripe-tailed Yellow-finch (*Sicalis citrina*) in Central Brazilian cerrado. Ornitol. Neotrop. 22: 319–327.

Hoffmann, D., & M. Rodrigues. 2011. Breeding biology and reproductive success of *Polystictus superciliaris* (Aves: Tyrannidae), an uncommon tyrant-flycatcher endemic to the highlands of eastern Brazil. Zoologia 28: 305–311.

IBAMA. 2003. Lista das Espécies da Fauna Ameaçada de Extinção. Instrução Normativa n° 3, de 27/maio/2003. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA), Ministério do Meio Ambiente, Brasília, DF, Brazil.

Ihering, H. von. 1900. Catálogo crítico-comparativo dos ninhos e ovos das aves do Brasil. Rev. Mus. Paul. 4: 191–300.

IUCN. 2008. 2008 IUCN Red list of threatened species. Version 2009.1. Downloaded on 2 February 2009 from http://www.iucnredlist.org.

Janzen, D. H. 1986. Guanacaste National Park: Tropical Ecological and Cultural Restoration. Editorial Univ. Estatal a Distancia, Fundación Tinker, & Fundación Parque Nacionales, San José, Costa Rica.

Johnson, E. I., P. C. Stouffer, & J. Bierregaard. 2012. The phenology of molting, breeding and their overlap in central Amazonian birds. J. Avian Biol. 43: 141–154.

Klink, C. A., A. G. Moreira, & O. T. Solbrig. 1993. Ecological impact of agricultural development in the Brazilian cerrados. Pp. 259–282 *in* Young, M. D., & O. T. Solbrig (eds). The world's savannas. Economic driving forces, ecological constraints and policy options for sustainable land use, 12. UNESCO, Paris, France.

Lima, A. M. X., & J. J. Roper. 2009. Population dynamics of the Black-cheeked Gnateater (*Conopophaga melanops*, Conopophagidae) in southern Brazil. J. Trop. Ecol. 25: 605–613.

Lopes, L. E., & M. Â. Marini. 2005a. Biologia reprodutiva de *Suiriri affinis* e *S. islerorum* (Aves: Tyrannidae) no Cerrado do Brasil central. Pap. Avul. Zool. 45: 127–141.

Lopes, L. E., & M. Â. Marini. 2005b. Low reproductive success of Campo Suiriri (*Suiriri affinis*) and Chapada Flycatcher (*S. islerorum*) in the central Brazilian Cerrado. Bird Conserv. Int. 15: 337346.

Manica, L. T., & M. Â. Marini. 2012. Helpers at the nests of White-banded Tanager (*Neothraupis fasciata*) benefit male breeders but do not increase reproductive success. J. Ornithol. 153: 149–159.

Marchant, S. 1959. The breeding season in SW Ecuador. Ibis 101: 137–152.

Marchant, S. 1960. The breeding of some SW Ecuadorian birds. Ibis 102: 349–382.

Marini, M. Â. 1992. Notes on the breeding and reproductive biology of the Helmeted Manakin. Wilson Bull. 104: 168–173.

Marini, M. Â., & F. I. Garcia. 2005. Bird conservation in Brazil. Conserv. Biol. 19: 665–671.

Marini, M. Â., J. C. Motta-Júnior, L. A. S. Vasconcellos, & R. B. Cavalcanti. 1997. Avian body masses from cerrado region of central Brazil. Ornitol. Neotrop. 8: 93–99.

Marini, M. Â., & R. Durães. 2001. Annual pattern of molt and reproductive activity of passerines in south-central Brazil. Condor 13: 767–775.

Marini, M. Â., F. J. Borges, L. E. Lopes, L. França, C. Duca, L. V. Paiva, L. T. Manica, D. T. Gressler, & N. M. Heming. 2010. Breeding biology of Columbidae in Central Brazil. Ornitol. Neotrop. 21: 581–590.

Marini, M. Â., N. O. M. Sousa, F. J. A. Borges, & M. B. Silveira. 2009a. Biologia reprodutiva de *Elaenia cristata* (Tyrannidae) no Cerrado do Brasil Central. Neotrop. Biol. Conserv. 4: 3–12.

