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THE NEST OF THE BAY-RINGED TYRANNULET (*PHYLLOSCARTES SYLVIOLUS*), A LITTLE-KNOWN ATLANTIC FOREST ENDEMIC, SUPPORTS A CLOSE RELATIONSHIP BETWEEN *PHYLLOSCARTES* AND *POGONOTRICCUS*

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Resumen. – El nido de la Mosqueta Cara Canela (*Phylloscartes sylviolus*), una especie poco conocida y endémica de la Mata Atlântica, apoya el estrecho parentesco entre *Phylloscartes* y *Pogonotriccus*. – Existen pocos datos sobre la biología reproductiva de la Mosqueta Cara Canela *Phylloscartes sylviolus*. Aquí describimos cuatro nidos encontrados en varios momentos durante la etapa de construcción, en el este de Paraguay, noreste de Argentina y sudeste de Brasil. Todos los nidos se pueden describir como cerrado/esférico/lateral o quizás cerrado/retorta/colgado, según el esquema reciente para la clasificación de los nidos de las aves Neotropicales. Los nidos eran mayormente verdes, construidos de musgo vivo, pelusa de semillas, otras fibras vegetales, tela de araña, y líquenes. Los dos adultos contribuyeron con la construcción del nido. El único huevo que observamos era blanco limpio. Recientes estudios moleculares han encontrado fuerte apoyo para un parentesco cercano entre *Phylloscartes* y el género *Pogonotriccus*, e incluso han sugerido que un mayor muestreo podría apoyar la reunificación de estos géneros; un estudio reciente de arquitectura de nidos, en contraste, propone que *Phylloscartes* se asemeja más a *Leptopogon* y *Mionectes*. Nuestra revisión de los datos de arquitectura de nidos para estos géneros sugiere un grado mucho mayor de plasticidad que lo que ha sido reconocido, por lo menos dentro de *Phylloscartes*, y similitudes llamativas entre los nidos de *Phylloscartes* y *Pogonotriccus*. Otros géneros cercanos, especialmente *Mionectes* y *Leptopogon*, construyen nidos obviamente diferentes. El sistema para clasificar nidos, presentado por Simon & Pacheco (2005), aunque no es perfecto, merece mayor uso por los ornitólogos describiendo nidos, para facilitar las comparaciones.

Abstract. – There are few data concerning the breeding biology of the Near Threatened Atlantic Forest endemic, the Bay-ringed Tyrannulet *Phylloscartes sylviolus*. Here, we describe four nests from eastern Paraguay, northeast Argentina and southeast Brazil, all found at various stages of construction. All four nests can be described as closed/globular/lateral, or perhaps closed/retort/pensile, according to the recent classification scheme for nests of Neotropical birds. Nests were mostly green, constructed of live moss, seed down, other plant fibers, spider webs, and lichen. Both adults contributed to nest-building. The single egg we observed was clean white. Recent molecular studies have found strong support for a close relationship between *Phylloscartes* and the genus *Pogonotriccus*, and have even suggested that

additional sampling might support their reunification; a recent study of nest architecture, in contrast, proposes that *Phylloscartes* is more similar to *Leptopogon* and *Mionectes*. Our review of nest architecture data for these genera suggests a much greater degree of plasticity than has heretofore been recognized, at least within *Phylloscartes*, and striking similarities between the nests of *Phylloscartes* and *Pogonotriccus*. Other genera, especially *Mionectes* and *Leptopogon*, build obviously different types of nests. The system for categorizing nests of Neotropical birds devised by Simon & Pacheco (2005), while not always perfect, merits greater use by ornithologists describing nests, in order to facilitate future comparisons. *Accepted 8 August 2010.*

Key words: Atlantic Forest, Bay-ringed Tyrannulet, nesting, *Phylloscartes sylviolus*, *Pogonotriccus*.

