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NESTING AND SOCIAL ROOSTING OF THE OCHRE-COLLARED PICULET (*PICUMNUS TEMMINCKII*) AND WHITE-BARRED PICULET (*PICUMNUS CIRRATUS*), AND IMPLICATIONS FOR THE EVOLUTION OF WOODPECKER (PICIDAE) BREEDING BIOLOGY

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Resumen. – Nidificación y pernocte social del Carpinterito Cuello Canela (*Picumnus temminckii*) y Carpinterito Común (*Picumnus cirratus*), e implicaciones para la evolución de la biología reproductiva de los pájaros carpinteros (Picidae). – Para entender la evolución de las estrategias reproductivas y del comportamiento social en los pájaros carpinteros (Picidae), es útil comparar la biología reproductiva entre las dos mayores subfamilias: Picinae (verdaderos pájaros carpinteros) y Picumninae (carpinteritos). Picumninae incluye cuatro especies del viejo mundo (*Sasia*, *Verreauxia*, y *Picumnus* spp.) y una radiación reciente de 25 especies de *Picumnus* en el Neotrópico; sin embargo, es limitada la información sobre su biología reproductiva. Estudiamos cuatro nidos y un pernocte de Carpinterito Cuello Canela (*Picumnus temminckii*) en la Selva Atlántica y ocho nidos de Carpinterito Común (*Picumnus cirratus*) en la región Chaqueña, de Argentina, y revisamos la literatura publicada sobre otras especies de *Picumnus*. Las cavidades fueron excavadas en ramas y troncos secos de árboles. El diámetro

de su entrada era $2,2 \pm 0,2$ cm (media \pm EE) para el Carpinterito Cuello Canela y $2,5 \pm 0,1$ cm para el Carpinterito Común. En ambas especies, macho y hembra excavaron las cavidades, incubaron los huevos, alimentaron los pichones y mantuvieron la cavidad limpia de heces. En el Carpinterito Cuello Canela, el período de incubación duró 13 días, los turnos de incubación duraron 42 ± 4 min (\pm EE) para hembras y 48 ± 7 min para machos, y la atención en el nido fue casi 100% durante la incubación y los primeros 10 días después del nacimiento de los pichones. Los pichones de Carpinterito Cuello Canela nacieron sin plumas; sus ojos y los canutos en las alas abrieron el día 13, y volaron los días 26 y 27. Los pichones de ambas especies fueron alimentados con larvas de hormigas y otras presas pequeñas. En el Carpinterito Cuello Canela, la tasa de entrega de alimentos (especialmente por la hembra) aumentó con la edad de los pichones. Las hembras extrajeron el 71% de los sacos fecales y los machos 29%. Los volantes de *Picumnus* tienen corona oscura y se parecen a las hembras adultas, lo que los diferencia de *Sasia*, *Verreauxia*, y la mayoría de los Picinae. A diferencia de los Picinae, los padres de *Picumnus* duermen juntos en su cavidad nido antes de la puesta, a lo largo de la anidación, y (acompañados de sus crías) después de que vuelan los pichones. También pernoctan en parejas o grupos cuando no están criando. Si los carpinteritos del viejo mundo también pernoctan en grupos, el rasgo puede reflejar una condición ancestral de los pájaros carpinteros.

Abstract. – To understand the evolution of reproductive strategies and social behavior in woodpeckers (Picidae), it is useful to compare breeding biology between the two largest subfamilies: Picinae (true woodpeckers) and Picumninae (piculets). The piculets include four species in the Old World (*Sasia*, *Verreauxia*, and *Picumnus* spp.) and a recent radiation of 25 *Picumnus* spp. in the Neotropics; however, information about their breeding biology is limited. We studied four nests and one roost of the Ochre-collared Piculet (*Picumnus temminckii*) in the Atlantic Forest of Misiones and eight nests of the White-barred Piculet (*Picumnus cirratus*) in the Chaco region, of Argentina, and reviewed the published literature on other species of *Picumnus*. Cavities were excavated in dead branches and tree trunks. Entrance diameters were 2.2 ± 0.2 cm (mean \pm SE) for the Ochre-collared Piculet and 2.5 ± 0.1 cm for the White-barred Piculet. In both species, both parents excavated cavities, incubated eggs, fed nestlings, and maintained the cavity clean of feces. In the Ochre-collared Piculet, incubation lasted 13 days, on-bouts were 42 ± 4 (\pm SE) min for females and 48 ± 7 min for males, and nest attentiveness was nearly 100% during incubation and the first 10 days after hatching. Nestling Ochre-collared Piculets hatched without feathers, their eyes and pin feathers opened on day 13, and they fledged on days 26 and 27. Nestlings of both species were fed ant larvae and other small prey. In Ochre-collared Piculets, the rate of food delivery (especially by the female) increased with nestling age. Females removed 71% and males 29% of fecal sacs. Fledgling *Picumnus* have dark crowns and look like adult females, which is different from *Sasia*, *Verreauxia*, and most Picinae. Unlike Picinae, *Picumnus* parents roost together in their nest cavity before laying, throughout nesting, and (accompanied by their offspring) after fledging. They also roost in pairs or groups when not breeding. If Old World piculets also roost socially, this trait may reflect an ancestral condition of the woodpeckers.

Key words: Argentina, incubation, nest, Ochre-collared Piculet, parental care, *Picumnus temminckii*, *Picumnus cirratus*, social roosting, White-barred Piculet, woodpecker.

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INTRODUCTION

The family Picidae (woodpeckers and their allies) has a complex evolutionary history and includes a fascinating diversity of morphological, life history, and behavioral traits (Spring 1965, Winkler & Christie 2002, Manegold & Töpfer 2013). Picidae likely arose in the Old

World, and includes (in order of divergence): the basal Jynginae (wrynecks), Picumninae (piculets), *Nesocittes micromegas* (the monotypic Antillean ‘Piculet’) and Picinae (true woodpeckers; Webb & Moore 2005, Benz *et al.* 2006, Fuchs *et al.* 2006). Picumninae is the second largest subfamily (after Picinae), with at least 29 species of tiny woodpeckers in

three genera: *Sasia*, *Verreauxia*, and *Picumnus* (Benz *et al.* 2006, Fuchs *et al.* 2006, Rêgo *et al.* 2014). *Sasia* includes two species in Asia, and *Verreauxia* one species in Africa (Fuchs *et al.* 2006). *Picumnus* is unusual – perhaps unique – among bird genera, in having a pantropical distribution, with 1 species in Asia and at least 25 in the Neotropics (Benz *et al.* 2006, Fuchs *et al.* 2006, Rêgo *et al.* 2014). Molecular evidence suggests that the split between *Picumnus* and *Sasia* + *Verreauxia* may have occurred around the same time (either before or after) the split between Picinae and Picumninae, and that the most basal of the *Picumnus* is the Asian *P. innominatus* (Benz *et al.* 2006, Fuchs *et al.* 2006). Thus, all three genera in the Picumninae are thought to have originated in the Old World, with *Picumnus* later radiating in the Neotropics (Fuchs *et al.* 2006). Taking into consideration the phylogeny, morphology, and natural history of extant woodpeckers and allies, several suppositions can be made about the last ancestors of modern woodpeckers and piculets. Likely, these ancestors (1) were small and strictly arboreal, (2) lacked stiffened rectrices, (3) did not climb trees vertically, (4) excavated nesting cavities, and (5) carried food to nestlings in their bills (as opposed to regurgitating; Benz *et al.* 2006, Manegold & Töpfer 2013). In all of these traits, they would have resembled modern *Picumnus*.

