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BREEDING BIOLOGY AND NATURAL HISTORY OF THE SLATE-THROATED WHITESTART IN VENEZUELA

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ABSTRACT.—We provide details on the breeding biology of the Slate-throated Whitestart (*Myioborus miniatus*) from 126 nests found during seven breeding seasons, 2002–2008, at Yacambú National Park, Venezuela. Nesting activity peaked in late April and May. Only the female built the nest and incubated the eggs. Males rarely visited the nest during these stages. Mean clutch size (2.1 ± 0.04 eggs, $n = 93$) was the smallest recorded for the Slate-throated Whitestart. Incubation and nestling period lengths were 15.3 ± 0.31 ($n = 21$) and 10.8 ± 0.24 ($n = 7$) days, respectively. Attentiveness (% of time on the nest) during incubation (59 ± 1.6%, $n = 52$) was similar to other tropical warblers and much lower than northern relatives. This caused a relatively low egg temperature (34.40 ± 0.33° C, $n = 6$ nests, 20 days) compared with north temperate birds. Both parents fed nestlings and increased their provisioning rates with nestling age. Growth rate based on nestling mass ($k = 0.521 \pm 0.015$) was faster than for other tropical passerines but slower than northern relatives. Predation was the main cause of nesting failure and rate of predation increased with age of the nest. An estimated 15% of nests were successful based on an overall Mayfield daily predation rate of 0.053 ± 0.007. This study confirms a strong latitudinal variation in life history traits of warblers. *Received 17 September 2009. Accepted 12 March 2010.*

New World wood warblers (Parulidae) are a small-sized and mostly insectivorous group of birds. Much work has been done on north temperate species, but resident tropical warblers are relatively poorly studied (but see Skutch 1945, 1954; Greeney et al. 2008; Cox and Martin 2009; Morales-Rozo et al. 2009). One of the most broadly distributed genera of this family is *Myioborus*, which consists of 12 species (Sibley and Monroe 1990, Curson et al. 1994, Ridgely and Tudor 1994). The most widespread species of the genus is the Slate-throated Whitestart (*M. miniatus*) which is a resident of mountain ranges between 700 and 2,500 m elevation in humid and wet forests (Ridgely and Tudor 1994). It occurs from Mexico to southern Bolivia, and unconfirmed data extend its distribution to northern Argentina (Di Giacomo 1995). It also is vagrant in southern Arizona, New Mexico, and west Texas (Dunn and Garrett 1997). However, the most northern breeding record is in the Sierra Madre Oriental, Mexico (McCormack et al. 2005).

Slate-throated Whitestart populations are not threatened anywhere within their range and tolerate nesting in disturbed areas (Collins and Ryan 1994, Curson et al. 1994, Mumme 2010). For these reasons, the species is evaluated as one of Least Concern (IUCN 2009).

The wide distribution of this species, which is almost equal to that of the entire genus, makes the Slate-throated Whitestart an interesting species for examining geographical variation. The Slate-throated Whitestart has great plumage and genetic variability along its range (Pérez–Emán 2005). The 12 subspecies recognized show a cline in belly colors from red to orange and yellow from North to Central and South America (Curson et al. 1994). Yet, intraspecific and interspecific comparisons in life-history traits of *Myioborus* are scarce (Skutch 1945, 1954; Collins and Ryan 1994; Mumme 2010).

M. m. ballux is the most common race in the Andes of Venezuela, Colombia, and part of Ecuador. Genetic information for our study site (Yacambu National Park, Venezuela) is lacking, but geographical proximity to Cubiro as well as the occurrence of some slight orange in the breast suggests *M. m. ballux* is also the race occurring in Yacambú (Phelps and Phelps 1950; J. L. Pérez-Emán, pers. comm.).

Our objective is to provide new information on the breeding biology of the Slate-throated Whitestart in a montane forest in northwest Venezuela. We compare our results with life-history traits recorded for other warblers, especially other *Myioborus* species.

METHODS

Study Area.—This study was conducted during seven consecutive breeding seasons, from early March to early July in 2002 to 2008 at Yacambú

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National Park (09° 42′ N, 69° 42′ W) in Lara State, Venezuela. This is a montane forest consisting mainly of primary forest in the northern part of the Andes. The park ranges from 500 to 2,200 m, but our study plots were restricted to 1,350–2,000 m elevation (Fierro-Calderón and Martin 2007). The rainy season spans from mid-April to mid-July with a peak from May to June.

