

# Divergence in nest placement and parental care of Neotropical foliage-gleaners and treehunters (Furnariidae: Philydorini)

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**ABSTRACT.** The Neotropical ovenbirds (Furnariidae) are an adaptive radiation of suboscines renowned for the diversity of their nests. Like most altricial insectivores, they generally exhibit biparental care. One tribe, Philydorini, includes 46 species thought to nest in either underground burrows or tree cavities, nest types traditionally treated as equivalent in phylogenetic studies. Their parental care systems are poorly known, but could help illuminate how uniparental care – typically associated with frugivory – can arise in insectivores. We examined the extent to which nest placement, parental care, and associated reproductive traits map onto two major clades of Philydorini identified by genetic hypotheses. We review published literature and present new information from the Atlantic Forest of Argentina, including the first nest descriptions for Ochre-breasted Foliage-gleaners (*Anabacerthia lichtensteini*) and Sharp-billed Treehunters (*Heliobletus contaminatus*). In the *Automolus-Thripadectes-Clibanornis* clade (including *Philydor rufum*), 134 of 138 reported nests were in underground burrows. In the *Syndactyla-Anabacerthia-Anabazenops* clade (including *Heliobletus*, *Philydor atricapillus*, and *Philydor erythrocercum*), 44 of 48 nests were in tree cavities. Remaining nests were in buildings or species-level identification was unclear. At least eight species in the first clade, but none in the second clade, excavated their nest sites. Biparental care was confirmed for nine species in the first clade and one species in the second clade. In contrast, nests of *A. lichtensteini* and *H. contaminatus* were attended by a single secretive adult. We propose that species in the *Automolus-Thripadectes-Clibanornis* clade are underground burrow excavators, and those in the *Syndactyla-Anabacerthia-Anabazenops* clade are secondary tree-cavity nesters (nonexcavators). We also note that parental care strategies in Furnariidae vary with nest complexity and conspicuousness – from uniparental care in secretive tree-cavity nesters to cooperative breeding in highly vocal builders of elaborate nests – suggesting evolutionary links among nest-building, concealment, and parental care strategies.

## RESUMEN. Divergencia en ubicación de nidos y cuidado parental en Philydorini (Furnariidae: Philydorini)

La familia Furnariidae es una radiación adaptativa de suboscines reconocida por la alta diversidad de sus nidos. Como la mayoría de los insectívoros nidícolas, generalmente tienen cuidado biparental. Una de las tribus, Philydorini, incluye 46 especies que anidarían en excavaciones subterráneas o en cavidades de árboles, dos tipos de nido que los estudios filogenéticos tradicionalmente han tratado como equivalentes. Son tradicionalmente considerados como equivalentes en estudios filogenéticos. El sistema de cuidado parental en esta tribu es poco conocido, pero puede contribuir a comprender cómo el cuidado uniparental – típicamente asociado con frugivoría – puede surgir en insectívoros. Examinamos hasta qué punto la ubicación de los nidos, el cuidado parental y los caracteres reproductivos asociados se correlacionan con los dos clados principales de Philydorini identificados por hipótesis genéticas. Revisamos la literatura y presentamos información nueva de la Selva Atlántica de Argentina, incluyendo las primeras descripciones del nido de *Anabacerthia lichtensteini* y de *Heliobletus contaminatus*. En el clado de *Automolus-Thripadectes-Clibanornis* (incluyendo *Philydor rufum*), 134 de los 138 nidos reportados fueron en excavaciones subterráneas. En el clado de *Syndactyla-Anabacerthia-Anabazenops* (incluyendo *Heliobletus*, *Philydor atricapillus* y *Philydor erythrocercum*), 44 de los 48 nidos fueron en cavidades de árboles. Los nidos restantes fueron en edificios o la identificación a nivel de especie no fue clara. Al menos ocho de las especies en el primer clado, pero ninguna del segundo clado, excavaron sus sitios de anidación. Confirmamos el cuidado biparental en nueve especies en el primer clado y una especie en el segundo clado. En contraste, nidos de *Anabacerthia lichtensteini* y *Heliobletus contaminatus* fueron cuidados por un único adulto sigiloso. Proponemos que las especies en el clado de *Automolus-Thripadectes-Clibanornis* son excavadores de túneles subterráneos y que las especies en el clado de *Syndactyla-Anabacerthia-Anabazenops* son adoptadores de cavidades de árboles. También resaltamos que las estrategias de cuidado parental en Furnariidae varían con la complejidad y conspicuidad del nido – desde cuidado uniparental en especies sigilosas que anidan en cavidades

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de árboles hasta cría cooperativa en especies altamente vocales que construyen nidos elaborados – sugiriendo asociaciones evolutivas entre la construcción de los nidos, su encubrimiento y las estrategias de cuidado parental.

*Key words:* *Anabacerthia*, burrow, cavity nest, *Heliobletus*, life history, parental care, phylogeny, tree cavity

The ovenbirds (Furnariidae) are a large family of insectivorous passerines that has diversified throughout the Neotropics to occupy nearly all terrestrial habitats from Mexico to Tierra del Fuego and from sea level to the high Andes (Irestedt et al. 2002, Remsen 2003, Seeholzer et al. 2017). Furnariids exhibit an extraordinary diversity of nest types (Skutch 1969, Sick 1993, Remsen 2003), which has been used to propose phylogenetic relationships (Vaurie 1980, Zyskowski and Prum 1999). Genetic studies of Furnariidae have revealed multiple cases of convergent morphology and polyphyly (Irestedt et al. 2002, Chesser et al. 2007, Claramunt et al. 2010, 2013, Derryberry et al. 2011), but have generally supported phylogenetic hypotheses that used nest architecture (Irestedt et al. 2006, 2009). DNA-based phylogenies now suggest that the ancestors of modern furnariids nested in cavities in trees or in underground burrows, and that building vegetative nests evolved multiple times in the family (Irestedt et al. 2006, 2009).