Information about traits shared within and between subfamilies can help illuminate woodpecker evolution and ecology. While sharing the trait of cavity-excavation, the Picinae have diverged widely in mating and social systems, as well as nestling diets and reproductive traits (Manegold & Töpfer 2013). In comparison, little is known about the life history and social systems of Picumninae. Nesting details have been described for 8 of the 25 species of Neotropical piculets: Lafresnaye's Piculet (*Picumnus lafresnayi*; Skutch 1948), Arrowhead Piculet (*Picumnus minutissimus*;

Haverschmidt 1951), White-barred Piculet (*Picumnus cirratus*; Hartert & Venturi 1909, Pergolani 1940, Giraudo *et al.* 1993, de la Peña 2005), White-wedged Piculet (*Picumnus albosquamatus*; Gussoni *et al.* 2009), Ochraceous Piculet (*Picumnus limae*; da Silva *et al.* 2012), Mottled Piculet (*Picumnus nebulosus*; Pichorim 2006), Olivaceous Piculet (*Picumnus olivaceus*; Skutch 1948, 1969, 1998), and Grayish Piculet (*Picumnus granadensis*; Sedano *et al.* 2008). Even for these species, key elements of nesting biology are often missing. For example, incubation period has been reported for only two species of Neotropical piculets (13–14 days for Olivaceous Piculet and 17 days for Mottled Piculet; Skutch 1948, 1969; Pichorim 2006). Basic descriptions of nesting, including male and female contributions to parental care, and length of incubation and nestling periods, are critical to understanding the life history evolution and social behavior of piculets and other woodpeckers.

The Ochre-collared Piculet (*Picumnus temminckii*) is endemic to the Atlantic Forest of Brazil, Paraguay and Argentina, and its breeding biology is poorly understood (Winkler & Christie 2002). A common inhabitant of primary forest, bamboo thickets, secondary forest, and edges, it forages primarily on thin dead branches, stalks, and bamboo in the understory and midstory (Partridge *in* Chebez 1995, Winkler & Christie 2002, Bodrati *et al.* 2010, pers. observ.). In winter, Ochre-collared Piculets are frequently found in mixed-species flocks (Partridge *in* Chebez 1995, pers. observ.). Three nests have been mentioned briefly, all from Brazil. First, Ihering (1900) described two greenish white eggs measuring 15 x 12 mm, in a circular tree cavity, 2.3 cm in diameter and 13 cm in depth, at Iguape, state of São Paulo. Second, on 22 October 2007 a male was observed taking food to a tree hole about 2.5 m above the ground in a small grove of trees at Ilha Comprida, state of São Paulo (Kirwan 2009). Third, on 26 November

2011, two adults were observed taking food to nestlings in a hole about 2.5 m high in a dead tree at the edge of a forest fragment at Campo Bom, state of Rio Grande do Sul (Mauricio *et al.* 2013). Other details of nesting, such as incubation and nestling periods, nest attentiveness, nestling diet, and division of parental care between the sexes, remain unknown.

The White-barred Piculet is considered as sister species of the Ochre-collared Piculet (Fuchs *et al.* 2006). It has a disjunct distribution including northern Brazil and Guyana, as well as southern Bolivia, Paraguay, southeastern Brazil, and northern and central Argentina (Winkler & Christie 2002). In recent years, its range has expanded in central Argentina and in areas previously covered by Atlantic Forest in Paraguay and Argentina (Bodrati *et al.* 2001, pers. observ.). At least 24 nests of White-barred Piculets have been reported to date, but, with the exception of a nest followed by Giraudo *et al.* (1993), studies were basically limited to descriptions of the nest cavity and clutch of 3–4 eggs (Hartert & Venturi 1909, Pergolani 1940, de la Peña 2005). Both sexes contribute to excavation, nestling feeding and sanitation (Giraudo *et al.* 1993, de la Peña 2005). However, many aspects of White-barred Piculet reproduction remain uncertain. For example, nest attendance has not been studied, and it is not known which parent is responsible for night care.

Here, we present new information about the breeding and roosting ecology of the Ochre-collared Piculet, including details of nest construction, incubation and nestling period, parental care, and family life after fledging, from four nests and one roost in the Atlantic Forest of Argentina. For comparative purposes, we also present unpublished details of breeding and roosting ecology of the White-barred Piculet from eight nests in the Chaco of Argentina. Our objective was not to

provide a full account of White-barred Piculet nesting, but to enhance comparisons with the Ochre-collared and other piculets. Finally, we provide a preliminary comparison of reproductive traits within and between the two major subfamilies of woodpeckers (Picumninae and Picinae) to shed light on their common origins and patterns of divergence.

METHODS

Nests of Ochre-collared Piculets were found as part of a long-term study on the ecology of cavity-nesting birds from 2006 to 2014 (Cockle *et al.* 2012, 2015) at Parque Provincial Cruce Caballero and surroundings, San Pedro, Misiones, Argentina (26°31'S, 54°00'W, 550–600 m a.s.l.). Ochre-collared Piculets are normally common in the study area, but had low abundance from 2006 to 2011 during a mass die-off of *Merostachys clausenii* bamboo (Bodrati *et al.* 2010). Each spring (September–December, the main breeding season for most birds in our study area), we searched for nests in primary and selectively logged forest. The natural forest in this region conforms to Cabrera's (1976) mixed forest with laurel (*Nectandra* spp. and *Ocotea* spp.), guatambú (*Balfourodendron riedelianum*), and Paraná pine (*Araucaria angustifolia*). To find nests, we walked along pre-established trails and roads, a grid of transects spaced every 500 m, and off-trail; listened for sounds of excavation, looked for birds entering or emerging from cavities, listened for nestlings' begging, and monitored cavities that were used in previous years.

Nests of the White-barred Piculet were found between 1997 and 2009 during bird surveys and systematic nest searching at six localities in the Chaco region of Argentina. These included, in the humid Chaco, Parque Nacional Chaco (Sargento Cabral department, province of Chaco, 26°48'S, 59°36'W); and in the dry Chaco, Sachayoj (Alberdi

department, province of Santiago del Estero, 26°41'S, 61°50'W), Río Dulce (Loreto department, province of Santiago del Estero, 28°19'S, 64°14'W), Embalse del Río Tercero (Calamuchita department, province of Córdoba, 32°12'S, 64°23'W), Cruz del Eje (Cruz del Eje department, province of Córdoba, 30°44'S, 64°48'W), and Los Morteros (El Alto department, province of Catamarca, 28°27'S, 65°11'W).

For Ochre-collared Piculets, we monitored the contents of cavities up to a height of 15 m every 1–7 days (every 1–2 days during laying and around the expected hatch date) using a small color video camera. The camera was inside one end of a horizontal tube 1.7 cm in diameter and 25 cm long, and the other end of the tube was mounted on the tip of a 15-m telescoping pole. We used the telescoping pole to measure cavity height (from lower lip of entrance to ground). To estimate the diameter of the cavity entrance we placed the camera inside and compared the width of the entrance to the width of the 1.7 cm diameter tube holding the camera. With a series of accessible cavities, we corroborated that this method provides a reasonable estimate of cavity entrance size (within 0.5 cm for small cavities). We did not have the pole-mounted camera at White-barréd Piculet nests, so we inspected them with a flashlight and mirror, and measured them with a tape, sometimes employing a ladder. We measured tree diameter at breast height (DBH) at nests of Ochre-collared Piculets.

We also watched cavities from the ground using binoculars or a telescope, to study the behavior of adults, older nestlings, and fledglings. During incubation, observations of Ochre-collared Piculet nests totaled 28 h 43 min, evenly spread across incubation days 1–12 (60–141 min of observation/nest/day, except days 3, 8, and 11 when we did not watch nests). During the nestling period, we observed Ochre-collared Piculet nests for a

total of 55 h 59 min during nestling days 0–27. In an effort to witness fledging, we increased our observations from a mean of 39 min/nest/day in the first 21 days after hatching to a mean of 138 min/nest/day in the last 6 days before fledging. Altogether we spent 4 h 17 min at Ochre-collared Piculet roosts. Observations of White-barréd Piculet nests totaled 2.5 h during laying and incubation, and 11.5 h during the late nestling period. A cavity was considered an active nest if it contained eggs or nestlings, or if adults spent long periods inside the cavity or brought food to the cavity. It was considered to be a roost if it was empty during the day but occupied by one or more birds at night.

