

Nesting and natural history of the Plain-winged Woodcreeper (*Dendrocincla turdina*): foraging associations and uniparental care

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ABSTRACT—*Dendrocincla* woodcreepers (Furnariidae: Dendrocolaptinae) are known for their foraging associations with army ants and mammals and for their emancipated males, which provide no parental care. Little is known of the natural history of the Plain-winged Woodcreeper (*Dendrocincla turdina*), an Atlantic Forest endemic. In Paraguay (2000–2002) and Argentina (2000–2016), we nearly always found Plain-winged Woodcreepers foraging in association with black capuchin monkeys (*Sapajus nigritus*), unless they were attending a nest, when they foraged alone, often by sally-gleaning. In our main study area, Parque Provincial Cruce Caballero, encounter rates of both monkeys and Plain-winged Woodcreepers increased dramatically after 2012. We found 2 nests, 1 with 2 eggs and the other with 2 nestlings, both in deep, nonexcavated tree cavities in shady forest understory. One secretive adult attended each nest; there was no evidence of a pair bond with another adult. During incubation, nest attentiveness was 62%, on-bouts were mean 35 (SE 5) min (range 3–83; $n = 21$) and off-bouts averaged 16 (SE 1) min (range 8–28; $n = 24$). The adult brought lichens and a few other nesting materials throughout the incubation period and sometimes used them to cover the eggs when it left the nest. Once the eggs hatched, nest attentiveness declined rapidly, although the adult roosted with the nestlings until they were 14 days old. Nestling diet included arthropods (especially Orthoptera, Lepidoptera, Hemiptera, and Coleoptera) and vertebrates (bat and frog) but differed between the 2 nests, suggesting opportunism. The adult brought food much more frequently around sunrise (7.93 [SE 0.69] visits/h) and sunset (8.03 [1.19] visits/h) than during the rest of the day (3.26 [0.22] visits/h). Nestling development was slower than for coexisting Dendrocolaptinae with biparental care, and the nestlings fledged when 26–27 days old. Uniparental care is unusual in forest insectivores but has arisen at least twice in Dendrocolaptinae and seems to be associated with hiding of eggs, secretive behavior, and slow nestling growth. Received 15 May 2017. Accepted 18 October 2017.

Key words: *Dendrocincla turdina*, foraging association, monkey, nest concealment, nestling development, nestling diet, uniparental care.

Nidificación e historia natural de *Dendrocincla turdina*: asociaciones de forrajeo y cuidado uniparental

RESUMEN (Spanish)—Los integrantes del género *Dendrocincla* (Furnariidae: Dendrocolaptinae) son conocidos por sus asociaciones mientras forrajean con correcciones de hormigas y grupos de mamíferos, y por sus machos emancipados, que no proporcionan cuidado parental. Poco se sabe de la historia natural de *Dendrocincla turdina*, una especie endémica de la Selva Atlántica. En Paraguay (2000–2002) y Argentina (2000–2016), a menudo encontramos *Dendrocincla turdina* forrajeando en asociación con monos capuchinos negros (*Sapajus nigritus*), a menos que estuviesen en un nido, cuando se alimentaban solos, a menudo con vuelos hasta la superficie de ramas, troncos e incluso hojas. En nuestra principal área de estudio, Parque Provincial Cruce Caballero, las tasas de encuentro de monos y *Dendrocincla turdina* aumentaron drásticamente después de 2012. Encontramos dos nidos, uno con dos huevos y el otro con dos pichones, ambos en cavidades profundas, no excavadas, en sotobosques sombrío. Un adulto sigiloso asistió a cada nido; no hubo evidencia de un vínculo de pareja con otro adulto. Durante la incubación, la atención del nido fue de 62%, con turnos de 35 \pm 5 min (promedio \pm EE; rango: 3–83; $n = 21$) y recesos de 16 \pm 1 min (rango: 8–28; $n = 24$). El adulto trajo líquenes y otros materiales al nido a lo largo del período de incubación, y a veces los utilizó para cubrir los huevos cuando salía del nido. Una vez que los huevos eclosionaron, la atención del nido disminuyó rápidamente, aunque el adulto durmió con los pichones hasta que tenían 14 días de edad. La dieta de los pichones incluyó artrópodos (especialmente Orthoptera, Lepidoptera, Hemiptera y Coleoptera) y vertebrados (murciélago y rana), pero difirió entre los dos nidos, lo que sugiere oportunismo. El adulto trajo alimento mucho más frecuentemente al amanecer (7,93 \pm 0,69 visitas/h) y al atardecer (8,03 \pm 1,19 visitas/h) que durante el resto del día (3,26 \pm 0,22 visitas/h). El desarrollo de los pichones fue más lento que en Dendrocolaptinae coexistentes que exhiben cuidado biparental, y los pichones abandonaron el nido a los 26–27 días de edad. El cuidado uniparental es inusual en insectívoros de bosque pero ha surgido por lo menos dos veces en Dendrocolaptinae y parece estar asociado con comportamientos crípticos, el encubrimiento de los huevos, y el crecimiento lento de los pichones.