INTRODUCTION

Limited data are available concerning the breeding biology of the Bay-ringed Tyrannulet *Phylloscartes sylviolus*, a poorly known and Near Threatened endemic of the Atlantic Forest, which ranges from Espírito Santo south to Santa Catarina, Brazil, as well as through the province of Misiones in northeast Argentina and eastern Paraguay (Fitzpatrick 2004, BirdLife International 2009). Narosky & Salvador (1998) briefly reported observations of two nests under construction in Parque Nacional Iguazú, Misiones, Argentina, the first in October 1970 (M. Rumboll) and the second in August 1991 (C. Saibene). Nests were 10 m and 16 m above ground, attached to horizontal branches, and constructed mainly of moss with a lateral entrance hole; the first nest was apparently ëhangingí but the second was attached to the branch and hidden within a bunch of *Rhipsalis* (Cactaceae). At the second nest , both members of the pair were observed carrying nest materials. Lowen *et al.* (1996) report a nest, also under construction, in the canopy of a 30-m-tall *Aspidosperma polyneuron* (Apocynaceae) tree at Reserva Natural Privada Itabó, eastern Paraguay, in mid-October 1995. No details on materials or structure were presented, but one of the observers, M. Pearman (*in litt.* 2010), recalled that it was placed on top of a large horizontal branch c. 25 m above the ground. Remold (2002) presents a photograph of a nest found in mid-October 1999 at Picinguaba, east of Ubatuba, São Paulo, in southeast Brazil. It is not possible to gain a clear impression of the materials used, but the closed nest was high above the ground, well attached to a 'pocket' in a branch, at a point where the latter was broadly vertical, and the nest was obviously longer top to bottom than it was wide, with a lateral entrance, and was pensile but not pyriform. Finally, Aleixo & Galetti (1997) report adults with fledged young in February in southeastern Brazil.

Here, we report on four nests of *P. sylviolus* and present more detailed information than has appeared in the literature previously. We review knowledge concerning the nest architecture of the genus *Phylloscartes* in general, and that of its apparent closest relative, *Pogonotriccus*. We offer remarks on the relationship between these two genera based on our findings and contrast these with that of another recent publication that addressed this problem (Greeney 2009).

METHODS

Nests were found between 2001 and 2009 at three sites in the Atlantic Forest. The first nest was at Reserva Privada Itabó (Rivas) (24º30'S, 54º38'W), a 5000-ha private forest reserve in the department of Canindeyú, Paraguay (the same site as the nest mentioned by Lowen *et al.* 1996). The second and third nests were at Parque Provincial Cruce Caballero (26º31'S, 53º59'W), a 600-ha protected area situated between a large privately owned

secondary forest (in the valley of the Arroyo Alegría) and an area of small farms with remnant forest, in the province of Misiones, Argentina. The fourth nest was at Parque Estadual Intervales (24º15'S, 48º10'W), a 41,700-ha conservation unit in southern São Paulo state, Brazil. We found all nests during the construction phase and watched them using binoculars, making documentary photographs of the nests and adults, and sound-recordings of the adults in several instances. These photographs and sound-recordings are available on request from the authors. We climbed to one of the Argentine nests and measured it using a 15-cm wing-rule.

RESULTS

The first nest was discovered at c. 300 m a.s.l. and c. 400 m from the Arroyo Pozuelo at Reserva Privada Itabó in late November 2001. This nest was attached to the trunk of a large cedro (*Cedrela fissilis*; Meliaceae) that formed part of the native tree canopy over an 80-ha plantation of shade-grown yerba mate within the reserve (see Cockle *et al.* 2005). The nest was c. 17 m above the ground, at the base of a small epiphytic guembé (*Philodendron* sp.; Araceae) surrounded by epiphytic bromeliads. The nest was hidden but we could see that it was globular, with a closed top and a lateral hole in the top third of the side, pointing 90º from the tree trunk. The adults made repeated trips to a nearby cedro to collect nest material. One of the adults would search for and collect nest material from behind some epiphytic bromeliads on this tree, then after some time among these plants it would fly to the nest. AB & KC observed this behavior on several different days, in the last week of November 2001. One of the adults made the trips to collect nest material and the other sometimes accompanied it, but did not seem to directly assist. In late February 2002, the same observers saw an adult feeding a juvenile in the native canopy of the same plantation.

The second nest was discovered by KC on 22 October 2006, at c. 600 m a.s.l., 300 m from the camping area in Parque Provincial Cruce Caballero. The nest was in primary forest, 18 m above the ground on the trunk of a 30-m tall Paraná Pine (*Araucaria angustifolia*; Araucariaceae). It could only be observed from the bottom, and was in the early stages of construction. It appeared as a thin, partial sphere of soft, pale green materials, attached among small ferns and moss on the vertical tree trunk, well below the lowest branches. Both members of the pair added material inside the nest, entering through the bottom. On 23 October, KC watched the nest from 08:14 to 08:26 h and saw the pair enter the nest six times, but she was unable to ascertain whether the birds were bringing new material or only adjusting what was already there. On 27 October, the nest had changed little and was still far from completion. The adults were not seen in this area again, despite weekly visits throughout November.