To test for changes in feeding rate over the course of the nestling period, we used general linear models in the stats package in R version 3.0.3 (R Core Team 2014) to predict feeding rate (visits/hour) as a function of nestling day. The two nests were combined for the analysis, but males and females were modeled separately. A preliminary mixed model analysis, which included nest identity as a random effect, yielded qualitatively similar results. We did not combine the sexes into a single model with an interaction between nestling day and sex, because low parental effort by one partner during a given period is likely to be compensated by increased effort from the other partner (Paredes *et al.* 2005, Wiebe 2010), which would violate the assumption that observations are independent.

RESULTS AND DISCUSSION

We found four nest cavities and one roost cavity used by Ochre-collared Piculets (Table 1, nests 1–4, roost 1), and eight nest cavities used by White-barréd Piculets (Table 1, nests 5–12). We monitored two Ochre-collared Piculet nests (nests 3 and 4) from excavation to fledging. The other two Ochre-collared

TABLE 1. Nests and roosts of Ochre-collared Piculet (*Picumnus temminckii*) and White-barred Piculet (*P. cirratus*) in Argentina. PPCC = Parque Provincial Cruce Caballero, Misiones. Exact nest coordinates are given when known.

ID	Species	Location	Date found	Stage monitored
Nest 1	Ochre-collared	PPCC	11 Nov 2006	Nestling
Nest 2	Ochre-collared	PPCC (26°30'46"S, 53°59'35"W)	21 Sep 2012	Incubation, nestling
Nest 3	Ochre-collared	PPCC (26°31'17"S, 53°59'24"W)	4 Oct 2013	Excavation-fledgling
Nest 4	Ochre-collared	PPCC (26°31'01"S, 53°59'26"W)	4 Aug 2014	Excavation-fledgling
Roost 1	Ochre-collared	PPCC (26°31'18"S, 53°59'00"W)	18 Nov 2014	Excavation-roosting
Nest 5	White-barred	Sachayoj, Santiago del Estero	20 Nov 1997	Nestling
Nest 6	White-barred	Parque Nacional Chaco, Chaco	29 Nov 1998	Nestling
Nest 7	White-barred	Parque Nacional Chaco, Chaco	23 Nov 1999	Nestling
Nest 8	White-barred	Parque Nacional Chaco, Chaco	7 Jan 2000	Nestling
Nest 9	White-barred	Los Morteros, Catamarca	7 Oct 2001	Excavation, fledgling
Nest 10	White-barred	Cruz del Eje, Córdoba	26 Nov 2005	Incubation
Nest 11	White-barred	Río Dulce, Santiago del Estero	6 Dec 2007	Nestling
Nest 12	White-barred	Embalse Río Tercero, Córdoba	15 Dec 2009	Laying-incubation

Piculet nests (nests 1 and 2) were not studied in detail because of difficult access (although we watched nest 2 from the ground during the incubation and nestling periods). We were unable to monitor nests of White-barred Piculets through the entire nesting period because we found them during short field-trips with other objectives. Three of the White-barred Piculet nests (nests 6, 7, and 8) were in two adjacent trees in consecutive years and may have belonged to the same pair.

Timing of reproduction. The earliest day we saw Ochre-collared Piculets excavating their nest cavities was 4 August (nest 4). The earliest day we observed incubation was 21 September (nest 2). Nest 3 contained two eggs on 26 October and a complete clutch of four eggs on 30 October; nest 4 was empty on 5 November and contained a complete clutch of four eggs on 13 November. Assuming that eggs were laid on consecutive days (as in the White-barred Piculet; Hartert & Venturi 1909, this study), laying began on 25 October at nest 3 and between 6 and 10 November at

nest 4. Fledging occurred on 7 December at nest 3 and 22 December at nest 4.

Our earliest observation of cavity excavation by White-barred Piculets was on 7 October at Nest 9. The cavity was checked on 7, 8, and 9 October, but did not contain eggs. On 5 December, two adults and two fledglings roosted in the cavity. The latest nest we observed for White-barred Piculets was nest 8, with well-feathered nestlings on 17 January.

Nest and roost trees. Ochre-collared Piculet cavities were found in primary Atlantic Forest (nests 2, 3, and 4), logged forest (nest 1), and forest edge (roost 1). White-barred Piculet cavities were found in dry forest (nests 10, 11), small forest patches within grassland (nests 6, 7, and 8), a patch of burned forest (nest 5), a garden on a farm (nest 9), and a monospecific stand of chañar (*Geoffroea decorticans*) at the edge of an artificial lake (nest 12). All Ochre-collared and White-barred Piculet cavities were excavated in dead branches or dead trunks, and faced sideways or slightly downward (Table 2, Fig. 1). Excavation of

TABLE 2. Characteristics of nest and roost cavities of Ochre-collared Piculet (*Picumus lemniskii*) and White-barred Piculet (*P. atratus*) from Argentina. DBH = tree diameter at breast height. Missing values indicate measurements not taken. See Table 1 for dates and localities.

ID	Piculet species	Tree species	Tree condition	DBH (m)	Cavity height (m)	Substrate condition	Entrance diameter (m)	Cavity depth (cm)
Nest 1	Ochre-collared	<i>Prunus myrsiflora</i>	living		9	dead		
Nest 2	Ochre-collared	<i>Apuleia leiocarpa</i>	dead	65	20	dead		
Nest 3	Ochre-collared	<i>Cabralia canjerana</i>	living	58	13.3	dead	2.1	
Nest 4	Ochre-collared	<i>Nectandra lanzeolata</i>	living	40	13.7	dead	2.5	
Roost 1	Ochre-collared	indet.	dead	51	13.5	dead	2.0	
Nest 5	White-barred	<i>Aspidosperma quebracho-blanco</i>	dead		2.2	dead	2.5	9.5
Nest 6	White-barred	<i>Erythrina crista-galli</i>	living		2.4	dead	2.5	12
Nest 7	White-barred	<i>Erythrina crista-galli</i>	living		2.2	dead	2.3 x 2.4	
Nest 8	White-barred	<i>Erythrina crista-galli</i>	living		2.7	dead	2.4 x 2.5	
Nest 9	White-barred	<i>Ligustrum lucidum</i>	dead		3.5	dead	2.3	9
Nest 10	White-barred	<i>Acacia</i> sp.	dead		1.6	dead	2.7	11
Nest 11	White-barred	<i>Zeriphus mistol</i>	living		4.5	dead		
Nest 12	White-barred	<i>Geoffroea decorticans</i>	dead		1.2	dead	2.6 x 2.9	12



FIG. 1. Nests of Ochre-collared Piculet (*Picumnus temminckii*) at Parque Provincial Cruce Caballero, Misiones, Argentina. Left: male looking from cavity entrance of nest 2. Top right: female provisioning food at nest 3. Bottom right: male looking from cavity entrance of nest 4. Nest numbers correspond to those in Tables 1 and 2. Note cavity-starts above nests 2 and 3, and a possible cavity below nest 2; birds were never seen to use these excavations. Photos by Martjan Lammertink.

cavities in dead wood is typical for New World piculets (Skutch 1948, 1969, 1998; Haverschmidt 1951, Giraudo *et al.* 1993, de la Peña 2005, Pichorim 2006, Sedano *et al.* 2008, Gussoni *et al.* 2009, da Silva *et al.* 2012, Mauricio *et al.* 2013). White-wedged Piculets have even been found nesting in a loose branch suspended in a vine tangle (Gussoni *et al.* 2009). The African Piculet (*Verreauxia africana*) also apparently only makes cavities in wood stubs; however, the three Asian piculets, Speckled Piculet (*Picumnus innominatus*), White-browed Piculet (*Sasia ochracea*), and Rufous Piculet (*Sasia abnormis*), all make cavities in both wood stubs and bamboo (Winkler

et al. 1995). Although the Ochre-collared Piculet frequently forages on bamboo and although there are large-diameter bamboo stems in its Atlantic Forest habitat, no cavities of this species have yet been found in bamboo.