Although nest architecture has long been recognized as phylogenetically informative in the Furnariidae, most studies have treated the excavation of underground burrows as equivalent to the use of existing tree cavities (Zyskowski and Prum 1999, Irestedt et al. 2006, 2009). Grouping these two types of nest placement allowed researchers to include problematic species and genera reported to nest both in underground burrows and in tree cavities (Lillo 1902, Vaurie 1980, Hilty 2003, Remsen 2003). However, Kratter and Parker (1997) recognized the importance of distinguishing tree cavities from underground burrows when they argued that Dusky-cheeked Foliage-gleaners (*Anabazenops dorsalis*), which nest in bamboo cavities (Kratter 1994), should be removed from the genus *Automolus*, whose members nest in underground burrows, and placed in the genus *Anabazenops*, a decision now supported by genetic data (Derryberry et al. 2011). Given morphological similarities among many furnariids, species-level identifications by early naturalists were prone to error. Moreover, some genera

lumped as “cavity nesters” by Zyskowski and Prum (1999) are now known to be polyphyletic (Chesser et al. 2007, Derryberry et al. 2011, Claramunt et al. 2013). Here, we revisit Kratter and Parker’s (1997) idea that nest placement – in an underground burrow versus a tree cavity – can be phylogenetically informative.

Mating systems and parental care are considered to vary little within the Furnariidae; most species are socially monogamous, with stable territories and biparental care of young (Remsen 2003). However, some are cooperative breeders, and a few have lek-like mating systems and uniparental (female-only) care (Skutch 1969, Willis 1972, Sick 1993, Willis and Oniki 1995, Remsen 2003). Female-only care occurs in about 8% of bird species globally (Cockburn 2006) and, among altricial species of birds, is generally associated with polygyny and frugivory in environments with long periods of fruit availability, where the ease of acquiring food for nestlings is hypothesized to reduce the value of paternal provisioning (Snow 1976, Cockburn 2006, Barve and La Sorte 2016). Even in insectivorous passerines, lek-like mating systems and uniparental care are usually associated either with elevated levels of frugivory or exceptionally food-rich habitats such as marshes (Schulze-Hagen et al. 1999, Barve and La Sorte 2016), conditions that do not appear to apply to forest furnariids (Cockburn 2006). Lill (1986) hypothesized that female-only care may be enabled by small broods and slow nestling growth that reduce daily brood-care expenditures. Small broods (Skutch 1949) and female-only care (Snow 1976, Schulze-Hagen et al. 1999, Lill 1986) might also facilitate nest concealment. If we can identify lineages with uniparental care within the furnariid radiation, we can begin to examine the conditions that favor emancipation of males from parental duties in forest insectivores.

One of the most problematic groups of Furnariidae, in terms of understanding nest placement and parental care, is Philydorini (sensu Derryberry et al. 2011), a tribe of 46 forest-dwelling foliage-gleaners in the

subfamily Furnariinae whose convergent morphologies have led to a long history of taxonomic controversy (Remsen 2003, Claramunt et al. 2013, Remsen et al. 2017). All species of *Philydorini* appear to place their nests in some kind of cavity – tree cavities, underground burrows, or human-made structures (Irestedt et al. 2006). All *Philydorini* (and indeed all Furnariinae) were inferred by Cockburn (2006) to exhibit biparental care (but see Remsen 2003). Nesting materials vary within *Philydorini* (Vaurie 1980, Zyskowski and Greeney 2010), but other details about breeding biology are available for few species and the nests of many remain completely unknown (Remsen 2017).

Genetic data (Derryberry et al. 2011) suggest that the *Philydorini* can be subdivided into two major clades: (i) the genera *Automolus*, *Clibanornis*, *Thripadectes*, *Ancistrops strigilatus*, *Philydor erythropterum*, and *Philydor rufum* (hereafter “*Automolus-Thripadectes-Clibanornis* clade”), and (ii) the genera *Syndactyla*, *Anabacerthia*, *Anabazenops*, *Heliobletus*, *Cichlocolaptes*, *Megaxenops*, and several other members of the polyphyletic *Philydor* (hereafter “*Syndactyla-Anabacerthia-Anabazenops* clade”). Here, we aimed to determine the extent to which nest placement, parental care, and associated reproductive traits map onto these two clades, by reviewing published literature and by presenting new information from the Atlantic Forest of northeastern Argentina, including the first nest descriptions for Ochre-breasted Foliage-gleaners (*Anabacerthia lichtensteini*) and Sharp-billed Treehunters (*Heliobletus contaminatus*).

## METHODS

We follow the taxonomy of Remsen et al. (2017). We reviewed the literature for nest descriptions for all members of the tribe *Philydorini*, by consulting general references about nesting of Furnariidae (Skutch 1969, Vaurie 1980, Narosky et al. 1983, Belton 1984, Sick 1993, Zyskowski and Prum 1999, Remsen 2003, 2017, de la Peña 2005, Kirwan 2009, Zyskowski and Greeney 2010, Londoño 2014) and references cited therein. We also used Google Scholar to search for each genus in *Philydorini*, in combination with the terms “nest”, “nido”, or “ninho.”

Finally, we consulted colleagues for details about nests they had found or about which they had written. We included comments such as “breeds in tree cavities” in our compilation (Table 1), but, when tallying nest types for each clade, we only counted nests that were specifically identified (e.g., by observer or locality).