Field Procedures.—Slate-throated Whitestart nests were found almost solely by observing parental behavior, especially during nest building when it is easiest to find them (Martin and Geupel 1993). Nests were checked every other day, except at stage-changing events (hatching or fledging), when they were checked every day or twice per day. Nest size was measured using a ruler with an accuracy of 0.01 cm for outer diameter (from edge to edge of nest) and height (exterior bottom-to-top of nest), and inner diameter (from edge to edge of cup) and height (bottom-to-top of cup). Eggs and nestlings were weighed with a portable electronic scale (ACCU-LAB, Elk Grove, IL, USA) with an accuracy of ±0.001 g. Mean egg mass was calculated only for eggs weighed between days 0 (last egg laid) and 2 of incubation. We measured the tarsus of nestlings using digital calipers (Mitutoyo, Kingsport, TN, USA) with an accuracy of 0.01 mm.

We videotaped nests during incubation and nestling periods in 6–8 hr sessions, starting within 30 min of sunrise (Martin and Ghalambor 1999, Fierro-Calderón and Martin 2007). This allowed us to calculate parental attentiveness (percentage of time on nest for incubating or brooding), as well as on- and off-bout duration and parental provision rates. We sought to videotape incubation in three periods to examine age-related changes in behaviors: early (2–3 days after the last egg was laid), middle (days 6–10) and late (2–3 days before average hatching date) incubation. We recorded parental behavior in two stages during the nestling period: early (day 2–3 after hatch day) and pin break (day in which the eighth pin feather broke its sheath). The latter is possible because pin feather tips turn white the day before they break. Activity recorded in videotapes as well as observation of predation events during nest checks allowed us to identify some of the predators.

We recorded egg temperatures by inserting thermisters on day 1 or 2 of the incubation period into one egg in a nest and the hole was sealed with glue (Weathers and Sullivan 1989). The wire was passed through the back of the nest and connected to a HOBO Stowaway XTI datalogger (Onset Corp., Bourne, MA, USA) that recorded temperatures every 12–24 sec for 5–7 days per nest, unless the nest was depredated earlier (Martin et al. 2007).

Statistical Analyses.—All means are reported with their standard errors (SE). Sample sizes are number of nests in all cases unless otherwise noted. Mean initiation date was calculated only for nests in which the exact egg laying date was known. Nesting season length was estimated as the number of days for the middle 90% of nests initiated (excluding the earliest and latest 5% of initiations) following Martin (2007). We calculated the incubation period as the number of days between the last egg laid and the last egg hatched (Briskie and Sealy 1990, Martin 2002). Incubation periods were only calculated for nests in which the exact day the last egg was laid and exact hatch day were known. We quantified the nestling period as the number of days between the last egg hatching and the last nestling fledging, again based only on exact observations. We used analyses of variance (ANOVA) with significance at $\alpha = 0.05$ to test changes in parental behavior during incubation and nestling stages, and used LSD *post-hoc* tests among periods. Nestling growth curves were calculated following Remeš and Martin (2002). We included measurements of mass and tarsus length for nestlings in which the exact age was known for these analyses. Mortality and survival analyses of nests were calculated considering the elapsed time of the observations to allow inclusion of nests found in different stages following Mayfield (1975). Nests that failed because of experimental activities were excluded from estimation of daily survival or mortality.

RESULTS

Nest Description.—The highest nest located was at an elevation of 1,674 ± 5 m asl; we did not see or hear any Slate-throated Whitestarts above this elevation even though we worked to 2,000 m. Nests were in small nooks on banks or slopes and often built in open or disturbed areas, including road banks or human-made trails inside the forest. However, nests were also found on slopes within undisturbed forest. Nests were highly cryptic because they were usually hidden by surrounding shrubs, ferns, or grasses. Only the female was observed going to and from the nest (mainly in

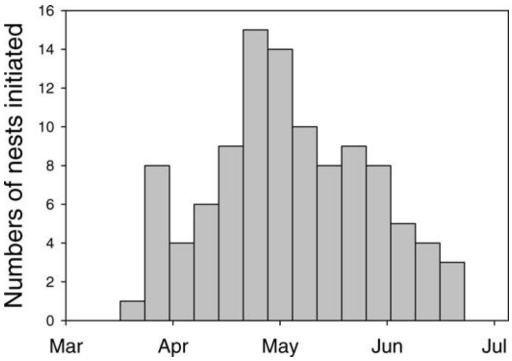

FIG. 1. Numbers of nests initiated (i.e., first egg laid) each week beginning 1 March for Slate-throated Whitestarts at Yacambú National Park, Venezuela during 2002–2008. Only nests for which initiation date was observed are included (n = 106).

morning hrs) to build the nest. The male was nearby in the surrounding trees, usually singing and hunting insects. The first nests of the season were often built over 2 to 4 weeks in a rhythm that started with several nest-building visits per day that slowly increased over time to much more active building. Nests of later attempts were built over 3 to 4 days in much more active behavior.