Ochre-collared Piculets excavated in the same tree species used by many other cavity-nesting birds in our Atlantic Forest study area (Table 2; Cockle *et al.* 2012). Some of these species have relatively hard wood (e.g., *Apuleia leiocarpa*). In contrast, White-barrred Piculets and many other species of *Picumnus* appear to select tree species with soft wood, such as *Heliocarpus*, *Baccharis*, and *Erythrina* spp. (Table

2; Skutch 1948, Haverschmidt 1951, Winkler & Christie 2002, Pichorim 2006; but see de la Peña 2005). Woodpecker species vary in morphology and excavation ability (Spring 1965, Lorenz *et al.* 2015), and a lack of stiffened rectrices has been hypothesized to make cavity-excavation more difficult in the piculets (Manegold & Töpfer 2013). Further studies should examine the relationships among tree species traits (such as wood density and decay-resistance), wood decay by heart-rot fungi, and nest-site selection by piculets and other Neotropical woodpeckers.

Three of the four nesting cavities of Ochre-collared Piculets and four of the eight nesting cavities of White-barred Piculets were within 1 m of a similar-sized excavated cavity or cavity-start (Fig. 1), as described for Ochraceous Piculet, Olivaceous Piculet, and Grayish Piculet (Skutch 1948, Sedano *et al.* 2008, da Silva *et al.* 2012). Cavity-starts are shallow excavations that may be further excavated into a cavity at a later date. They are common in many woodpecker species, and may represent trials to find the best substrate for excavation, or wounding of the wood to create an infection site for wood-decaying fungi (Jackson & Jackson 2004).

Nest and roost cavities. Cavity shape and size are very consistent among the *Picumnus*. We found cavity entrances to be circular or slightly oval, with diameters of 2.2 ± 0.2 cm (mean \pm SE) for Ochre-collared Piculets and 2.5 ± 0.1 cm for White-barred Piculets (Table 2). All other described *Picumnus* cavities were also round, and 2.0–2.5 cm in diameter (Ihering 1900, Hartert & Venturi 1909; Skutch 1948, 1969; Giraudo *et al.* 1993, Winkler & Christie 2002, Pichorim 2006, Sedano *et al.* 2008, Gussoni *et al.* 2009), except those of Ochraceous Piculets which averaged 2.5 ± 0.3 cm and reached 3 cm in diameter (da Silva *et al.* 2012, M. da Silva *in litt.*) and those of White-barred Piculets which can reach 3.7 cm in diameter (Pergolani

1940, de la Peña 2005). With an average body mass of 10 g (range: 9–14 g; Dunning 2008), White-barred Piculets are among the smallest Neotropical piculets whose nests have been studied, so their use of larger cavities is not explained by their body size. Instead, cavities >3 cm in diameter appear to be exceptional, and may have been excavated or enlarged by another woodpecker species. Cavity depth was not measured for Ochre-collared Piculets, but was 10.7 ± 0.6 cm for White-barred Piculets (Table 2), similar to other piculet nests that have been measured (Skutch 1969, Giraudo *et al.* 1993, Pichorim 2006, Sedano *et al.* 2008, Gussoni *et al.* 2009, da Silva *et al.* 2012). The bottom of Ochre-collared and White-barred Piculet nests contained wood chips, as in many woodpeckers and piculets (Winkler & Christie 2002).

Cavity height above ground was 13.9 ± 1.8 m (range: 9–20 m) for Ochre-collared Piculets and 2.5 ± 0.4 m (range: 1.2–4.5 m) for White-barred Piculets. The Ochre-collared Piculet nests and roosts that we found in Argentina were considerably higher than the nests previously reported for Ochre-collared Piculets (two nests at 2.5 m, in Brazil; Kirwan 2009, Mauricio *et al.* 2013) and other *Picumnus* (cf. Table 3). Most published descriptions of *Picumnus* cavities have resulted from chance discoveries, and may be biased toward low nests that are easiest to find and confirm. However, like us (see Methods), Skutch (1969) searched for nests quite systematically, and found that Olivaceous Piculets almost always nested below 5 m. He suggested they may be limited to lower nest sites, to access wood soft enough to excavate but also stable enough to last the breeding season. In our study in primary Atlantic Forest, Ochre-collared Piculets were apparently able to find wood that was sufficiently soft and stable, and still quite high.

Likely, the Ochre-collared Piculets' ability to use a very small cavity, high above the

TABLE 3. Reproductive traits for New World piculets (*Picumnus* spp.). Cavity height is reported as mean \pm SE [range] (n), wherever possible. Sources: Lafresnaye's Piculet: Skutch 1948; Arrowhead Piculet: Haverschmidt 1951; White-barred Piculet: Hartert & Venturi 1909, Pergolani 1940, Pereyra 1951, Giraudo *et al.* 1993, Bodrati *et al.* 2001, de la Peña 2005, this study; Ochre-collared Piculet: Kirwan 2009, Mauricio *et al.* 2013, this study; White-wedged Piculet: Gussoni *et al.* 2009; Ochraceous Piculet: da Silva *et al.* 2012, M. da Silva *in litt.*; Mottled Piculet: Pichorim 2006; Olivaceous Piculet: Skutch 1948, 1969, 1998; Grayish Piculet: Sedano *et al.* 2008. Empty cells indicate that no information is available.

Species	Latitude	Cavity height (m)	Clutch size	Length of incubation period (d)	Mean length of incubation on-bouts (min)	% attentiveness during incubation	Length of nestling period (d)
Lafresnaye's Piculet	1°S	3 (1)	2		M: 46, F: 56	92	
Arrowhead Piculet	6°N	8 (1)			F: 48		~ 28
White-barred Piculet	~ 30°S	2.5 \pm 0.2 [1-5] (32)	3-4			~ 100	
Ochre-collared Piculet	27°S	10.6 \pm 2.4 [2.5-20] (7)	4	13	M: 48, F: 42	~ 100	26-27
White-wedged Piculet	22°S	5 (1)					
Ochraceous Piculet	5°S	2.0 \pm 0.2 (17)					
Mottled Piculet	25°S	0.85 (1)	4	17	M: 31, F: 53	~ 100	22-25
Olivaceous Piculet	9°N	[0.9-9.1] (14)	2-3	13-14	M: 55, F: 53	91	24-26
Grayish Piculet	4°N	6.3 \pm 1.0 [1.5-18] (4)	1-3		M: 37, F: 30	70	25

ground, is an advantage for avoiding nest predators. In our study area, small cavity-nesting birds experience their highest rates of daily nest survival in cavities with small entrances, high above the ground (Cockle *et al.* 2015). Indeed, we recorded no instances of predation at Ochre-collared Piculet nests, compared to an 81% failure rate for nests of the larger Green-barred Woodpecker (*Colaptes melanochloros*), whose cavities were 7 \pm 0.5 cm in diameter and 7 \pm 1 m high (Cockle *et al.* 2011, 2015).

Cavity excavation and courtship. Both sexes of Ochre-collared and White-barred Piculets contributed to excavation of nesting and

roosting cavities, as with all *Picumnus* that have been studied (Table 4). Ochre-collared Piculets were seen excavating 94 and 8 days before the first egg was laid (nest 4). Although they probably excavated on other days, their efforts must have been sporadic because their nest was right above a main trail, and we passed under it several times daily throughout this period, without detecting excavation. A pair of Ochre-collared Piculets was observed roosting together in their nest cavity about 5 days before the first egg was laid (nest 4). In White-barred Piculets, the cavity may be fully excavated and used for roosting even months in advance of egg-laying (Giraudo *et al.* 1993), unlike in true

TABLE 4. Division of labor between adult males (M) and females (F) at nests of New World piculets (*Picumnus* spp.). In the column on night care, “pair” indicates that the two adults roosted in the cavity simultaneously. > is used where one sex made a larger contribution. = indicates that the two sexes contributed equally. M+F indicates both parents contributed but their relative contribution was not calculated. Empty cells indicate that no information is available. Sources as in Table 3.