The third nest (Fig. 1A) was discovered by AB at 600 m a.s.l. in the camping area of Parque Provincial Cruce Caballero, c. 300 m from the second nest and c. 20 m from a small creek, on 16 November 2008 and observed daily until 22 November. It was 15 m above the ground, behind a dead epiphytic cactus (*Rhipsalis* sp.; Cactaceae), 2 m above an active ant nest, attached firmly to a large, mossy, vertical branch of a Grapia (*Apuleia leiocarpa*; Fabaceae) c. 25 m tall. Some branches of the cactus passed through the underside of the nest, helping to support it. On 16 November, the nest was discovered when both adults arrived together at 17:35 h. The nest would later be closed and globular, with a very short lateral entrance 'tunnel' in the top third of the side pointing 90º from the tree trunk (Fig. 1B); however, on 16 November the adults were still visible inside the nest

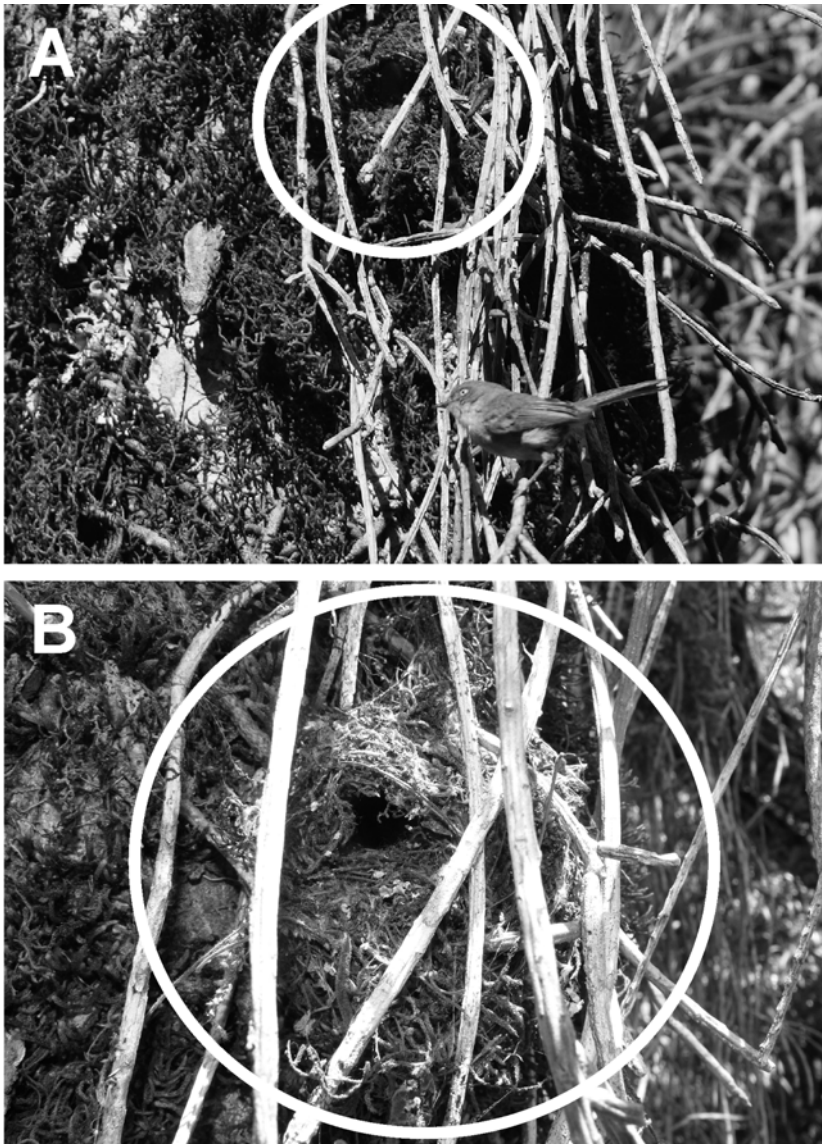

FIG. 1. Nest of Bay-ringed Tyrannulet *Phylloscartes sylviolus* in different phases: A) Adult *P. sylviolus* with Nest 3 in construction on 19 November 2008 at Parque Provincial Cruce Caballero, Argentina (M. Lammertink), B) Nest 3 completed and containing one egg on 22 November 2008 at Parque Provincial Cruce Caballero, Argentina (K. Cockle).