Marini, M. Â., Y. Lobo, L. E. Lopes, L. F. França, & L. V. Paiva. 2009b. Biologia reprodutiva de *Tyrannus savana* (Aves, Tyrannidae) em cerrado do Brasil Central. Biota Neotrop. 9: 54–63.

Martin T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. Proc. R. Soc. Lond. Ser. B 269: 309–316.

Medeiros, R. C. S., & M. Â. Marini. 2007. Biologia reprodutiva de *Elaenia chiriquensis* (Lawrence, 1865) (Aves: Tyrannidae) em cerrado do Brasil

Central. Rev. Bras. Zool. 24: 12–20.

MMA. 1999. Áreas prioritárias para a conservação da biodiversidade do Cerrado e do Pantanal. MMA, Funatura, Conservation International, Fundação Biodiversitas, Univ. de Brasília, Brasília, DF, Brazil.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Fonseca, & J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nimer, E. 1979. Climatologia do Brasil. IBGE & SUPREN, Rio de Janeiro, RJ, Brazil.

Nóbrega, P. F. A., & J. B. Pinho. 2010. Biologia reprodutiva e uso de habitat por *Cantorchilus leucotis* (Lafresnaye, 1845) (Aves, Troglodytidae) no Pantanal, Mato Grosso, Brasil. Pap. Avulsos Zool. (São Paulo) 50: 511–516.

Oniki, Y., & E. O. Willis. 1983a. A study of breeding birds of the Belém area, Brazil: V. Troglodytidae to Coerebidae. Cienc. Cult. 35: 1875–1880.

Oniki, Y., & E. O. Willis. 1983b. A study of breeding birds of the Belém area, Brazil: VI. Tyrannidae. Cienc. Cult. 35: 1880–1885.

Oniki, Y., & E. O. Willis. 1983c. Breeding records of birds from Manaus, Brazil, IV. Tyrannidae to Vireonidae. Rev. Brasil. Biol. 43: 45–54.

Paiva, L. V., & M. Â. Marini. In press. Timing of migration and breeding of the Lesser Elaenia (*Elaenia chiriquensis*) in a Neotropical savanna. Wilson J. Ornithol.: – .

Pereira, Z. P. 2011. Influência dos recursos alimentares sobre a reprodução de *Neothraupis fasciata* (Aves, Thraupidae). M.Sc. thesis, Univ. de Brasília, Brasília, DF, Brazil.

Piratelli, A. J., M. A. C. Siqueira, & L. O. Marcondes-Machado. 2000. Reprodução e mudas de penas em aves de sub-bosque na região leste de Mato Grosso do Sul. Ararajuba 8: 99–107.

Prado, A. D. 2006. *Celeus obrieni*: 80 anos depois. Atual. Ornitol. 134: 4–5.

Ratter, J. A., J. F. Ribeiro, & S. Bridgewater. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. Ann. Bot. 80: 223–230.

Remsen, J. V., Jr., C. D. Cadena, A. Jaramillo, M. Nores, J. F. Pacheco, J. Pérez-Emán, M. B. Robbins, F. G. Stiles, D. F. Stotz, & K. J. Zimmer. Version 2012. A classification of the bird species of South America. American Ornithologists Union. Available from http://www.museum.lsu.edu/~Remsen/SACCBaseline.html.

Repenning, M., & C. S. Fontana. 2011. Seasonality of breeding, moult and fat deposition of birds in subtropical lowlands of southern Brazil. EMU 111: 268–280.

Ribeiro, J. F., & B. M. T. Walter. 1998. Fitofisionomias do bioma Cerrado. Pp. 89–166 *in* Sano, S. M., & S. P. Almeida (eds). Cerrado: ambiente e flora. Embrapa, Planaltina, D.F., Brazil.

Ricklefs, R. E. 1969a. The nesting cycle of songbirds in tropical and temperate regions. Liv. Bird 15: 33–41.

Ricklefs, R. E. 1969b. An analysis of nesting mortality in birds. Smiths. Contrib. Zool. 9: 1–48.

Robinson, W. D., T. R. Robinson, S. K. Robinson, & J. D. Brawn. 2000. Nesting success of understory forest birds in Central Panama. J. Avian Biol. 31: 151–164.