We studied nests of *Philydorini* from 2003 to 2016 in the Atlantic Forest of Misiones, Argentina. Most (90%) of our search effort was spent at Parque Provincial Cruce Caballero (26°31'S 53°58'W), where we studied tree-cavity-nesting birds from September to December each year from 2006 to 2016 (Cockle et al. 2015). A few nests were also found at Tobuna (26°28'S 53°53'W), Parque Nacional Iguazú (25°42'S 54°22'W), Área Experimental Guaraní (26°56'S 54°13'W), Parque Provincial Caá Yari (26°52'S 54°13'W), Reserva Privada Yaguaroundi (26°42'S 54°16'W), and Parque Provincial de la Araucaria (26°38'S 54°07'W). We found nests of *Philydorini* by searching for birds that vocalized repeatedly in the same location, watching their behavior (e.g., carrying nest material, food, or fecal sac), inspecting tree cavities and underground burrows, and accidentally flushing adults. We took photographs, audio-recordings, and videos of *A. lichtensteini* and *H. contaminatus* attending their nests, to confirm species identification.

We inspected tree cavities and burrows by inserting a small camera mounted on the end of a rod or hose, illuminating the interior with a flashlight, or reaching inside to touch eggs or nestlings. Tree cavities were accessed using a 10-m ladder, single-rope tree-climbing system, or telescoping pole (up to 22 m). Nests of Buff-browed Foliage-gleaners (*Syndactyla rufosuperciliata*), *A. lichtensteini*, and *H. contaminatus* were also watched using binoculars for a total of 24.4 h, 6.2 h, and 8.8 h, respectively. We only counted nests where we saw eggs, nestlings, or adults carrying food, nest material, or fecal sacs. We considered nests to be successful if fledglings were observed around the nest site, or at least one feathered nestling was observed in the nest and there was no subsequent evidence of predation. We considered nests to have failed if they were found empty several days before nestlings could have fledged. After nests either failed or fledged, we used measuring tapes to

determine cavity dimensions and height above or below ground. In some cases, we used a hooked stick to extract nest material.

## RESULTS

Our literature review and field data (see species accounts below) revealed nesting information for 28 species in the Philydorini (Table 1). At least 138 nests were reported for species in the *Automolus-Thripadectes-Clibanornis* clade (we counted one nest in cases where authors reported an unspecified number of nests). Of these, at least 134 were in underground burrows (Table 1). The only exceptions involve Buff-fronted Foliage-gleaners (*P. rufum*), which were mentioned nesting in buildings (Schwartz in Vaurie 1980), one stick nest (Fiebrig 1921), and two (Olrog in Narosky et al. 1983) or possibly four (Olrog in Vaurie 1980) tree cavities. The stick nest and tree cavity records appear to have resulted from species misidentification (see below). At least eight species in the *Automolus-Thripadectes-Clibanornis* clade excavated their own burrows (Table 1).

In contrast, of 48 reported nests for the *Syndactyla-Anabacerthia-Anabazenops* clade, 44 were in pre-existing cavities in either trees or bamboo and two were in buildings (Table 1). Reports of nests in underground burrows are unconfirmed, and correspond to species that have been recorded nesting in tree or bamboo cavities (Table 1). Ruschi (1981) reported Black-capped Foliage-gleaners (*Philydor atricapillus*) nesting in underground burrows; Sick (1993) appears to have repeated this idea, but Zyskowski and Prum (1999) doubted the species identification. Confusingly, Ruschi's (1981) descriptions combined nests of *P. atricapillus* with nests of *P. rufum*. Pacheco (1995) and Pacheco and Bauer (2001) revealed serious inconsistencies in some of Ruschi's work and suggested that all of his findings should be revisited. Recently, Mitsuo Tanaka et al. (2016) photographed *P. atricapillus* nesting in a bamboo cavity. Another nest in an earth bank was photographed by an unidentified photographer and attributed to Rufous-rumped Foliage-gleaner (*Philydor erythrocerum*; Londoño 2014), but no details were provided. *Philydor erythrocerum* has been observed nesting in a tree cavity (Tostain et al. 1992). Finally,

Kirwan (2009) observed a Rufous-tailed Foliage-gleaner (*Anabacerthia ruficaudata*) visiting a hole in an earth bank, but recognized there was no evidence that the bird was nesting.

We found evidence of biparental care for 10 species in the *Automolus-Clibanornis-Thripadectes* clade, but only *S. rufosuperciliata* in the *Syndactyla-Anabacerthia-Anabazenops* clade (Table 1). We found evidence of uniparental care for three species in the *Syndactyla-Anabacerthia-Anabazenops* clade (Table 1).

**White-eyed Foliage-gleaner (*Automolus leucophthalmus*).** Four nests have been described, all in burrows (Euler 1900, JCR Magalhães in Novaes 1961, Marini et al. 2007). We observed two nests in the forest at Parque Provincial Cruce Caballero. One was in a horizontal tunnel ~80 cm long in the bank of a stream with at least two eggs in a loose cup of rachises on 10 November 2012. The second was in a horizontal tunnel ~40 cm below the edge of a large natural hole ~1 m deep and 1 m wide, in the ground near a spring. On 27 November 2014, it contained two white eggs in a cup of rachises or other flexible material, including leaves of *Merostachys clausenii* (Poaceae) bamboo (C. A. Ferreyra *in litt.*). At both of these nests, as well as at a nest found by J. C. R. Magalhães (in Novaes 1961), two adults were seen near burrow entrances, but the extent to which each sex might have contributed to incubating eggs was not determined. When one adult entered the tunnel, the other often remained near the entrance. Members of the pair maintained contact through vocalizations (both the regular song and contact notes) around their nest. We have also observed an adult excavating a tunnel in a stream bank near Tobuna.