Species	Excavation	Diurnal incubation	Night care	Feeding nestlings	Sanitation
Lafresnaye's Piculet		M+F	pair		
Arrowhead Piculet	M+F	M+F	pair	M<F	M+F
White-barred Piculet	M+F	M+F	pair	M+F	M+F
Ochre-collared Piculet	M+F	M=F	pair	M<F	M<F
White-wedged Piculet				M<F	M<F
Ochraceous Piculet	M+F	M+F		M+F	M
Mottled Piculet		M<F		M+F	M
Olivaceous Piculet	M+F	M=F	pair	M+F	M+F
Grayish Piculet	M+F	M=F	pair	M=F	M+F

woodpeckers (Picinae; Winkler & Christie 2002).

Some excavation continued even during the incubation and nestling periods. For example, at nest 3 the female removed wood chips 97 times in a span of 11 min on day 12 of the incubation period. Excavation or tapping sounds were heard occasionally from inside the cavity up to days 22 and 23 of the nestling period (nests 3 and 4, respectively). At least sometimes, these sounds were made by older nestlings, occurring when both adults were outside of the cavity. On some occasions, adult birds may have been producing fresh wood-chips, which help absorb nestling feces on the cavity floor, as observed for Acorn Woodpeckers (*Melanerpes formicivorus*; Koenig *et al.* 1995).

We observed one copulation of Ochre-collared Piculets, at around 09:00 h on 9 November 2014. We first noticed a male and two birds in female plumage hopping and flitting restlessly from branch to branch, about 30 m from nest 4. One of the female-plumaged birds perched on a horizontal branch about 4 m high; the male flew to the branch, vocalized softly, positioned himself very close

to the female, then mounted her for a few seconds. The other female-plumaged bird flew away. After copulating, the male and female flew in the same direction as the female-plumaged bird, which might have been one of their offspring from the previous season.

Eggs, incubation, and parental behavior. Complete clutches for both Ochre-collared and White-barred Piculets contained four white eggs (nests 3, 4, 10, and 12; other nests were inaccessible or found only at the nestling stage). A nest of Mottled Piculets at similar latitude also contained 4 eggs (Pichorim 2006); in contrast, piculets inhabiting lower latitudes laid smaller clutches of 1–3 eggs, consistent with the well-documented positive correlation between avian clutch size and latitude (Table 3; Lack 1948, Jetz *et al.* 2008). White-barred Piculet nest 12 contained two eggs on 15 December, three eggs on 16 December, and four eggs on 17 December, by which we conclude that eggs were laid on consecutive days, as previously suggested by Hartert & Venturi (1909). Three of the four Ochre-collared Piculet eggs hatched at nest 3 (the first two on 10 Novem-

ber, and the third on 11 or 12 November), and one of the four eggs hatched at nest 4 (on 26 November). Assuming incubation began when the last egg was laid, the incubation period was 13 days at nest 3, and at least 13 days at nest 4, similar to the 13–14 days reported for Olivaceous Piculets but shorter than the 17 days recorded at a single nest of the Mottled Piculet (Skutch 1948, 1969, 1998; Pichorim 2006).

Both parents contributed to incubation at Ochre-collared and White-barred Piculet nests. In Ochre-collared Piculets, both parents roosted in the nest overnight during incubation (day 3 at nest 3; days 4, 9, and 12 at nest 4), as with all other piculet species that have been studied (Table 4). Male and female Ochre-collared Piculets contributed evenly and attended the nest almost constantly (Table 5); nest attentiveness was low (18%) during our 2-h watch on day 1, but rose to 100% on days 3–12 (nests 3 and 4). For White-barred Piculets, only the female was seen inside the cavity during the laying period (nest 12). Nest attentiveness of White-barred Piculets was 100%, and the male fed the female at least twice at the cavity entrance during 5 h of observations on day 0 at nest 12. Other piculets also exhibit biparental care during incubation, with relatively equal contributions of the sexes and high nest attentiveness (Tables 3 and 4; but see Sedano *et al.* 2008). Courtship feeding, however, has not been mentioned for other piculets; although common in wrynecks (Jyninae), it is unusual in woodpeckers (Winkler & Christie 2002).

Ochre-collared Piculet incubation bouts lasted 42 ± 4 min for females ($n = 9$ observations) and 48 ± 7 min for males ($n = 8$), similar to other piculets that have been studied (Table 3). When switching, the incoming adult normally ascended from the understory through midstory vegetation, until near the cavity, and its wings were audible as it flitted up to the nest. It then usually emitted a short

soft trill, which was only rarely answered by the adult inside the cavity. The incoming adult normally entered the cavity head first, turned and looked out, then descended; the outgoing adult then looked out of the entrance and exited the cavity 0–2 min later, similar to the Olivaceous Piculet (Skutch 1969, 1998). In contrast, at nests of Lafresnaye's Piculet and Arrowhead Piculet, the outgoing adult emerged before its mate entered (Skutch 1948, Haverschmidt 1951), as is the common practice among woodpeckers (Winkler & Christie 2002).

Nestlings. Our description of nestling development is based on video images. The development of Ochre-collared Piculet nestlings was similar to that of other piculets that have been studied. On hatching, Ochre-collared Piculet nestlings had pink skin and closed eyes, and were devoid of feathers, like all woodpeckers. Pin feathers were first seen under the skin of the wings day 6 (vs. day 5 for Olivaceous Piculets; Skutch 1969), and remained visible under the skin on day 11. However, feathers were emerging from pins on the wings by day 13 (vs. day 16 for Olivaceous Piculets; Skutch 1969). Eyes opened on day 12 or 13 (vs. day 13 for Mottled Piculets; Pichorim 2006). Nestlings were fully feathered with a black crown but short tails on day 19; their tails remained about half the adult length on day 24. Nestlings were observed at the cavity entrance, where the parents fed them, beginning on day 22 at nest 3 and day 18 at nest 4 (vs. 22 days for Olivaceous Piculet and 26 days for Arrowhead Piculet; Haverschmidt 1951, Skutch 1969). From day 23 on, nestlings frequently looked from the cavity entrance and vocalized with very short trills.

For Ochre-collared Piculets, nestling survival was 100% from hatching to fledging (three nestlings hatched and fledged at nest 3; one nestling hatched and fledged at nest 4). For White-barred Piculets, we observed three

TABLE 5. Attentiveness of incubating adult male (M) and female (F) at two nests of the Ochre-collared Piculet (*Picumnus temminckii*) at Parque Provincial Cruce Caballero, Misiones, Argentina.

Nest	Observer effort (min)	% time M alone in nest	% time F alone in nest	% time M & F together in nest	% time nest unattended
3	830	37	43	8	12
4	893	43	39	17	0

nestlings with pin feathers in nest 5, two unfeathered nestlings in nest 6, and two feathered nestlings that came to the cavity entrance at nest 11.

The three Ochre-collared Piculet chicks from nest 3 fledged on day 27, and the single chick at nest 4 fledged on day 26; these are among the longest nestling periods reported for piculets (Table 3). Fledgling Ochre-collared and White-barred Piculets looked like adult females, with the following differences: fledglings of both species lacked white spots on their black crowns, and fledgling White-barred Piculets had less-defined coloring on the breast compared to adult females. Likewise, fledglings of White-barred, Arrowhead, Ochraceous, Olivaceous, and Mottled Piculets have all been described as similar to adult females (crowns dark, where males are brightly-colored), but lacking or with less obvious white spotting on the crown (Pergolani 1940, Haverschmidt 1951, Skutch 1969, Pichorim 2006, da Silva *et al.* 2012).