Palabras claves: asociaciones de forrajeo, cuidado uniparental, *Dendrocincla turdina*, desarrollo de pichones, dieta de pichones, mono, ocultamiento del nido.

Dendrocincla is a genus of Neotropical woodcreepers (Furnariidae: Dendrocolaptinae) that currently includes 6 species: Tyrannine Woodcreeper

(*Dendrocincla tyrannina*), White-chinned Woodcreeper (*D. merula*), Ruddy Woodcreeper (*D. homochroa*), Plain-brown Woodcreeper (*D. fuliginosa*), Tawny-winged Woodcreeper (*D. anabatina*), and Plain-winged Woodcreeper (*D. turdina*; AOU 1998, Remsen et al. 2017). *Dendrocincla turdina* is endemic to the Atlantic Forest of eastern Paraguay, southeastern Brazil, and northeastern Argentina (Marantz et al. 2003). Although previously included within *D. fuliginosa*, it is now

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considered a separate species on the basis of vocalizations and genetic data (Willis 1983, Weir and Price 2011, Remsen et al. 2017).

Dendrocincla woodcreepers are well known for their foraging associations in which they sally-glean insects and other organisms flushed by swarming army ants (e.g., *Eciton* and *Labidus* spp.; Willis 1960, 1972, 1983; Skutch 1969; French 1973; Willis and Oniki 1978, 1995). They also occur in mixed species flocks of birds, accompanying ant swarms or not (Davis 1946, Wiley 1971, Poulsen 1996, Develey and Peres 2000). In parts of their range, *D. anabatina*, *D. fuliginosa*, and *D. turdina* also forage on arthropods and vertebrates flushed by groups of coatís (*Nasua nasua*) or primates, including black capuchin monkeys (*Sapajus nigritus*) and squirrel monkeys (*Saimiri oerstedii*; Terborgh 1983, Boiniski and Scott 1988, Willis and Oniki 2002, de Mello Beisiegel 2007).

Like other woodcreepers, members of *Dendrocincla* nest in cavities in trees, palms, or bamboo (Skutch 1969, Zeledón in Wetmore 1972, Willis 1972, French 1973, Narosky et al. 1983, Greeney et al. 2009). Unlike most woodcreepers, *Dendrocincla* do not seem to form a pair bond (Skutch 1969, Willis 1972, Willis and Oniki 1995). Only the female cares for the eggs and nestlings, which is similar to genera *Xiphorhynchus* and *Sittasomus* but contrasts with the biparental care exhibited by genera *Dendroplex*, *Campylorhamphus*, *Dendrocolaptes*, *Xiphocolaptes*, *Lepidocolaptes*, and most other Furnariidae (Marantz et al. 2003, Bodrati et al. 2012b, Majewska and Oteyza 2013, Cockle and Bodrati 2017). Several nests have been described for *Dendrocincla fuliginosa* (Narosky et al. 1983), but only one can be attributed to *D. turdina*: 2 white eggs, frequently left unattended, on a woodchip lining in a natural cavity 1.5 m high in a tree trunk by a forest road at Barreiro Rico (Brazil), on 8–10 November 1976 (Willis 1983). Saibene et al. (1996) listed *D. turdina* as a breeding resident at Parque Nacional Iguazú (province of Misiones, Argentina). Little else is known about its breeding, nest attentiveness, nestling diet, or care of young (Majewska and Oteyza 2013). We present observations of foraging and nesting of *D. turdina*, highlighting behaviors and reproductive parameters that may be associated with uniparental care in woodcreepers.

Methods

We conducted bird surveys throughout the Atlantic Forest of Argentina (2000–2016) and Paraguay (2000–2002) in mixed forest with laurel (*Nectandra* and *Ocotea* spp.) and guatambú (*Balfourodendron riedelianum*); mixed forest with laurel, guatambú, and palo rosa (*Aspidosperma polyneuron*); and mixed forest with laurel, guatambú, and Paraná pine (*Araucaria angustifolia*; Cabrera 1976; Guyra Paraguay 2004; Bodrati and Cockle 2006, 2013; Bodrati et al. 2010, 2012a). We focused in particular on 400 ha of primary forest at Cruce Caballero Provincial Park (Misiones, Argentina; 26°31'S, 53°59'W).