**Buff-fronted Foliage-gleaner (*Philydor rufum*).** Much confusion surrounds nest placement by *P. rufum*. Fiebrig (1921) attributed a pendant stick nest to *P. rufum*, but that was almost certainly an error (Vaurie 1980, Narosky et al. 1983, Bodrati and Salvador 2015). *P. rufum* is generally assumed to nest in both burrows and tree cavities (Hilty 2003, van der Hoek et al. 2017, Remsen 2017), but all records of nesting in tree cavities can be traced to two (Narosky et al. 1983) or possibly four (Vaurie 1980) nests that C. C. Olrog claimed to have found in 1949.

Although abundant in Parque Provincial Cruce Caballero (Bodrati et al. 2010), we have

Table 1. Number of nests found in underground burrows, tree cavities, or other sites, for two clades within Philydorini (Furnariidae).

| Species  | Underground burrow | Tree or bamboo cavity | Other site | Excav. | Parental care | Source   |
|--|--------------------|-----------------------|------------|--------|---------------|--|
| <b><i>Automolus-Thripadectes-Clibanornis</i> clade</b> |                    |                       |            |        |               |  |
| <i>Automolus leucophthalmus</i>                        | 2                  | -                     | -          | -      | -             | Marini et al. (2007)   |
| <i>Automolus leucophthalmus</i>                        | 1                  | -                     | -          | -      | -             | Euler (1900)   |
| <i>Automolus leucophthalmus</i>                        | 1                  | -                     | -          | -      | [B]           | Magalhães<br>in Novaes (1961)  |
| <i>Automolus leucophthalmus</i>                        | ns                 | -                     | -          | -      | -             | Sick (1993)  |
| <i>Automolus leucophthalmus</i>                        | 2                  | -                     | -          | E      | [B]           | This study   |
| <i>Automolus paraensis</i>                             | > 1                | -                     | -          | -      | -             | Sneathlage (1935)  |
| <i>Automolus paraensis</i>                             | 4                  | -                     | -          | -      | -             | Pinto (1953)   |
| <i>Automolus infuscatus</i>                            | 1                  | -                     | -          | -      | -             | Londoño (2014)   |
| <i>Automolus ochrolaemus</i>                           | 11                 | -                     | -          | E      | B             | Skutch 1952, 1969)   |
| <i>Automolus ochrolaemus</i>                           | 1                  | -                     | -          | -      | -             | Londoño (2014)   |
| <i>Automolus subulatus</i>                             | 1                  | -                     | -          | -      | -             | Wheelwright in<br>Hilty (2003)   |
| <i>Automolus melanopezus</i>                           | 1                  | -                     | -          | -      | -             | Londoño (2014)   |
| <i>Automolus rufipileatus</i>                          | 1                  | -                     | -          | -      | -             | Londoño (2014)   |
| <i>Thripadectes rufobrunneus</i>                       | 1                  | -                     | -          | -      | -             | Worth (1939)   |
| <i>Thripadectes rufobrunneus</i>                       | 1                  | -                     | -          | -      | B             | Hartman (1957)   |
| <i>Thripadectes rufobrunneus</i>                       | 1                  | -                     | -          | -      | B             | Skutch (1969)  |
| <i>Thripadectes rufobrunneus</i>                       | > 3                | -                     | -          | E      | -             | Stiles, Marín,<br>Schmitt,<br>and Catchick in<br>Zyskowski and<br>Greeney (2010) |
| <i>Thripadectes melanorhynchus</i>                     | 2                  | -                     | -          | -      | B             | Zyskowski and<br>Greeney (2010)  |
| <i>Thripadectes melanorhynchus</i>                     | 1                  | -                     | -          | -      | -             | Kiff et al. (1989)   |
| <i>Thripadectes virgaticeps</i>                        | 1                  | -                     | -          | -      | B             | Zyskowski and<br>Greeney (2010)  |
| <i>Thripadectes virgaticeps</i>                        | 1                  | -                     | -          | -      | -             | Marín and<br>Carrion B. (1994)   |
| <i>Thripadectes virgaticeps</i>                        | 5                  | -                     | -          | -      | -             | Hilty and<br>Brown (1986)  |
| <i>Thripadectes holostictus</i>                        | 2                  | -                     | -          | E      | -             | Greeney and Nunnery<br>(2006), Zyskowski<br>and Greeney (2010)                   |
| <i>Thripadectes holostictus</i>                        | 4                  | -                     | -          | -      | [B]           | Smith and<br>Londoño (2013)  |
| <i>Thripadectes flammulatus</i>                        | 2                  | -                     | -          | -      | B             | Zyskowski and<br>Greeney (2010)  |
| <i>Thripadectes flammulatus</i>                        | 1                  | -                     | -          | -      | B             | Botero-Delgadillo<br>and Guayara (2009)  |
| <i>Thripadectes scrutator</i>                          | 2                  | -                     | -          | -      | -             | Whitney in<br>Zyskowski and<br>Greeney (2010)                                    |
| <i>Thripadectes ignobilis</i>                          | 3                  | -                     | -          | E      | B             | Strewe (2001)  |
| <i>Clibanornis erythrocephalus</i>                     | 17                 | -                     | -          | E      | B             | Miller et al. (2012)   |
| <i>Clibanornis rubiginosus</i>                         | 1                  | -                     | -          | -      | -             | Rowley (1966)  |
| <i>Clibanornis rubiginosus</i>                         | 1                  | -                     | -          | -      | -             | Londoño (2014)   |
| <i>Clibanornis rubiginosus</i>                         | 1                  | -                     | -          | -      | -             | Marin A. and<br>Carrion B. (1991)  |