Nestling diet and provisioning. In Ochre-collared Piculets and White-barred Piculets, both adults contributed to feeding the nestlings, as with all other piculet species that have been studied (Table 3). Food was often visible, overflowing from the adults' bills, but it was difficult to identify. We observed Ochre-collared Piculets with bills full of ant larvae on 4 occasions, lepidopteran larvae on 2 occasions, a greenish insect with legs on 1 occasion, and unidentified white larvae on 12 occasions. One of the lepidopteran larvae was regurgi-

tated by the male at nest 4 on day 18. The adults from nest 4 frequently brought food items extracted from the dead culms of *Merostachys clausenii* bamboo within 20 m of their cavity. Those from nest 3 often foraged among the pendant dead petioles of tree ferns (*Alsophila procera*), 20–60 m from their nest tree. Adult White-barred Piculets brought their nestlings beetle and ant larvae obtained from dead twigs and branches, which were often in advanced stages of decay. They also brought wasp nymphs, which they pecked from mud nests, to nestlings with pin feathers (nest 5). Nest 5 was in a small burned patch within Chaco forest, and the adults were only observed foraging in the branches of the burned trees, never outside the burned patch. Previous studies of piculet nests have also reported food carried in the bill, and very similar nestling diets. At other nests of White-barred Piculet, adults brought larvae and ant eggs (Giraud *et al.* 1993, de la Peña 2005). Ochraceous Piculets brought beetle larvae (Da Silva *et al.* 2012); Olivaceous Piculets brought small white objects that appeared to be the larvae and pupae of ants and other insects (Skutch *et al.* 1969); and Grayish Piculets brought white larvae (Sedano *et al.* 2008). Like the piculets, wrynecks and many true woodpeckers carry food in the bill; however, *Dryocopus*, *Colaptes*, and other woodpeckers in the Malarpicini (Picinae) typically feed by regurgitation (Winkler & Christie 2002, Manegold & Töpfer 2013).

The diets of adult *Picumnus* also appear to be composed primarily of ants and beetles.

White-barred Piculet stomachs contained ants (Formicidae, including genera *Solenopsis*, *Pheidole*, and *Pseudomyrma*), wood-boring larvae (especially beetles in the families Tenebrionidae, Buprestidae, and Cerambycidae), fly larvae (Diptera), and spiders (Araneae; Alabarce 1981, Lopes *et al.* 2005). White-wedged Piculet stomachs contained ants (Alves Lima *et al.* 2010). Olivaceous Piculets were frequently observed foraging on adult ants and their larvae and pupae (Skutch 1969). Their stomachs contained mostly ants (genera *Camponotus*, *Cramatogaster*, and *Pseudomyrmex*), but also cockroach (Blattaria) oothecae and beetles (Otvos 1967). While a female Grayish Piculet was attending nestlings, her feces contained white larvae and ants, including *Topinoma melanocephala* (Sedano *et al.* 2008).

The visitation rate of female Ochre-collared Piculets increased strongly over the nestling period, whereas the male rate increased only slightly (Fig. 2). Thus by the end of the nestling period (days 22–27), females were making 3.0 ± 0.5 trips/h and males 1.6 ± 0.3 trips/h ($n = 9$ observation periods at nests 3 and 4). Our observation of an increase in feeding rate over time is similar to observations at a nest of Mottled Piculets, but contrasts with a nest of Arrowhead Piculets, which showed no strong trend in feeding rate over time (Pichorim 2006, Haverschmidt 1951). Overall, visitation rate was similar between nest 3 (three nestlings) and nest 4 (one nestling; Fig. 2). Even during the observation period with the highest feeding rate, the two adult Ochre-collared Piculets did not make more than eight visits/hour (Fig. 2). Mauricio *et al.* (2013) reported a visit every 1–3 min for the same species; however, this rate was calculated from a very short sampling period (10–15 min; I. Franz *in litt.*) and likely represents a short burst of activity that could not be sustained over a long period. White-barred Piculets visited nest 11 every 5–10 min on 6 December

2007, feeding two nestlings at the cavity entrance.

Brooding and nest attendance during the nestling period. Male and female Ochre-collared Piculets spent similar amounts of time in the cavity during the nestling period, occasionally staying together in the cavity during the day. Males alone accounted for 46% and 51% of nest attendance at nests 3 and 4, respectively, females alone for 47% and 39%, and both adults together for 7% and 10%. For example, a video (available from <http://macaulaylibrary.org/video/475246>) taken on day 10 at nest 3 shows the adult female arriving with food while the male is inside the cavity. The adults are in the cavity together for 31 s until the male leaves (the female stays inside). At least one adult was always in attendance (possibly brooding) when we watched nests before day 10 (7 h 8 min of observation); after that, nest attendance declined (days 12–27: $34 \pm 6\%$; $n = 19$ observations over 44 h 34 min; Fig. 3).

The drop in nest attendance around days 12–15 (Fig. 3) coincided with the emergence of feathers between day 12 and day 13 (above), and an increase in feeding rate (especially by females) around day 14–15 (Fig. 2). Possibly, as nestlings began to thermoregulate, females were freed from the necessity of brooding and could dedicate more time to foraging and bringing food to the nest (see Jackson 1976, Johnson & Best 1982).

In Ochre-collared and White-barred Piculets, the adults of both sexes roosted overnight in the cavity during the nestling period (eight observations covering most of the nestling period, at nests 3, 4, 7, and 8), as do all other piculet species that have been studied (Table 4).

Nest sanitation. Ochre-collared and White-barred Piculets kept their nest interior clean,

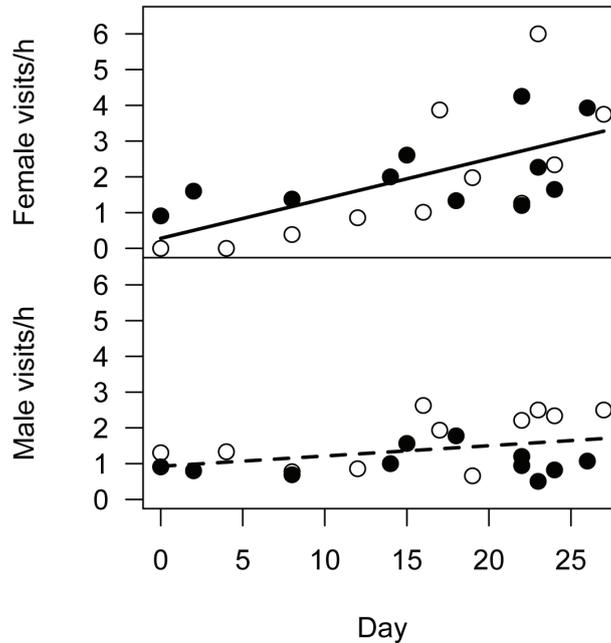


FIG. 2. Adult female (above) and male (below) visitation rates for Ochre-collared Piculets during the nestling period at nests 3 (open circles) and 4 (filled circles) at Parque Provincial Cruce Caballero, Misiones, Argentina. Predicted values of the general linear model (feeding rate \sim day) are shown by the solid line for females (statistically significant: $b_{\text{day}} = 0.11$, $SE = 0.03$, $t = 3.66$, $p = 0.0016$, $r^2 = 0.40$) and broken line for males (marginally significant: $b_{\text{day}} = 0.029$, $SE = 0.017$, $t = 1.74$, $p = 0.098$, $r^2 = 0.13$).