The nest was a dome-shaped construction entirely built with dry material including pieces of grass, several types of dry leaves, roots, and small twigs. The lining consisted of fine and soft dry fibers. The entrance was circular to elliptical (wider than higher). Nest orientation at 73 nests spanned from 1 to 334° with no orientation preferences. The internal dimensions of the cup averaged 49.1 ± 4.7 mm in diameter and 31.4 ± 9.5 mm in height (n = 66). The outer dimensions of the nest averaged 103.9 ± 21.2 mm and 64.8 ± 25.0 mm for diameter and height, respectively.

Nesting Chronology.—The nesting period of Slate-throated Whitestarts in Yacambú spanned from late March to late June based on 126 nests over seven breeding seasons. The earliest and latest nests across all years of study were initiated on 26 March and 23 June, respectively. Both nests were found before the first egg was laid, yielding precise documentation of these extremes, but even back-calculating nests that were already initiated when found did not exceed these extremes. The mean initiation date was 7 May (± 2.2 days, n = 106) and highest nesting activity occurred at the end of April and through May (Fig. 1).

Re-nesting activities were observed within 6–8 days after a nest failed and within a 15-m radius of the previous nest (n = 10). Banded individuals allowed confirmation that it was a re-nesting attempt by a particular pair of individuals. The nesting season of the Slate-throated Whitestart in Yacambú was 77 days, but this species appears to be single brooded; we did not observe any breeding activity of the same pair in the same season after a successful brood.

Clutch Size and Eggs.—Mean clutch size for the Slate-throated Whitestart was 2.1 ± 0.04 eggs (n = 93). We recorded one instance of a single egg clutch (1%), 15 nests had three eggs (16%), and the rest had two eggs (83%). Three-egg clutches did not exceed 25% of the clutches in any year, but three-egg clutches were observed in all years except 2004 (n = 14 in 2004).

Eggs were laid on consecutive days and generally early in the morning (i.e., before 0800 hrs). The eggs were elliptical to sub-elliptical and the shell was dull white with irregularly distributed dark red to brown spots. Mean egg mass was 1.61 ± 0.01 g (n = 152 eggs) and ranged from 1.20 to 1.94 g. The mean egg mass represented 19% of adult female body mass (10.1 ± 0.15 g, n = 20 females).

Incubation Period.—Incubation began when the last egg was laid, but nest attentiveness was highly variable on that day. Eggs hatched synchronously in all cases. Only the female incubated, and the male rarely visited the nest to feed the female. The male did not visit during 6–8 hrs of video observations at 31 of 52 nests sampled during incubation. Overall, the male averaged 0.11 ± 0.02 trips/hr to the nest (n = 52) during incubation.

The incubation period of the Slate-throated Whitestart averaged 15.3 ± 0.31 days (n = 21) varying from 14 to 18 days. Overall, nest attentiveness (percent of time spent on the nest incubating) during this stage averaged 59 ± 1.6% (n = 52). Nest attentiveness increased ($F_{2,49}$ = 15.8, $P < 0.001$) from early incubation to mid-incubation but did not continue to increase in late incubation (Fig. 2A). The increase in nest attentiveness was caused by reduction in duration of off-bouts with increasing age of the embryo (Fig. 2B; $F_{2,49}$ = 5.4, P = 0.008). Duration of on-bouts did not change ($F_{2,49}$ = 1.49, P = 0.17) with age of the embryo (Fig. 2B). On- and off-bouts averaged 33.4 ± 1.63 min and 22.8 ± 2.65 min (n = 52 in both cases), respectively. Temperature of Slate-throated Whitestart eggs averaged 34.40 ± 0.33° C over 24-hr periods (n =