AB conducted surveys throughout the year by walking slowly along trails, detecting birds by sound or sight, in all types of forest from predawn until midday and again for 3–4 h from midafternoon until dark. Relative abundance (encounter rate) of birds was recorded on daily lists as rare (1 individual), scarce (2–5), frequent (5–10), common (10–20), or abundant (>20). Later, these encounter rates were summarized over multiple visits to the same sites, as rare (low numbers and not recorded on all visits to the site), scarce (1–2 records each 2–3 d), frequent (1–5 records/d almost every day), common (5–10 records/d every day), abundant (>10 records/d every day) or occasional (1–5 times in >100 d of field work; Bodrati et al. 2010). On a few occasions before 2010, we used playback to search for *Dendrocincla turdina* in Parque Provincial Cruce Caballero.

We and our field assistants searched for nests by observing adult birds at Parque Provincial Cruce Caballero each September–December (main breeding season for birds in Misiones) from 2006 to 2016 (Cockle et al. 2015). We inspected nests using a ladder or pole and a small camera on a 2 m hose and watched them from the ground opportunistically throughout the day using binoculars or telescope, sometimes aided by photographs. Observation bouts lasted 20–347 min (mean: 130 min) for a total of 24 h 11 min during the incubation period and 95 h 5 min during the nestling period. We attempted to observe nests at least once per day during the nestling period, although we missed days 0, 3, 7, and 18 at nest 1 and days 0–15, 25, and 27 at nest 2. When nests were completed, we used tapes to measure cavity dimensions, height above ground, and tree diam-

eter at breast height (DBH); a compass to determine cavity entrance orientation; a laser rangefinder to estimate tree height; and a concave spherical crown densiometer to estimate percent cover of vegetation at cavity height, 1 m in front of the cavity entrance.

We observed stage transitions at nest 1, which allowed us to estimate the length of the nestling period (26–27 d, discussed later). Nest 2 was found with nestlings, whose age we estimated by working backward from the date of fledging, assuming a nestling period of 27 d. To test for changes in feeding rate over the course of the day and the nestling period, we compared general linear models (lm command in R 3.2.2; R Core Team 2015) that predicted feeding rate (visits/h) as a function of different combinations of the following predictor variables: “nest identity” (categorical, 2 levels), “nestling age” (continuous), and “time of day” (categorical, 3 levels). Time of day was divided into “sunrise” (15 min before to 15 min after sunrise), “daytime” (15 min after sunrise until 15 min before sunset), or “sunset” (15 min before to 15 min after sunset). We used Akaike information criterion (corrected for small sample size; AICc) and Akaike weights (w_i) to weigh support for each model (Burnham and Anderson 2002). If a model had $\Delta\text{AICc} < 2$ we considered it well supported by the data. We used t -tests to assess whether slope parameters (b) differed significantly from zero ($\alpha = 0.05$; Tabachnick and Fidell 2001).

Results

Foraging associations and habitat

Throughout the Atlantic Forest of Misiones (Argentina) and eastern Paraguay, we have almost always recorded *D. turdina* accompanying groups of black capuchin monkey, sometimes so close that the monkeys attempted, unsuccessfully, to catch them. On a few occasions we have seen them with coatís (at Parque Nacional Iguazú; 25°35'S, 54°19'W; elevation 250 m). Once, at Parque Provincial Cruce Caballero on 22 May 2005, we saw 2 individuals foraging low to the ground at a swarm of ants. They were in a mixed species flock of birds that included Giant Antshrike (*Batara cinerea*), Spot-backed Antshrike (*Hypodaleus guttatus*), Variable Antshrike (*Thamnophilus caerulescens*), White-shouldered Fire-eye (*Pyriglena*

leucoptera), Plain Antvireo (*Dysithamnus mentalis*), Tufted Antshrike (*Mackenziaena severa*), Large-Tailed Antshrike (*Mackenziaena leachii*), Olivaceous Woodcreeper (*Sittasomus griseicapillus*), Buff-browed Foliage-gleaner (*Syndactyla rufosuperciliata*), and Rufous-capped Spinetail (*Synallaxis ruficapilla*). We also occasionally saw *Dendrocincla turdina* in mixed-species flocks of birds away from ants or monkeys; however, they seem to not participate in such flocks as regularly as other woodcreepers, including White-throated Woodcreeper (*Xiphocolaptes albicollis*), Planalto Woodcreeper (*Dendrocolaptes platyrostris*), Olivaceous Woodcreeper, Black-billed Scythebill (*Campylorhamphus falcularius*), or Scalloped Woodcreeper (*Lepidocolaptes falcinellus*). We rarely saw 2 *Dendrocincla turdina* individuals together, but sometimes detected 2 individuals 30–50 m apart within the same group of mammals or birds.