with no feces or fly larvae. Both sexes participated in sanitation. Ochre-collared Piculets were observed removing fecal sacs beginning on day 14 and they continued until the chicks fledged. Eggshells and unhatched eggs remained in the nest for 4–5 days at nest 3 and at least 11 days at nest 4, similar to Olivaceous Piculet (Skutch 1969). The male was seen removing pieces of egg shell from nest 4 on nestling day 10. The female threw some debris, apparently insect parts, from the entrance on day 22 at nest 4. Olivaceous Piculets also keep their nest clean of feces up to the day of fledging (Skutch 1969, 1998). In contrast, in many species of true woodpeckers, the parents, especially females, stop removing feces in the last days of the nestling period, leaving their cavities soiled when the

chicks fledge (Tutt 1956, Jackson 1976, Koenig *et al.* 1995, Jackson & Ouellet 2002, Winkler & Christie 2002, Gorman 2011). By maintaining the cleanliness of their nest cavity, piculets probably keep it in good condition for social roosting during the late nestling and post-fledging periods, in contrast to other woodpeckers which move to other roost sites after fledging (see below). In many birds with stiffened rectrices (including most woodpeckers), adults and older nestlings roost vertically, clinging to a cavity wall, propped up by their stiff tails (Tutt 1956, Skutch 1969, van Els & Whitney 2011). Piculets, however, do not have stiff tails and it is not known whether they can cling vertically overnight; instead, they might roost on the cavity floor, like the short-tailed *Hemicircus* woodpeckers, which are basal to the

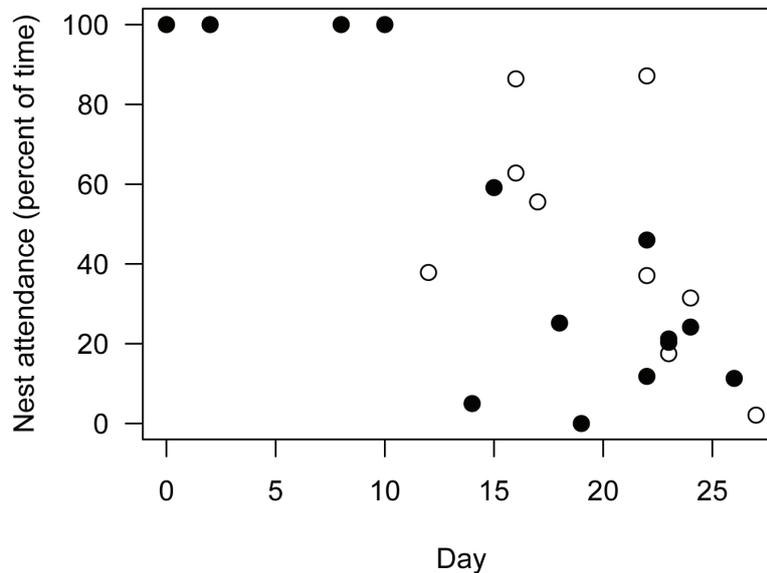


FIG. 3. Daytime nest attendance (percent of time at least one adult was in the cavity) for Ochre-collared Piculets during the nestling period at nests 3 (open circles) and 4 (filled circles) at Parque Provincial Cruce Caballero, Misiones, Argentina. Nest 3 was also watched for 92 and 90 min, respectively, on days 0 and 4, but we could not determine nest attendance because the female was never seen. Given the 100% attendance at nest 4 up to day 10, it now seems likely that the female at nest 3 was in the cavity during our entire observation periods on days 0 and 4.

rest of the Picinae (Lammertink 2011, Manegold & Töpfer 2013). If so, older nestlings, fledglings, and adults might spend considerable time on the cavity bottom, making cleanliness a higher priority for piculets than for most woodpeckers.

The female Ochre-collared Piculet was responsible for 10 of 13 fecal sac removals we observed at nest 3, and 10 of 15 at nest 4 (overall 71%). For several other piculet species, there is evidence that females may take on more feeding and sanitation work than males (Table 4). Nevertheless, observations at several Olivaceous Piculet nests suggest that the relative contribution of males and females may vary considerably among breeding pairs within a single species, with the male taking on a larger proportion of the work in some cases (Skutch 1998).

Fledging. The three Ochre-collared Piculet chicks at nest 3 fledged within a span of 32 min, at 07:24, 07:42, and 07:56 h. Likewise, same-day fledging was observed for a brood of two White-wedged Piculets (Gussoni *et al.* 2009) and a brood of two Grayish Piculets (Sedano *et al.* 2008). In contrast, the first and last nestlings in a Mottled Piculet brood fledged three days apart (Pichorim 2006). The Ochre-collared Piculet chick at nest 4 fledged at 09:20 h.

Nestling Ochre-collared Piculets vocalized incessantly during the day before fledging at nest 4, and in the last hours before fledging (not the previous day) at nest 3. Adults also vocalized incessantly at nest 3 in the hours before the chicks fledged. For 2–3 min before fledging, nestlings emerged part way and re-entered the cavity repeatedly, as if

uncertain whether to leave. They first made short flights (estimated 50 cm at nest 4) to adjacent branches or trees, then flew farther and could be heard vocalizing near the adults. They flew quite well (similar to adults). The whole family from nest 3 remained together when the chicks fledged. We observed adults feeding the fledglings near the cavity 1, 3, and 4 days after fledging.

Roosting and social behavior. Whether breeding or not, two or more piculets roost together in a single cavity. The two adult Ochre-collared Piculets from nest 3 and their three fledglings were observed on several occasions in and around their old cavity. The day after fledging (8 December), 40 min after sunrise, fledglings and adults were observed foraging in front of the nest cavity. The parents fed the nestlings, and the male entered the cavity briefly (with food, which he then provided to a nestling outside the cavity). That night, at least three individuals roosted in the vacated nest cavity. Two days later, the cavity entrance was dramatically and irregularly enlarged, as if another woodpecker had attempted to access the contents. All five members of the Ochre-collared Piculet family were observed near the cavity that evening, two of them entering and apparently inspecting it; however, they did not sleep in the cavity that night. The following day at 08:52 h, the five individuals were again observed in the area of their old nest cavity. Additionally, two adult Ochre-collared Piculets slept in roost 1 on the nights of 23 and 29 November 2014, shortly after they finished excavating the cavity, and at least three individuals entered the nest 2 cavity to roost on 28 October 2012, when nesting may or may not have been completed. At least three White-barred Piculets roosted in the cavity from nest 6 in May 1999, about 6 months after the cavity was used for nesting. Another family of White-barred Piculets (male, female, and one juvenile) was observed sharing a

roost cavity outside the breeding season (Bodrati *et al.* 2001). Likewise, families of Oliveaceous Piculets returned to sleep in their nest cavity the day they fledged, and continued to use it as a dormitory for several months (Skutch 1969). In contrast, there is no evidence that piculets ever roost alone (Table 4; Skutch 1948, 1969; Haverschmidt 1951, Giraudo *et al.* 1993, this study). Several species of piculets, including Ochre-collared Piculets and White-barred Piculets, are found in groups of 3–5 outside the breeding season, suggesting that families may spend days, as well as nights, together (Skutch 1969, Partridge in Chebez 1995, AB and ML pers. observ.).

At Ochre-collared Piculet cavities, the first individual emerged 18 ± 6 min after sunrise ($n = 4$ observations at 2 nests and 1 roost). The second adult entered to roost 39 ± 5 min before sunset ($n = 7$ observations at 2 nests and 1 roost). Most other diurnal birds (e.g., Golden-Crowned Warbler *Basileuterus culicivorus*, White-browed Warbler *Myiothlypis leucoblephara*, Black-goggled Tanager *Trichothraupis melanops*, Ruby-crowned Tanager *Tachyphonus coronatus*, Red-crowned Ant-tanager *Habia rubica*, Plumbeous Kite *Ictinia plumbea*) were still active and singing at this time, and crepuscular birds (e.g., Barred Forest-falcon *Micrastur ruficollis*, Rufous-capped Motmot *Baryphthenus ruficapilla*, Planalto Woodcreeper *Dendrocopos platyrostris*) had not yet begun to vocalize, suggesting that Ochre-collared Piculets enter their roost earlier than other species of birds. Nevertheless, they remained awake, occasionally looking out of the cavity entrance or vocalizing inside the cavity, up to 40 min after entering.