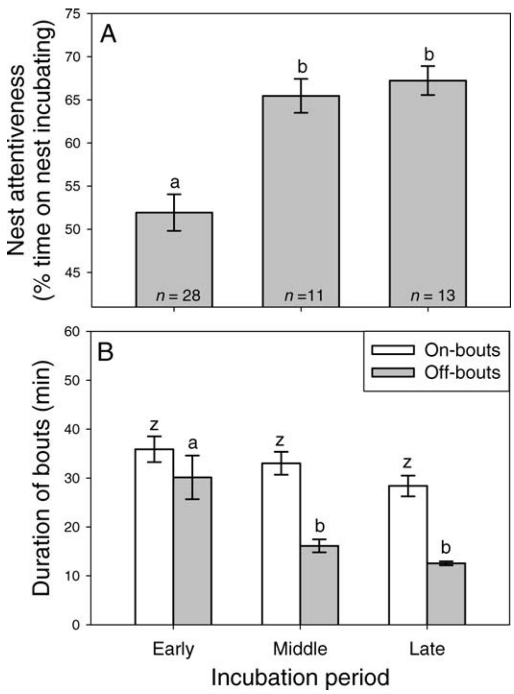

FIG. 2. Mean ± SE for (A) nest attentiveness, and (B) on- and off-bout durations across three periods of incubation: early (days 1–5), middle (days 6–10), and late (days 11–17) for Slate-throated Whitestarts at Yacambú National Park, Venezuela. Sample sizes reflect numbers of nests. Different letters among periods indicate significant difference ($\alpha = 0.05$) level based on LSD tests of each bout type (on- vs. off-bouts) separately.

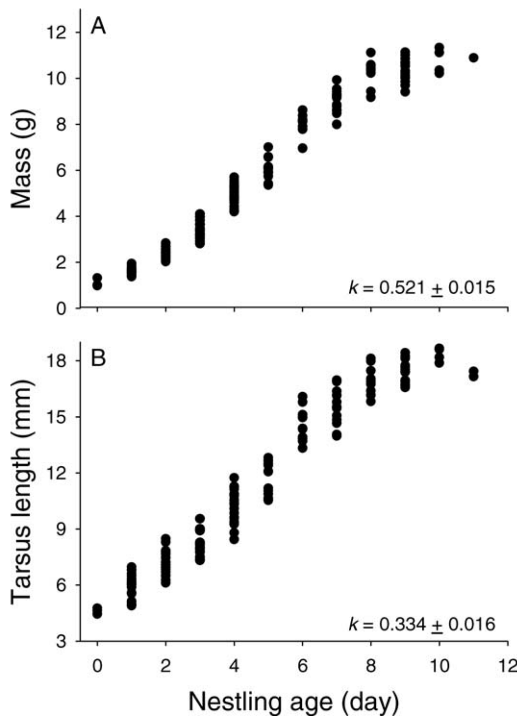

FIG. 3. (A) Mass and (B) tarsus length measurements of Slate-throated Whitestart nestlings at Yacambú National Park, Venezuela plotted against age. Growth rate constant (k) is indicated in each graph.

6 nests, 20 days of sampling) based on an overall mean taken from the means of each nest.

Nestling Period.—Hatchlings had sparse natal down with pink-orange skin, and were blind. The eighth primary feather broke its sheath on days 6 or 7. Brooding attentiveness was by females alone and averaged 63 ± 2.9% (n = 10) at the beginning of the nestling period (days 0–3 of age) and decreased dramatically ($F_{1,15} = 92.6$, $P < 0.001$) to 11 ± 4.9% (n = 7) at pin break. Both females and males provisioned the nestlings at an average rate of 3.77 ± 0.44 trips/hr (n = 10) early in the nestling period (days 0–3), but provisioning rate markedly increased ($F_{1,15} = 25.7$, $P < 0.001$) to 9.41 ± 1.18 trips/hr (n = 7) at pin break.

Nestlings fledged in 10.8 ± 0.24 days (n = 7) after hatching, ranging from 10 to 11.5 days. Growth rate based on nestling mass (Fig. 3A) was greater than when based on tarsus length (Fig. 3B). Nestling weights on the last 2 days in the nest (days 10 and 11) averaged 10.78 ± 0.22 g (n = 5 fledglings) compared with mean adult mass (10.1 ± 0.15 g for the female [n = 20] and 10.1 ± 0.11 g for the male [n = 36]).

Nest Survival.—Eighteen of 126 nests were excluded from nest survival analyses because of disruption by experimental activities or because they were abandoned before egg-laying. Overall daily mortality rate for the remaining nests was 0.065 ± 0.008 (n = 108 nests; 1,084.5 exposure days) and only 15% of the nests were successful (based on a total nesting period of 30.2 days). Overall daily nest predation rate was 0.053 ± 0.007. Daily nest predation rates increased with age of the nest from 0.037 ± 0.021 (n = 81.5 exposure days) during egg-laying to 0.052 ± 0.008 (n = 736 exposure days) during incubation to 0.060 ± 0.015 (n = 267.0 exposure days) during the nestling stage. Predators included mostly birds (e.g., small raptors, jays, and woodwrens) but also small mammals (e.g., squirrels and tayra [*Eira barbara*]).