We have found the highest encounter rates of *D. turdina* in laurel, guatambú, and palo rosa forest, especially in patches of palo rosa, palmito (*Euterpe edulis*) palms, or takuarusú (*Guadua chacoensis*) bamboo. In riparian forest of the Iguazú and Paraná rivers in northern Misiones, where takuarusú bamboo dominates the vegetation (e.g., at Parque Nacional Iguazú and Puerto Bemberg; 25°55'S, 54°37'W; elevation 130 m), *Dendrocincla turdina* is by far the most frequently detected woodcreeper (abundant, >10 records/d); the larger *Xiphocolaptes albicollis* and *Dendrocolaptes platyrostris* are scarce (1–2 records every 2–3 d) or locally absent (Bodrati et al. 2012a). We also categorized *Dendrocincla turdina* as abundant (>10 records/d) in takuarusú forest with emergent palo rosa and nearby patches of palmito at Estancia Itabó Rivas, Canindeyú, Paraguay (24°28'S, 54°36'W; elevation 370 m).

Parque Provincial Cruce Caballero is somewhat higher than these sites, at 600 m elevation; it lacks palo rosa, palmito, and takuarusú and instead falls within the district of laurel, guatambú, and Parana pine. From 2003 to 2010, we obtained <5 records of *D. turdina* in 341 d of field work in the park, could not determine its seasonal presence, and had no evidence of breeding (Bodrati et al. 2010). We rarely observed black capuchin monkeys during this time (2003–2010). Then, from 2012 to 2016 we began to detect both black capuchin monkeys and *D. turdina* nearly every day, usually foraging



Nest 1



Nest 2

Figure 1. Plain-winged Woodcreeper (*Dendrocincla turdina*) adults at their nest cavities in Parque Provincial Cruce Caballero, Misiones, Argentina. Nest 1 photographed by Martjan Lammertink on 21 Oct 2015. Nest 2 photographed by KLC on 20 Nov 2016.

together, and in areas of the park where we had not previously found them, even using playback. We now characterize *D. turdina* as frequent (1–5 records/d, nearly every day) in Parque Provincial Cruce Caballero.

Nest site

We found 2 *D. turdina* nests, both in non-excavated tree cavities surrounded by tree ferns (*Alsophila procera*) in the shady low-midstory of primary forest, >1.3 km from the forest edge (Fig. 1). The first cavity (nest 1) was at a height of 4.5 m in the main stem of an unhealthy *Alchornea triplinervia* 17 m tall and 28 cm DBH. The cavity was 64 cm deep and 10 cm in internal diameter and lined with pieces of lichen and a few small sticks and stems. Its entrance measured 21 cm (vertical) by 3.8 cm (horizontal) and faced 162°. The leaves of the tree ferns unfurled about a week

before the eggs hatched, hiding the cavity from above and below and obstructing sunlight throughout the day. Vegetation cover was 100% above the cavity and 99% in a 10 m radius. The tree was dead by the end of the breeding season and fell within 10 months. The second nest (nest 2) was 670 m from nest 1 and 10 m from a small stream. The cavity was at a height of 3.7 m in the main trunk of an unhealthy *Cedrela fissilis* 9 m tall and 17 cm DBH. It was 48 cm deep and 8 cm in internal diameter; its entrance was 54 cm (vertical) by 4 cm (horizontal) and faced due north (0°). Vegetation cover was 100% above the cavity and 92% in a 10 m radius.

Eggs and nestlings

Nest 1 contained a complete clutch of 2 white eggs on 18 October 2015; they hatched between 1630 h Argentina Time on 31 October and 1524 h

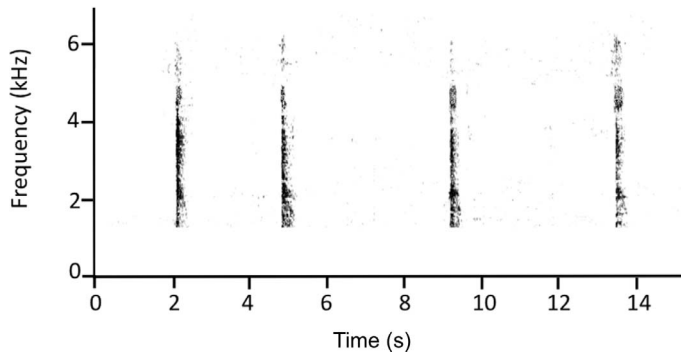


Figure 2. Vocalizations *kkjjjj* of adult Plain-winged Woodcreeper (*Dendrocincla turdina*) attending nest 1. Recorded by FGD at 0623 h on 26 Nov 2015 using an H4N digital recorder (Zoom Corporation) and Sennheiser ME-66 shotgun microphone. Audio available from: <https://www.xeno-canto.org/421258>

on 2 November. One chick fledged between 0945 h on 27 November and 0545 h on 28 November and the other at 0700 h on 28 November. We considered 1 November to be day 0 and estimated the nestling period as 26–27 d. Nest 2 was found with 2 nestlings on 18 November 2016; they were in the nest, fully feathered, at 1824 h on 29 November but were absent (presumed to have fledged) the following day at 1710 h. Assuming a nestling period of 27 d, the nestlings were about 15 days old when nest 2 was discovered.