because the tunnel was not constructed and the top of the nest chamber not fully closed. AB watched the nest until 18:55 h and witnessed two further visits, with both adults adding or adjusting material inside the nest. On one of the visits the adults copulated

briefly c. 2 m above the nest. On 17 November, AB watched the nest from 06:25 to 08:30 h, observing 19 visits to bring or adjust material in the nest. All construction occurred inside the nest, which was still relatively open around the entrance and roof. Sometimes both individuals entered the nest. Other times, only one individual entered while the other bird waited in a smaller nearby tree. During this period, they copulated twice. One of the individuals seemed to have a paler cinnamon color to the face. This individual appeared to be more involved in the nest construction and spent more time in the nest. In the evening, the nest was observed for 1 h 40 min, during which time the adults visited it three times. One individual brought material each time, and the other only once. On 18 November, AB watched the nest from 06:40 to 07:40 h. The nest had advanced considerably and the entrance tunnel appeared to be under construction. At 06:45 h one of the adults entered the nest, remaining there for six minutes. It was no longer visible inside the nest because the entrance had been built up. The other bird remained nearby. Both vocalized, including the bird inside the nest. They seemed to maintain vocal contact even though the individual outside the nest flew to about 20 m away. A pair of Piratic Flycatchers *Legatus leucophaius* had a nest with two chicks, c. 13 m away. At one point the pair of *Legatus* foraged for insects among the epiphytes along the branch less than 30 cm from the nest of *P. sylviolus*. A *Phylloscartes* in the nest did not react. That evening the nest was watched from 16:25 to 17:40 h. One individual was heard vocalizing away from the nest. On 19 November, the nest appeared complete. AB observed it from 06:25 to 09:20 h. The pair arrived three times; each occasion one individual entered the nest for 3–11 min, maintaining vocal contact with the other. AB sound-recorded these vocalizations and M. Lammertink photographed one of the adults (Fig. 1A). On 20 November, during 2.5 h of observation, only one individual was seen and it did not enter the nest. On 21 November there was no activity in 3 h of observation by J. Segovia and E. Jordan, and we suspected the nest might have been abandoned. On 22 November, the adults were not seen during the morning and KC inspected the nest. It measured 86 mm tall × 65 mm side to side × 85 mm front to back. Its internal horizontal depth was 73 mm from the inside of the entrance tunnel to the back of the nest chamber. Although the entrance was covered completely by the tunnel roof, the lower lip of the entrance tunnel was shorter (c. 3 cm). The nest did not swing freely but was set firmly among living and dead epiphytes attached to the tree trunk (Fig. 1B). The outside of the nest was constructed of moss, spider web, some relatively hard plant fibres, and white and orange lichen. The egg chamber was covered in soft white plant fibres, probably seed down. The nest contained one white egg (presumably an incomplete clutch, given that clutch size is apparently three in *P. ventralis*: Dabbene 1919, Smyth 1928, Narosky & Salvador 1998).

The fourth nest was discovered, by GMK, at c. 650 m a.s.l. beside the Carmo road, in Parque Estadual Intervales on 30 October 2009, and was observed again on 31 October, as well as more extensively on 1 November, for a total of c. 2 hours. The nest, which was still under construction, was sited c. 15 m above the ground on one of the principal trunks of a "bico do pato" (*Machaerium* sp., Fabaceae) tree at a point where it was near-vertical, smooth, and covered in live lichens and *Tillandsia* (Bromeliaceae). The tree was sited on the steep slopes of a valley. The nest was closed and globular, and its outer layer appeared to be mainly constructed of moss and or *Tillandsia*. Its dimensions were difficult to determine at the distance (c. 25 m) from which observations were made, but it was c. 10 cm in overall length and approximately