Table 1. Continued

| Species   | Underground burrow | Tree or bamboo cavity | Other site     | Excav.         | Parental care  | Source  |
|---|--------------------|-----------------------|----------------|----------------|----------------|---|
| <i>Clibanornis rubiginosus</i>                          | ns                 | -                     | -              | -              | -              | Gómez de Silva G. et al. (1999)                   |
| <i>Clibanornis rectirostris</i>                         | 20                 | -                     | -              | E              | B              | Faria et al. (2008)                               |
| <i>Clibanornis rectirostris</i>                         | ns                 | -                     | -              | E              | -              | Sick (1993)                                       |
| <i>Philydor rufum</i>                                   | 24                 | -                     | -              | E              | -              | This study  |
| <i>Philydor rufum</i>                                   | 1                  | -                     | -              | -              | B              | Maillard Z. et al. (2006)                         |
| <i>Philydor rufum</i>                                   | 1                  | -                     | -              | -              | B              | Hilty and Brown (1986)                            |
| <i>Philydor rufum</i>                                   | 2                  | -                     | -              | -              | -              | Kirwan (2009)                                     |
| <i>Philydor rufum</i>                                   | 1                  | -                     | -              | -              | -              | Marini et al. (2007)                              |
| <i>Philydor rufum</i>                                   | 1                  | -                     | -              | -              | -              | Marinkelle in Vaurie (1980)                       |
| <i>Philydor rufum</i>                                   | 1                  | -                     | -              | -              | -              | C. A. Ferreyra <i>in litt.</i>                    |
| <i>Philydor rufum</i>                                   | 1                  | -                     | -              | -              | -              | B. Wilcox and K. Murphy <i>in litt.</i>           |
| <i>Philydor rufum</i>                                   | ns                 | -                     | -              | -              | -              | Willis and Oniki (2002)                           |
| <i>Philydor rufum</i>                                   | ns                 | -                     | ns             | -              | -              | Schäfer and Schwartz in Vaurie (1980)             |
| <i>Philydor rufum</i>                                   | ns                 | -                     | ns             | -              | -              | Sick (1993)                                       |
| <i>Philydor rufum</i>                                   | ns <sup>a</sup>    | -                     | -              | E <sup>a</sup> | B <sup>a</sup> | Ruschi (1981)                                     |
| <i>Philydor rufum</i>                                   | -                  | 2 or 4                | -              | -              | -              | Olrog in Vaurie (1980), /in Narosky et al. (1983) |
| <i>Philydor rufum</i>                                   | -                  | -                     | 1 <sup>b</sup> | -              | -              | Fiebrig (1921)                                    |
| <b><i>Syndactyla-Anabacerthia-Anabazenops</i> clade</b> |                    |                       |                |                |                |   |
| <i>Syndactyla subalaris</i>                             | -                  | 1                     | -              | N              | -              | Greeney (2012)                                    |
| <i>Syndactyla rufosuperciliata</i>                      | -                  | 18                    | -              | N              | B              | Cockle et al. (2012), this study                  |
| <i>Syndactyla rufosuperciliata</i>                      | -                  | 1                     | -              | -              | B              | Belton (1984)                                     |
| <i>Syndactyla rufosuperciliata</i>                      | -                  | 11                    | -              | N              | B              | Auer et al. (2007)                                |
| <i>Syndactyla rufosuperciliata</i>                      | -                  | 1                     | -              | -              | B              | de la Peña (2005)                                 |
| <i>Syndactyla rufosuperciliata</i>                      | -                  | 1                     | -              | -              | -              | Calo and Calo in Remsen (2003)                    |
| <i>Syndactyla rufosuperciliata</i>                      | -                  | 1                     | -              | -              | -              | Endrigo in Remsen (2003)                          |
| <i>Syndactyla rufosuperciliata</i>                      | -                  | ns                    | -              | N              | -              | Venturi in Hartert and Venturi (1909)             |
| <i>Syndactyla rufosuperciliata</i>                      | -                  | ns                    | -              | -              | -              | Sick (1993)                                       |
| <i>Syndactyla rufosuperciliata</i>                      | -                  | -                     | 2              | N              | -              | Di Giacomo and López Lanús (1998)                 |
| <i>Syndactyla rufosuperciliata</i>                      | ns                 | ns                    | ns             | -              | -              | Lillo 1902  |
| <i>Anabacerthia variegaticeps</i>                       | -                  | 1                     | -              | N              | -              | Wagner (1980)                                     |
| <i>Anabacerthia lichtensteini</i>                       | -                  | 1                     | -              | N              | U              | This study  |
| <i>Anabacerthia lichtensteini</i>                       | -                  | 1                     | -              | -              | -              | Saibene (1995)                                    |
| <i>Anabacerthia lichtensteini</i>                       | -                  | 1                     | -              | -              | -              | Alonso in Remsen (2003)                           |
| <i>Anabacerthia striaticollis</i>                       | -                  | 1                     | -              | -              | -              | Schäfer in Vaurie (1980)                          |
| <i>Anabacerthia striaticollis</i>                       | -                  | 1                     | -              | -              | -              | T. McNish M./VIREO <sup>c</sup>                   |
| <i>Philydor atricapillus</i>                            | -                  | 1                     | -              | N              | -              | Mitsuo Tanaka et al. (2016)                       |