DISCUSSION

The nesting season for Slate-throated Whitestart in Yacambú (late Mar to late Jun) was almost identical to reports elsewhere in Venezuela (Collins and Ryan 1994), and Costa Rica (Skutch 1954, Mumme 2010). In general, the highly seasonal breeding activity began at the end of the dry season and continued through the rainy season.

Behavior during nest building was consistent with previous observations reported by Skutch (1945, 1954) and Mumme (2010) in Central America, and for other *Myioborus* species (e.g., *M. pictus* [Marshall and Balda 1974] and *M. flavivertex* [Morales-Rozo 2009]). Characteristics of Slate-throated Whitestart nests appear to be highly conservative along the broad range of the species. Slate-throated Whitestart nests in Yacambú were in the same types of places reported from Central America (Skutch 1954, McCormack et al. 2005, Mumme 2010) and Venezuela (Ewert 1975, Collins and Ryan 1994). Slate-throated Whitestart nests were quite similar to some other members of the genus, including *M. melanocephalus* (Greeney et al. 2008), *M. torquatus* (Skutch 1954), *M. brunniceps* (Auer et al. 2007), and *M. flavivertex* (Morales-Rozo et al. 2009). However, some tropical *Myioborus* species, such as *M. ornatus*, apparently build open cup nests (Curson et al. 1994; O. Cortés, pers. comm.). Painted Redstart (*M. pictus*), the most northern species of the group, only occasionally builds an enclosed nest, and more often makes an open cup with the roof substituted by natural overhangs such as rocks, logs, and pine needles (Marshall and Balda 1974). Open-cup nests are common for warblers outside of the tropics. The placement of nests in small holes in the ground is also typical of some North American parulids, such as ground-nesting *Vermivora*, which do not build a roof (Martin 1993).

Clutch size for Slate-throated Whitestart at our study site was relatively constant with 83% of nests containing two eggs. The mean clutch size in Yacambú (2.1 eggs) was relatively small compared with that of *M. m. pallidiventris* only 250 km from our study site, which averaged 2.7 eggs based on six nests (Collins and Ryan 1994). This difference may reflect sample size issues, but it is notable that four of their six nests (67%) had three eggs, while only 15 of 93 nests (16%) had three eggs in our study. Moreover, we did not find more than 25% of nests with three eggs in any individual year. Other *Myioborus* species near the equator also had two-egg clutches. *M. melanocephalus* in Ecuador had two eggs in all of seven nests (Greeney et al. 2008), and *M. flavivertex* in Colombia had two eggs in the only nest observed (Morales-Rozo et al. 2009). *Basileuterus tristriatus* in Yacambú had a mean clutch size of 1.96 eggs and only one of 96 clutches had three eggs (Cox and Martin 2009). Thus, two eggs near the equator may be more typical of warblers, but the frequency of occurrence of three eggs needs further study in *Myioborus*.

Variation in clutch size among latitudes is clear. *M .m. aurantiacus* in Costa Rica usually laid three eggs with mean clutch sizes of 2.84 eggs from 13 nests (Skutch 1954) and 2.89 from 82 nests (Mumme 2010). The only nest observed for *M. m. hellmayri* in Guatemala had three eggs (Skutch 1954), *M. brunniceps* in Argentina had a mean clutch size of 2.6 eggs (Auer et al. 2007), while *M. pictus* in Arizona had a mean clutch size of 3.7 eggs (Marshall and Balda 1974). In contrast, warblers in the north temperate region typically have mean clutch sizes of 4–5 eggs (Martin 1988). Thus, tropical warblers have a strong reduction in clutch size compared to north temperate warblers, but variation within the tropics and subtropics both in Slate-throated Whitestart races and among congeners also appears evident.