two-thirds as wide, i.e. probably broadly similar to the nests at Parque Provincial Cruce Caballero and a nest of Serra do Mar Tyrannulet *Phylloscartes difficilis* (Kirwan 2009), and had a lateral side entrance. Both members of the pair brought materials, usually alone but occasionally together (twice during a one-hour observation period on 1 November, but also on other occasions on the other days). However, when this happened, only one individual would visit the nest, whilst the other remained 'on guard' in the same tree approximately 5 m away ('mate guarding'). As at nest 3, both members of the pair vocalized quite regularly. Visits were usually at a rate of one per ten minutes, but during each period when a bird or birds were at the nest they would visit 2–3 times either with different items or return to adjust material already present. During periods when both birds were present they would stay longer in the vicinity and visit the nest more frequently. On each occasion a bird visited the nest, it was usually for < 10 seconds, but occasionally longer. On c. 50% of visits the birdís tail would be visible when it was entering the nest. Usually the birds sought materials some distance from the nest (flying out of sight when leaving the vicinity) but sometimes they collected materials in the immediate vicinity, especially in the nest tree itself and two adjacent *Cecropia* (Urticaceae) trees (including once some vegetable matter from within a clump of dead leaves). Regular perches were utilized to approach or stay in the general vicinity of the nest, c. 5 of these were in the most adjacent *Cecropia*, and two were in the nest tree, all of them within a 5-m radius of the nest. When approaching from long distance, the birds always staged in two or three trees en route to the nest, and sometimes hovered briefly in front of it before entering, but generally the final approach was direct. However, a small snag immediately (c. 5 cm) below the nest was utilized only occasionally. Items brought generally could not be determined, but included a c. 2 cm-long plant fibre, some seed down, parts of dead leaves, and twice parts of live leaves, suggesting that the birds were finalizing the egg chamber. The altitude at which this nest was discovered is marginally higher than the published elevational range of the species (Fitzpatrick 2004, Ridgely & Tudor 2009).

DISCUSSION

The nests of *P. sylviolus* we found were broadly similar to those previously reported for the species. They were sited high on large vertical branches or trunks of large live trees. The two that could be observed closely were globular, constructed mostly of moss, and at least three of the four had lateral entrances.

In recent decades, especially, there have been several large-scale and numerous smaller-scale contributions to the debate over generic relationships within the Tyrannidae. In addition to the obvious studies of DNA, anatomy and morphology, voice, behavior and nest architecture, amongst other characters, are being increasingly mobilized in efforts to create a robust phylogeny for this diverse family. Treatment of the genus *Phylloscartes* has varied during this period; it sometimes has been expanded to include *Pogonotriccus* (bristle tyrants). Relatively few species of *Phylloscartes* have been sampled genetically to date; the recent nuclear DNA study by Tello *et al.* (2009) included just three species (Black-fronted Tyrannulet *P. nigrifrons*, Mottle-cheeked Tyrannulet *P. ventralis*, and Oustaletís Tyrannulet *P. oustaleti*), as well as one species of *Pogonotriccus*, Marble-faced Bristle Tyrant *P. ophthalmicus*. Tello *et al.* (2009), like Ohlson *et al.* (2008), recovered evidence of a sufficiently close relationship between these two genera to suggest that Traylor (1977: 154) might have been correct to consider them congeneric. Traylor also considered *Leptotriccus* (see below) part of his

expanded *Phylloscartes*. Traylor also included *Capsiempis* (Yellow Tyrannulet *C. flaveolus*), but this suggestion has been refuted (e.g., Lanyon 1988).

The genus *Phylloscartes* is currently usually treated as constituting 16 species of primarily circum-Amazon distribution, one of which, Yellow-green Tyrannulet *P. flavovirens*, is restricted to eastern Panama (Fitzpatrick 2004, Ridgely & Tudor 2009). Intra-generic relationships within this circumscribed view of *Phylloscartes* also have intrigued taxonomists working with Tyrannidae. Several superspecies groupings have been suggested, most notably that *P. nigrifrons*, Rufous-browed Tyrannulet *P. superciliaris*, Rufous-lored Tyrannulet *P. flaviventris*, Cinnamon-faced Tyrannulet *P. parkeri*, Minas Gerais Tyrannulet *P. roquettei*, and *P. sylviolus* might form an expanded superspecies, although it is possible that this close relationship should be confined to *P. flaviventris* and *P. parkeri* (Raposo *et al.* 2002, Fitzpatrick 2004, Maldonado-Coelho 2009). On the other hand, *P. sylviolus* has sometimes been removed to its own genus, *Leptotriccus* Cabanis & Heine, 1859, on the basis of minor structural features (e.g., Hellmayr 1927), and a separate genus is also available for *P. difficilis*, *Guracava*, H. von Ihering & R. von Ihering, 1907. However, Rheindt *et al.* (2008) recovered molecular evidence to suggest that *P. sylviolus* is closely related to *P. superciliaris* and, to a lesser extent, *P. ventralis*, but his sampling of the genus was limited to these three taxa.