We based our description of nestling development on nest 1. On day 1 the nestlings had pink skin, closed eyes, pink bill, yellow-white gape flanges (along three-fourths of the bill) and dark gray down on the back. By day 6 they appeared less downy and had pins under the skin on the wings and upper back. By day 10, pins had emerged from the skin on the wings and spine and were visible under the skin on the head and tail. Eyes remained closed. By day 15 the eyes were open and the gape flanges were less obvious, occupying about one-fourth of the bill. Each wing had a double line of pin feathers, the pins on the spine had opened, and those on the head and tail were beginning to open. Some bare patches remained visible on the flanks and neck. By day 19, nestlings had grayish-brown feathers on the back and wings, a dark head with whitish stripes, and a short tail. By day 25 they climbed the cavity walls and emitted begging calls or short, low-volume versions of the adult song when the adult entered or exited. On day 26, nestlings could occasionally be seen at the cavity entrance.

Fledglings (day 27) were similar to adults but had shorter tails, slight gape flanges, and a pink base to the mandible.

Parental care

Only one adult was seen at each nest. It was remarkably secretive, singing rarely and only at a considerable distance. A second adult was occasionally heard 50–100 m away. Once (nestling day 23, nest 2), a second adult sang within 15 m of the nest and, in response, the adult that attended the nest sang and flew to the same tree. When disturbed in any way (e.g., when 2 doves fought nearby), the adult that attended the nest instantly became alert. Initially, it hesitated to enter the nest in our presence. The first time we watched nest 1 (14 d before hatching), it waited 10 min to enter, emitting low vocalizations (*kkjjjj*, possibly an alarm call; Fig. 2), and then emerged after only 2 min. It often made this sound during incubation and the early nestling period, and the nestlings made a similar sound when they were near fledging. Two days later (12 d before hatching, nest 1), it spent 5 min clinging beside the entrance, entered, and seemed agitated, peering out of the entrance and dropping a feather outside the cavity before eventually descending inside. While incubating, the adult entered the cavity tail-first, frequently re-emerged to observe the surroundings before descending, and peered out for some time before leaving. By contrast, as soon as it was feeding nestlings (day 1, nest 1), it started entering rapidly, head first, and emerging directly. It entered the cavity completely to feed nestlings, only

Table 1. Food items delivered to 2 nests of Plain-winged Woodcreeper (*Dendrocincla turdina*) in Parque Provincial Cruce Caballero, Misiones, Argentina, 2015–2016, organized by phylum, subphylum, class, and order.

Taxon	Stage	Nest 1	Nest 2	Details
Arthropoda				
Hexapoda				
Insecta				
Blattodea	adult	0	1	
Coleoptera	larva	5	0	
	adult	32	0	includes 1 Curculionidae
Dermaptera	adult	1	0	
Diptera	adult	4	0	includes 2 Tabanidae
Hemiptera	adult	14	11	all Cicadidae
Hymenoptera	larva	>1	0	Formicidae
	adult	11	2	
Isoptera	adult	2	0	
Lepidoptera	larva	22	5	
	pupa	0	1	
	adult	17	5	includes 1 <i>Doxocopa</i> sp., 1 <i>Hamadryas februa</i>
Mantodea	adult	1	2	
Odonata	adult	3	1	
Orthoptera	adult	12	13	includes 7 Gryllidae, 6 Acridae, 1 Tettigoniidae
Phasmida	adult	0	1	
Neuroptera	adult	0	4	Chrysopidae
Chelicerata				
Arachnida				
Araneae	adult	6	3	
Opiliones	adult	2	0	
Myriapoda				
Chilopoda				
Geophilomorpha	adult	1	0	
Scolopendromorpha	adult	1	0	<i>Scolopendra</i> sp.
Unknown	adult	1	0	
Unknown	adult	1	0	
Chordata				
Amphibia				
Anura	adult	1	0	<i>Hypsiboas</i> sp.
Mammalia				
Chiroptera	juvenile	1	0	
Total		138	49	

feeding at the entrance occasionally in the last 3 days before fledging.

While incubating, the adult brought nest material, about 90% lichens, nearly every time it came to nest 1, until at least 27 October (5 d before hatching). It sometimes brought several items at once, including lichens, a blade of grass, and a small root; lichens and a tubular purple Bignoniaceae flower; leaves; lichens and a large piece of molted snake skin. Surprisingly, it also brought an insect (14 d before eggs hatched).