Incubation behavior and duration (15.3 days) of the Slate-throated Whitestart in Yacambú seems to be typical for tropical and subtropical warblers (see Cox and Martin 2009) and differ substantially from northern relatives. The mean incubation period was about a day longer than for other subspecies (Skutch 1954, Collins and Ryan 1994, Mumme 2010). However, other whitestart species and most tropical warblers have incubation periods ranging from 14 to 16 days (Martin et al. 2007, Cox and Martin 2009), and our results fit in the middle of this range. Longer incubation periods in the tropics and subtropics, compared to northern species, have been attributed to lower nest attentiveness which causes colder incubation temperatures (Martin 2002, Martin et al. 2007, Martin and Schwabl 2008, Londoño 2009). Nest attentiveness of Slate-throated Whitestarts at our study site was relatively low but similar to other tropical and southern warblers (Cox and Martin 2009). Skutch (1954) studied one nest of Slate-throated Whitestart in Guatemala during middle incubation, and both nest attentiveness (67.4%) and duration of bouts (on-bouts = 37.6 min; off-bouts = 18.2 min) were similar to our observations for mid-incubation (Fig. 2).

Length of the nestling period (10–11 days) had low variation within Yacambú and was similar to that observed for Slate-throated Whitestarts in other localities (Skutch 1954, Collins and Ryan 1994, Mumme 2010). Nestling periods in other species of *Myioborus* are similar to Slate-throated Whitestarts (Skutch 1954, Marshall and Balda 1974, Auer et al. 2007, Greeney et al. 2008). Most warblers have a nestling period within a range of 9–13 days (Cox and Martin 2009) even when including north temperate and tropical species (Elliot 1969, Martin 1995, Remeš and Martin 2002, Martínez et al. 2004, Di Giacomo 2005, Auer et al. 2007, Cox and Martin 2009). The duration of the nestling period appears to be a more conservative life-history trait within Parulidae than incubation period.

Slate-throated Whitestarts in Costa Rica made 20.3 provisioning trips/hr, on average, during nestling ages 5–9 days (Mumme 2010), which is twice the rate that we observed (9.41 trips/hr) for this species in Yacambú on days 6–7. Despite the much higher provisioning rate, nestlings averaged the same weight on days 7–8 in both places: 9.5 g in Costa Rica (Mumme 2010) and 9.5 ± 0.17g (n = 24) in Venezuela (this study). The larger clutch size in Costa Rica (Mumme 2010) may account for the higher provisioning rate and similar nestling size compared with our site. The larger clutch size and similarly sized nestlings with higher parental provisioning rates in Costa Rica (Mumme 2010) compared with our site may suggest that food is more limiting at our site for this species.

Growth rate estimates are scarce for tropical warblers. One estimate based on limited data for the Slate-throated Whitestart in Venezuela (Collins and Ryan 1994) found that nestlings grew at a rate ($k = 0.522$) based on mass almost identical to our estimate from Yacambú ($k = 0.521$, Fig. 3). Generally, tropical passerines grow more slowly than species in temperate regions (Ricklefs 1976, Cox and Martin 2009). Our estimated growth rate (Fig. 3) was slower than estimates for north temperate warblers (i.e., Remeš and Martin 2002, Cox and Martin 2009), but faster than for many other tropical passerines (Ricklefs 1976). This relatively fast growth of nestlings given slow embryonic development (i.e., long incubation periods) demonstrates that developmental rates in embryonic and post-natal stages are not constrained by each other.

Nest design is thought to be an important factor influencing predation rate and failure from weather (Collias and Collias 1984, Auer et al. 2007). The last may be especially important in tropical and subtropical montane forests where rains during the breeding season are quite intense. Enclosed nests in these environments may afford nest contents protection from rain (Collias and Collias 1984) as well as predation (Auer et al. 2007). The daily predation rate of Slate-throated Whitestarts in Yacambú was higher than the average for all non-cavity-nesting species studied at this site (0.041 ± 0.003, n = 38 spp.; TEM, unpubl. data). This average was remarkably similar to the average for 10 non-cavity-nesting species studied in Panama (Robinson et al. 2000). Thus, the domed ground nests of this warbler in Yacambú are readily found by predators.

The Slate-throated Whitestart in Yacambú had a relatively high daily predation rate, small clutch size, long incubation period, and low nest attentiveness during incubation, typical of many tropical passerines (Skutch 1954; Martin et al. 2000, 2007; Cox and Martin 2009). Warblers appear to have strong divergences among relatives across geographic space, making them an important group for studying latitudinal changes in life-history strategies. Some traits, such as clutch size seem to have geographic variation even within the tropics within this species and genus. Other features of Slate-throated Whitestart nesting behavior, including nest construction and placement, nestling period length, and growth rate are relatively conservative. Focusing effort on parulids in tropical latitudes in particular could strengthen many aspects of life history theory.

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