Given that nest architecture is recognized to be a taxonomically informative character among some suboscines (Sheldon & Winkler 1999, Zyskowski & Prum 1999, Miller & Greeney 2008), it is worthwhile to reconsider some of these suggested relationships in the light of recently published breeding data. To date, the nests of just six species of the genus *Phylloscartes* have been described, in varying levels of detail: Mottle-cheeked Tyrannulet *P. ventralis* (Dabbene 1919, Klimaitis 1984, Belton 1985, Narosky & Salvador 1998, Smith & Betuel 2006), Alagoas (Long-tailed) Tyrannulet *P. ceciliae* (B. M. Whitney *in* Collar *et al.* 1992), *P. sylviolus* (Lowen *et al.* 1996, Narosky & Salvador 1998; this paper), Restinga Tyrannulet *P. kronei* (Remold & Ramos Neto 1995), *P. roquettei* (Kirwan *et al.* 2004), and Serra do Mar Tyrannulet *P. difficilis* (Kirwan 2009). Only the eggs of *P. ventralis* (Dabbene 1919, Smyth 1928, Belton 1985, Narosky & Salvador 1998) and *P. sylviolus* (this paper) have been described (both are white).

Nests of Phylloscartes. The nests of *Phylloscartes* have provided us with a problem of categorization according to the classification system devised by Simon & Pacheco (2005). Although all appear to be closed with a lateral entrance, their attachment points may be considered 'pensile' (attached from above), 'lateral' (attached laterally to substrate) and sometimes even 'fork' (sitting in a fork). To some extent, the *P. sylviolus* nests described here present a midway point between closed/globular/lateral, or closed/retort/pensile, because the nests were somewhat pensile but also supported laterally (by the tree trunk). Nests 3 and 4 also were supported by vegetation on the trunk and did not move freely. A recently discovered nest of *P. difficilis* can also be considered ëmidwayí between pensile and lateral, and was also constructed on a vertical section of trunk (Kirwan 2009). Complicating the classification of nest architecture, at least some species of *Phylloscartes* may show considerable intraspecific variation in nest construction, as had already been noted by Simon & Pacheco (2005: 147) for some other Tyrannidae.

Among the *Phylloscartes*, nest architecture is best known for *P. ventralis*. We know of ten nests of this species, all pertaining to the nominate subspecies and *P. v. tucumanus*, and described as closed with lateral entrances, usually protected by a slight overhang, and

attached to trees or lianas at a height of 1.5–7.0 m above the ground. Four of the nests appeared somewhat longer than they were wide (Dabbene 1919, Klimaitis 1984, Narosky & Salvador 1998). Three were constructed using a variety of plant materials including small twigs, liana fibres, spider webs, dry leaves, lichens, and moss (Klimaitis 1984, Narosky & Salvador 1998). Two appeared to be constructed mostly of *Tillandsia usneoides* (Bromeliaceae; Dabbene 1919, Belton 1985); in one of these the bird appeared to have simply adapted a hanging clump of *Tillandsia* for its own use (Belton 1985). This latter nest was suspended from "a small tree" and another was suspended from "a thin branch" (Belton 1985). In contrast, the nest found by Klimaitis (1984) was placed within an accumulation of dead leaves and other litter between interlaced lianas and surrounded by *Rhipsalis* (Cactaceae), and the one found by Narosky & Saibene (per Narosky and Salvador 1998) was placed among branches to which it was attached using abundant spider webs above and in various places. Likewise, two nests found by AB (pers. observ.), in Buenos Aires and Entre Ríos, Argentina, were both attached laterally to trees at points where branches or twigs joined the main trunk, and a nest found by Smith & Betuel (2006: 21) was "placed on a thin, horizontal moss-covered branch with two further vertical branches providing a crotch-like support for the entrance". Some of these nests are difficult to characterise on the basis of the details presented, but most appear to be closed/globular/lateral. All were obviously closed and none sounds truly pyriform, although some do appear to have been pensile. *Contra* Fitzpatrick (2004: 299), we are unaware of any description of the nest of *P. v. angustirostris* (of eastern Peru to Bolivia). The nest ascribed to that race in the latter work is transcribed from Dabbene (1919), whose observations were made in Buenos Aires province (erroneously omitted from the speciesí range by Fitzpatrick) and therefore pertained to *P. v. ventralis*. Equally, the nest specifically mentioned for *P. v. tucumanus* seems to have been taken from Klimaitis (1984), which too was based on observations in Buenos Aires. Fitzpatrick (2004) considered the season to be October–December in Argentina, but Narosky & Salvador (1998) also mention a January nest, and, for Brazil, Belton (1985) reported various breeding data for most months between late August and December. The date of the only Uruguayan nest reported to date is unclear, but probably refers to the same general period (Rocha 2000).