Incubation on-bouts were mean 35 (SE 5) min (range: 3–83; $n = 21$ complete on-bouts), off-bouts

were 16 (SE 1) min (range 8–28; $n = 24$), and the adult was in the cavity 62% of the daytime. The first 3 times we inspected nest 1 during incubation, the adult flushed when we were about 25 m away, leaving the eggs on top of the nest material; the last 2 times (1 and 3 d before hatching), it took longer to flush and left the eggs partially covered by lichens.

We could identify 187 of 349 food items taken to the nestlings one at a time (Table 1). Adult Coleoptera and adult and larval Lepidoptera were the most frequent items at nest 1, whereas adult Orthoptera and Hemiptera were most frequent at

Table 2. Comparison of general linear models predicting visitation rate (visits/h) at 2 nests of Plain-winged Woodcreeper (*Dendrocincla turdina*) in Parque Provincial Cruce Caballero, Argentina. Observation periods $n = 61$. Lowest AICc = 135.3.

Model	k	ΔAICc	w_i
1. Nestling age + time of day + nest ID	5	2.12	0.21
2. Time of day + nest ID	4	0.00	0.79
3. Nestling age + nest ID	3	28.58	<0.0001
4. Nest ID	2	26.37	<0.0001

nest 2. The top model predicting visitation rate during the nestling period included time of day (sunrise, daytime, or sunset) but not nestling age (Table 2). According to this model, visitation rate was significantly higher at sunrise (7.93 [SE 0.69] visits/h, $b = 4.79$, SE = 1.39, $t = 3.44$, $P = 0.0011$) and sunset (8.03 [SE 1.19] visits/h, $b = 4.71$, SE = 0.84, $t = 5.63$, $P < 0.001$) compared to other times of day (3.26 [SE 0.22] visits/h; Fig. 3). Nestling age ($|t| < 1.5$, $P > 0.1$ for all models) and nest identity ($|t| < 1.8$, $P > 0.05$ for all models) were not significant predictors of feeding rate, nor were they significant in alternate models (not shown here) in which we analyzed daytime and crepuscular observations separately, or averaged feeding rates across all times of day. The adult removed fecal sacs at nests 1 (days 8–26) and 2 (until day 24). Diurnal nest attendance remained about 60% immediately after hatching (days 1–2) but declined rapidly thereafter to only 1% on days 9–27 (Fig. 3c). The adult roosted in the cavity at nest 1 until

the nestlings were 14 days old (on 5, 9, 10, 11, 12, 13, 14, and 15 Nov, but not on 16, 17, 24, 25, or 26 Nov).

While nesting, the attending adult foraged alone, dissociated from any other *D. turdina*, monkeys, or bird flocks. For example, at nest 1 on 25 November (nestling day 24), it searched for arthropods near the nest, flaking pieces off the trunks of tree ferns. At nest 2 on 26 November (nestling day 23), it emerged from the nest, climbed a thin trunk, and then flew upward to sally-glean a cicada (Hemiptera: Cicadidae), which it took to the nest. On emerging, it flew to the same perch, caught a green grasshopper (Orthoptera: Acrididae) on the wing, returned to perch on a nearby tree, and a few seconds later flew with the prey to the nest. It emerged with a fecal sac, perched on the same initial tree, flicked away the fecal sac, sally-gleaned a cicada from the underside of some leaves, beat it against a branch for more than 1 min, and took it to the nest. The following day the adult flew from the staging tree to the middle of a tall (~20 m) alcérin tree (*Holocalyx balansae*) where it performed a vertical flight into the crown and sally-gleaned a large spider from the leaves. It seemed to take advantage of momentarily abundant food sources. For example, within a period of 1 h on 24 November at nest 2 (nestling day 21), it captured at least 5 lacewings (Neuroptera: Chrysopidae) by sally-gleaning on trees next to the nest tree. It took 4 of them to the nest and ate the fifth; we did not see lacewings delivered to either of the nests on any other occasion.