Table 1. Continued

| Species                         | Underground burrow | Tree or bamboo cavity | Other site | Excav.         | Parental care  | Source                           |
|---------------------------------|--------------------|-----------------------|------------|----------------|----------------|----------------------------------|
| <i>Philydor atricapillus</i>    | ns <sup>a</sup>    | -                     | -          | E <sup>a</sup> | B <sup>a</sup> | Ruschi (1981)                    |
| <i>Philydor atricapillus</i>    | ns                 | -                     | -          | -              | -              | Sick (1993)                      |
| <i>Heliobletus contaminatus</i> | -                  | 1                     | -          | N              | U              | Cockle et al. (2012), this study |
| <i>Philydor erythrocerum</i>    | -                  | 1                     | -          | -              | [U]            | Tostain et al. (1992)            |
| <i>Philydor erythrocerum</i>    | 1                  | -                     | -          | -              | -              | Londoño (2014)                   |
| <i>Anabazenops dorsalis</i>     | -                  | 1                     | -          | N              | -              | Kratter (1994)                   |
| <i>Anabazenops fuscus</i>       | -                  | ns                    | -          | -              | -              | Sick (1993)                      |

“Excav.” indicates whether nest sites are excavated by the birds themselves (E) or formed by other species/processes (N). Parental care is categorized as either uniparental (U) or biparental (B) [square brackets indicate suspected, but not confirmed]. ns = number of nests not specified; - indicates no information in the given sources. Species order follows Derryberry et al. (2011; Fig. 1).

<sup>a</sup>Species identification doubted by Zyskowski and Prum 1999.

<sup>b</sup>Species identification doubted by Vaurie 1980, Narosky et al. 1983, and Bodrati and Salvador 2015.

<sup>c</sup>Academy of Natural Sciences of Drexel University, VIREO m42/1/092-094 <vireo.ansp.org>(27 March 2017).

never found *P. rufum* nesting in a tree cavity. Instead, we found 24 nests of *P. rufum* in underground burrows. Twenty-two were in the banks of small streams and springs (nine at Parque Provincial Cruce Caballero, eight at Área Experimental Guaraní, three at Parque Provincial Caá Yará, and two at Reserva Privada Yaguaroundi), one was in an abandoned well at Parque Provincial de la Araucaria, and one was in a small alluvial bank (1.6 m high) 15 m from the Río Iguazú at Parque Nacional Iguazú. All were in forest habitat. We often observed two adults vocalizing (regular song and metallic contact notes) near nest entrances. Burrows were ~1 m deep and contained cup nests apparently constructed of rachises, small twigs, and sometimes moss. We observed adults excavating five more underground tunnels in earth banks. C. A. Ferreyra (*in litt.*) also saw an adult feeding nestlings in a tunnel in an earth wall formed by the roots of a fallen tree at Parque Provincial Cruce Caballero on 22 October 2015. B. Wilcox and K. Murphy (*in litt.*) photographed an adult carrying moss into a tunnel in a roadside embankment at Reserva Ecológica de Guapiacu (22°27'S 42°46'W; Rio de Janeiro, Brazil) on 11 September 2017. Given the proximity of our study sites to those of Olrog (in Narosky et al. 1983), our extensive search and monitoring of tree cavities (Cockle et al.

2015), and evidence that all other known nests of *P. rufum* were located in underground burrows (or, occasionally, human-made structures; Table 1), we suspect that the nests in tree cavities reported by Olrog belonged to some other species of furnariid.

**Buff-browed Foliage-gleaner (*Syndactyla rufosuperciliata*).** The breeding biology of the Andean subspecies *S. rufosuperciliata oleaginea* has been studied (Di Giacomo and López Lanús 1998, Auer et al. 2007), but little is known about the subspecies (nominate *rufosuperciliata* and *acrita*) found in the Atlantic Forest and adjacent regions in southeastern Brazil, Uruguay, northeastern Argentina, and eastern Paraguay. Lillo (1902) stated that *S. rufosuperciliata* nested in banks, trees, and walls, but all nests that have been described have either been in tree cavities or human-made structures (Table 1). We found 17 nests in 12 tree cavities at Parque Provincial Cruce Caballero, and two nests in one tree cavity at Tobuna. Cavities averaged  $15.5 \pm 1.8$  (SE) m above ground ( $N = 13$ ),  $24 \pm 3$  cm deep ( $N = 11$ ), and  $4.0 \pm 0.5$  cm in entrance diameter ( $N = 11$ ). All nests were messy cups of crisscrossed rachises that often filled cavity bottoms ( $N = 10$ ). One nest included a little moss, another had an inflorescence, and one appeared to contain a few *Marasmius* rhizomes. Mean clutch size was  $3.3 \pm 0.3$  ( $N = 8$ ).

Two adults attended nests during both incubation ( $N = 5$ ) and nestling ( $N = 6$ ) periods. They frequently looked out of the nest cavity, clung beside the cavity, and maintained contact through loud vocalizations (song and contact notes). During incubation, nest attentiveness was 97% ( $N = 3$  nests, 3.35 h of observation). Nestlings were naked at hatching, had pin feathers by days 8–9, and appeared well-feathered by days 14–15. They were fed at an average rate of  $4.4 \pm 0.7$  visits/h ( $N = 7$  observations at 4 nests, total 9.9 h). Their diet included larvae ( $N = 6$ ), a cricket (Orthoptera), and a cockroach (Blattaria). We determined nest fate at 11 nests; all were successful, with an average of  $2.5 \pm 0.4$  fledglings/nest.

**Ochre-breasted Foliage-gleaner (*Anabacerthia lichtensteini*).** The literature contains two brief mentions of nests of *A. lichtensteini*. Saibene (1995) observed an adult carrying material into a cavity ~15 m high and near the end of a dead branch in Parque Nacional Iguazú, Argentina, and J. Alonso (in Remsen 2003:225) photographed an adult carrying an insect to a tree cavity, also in Parque Nacional Iguazú.