Few or no nests have been described for the remaining *Phylloscartes* species. Only one nest of *P. roquettei* has been described, and it was closed/retort/pensile (Kirwan *et al.* 2004). However, photographs of two recently discovered nests of *P. roquettei* posted on the internet, in both of which the identification of the adults appears correct, show moss-like nests supported against trunks and within tree forks (www.arkive.org and www.wikiaves.com), suggesting a structure that is closed/globular/lateral or even closed/globular/fork. One nest of *P. kronei* has also been described (Remold & Ramos Neto 1995); the side walls and back of the nest were supported by a total of five thin twigs (H. Remold *in litt.* 2010), so it can be considered closed/globular/lateral. Finally, there is a very brief description of a nest of *P. ceciliae* in Collar *et al.* (1992). The nest was a 45-cm pensile structure sited 6 m above the ground and consisting of three parts: a 10-cm attachment to the branch of the tree, the ball-like nest chamber with a side entrance, and a 20-cm tail of dangling material, all of them constructed of moss-like material (B. M. Whitney pers. comm.). This description suggests the nest was pensile, and quite different to all of the other nests of *Phylloscartes* species described to

date. Unlike the round nest of *P. roquettei* (Kirwan 2009) this nest appears to have been pyriform, albeit with an additional tail of material hanging below the nest chamber. To date, this description is by far the most disparate of all those available for the genus *Phylloscartes*.

Nests of Pogonotriccus. The nests of *Pogonotriccus* also are largely unknown. No nest descriptions are available for four species (Fitzpatrick 2004) and the description for a fifth species appears erroneous, leaving only two species - Southern Bristle Tyrant *P. eximius* (the type species of *Pogonotriccus*) (Bertoni 1901) and Marble-faced Bristle Tyrant *P. ophthalmicus* (Greeney 2009) - with valid nest descriptions. The nest of *P. eximius* found in Paraguay (Bertoni 1901) was a mossy oven-shaped ball constructed against a tree trunk, and clearly could be considered closed/retort/lateral in architecture. The nest of *P. ophthalmicus* discovered by Greeney (2009) was placed 7 m above the ground and in most general respects of form and structure closely matched the nests of *Phylloscartes sylviolus* (described here) and other *Phylloscartes*, as did that of another nest of *Pogonotriccus ophthalmicus* collected in Peru by T. S. Schulenberg (also described in Greeney 2009). We concur with Greeney (2009) that the nest of *P. ophthalmicus* mentioned in Hilty & Brown (1986) must either have been misidentified to species, or was described so imprecisely ("a mossy cup … on a small forked branch") as to unwittingly invite subsequent confusion. There is also confusion about the nest of the Variegated Bristle Tyrant *P. poecilotis*. The nest reported to belong to this species by Londoño & Muñoz (2006) was more likely that of a Slaty-capped Flycatcher *Leptopogon superciliaris* (see Greeney 2009, whose conclusions we support, for a thorough discussion of this nest). Hilty & Brown (1986) mentioned a 'July nest' of this species that had been reported to them, but without additional information. However, a video of a *P. poecilotis* nest filmed in eastern Ecuador, archived on the Internet Bird Collection (https://ibc.lynxeds.com) clearly shows a nest similar in form and structure to those of *Phylloscartes sylviolus* reported here and that of *Pogonotriccus ophthalmicus* reported by Greeney (2009, of which video evidence is also available on the Internet Bird Collection web site).