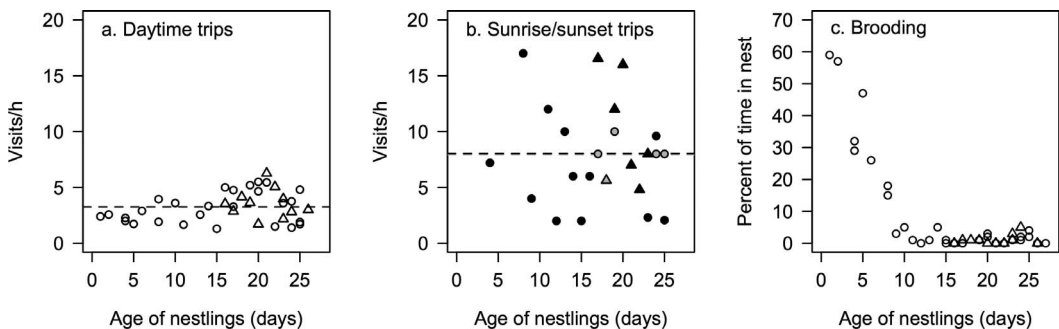


Figure 3. Nest attendance of adult Plain-winged Woodcreeper (*Dendrocincla turdina*) during the nestling period at nest 1 (circles) and nest 2 (triangles) in Parque Provincial Cruce Caballero, Misiones, Argentina. (a) Visitation rate (number of visits/h) during daytime (15 min after sunrise to 15 min before sunset). (b) Visitation rate at sunrise (15 min before to 15 min after sunrise; gray) and sunset (15 min before to 15 min after sunset; black). Dashed horizontal lines indicate means for each time of day. (c) Brooding behavior (percent of time in nest).

Fledging

At both nests, the adult began hesitating with food outside the cavity 3 d before the chicks fledged, vocalizing and showing the food to the nestlings up to 4 times before entering. At 0545 h (5 min after sunrise) on 28 November (nestling day 27, nest 1), FGD found both chicks vocalizing, one from the cavity entrance and the other from a nearby tree. Each time the adult fed the nestling at the cavity entrance, the nestling emerged a little more. When the adult was away, the nestling opened and closed its wings. At 0700 h, the adult hitched around the tree trunk with food in its bill; the nestling followed it up the trunk, was fed, and made its first flight to a nearby tree. Minutes later, the adult approached this chick with food and then flew to a nearby tree; the chick pursued the adult until both were lost from sight. In the next 30 min, the adult returned to the nest cavity twice with food but did not enter, instead taking the food to a fledgling that vocalized out of sight. At 0835 h the cavity contained beetle remains (elytra) and 2 fecal sacs.

Interactions with potential predators and competitors

A pair of Red-breasted Toucans (*Ramphastos dicolorus*) nested 8.8 m above nest 1, completely obscured by tree ferns. They laid their first egg on 4 or 5 October, presumably a few days before the *Dendrocincla*. Although they are important nest predators, these toucans probably could not access the woodcreeper's deep, narrow cavity (Cockle et al. 2016). On 22 October (10 d before hatching) the adult woodcreeper arrived at the cavity with nest material, but seeing one of the toucans hunting near the ground about 6 m away, it flushed and flew far away. Three minutes later when the toucan had gone, the woodcreeper adult returned quietly and cautiously, making short flights from tree to tree and looking attentively at the spot where the toucan had been. Likewise on 24 October (8 d before hatching), on one of its return trips to the nest, the woodcreeper was interrupted by one of the toucans crossing just above the nest, and spent 8 min flying from tree to tree inspecting the surroundings before entering. In general, however, the 2 species coexisted in harmony. If the toucans offered any protection

against other nest predators, it was not obvious; we never saw them chase any animals away.

A pair of *Dendrocolaptes platyrostris* also had a nest in a cavity about 50 m away. They were often 10–15 m from the *Dendrocincla turdina* nest, but normally the adult ignored them. On 25 November 2015, a *Dendrocolaptes* flew to the trunk 2 m below the *Dendrocincla* cavity entrance while the adult was inside feeding its 24-day-old nestlings. As soon as the *Dendrocolaptes* landed, the *Dendrocincla* flew out of the cavity (carrying a fecal sac) directly toward the *Dendrocolaptes* and chased it behind another tree while uttering an unusual, sharp, aggressive vocalization. The *Dendrocincla* quickly returned without the fecal sac, perched on the tree trunk 1.5 m below the cavity entrance, and then flew off to search for food. The following day, after feeding the nestlings, the adult *Dendrocincla* was searching for food when an adult *Dendrocolaptes platyrostris* landed on a tree about 10 m from the nest; the *Dendrocincla* attacked and pursued the intruder until both were out of sight.

On another occasion (21 Nov) the adult *Dendrocincla* was approaching nest 1 with food for its 20-day-old nestlings and noticed an adult *Sittasomus griseicapillus* perched on a trunk about 5 m away. The *Dendrocincla* changed course to fly directly at the *Sittasomus*, displacing it on the trunk, then flew to the cavity and fed the nestlings. When it emerged, it flew back to the same trunk, noticed the *Sittasomus* on another nearby tree, chased it away, and then flew off in another direction to forage.