*Anabacerthia lichtensteini* is a common resident at Parque Provincial Cruce Caballero (Bodrati et al. 2010), but we found only one nest in a decade of field work. The nest was discovered on 5 October 2015 when an adult was observed entering a cavity in a dead branch of a living tree (*Parapipadenia rigida*, Fabaceae; Fig. 1). The cavity was 21 m high (Fig. 2), 56 cm long, and the entrance measured 5 cm  $\times$  6 cm. The nest was 39 cm from the entrance (Fig. 2), and consisted of a cup-like base of crisscrossed leaf rachises lined with a mat of *Marasmius* spp. rhizomorphs. The three nestlings had down on their heads and backs, and pin feathers visible beneath their pink skin on 6 October. They had open pins on their wings and unopened pins on their backs on 14 October, and were fully feathered, except for tails, by 19 October.

Only one adult was observed at the nest. It always flew straight into and out of the cavity entrance across at least 30 m, and never paused or vocalized near the cavity. No other adult ever approached the nest, contrasting strongly with our observations of *Automolus leucophthalmus*, *P. rufum*, and *S. rufosuperciliata*. The adult made seven trips to

the cavity in 80 min of observation on 6 October, eight trips in 90 min on 10 October, and 14 trips in 130 min on 23 October. Food items of nestlings included two adult Orthoptera and one Lepidopteran.

**Sharp-billed Treehunter (*Heliobletus contaminatus*).** The only breeding information known for *H. contaminatus* is a brief mention of a nest in a non-excavated cavity in a living *Luehea divaricata* (Tiliaceae; Cockle et al. 2012). The cavity was 7.6 m above ground in a slim trunk near a small creek in primary forest at Parque Provincial Cruce Caballero. It measured 26 cm deep and 4.6  $\times$  4.9 cm in entrance diameter. On 1 November, the nest contained two white eggs on a loose cup of dry plant fibers, perhaps grass or rachises, with a few *Marasmius* rhizomes and moss. The first egg hatched on 20 November. Nestlings had little gray down, red mouth linings, and ivory-colored bills on day 0, pins under the skin by day 7, emerging pin feathers and open eyes by day 10, and open pin feathers (except on head and tail) by day 16 (when we left the site).

Only one adult, identified by missing tail feathers that grew back during the nesting period (Fig. 1), attended the nest. It was quiet around the nest, sometimes emitting short bursts of “tk” contact notes, but never songs. We sometimes heard singing by a second adult 40–100 m distant, but the two individuals did not appear to interact in any way. During incubation, overall nest attentiveness was 72%. On-bouts averaged  $32 \pm 2$  min ( $N = 32$ ) and off-bouts  $12 \pm 2$  min ( $N = 36$ ). During the nestling period, nest attentiveness by the adult was 48% on days 0–2, 37% on days 5–7, 26% on day 8, and 3% on day 11. Nestlings were fed at a relatively constant rate of  $3.6 \pm 0.3$  trips/h (days 0–11), and their diet included lepidopteran larvae ( $N = 14$ ) and an adult cricket (Orthoptera).

## DISCUSSION

Our results suggest that nest placement, either in underground burrows or tree cavities, is congruent with molecularly derived hypotheses about relationships within Philydorini. We propose that the two main clades within Philydorini can be characterized, respectively, as burrow excavators (*Automolus-Thripadectes-Clibanornis*) and secondary tree-





Fig. 1. Nesting of (A) Ochre-breasted Foliage-gleaner (*Anabacerthia lichtensteini*) and (B–D) Sharp-billed Treehunter (*Heliobletus contaminatus*) at Parque Provincial Cruce Caballero, Misiones, Argentina. (A) Adult *A. lichtensteini* flies from its nest cavity on 7 October 2015 (Photographed by Carlos A. Alderete). (B) Adult *H. contaminatus* carries nesting material on 3 November 2010 (Photographed by K. L. Cockle). (C) Adult *H. contaminatus* looks from its nest cavity on 3 November 2010 (Photographed by K. L. Cockle). (D) Video-monitor view of newly hatched nestling and unhatched egg of *H. contaminatus* on 20 November 2010 (Photographed by José M. Segovia).

cavity nesters (*Syndactyla-Anabacerthia-Anabazenops*). Although we cannot discard the hypothesis that some members of Philydorini exhibit plasticity in nest placement, there is currently no conclusive evidence that either *P. rufum* or any other member of the first clade nests in tree cavities or that *P. atricapillus*, *S. rufosuperciliata*, or any member of the second clade nests in burrows. Although tree-cavity nesting can sometimes arise in burrow-nesting lineages of Furnariidae, such as *Cinclodes* (Ojeda 2016), current evidence suggests that the nests of *Cichlocolaptes* and *Megaxenops* – which remain undescribed – will eventually be found in existing tree or bamboo cavities, like the nests of their relatives in *Anabacerthia*, *Heliobletus*, *Syndactyla*, and *Anabazenops*.

Our observations of nesting in *A. lichtensteini* correspond closely with the little

information that has been published about nesting in this species. The nest site – a tree cavity near the end of a dead branch – was similar to the site described by Saibene (1995). Although nesting material is thought to be phylogenetically informative in Furnariidae (Zyskowski and Prum 1999), the nesting material we found (a cup of crisscrossed rachises lined with *Marasmius*) differed from the only other nest described for the genus *Anabacerthia* (57 cm of moss mixed with plant fibers and stems; Wagner 1980), and was similar, instead, to nests of *S. rufosuperciliata* and *H. contaminatus*.