Nest architecture and the relationship between Phylloscartes *and* Pogonotriccus. Greeney (2009) considered relationships between *Phylloscartes*, *Pogonotriccus*, and other related small tyrannid genera. *Contra* the genetic data (cited above), nest architecture and behavioral innovations led him to speculate that *Phylloscartes* could be united with *Leptopogon* and *Mionectes*, whereas he considered *Pogonotriccus* to be closer to *Corythopis* and *Pseudotriccus* in nest characters. Greeney (2009) regarded *Phylloscartes* as building solely pendant nests. However, as reviewed above, *Phylloscartes ventralis* (Dabbene 1919, Klimaitis 1984, Belton 1985, Narosky & Salvador 1998, Smith & Betuel 2006; AB pers. obs.), *P. difficilis* (Kirwan 2009), *P. kronei* (H. Remold *in litt.* 2010), and *P. sylviolus* (this paper) often (but not exclusively) build nests that are supported laterally, in the same manner as the nest of *Pogonotriccus ophthalmicus* Greeney (2009) described. Like the nests of *Pogonotriccus*, they are also globular structures built more or less well above the ground (this seems to vary with the foraging strata of the species concerned, but nests are never sited below overhanging banks within root masses), and frequently using green materials such as live moss. In contrast, the nests of *Leptopogon* and *Mionectes* are more pyriform structures that hang from roots or low plants close to the ground, and are often constructed of brown materials such as dry plant fibres, though live moss can also be utilized to cover the outside, whilst those of *Mionectes* are sited toward the tip of long branches (e.g., Skutch 1960, Aguilar *et al.* 2000, Fitzpatrick 2004,

Greeney *et al.* 2006, Greeney 2009). To date, of the available descriptions, the only individual nest of *Phylloscartes* that could be described as hanging freely and pyriform is the sole nest found of *P. ceciliae* (Collar *et al.* 1992). It is also worth remarking in this respect that even the pensile nest of *P. roquettei* described in the literature (Kirwan *et al.* 2004) was still quite different from those of any known *Leptopogon* or *Mionectes*, in being placed high above the ground suspended (but not swinging wholly free) from a tree branch (in perhaps the same manner as some of the nests of *P. sylviolus* mentioned in the introduction), and in being strongly globular rather than pyriform. While few green materials, and no mosses, were used in its construction, this probably largely reflected their relative lack in the vicinity of the nest at this season (e.g., early October is still very dry in the region concerned).

Greeney (2009) also drew attention to what he considered to be probably a second distinction, in how the nest is attached to the substrate: 'stuffing' (in *Pogonotriccus*) versus 'draping' (*Phylloscartes*) the nest. However, it seems certain from our observations of *Phylloscartes sylviolus* and *P. difficilis* that these two species are also 'stuffers', i.e. rather than attaching their nest by draping material over an attachment point and building the nest chamber within the resulting curtain (as in *Leptopogon*), they stuff material into small spaces between epiphytic plants, effectively creating a nest that is part of an existing substrate. This is certainly true of *P. difficilis*, and seems very likely to have been the case in most or all of the *P. sylviolus* nests we observed. The obviously pensile nest of *P. sylviolus* found by Remold (2002) and at least one of the nests of *P. ventralis* found by Belton (1985) appear also to have been constructed using the advantages afforded by an already suitable substrate. As such, *contra* Greeney (2009) we consider that nest architecture, like the genetic data, points to a close relationship between *Pogonotriccus* and *Phylloscartes*, distinct from *Mionectes* and *Leptopogon*.

More information concerning the nests of all *Phylloscartes* and *Pogonotriccus* species is needed, not only for the role it can play in expanding our knowledge of their life histories, and aiding their conservation (several species are considered to be globally threatened), but also to help inform our knowledge of inter- and intra-generic relationships. We suspect that *Phylloscartes* might prove to be polyphyletic, but that in terms of some aspects of nest architecture the genus, as currently constituted, appears to sit somewhere in the middle of a continuum, with *Pseudotriccus* (which builds nests closely affixed to a trunk) and *Mionectes* (which constructs highly pensile nests) at opposite ends of this spectrum. To this end, further data for those species whose nests are already known, to a greater or lesser extent, also will be valuable, if only to evaluate the degree of plasticity in their breeding behavior (which is already evident for at least two species of *Phylloscartes*, *P. ventralis*, and *P. roquettei*). We believe that robust (correctly identified to species) and large samples are probably needed to infer patterns from nest architecture in at least some groups, especially genera of wide geographical range and habitat preferences. We also encourage nest finders and describers to use the system proposed by Simon & Pacheco (2005) for describing nests and to document the species whenever possible by sound-recording or photographs, thereby providing ready means for researchers to compare nest architecture between different species and genera.

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