Nest-guarding. On day 4 of incubation at nest 4, both Ochre-collared Piculet parents were in the cavity at 18:32 h, apparently settling down to roost, when a third individual in female plumage arrived. When the intruder came

within 1 m of the cavity, the nesting female emerged and chased it into the understory near the observer. The intruder returned to the nest 1 min later and attempted to enter. This time, the nesting male obstructed the entrance and pecked fiercely at the intruder's legs until 18:38 h, when the nesting female returned and chased the intruder away. Several minutes later the intruder returned, but was again chased away by the nesting female. At 18:47 h (12 min before sunset), the nesting female entered the cavity and remained there, with the male, to roost. In at least three species of piculets (Lafresnaye's, Arrowhead, and Olivaceous), researchers have observed a third individual, probably a young bird of an earlier brood, roosting with the parents in active nest cavities (Haverschmidt 1951, Skutch 1948, 1969). The Ochre-collared Piculet that intruded on nest 4 in our study may likewise have been a young bird from an earlier brood, attempting to roost with its parents.

We never observed Ochre-collared Piculets or White-barred Piculets chasing any other species away from their nest. When we lifted our pole-mounted camera to inspect Ochre-collared Piculet cavities, they only flushed at the last moment, and sometimes did not flush at all. They returned to the cavity within 2–6 min of our nest checks (as we were still removing equipment), faster than other birds in our Atlantic Forest study area (which remain absent until we leave). Ochre-collared Piculets looked out of the cavity when they heard people on the ground or birds (Maroon-bellied Parakeet *Pyrrhura frontalis*, White-spotted Woodpecker *Veniliornis spilogaster*, Olivaceous Woodcreeper *Sittasomus griseicapillus*, Black-goggled Tanager, and Ruby-crowned Tanager) within 1 m of their nest, and on one occasion when a Plumbeous Kite flew by and flapped its wings about 2 m from the nest. In contrast, Arrowhead Piculets on several occasions chased or attacked

larger birds near their nest (Haverschmidt 1951).

Both adults were outside nest 3 on nestling day 12, when a group of Black Capuchin Monkeys (*Sapajus nigritus*) was foraging on an adjacent tree. The female Ochre-collared Piculet remained away from the nest for 79 min and the male remained foraging around the nest tree for 96 min (and was seen with white larvae in the bill), without either adult returning to the cavity, until the monkeys had moved more than 100 m away. As a result, the nest was unattended for 74 min. In contrast, during previous observations at the same nest (day 8), trips away from the cavity were 47 and 55 min, and the nest was never left unattended. During our next observations (days 16 and 17), trips away from the cavity were 16 ± 4 min (range: 2–61 min, $n = 14$ observations), and the nest was left unattended for bouts of 8 ± 2 min (range: 1–22 min, $n = 15$ observations). As a result of the unusually long time spent away from the nest while monkeys were nearby, nest attendance on day 12 was low (38%) compared to days 8 (100%), 16 (86% in the morning and 63% in the evening), and 17 (56%; Fig. 3). We infer that the adult piculets may have stayed away from their nest to avoid revealing its location to the monkeys, which were implicated in depredations at the nests of other woodpeckers in our study area (Cockle *et al.* in press).

Conclusions. Breeding biology varies little within the Neotropical piculets and can be characterized as follows (from Tables 3 and 4, and references therein). Pairs build very small cavities (2–3 cm in entrance diameter and ~ 10 cm deep) in dead wood. Both parents participate in all aspects of nest-building, incubation, nest-guarding, nestling care, and sanitation. They exhibit high nest attentiveness (near 100% during incubation and early nestling period) and incubation bouts from about 30 to 60 min. Nestling diet is com-

prised mainly of ant eggs and larvae. Both parents sleep in the nesting cavity before laying, during incubation, with nestlings, and (accompanied by their offspring) after fledging. They also roost in pairs or small groups when they are not breeding.

In many ways, the breeding biology of Neotropical piculets resembles that of the true woodpeckers, and these shared traits may represent the condition of ancestral woodpeckers. Most members of both Picinae and Picumninae excavate their cavities primarily in dead branches or tree trunks (Winkler & Christie 2002). In both Picinae and Picumninae, both parents incubate the eggs and feed the young (Winkler & Christie 2002). Except for Mottled Piculets (Pichorim 2006), piculets have a long nestling period relative to their incubation period, with a nestling/incubation period ratio of ~ 2 , similar to other woodpeckers but higher than in most altricial birds (Yom-Tov & Ar 1993). Nestling piculets hatch without feathers, which take more than a week to emerge, and the nestling period is nearly 4 weeks, all within the typical range for woodpeckers (Winkler & Christie 2002).

Neotropical piculets diverge from most of the true woodpeckers in the division of labor between the sexes, social roosting, and fledging coloration. Female piculets provide an unusual amount of parental care compared to true woodpeckers. Female Ochre-collared Piculets increased their feeding rate to nearly double that of males in the last week before fledging, whereas in the true woodpeckers females often stop feeding completely during this last week, leaving males to attend the nestlings alone (Winkler & Christie 2002). An exception among the true woodpeckers are the multi-brooded *Melanerpes* spp., in which males may stop feeding during the last week, possibly freeing them to excavate a new cavity (Winkler & Christie 2002).

Piculet females (and sometimes a third individual) also consistently roost in the nest

cavity with the male, whereas in the true woodpeckers males alone are normally responsible for nocturnal care (Winkler *et al.* 1995, Winkler & Christie 2002). Social roosting during breeding is rare and apparently facultative in the true woodpeckers. Even in the highly social, cooperatively-breeding Acorn Woodpecker, the breeder male normally roosts alone in the nest cavity, only occasionally accompanied by another adult (Joste *et al.* 1982, Koenig *et al.* 1995). In the non-cooperatively breeding Magellanic Woodpecker (*Campyphilus magellanicus*), females sometimes join their mates in the nest cavity overnight (Ojeda 2004), but such behavior appears to be unusual (Chazarreta *et al.* 2011). Wrynecks (Jynginae), which are basal to both piculets and true woodpeckers, also normally roost alone, but fledglings may sometimes return to roost in the nest cavity with one or even two parents (Tarboton 1976, Glutz von Blotzheim & Bauer 1980). It will be interesting to determine whether social roosting occurs only in New World *Picumnus* piculets or also in the other Picumninae (African Piculet *Verreauxia africana* and the Asian piculets *Picumnus innominatus*, *Sasia abnormis*, and *S. ochracea*). Given that *Sasia* may have diverged from *Picumnus* around the time that Picumninae diverged from Picinae + Nesocitinae, and that *P. innominatus* is basal to the Neotropical piculets (Benz *et al.* 2006, Fuchs *et al.* 2006), a finding that parents share night duties in these species would raise the possibility that ancestral woodpeckers exhibited this behavior as well.

Juveniles have been described for 22 of the 26 *Picumnus* species (including the Asian *P. innominatus*), and all have female-like head patterns (Haverschmidt 1951, Skutch 1969, Winkler *et al.* 1995, Pichorim 2006, da Silva *et al.* 2012, this study). In contrast, in *Sasia*, *Verreauxia*, and the true woodpeckers (except *Celeus*) juveniles either (1) resemble the adults of their sex, or (2) have more extensive bright head coloration than adult males (Winkler *et*

al. 1995). Juvenile plumage may function to reduce aggression from adult birds (e.g., VanderWerf & Freed 2003), and in the case of Neotropical piculets this might facilitate group living and social roosting. Nevertheless, social roosting during the non-breeding season also occurs in woodpecker species whose juveniles resemble adult males, and further research is needed to understand the significance and evolution of juvenile plumage in woodpeckers (Koenig & Walters 2014).

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