Rodrigues, L. C., & M. Rodrigues. 2011. Size dimorphism, juvenal plumage, and timing of breeding of the Hyacinth Visorbearer (*Augastes scutatus*). Wilson J. Ornithol. 123: 726–733.

Rodrigues, M., L. M. Costa, G. H. S. Freitas, M. C. Santos, & D. F. Dias. 2009. Os ninhos do canário-do-campo *Emberizoides herbicola*, do canário-do-brejo *Emberizoides ypiranganus* e do rabo-mole-da-serra *Embernagra longicauda*. Rev. Bras. Ornitol. 17: 155–160.

Roper, J. J. 2000. Experimental analysis of nest-sites and nest predation for a Neotropical bird: stuck between a rock and a hard place. Ararajuba 8: 85–91.

Roper, J. J. 2003. Nest-sites influence predation differently at natural and experimental nests. Ornitol. Neotrop. 14: 1–14.

Roper, J. J., K. A. Sullivan, & R. E. Ricklefs. 2010. Avoid nest predation when predation rates are low, and other lessons: testing the tropical-temperate nest predation paradigm. Oikos 119: 719–729.

Rubio, T. C., & J. B. Pinho. 2008. Biologia reprodutiva de *Synallaxis albilora* (Aves: Furnariidae) no Pantanal de Poconé, Mato Grosso. Pap. Avulsos Zool. (São Paulo) 48: 181–197.

Santos, L. R., & M. Â. Marini. 2010. Breeding biology of the White-rumped Tanager (*Cypsnagra*

hirundinacea) in central Brazil. J. Field Ornithol. 81: 252–258.

Santos, M. P. D., & M. F. Vasconcelos. 2007. Range extension for Kaempfers Woodpecker *Celeus obrieni* in Brazil, with the first male specimen. Bull. Br. Ornithol. Club 127: 249–252.

Silva, J. M. C. 1995. Birds of the Cerrado region, South America. Steenstrupia 21: 69–92.

Silva, J. M. C., & J. M. Bates. 2002. Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. BioScience 52: 225–233.

Silva, J. M. C., & M. P. D. Santos. 2005. A importância relativa dos processos biogeográficos na formação da avifauna do Cerrado e de outros biomas brasileiros. Pp. 220–233 *in* Scariot, A., J. C. Souza-Silva, & J. M. Felfili (eds). Cerrado: ecologia, biodiversidade e conservação. Ministério do Meio Ambiente, Brasília, DF, Brazil.

Silveira, M. B., & M. Â. Marini. 2012. Timing, duration and intensity of molt in birds of a Neotropical savanna in Brazil. Condor 114: 435–448.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithol. Monogr. 36: 575–594.

Snow, D. W., & B. K. Snow. 1964. Breeding seasons and annual cycles of Trinidad landbirds. Zoologica 49: 1–39.

Sousa, N. O. M., & M. Â. Marini. 2007. Biologia de *Culicivora caudacuta* (Aves: Tyrannidae) no Cerrado, Brasília, DF. Rev. Bras. Ornitol. 15: 569–573.

Stutchbury, B. M., & E. S. Morton. 2001. Behavioral ecology of tropical birds. Academic Press, London, UK.

Stutchbury, B. M., & E. S. Morton. 2008. Recent advances in the behavioral ecology of tropical birds. Wilson J. Ornithol. 120: 26–37.

Willis, E. O., & E. Eisenmann. 1979. A revised list of birds of Barro Colorado Island, Panama. Smithsonian Institution Press, Washington, D.C., USA.

Wischhoff, U., F. Marques-Santos, & M. Rodrigues. 2012. Nesting of the Cinereous Warbling Finch (*Poospiza cinerea*) in southeastern Brazil. Wilson J. Ornithol. 124: 166–169.

Yom-Tov, Y., M. I. Christie, & G. J. Iglesias. 1994. Clutch size in passerines of southern South America. Condor 96: 170–177.

Zimmer, K. J., A. Whittaker, & D. C. Oren. 2001. A cryptic new species of flycatcher (Tyrannidae: *Suiriri*) from the Cerrado region of central South America. Auk 118: 56–78.