Although the *Automolus-Thripadectes-Clibaornis* clade appears to be characterized by biparental care, our results suggest that the *Syndactyla-Anabacerthia-Anabazenops* clade includes at least one species with biparental care and others with uniparental care.

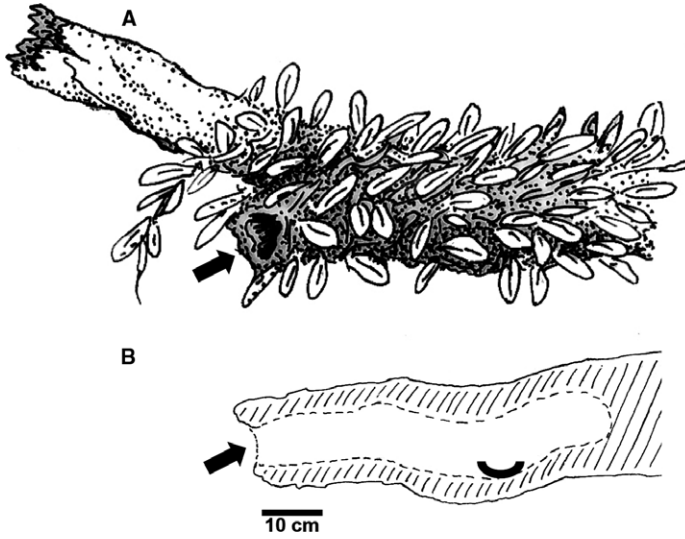


Fig. 2. Tree cavity used for nesting by an Ochre-breasted Foliage-gleaner (*Anabacerthia lichtensteini*) in Parque Provincial Cruce Caballero, Misiones, Argentina. (A) External characteristics of the cavity, with epiphytic ferns (*Microgramma* spp.) covering the branch. (B) Cut-away section showing internal cavity characteristics. Arrows indicate cavity entrance and saucer indicates placement of the nest in the cavity. Illustrator: Luis G. Pagano.

Although biparental care is the norm for Furnariidae (Remsen 2003), uniparental care has arisen at least twice in Furnariinae (*Pseudocolaptes*, Skutch 1969, *Anabacerthia* and *Heliobletus*, Tostain et al. 1992, this study) and at least twice in Dendrocolaptinae (*Xiphorhynchus*, Skutch 1996, Vega Rivera et al. 2003, *Dendrocincla* and *Sittasomus*, Willis 1972, Cockburn 2006, Bodrati et al. 2012). There are no obvious differences in nestling diets of furnariids with uniparental care and those with biparental care (Bodrati et al. 2012, this study). Neither feeding rates nor the rate of nestling development appeared dramatically lower for uniparental *H. contaminatus* and *A. lichtensteini* than for biparental *S. rufosuperciliata*, consistent with Skutch's (1949) observations of similar nestling periods among tyrant flycatchers with uniparental and biparental care. However, our data are very sparse and we were unable to determine the duration of nestling periods. Skutch (1969) reported that the uniparental Buffy Tuftedcheek (*Pseudocolaptes laurencii*) has an exceptionally long nestling period (29 d), apparently the longest known for any member of Furnariinae (Remsen 2003). There is currently insufficient

evidence to determine if uniparental care in furnariids is generally associated with slower nestling growth rates.

We propose that, in Furnariidae, parental care systems are related to nest complexity and concealment. At one end of the spectrum, cooperative breeding occurs among the builders of elaborate mud or stick nests (many of which also build extra "dummy" nests; e.g., *Furnarius*, *Phacellodomus*, *Anumbius*, *Pseudo-seisura*, *Coryphistera*, and *Acrobatornis*; Fraga 1979, Nores and Nores 1994, Whitney et al. 1996, Rodrigues and Carrara 2004, Areta and Bodrati 2007). These nests are often large and exposed. To maintain social bonds and organize territorial defense, adults perform frequent, loud duets and displays in and on their nests, and nestlings vocalize from within the nest, even duetting with adults (Fraga 1980, Sick 1993, Nores and Nores 1994, Pacheco et al. 1996, Zimmer and Whittaker 2000). At the other end of the spectrum, uniparental care appears to have arisen only among forest-dwelling tree-cavity nesters (Skutch 1969, 1996, Willis 1972, Tostain et al. 1992, Vega Rivera et al. 2003, Bodrati et al. 2012, this study). In contrast to their cooperative-breeding and biparental relatives, these species

exhibit extreme stealth around nests; the adult usually flies directly into and out of the cavity without vocalizing, and nestlings are silent (Skutch 1969, Willis 1972, Bodrati et al. 2012, this study). Almost nothing is known about pair bonds and territoriality in these species. Like most passerines with female-only care, *Dendrocincla* are generally considered not to form pair bonds (Skutch 1969, Willis 1972, Willis and Oniki 1995). Males of *Heliobletus* and *Sittasomus* appear to remain on a territory, vocalizing, without revealing nest locations (Bodrati et al. 2012, this study), but their mating systems are unknown. Expanding on Snow's (1976) hypothesis that nest concealment is linked to uniparental care in frugivorous cotingas (Cotingidae), we propose that by eliminating vocal interactions around the nest, uniparental species of Furnariidae can adopt a strategy of nest concealment (vs. active defense) against predators. The time-consuming construction of elaborate nests may promote (and be facilitated by) the evolution of helping behaviors. Nesting in a tree cavity may reduce the value, and increase the cost, of male help.

Our review suggests that if nests are well-studied and confirmed, placement of nests in a tree cavity versus burrow can be phylogenetically informative in Furnariidae. We strongly encourage researchers to study, in detail, new nests of *Philydorini*, which are necessary to explore the links between nest placement and parental care.

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