Discussion

Foraging and diet

When not attending a nest, *D. turdina* adults were nearly always found with black capuchin monkeys. Although we did not quantify the density of either species, the dramatic and simultaneous increases in detections at Parque Provincial Cruce Caballero from 2012 to 2016 suggest that the abundance of *D. turdina* in the interior (western) Atlantic Forest may be strongly tied to that of their foraging associates. While nesting, however, *D. turdina* adults foraged singly, away from mammals or other birds, likely because it would be inefficient to follow wide-ranging foraging associates while attending a nest in a

fixed location. *Dendrocincla fuliginosa* has also been reported to forage away from ant swarms while nesting (Willis 1972).

Nesting *D. turdina* foraged opportunistically on arthropods, frogs, and a bat, most actively at dawn and dusk. As the light failed and most birds went to roost, *D. turdina* caught and delivered multiple prey in quick succession, reminiscent of the flurries of activity at dusk (e.g., 14 visits in 33 min) described by Skutch (1969) for *Dendrocincla anabatina*. The diet of nestling *D. turdina* was similar to the stomach contents reported for *D. turdina* adults and diet of nestling *D. fuliginosa* (Willis 1972, Lopes et al. 2005). Small lizards seemed to be uncommon in our study area, and we observed none among the prey items of *D. turdina*, although they comprised 22 of 76 food items seen at a nest of *D. anabatina* (Skutch 1969) and at least one of the items at a nest of *D. fuliginosa* (Willis 1972).

Nest construction

The nest sites we describe for *D. turdina* are similar to those of other *Dendrocincla* (0.6–10 m high, 25–213 cm deep; Pinto 1953, Skutch 1969, Willis 1972, French 1973, Stiles and Skutch 1989, Greeney et al. 2009). Lichens comprised most of the nesting material observed for *D. turdina* in our study (although we did not observe the early days of nest construction), *D. anabatina* (Skutch 1969), and *D. tyrannina* (Greeney et al. 2009). However, the only previously described nest of *D. turdina* was lined with wood chips (Willis 1983); nests of *D. fuliginosa* contained dry moss, leaves, stems, *Marasmius* rhizomes, feathers, and plant down (Zeledón in Wetmore 1972, French 1973); and nests of *D. homochroa* contained moss, leaves, bark, and fibers (Stiles and Skutch 1989), suggesting flexibility in nesting material within and among species.

Uniparental care in Dendrocolaptinae

Only one adult attended each nest of *D. turdina*, coinciding with other species of *Dendrocincla* (Skutch 1969, Willis 1972). Only once did Skutch (1969) see a second adult near any nest of *D. anabatina*; it perched on the nest stub but did not approach the cavity or interact directly with the attending adult. In *D. fuliginosa* and *D. anabatina* the pair bond is brief, and in *D. tyrannina* the

mating system may approach an exploded lek (Skutch 1969, Willis 1972, Willis and Oniki 1995). No evidence exists that *Dendrocincla* males provide any support to the nesting female, not even nest or territory defense.

Uniparental (female-only) care is unusual in passerines and even more unusual among forest insectivores (Cockburn 2006). Although biparental care is the norm in Furnariidae (Remsen 2003), there is evidence that uniparental care has arisen at least twice in cavity-nesting Furnariinae (*Pseudocolaptes* and *Anabacerthia/Heliobletus*) and Dendrocolaptinae (*Xiphorhynchus* and *Dendrocincla/Sittasomus*; Cockle and Bodrati 2017). Predation risk increases with parental activity around the nest (Martin et al. 2000a, 2000b), and female-only care might facilitate nest concealment in passerines (Snow 1976, Lill 1986, Schulze-Hagen et al. 1999, Cockle and Bodrati 2017). In *Dendrocincla* and other Dendrocolaptinae, we propose that uniparental care is associated with a suite of nesting strategies and reproductive parameters, including secrecy at the nest, concealment of eggs, small clutch, long nestling period, and slow nestling growth.

The stealthy demeanor exhibited by *D. turdina* adults around their nests seems similar to the behavior described by Willis (1972) for *D. fuliginosa* and recalls other furnariids with uniparental care (Skutch 1969, Bodrati et al. 2012b, Cockle and Bodrati 2017) but contrasts with woodcreepers that exhibit biparental care (Cockle and Bodrati 2009, 2013; Bodrati and Cockle 2011). Twice we observed that an adult *D. turdina* had covered its eggs with nesting material, a behavior we likely missed on other occasions because we startled the adult on the nest. Uniparental *D. anabatina*, Buff-throated Woodcreeper (*Xiphorhynchus guttatus*), and *Sittasomus griseicapillus* also frequently cover eggs with nesting material (Skutch 1969, 1996; Bodrati et al. 2012b); by contrast, we have never observed such behavior in woodcreepers with biparental care, whose eggs are incubated nearly 100% of the time, including *Dendrocolaptes platystris*, *Xiphocolaptes albicollis*, Great Rufous Woodcreeper (*Xiphocolaptes major*), *Lepidocolaptes falcinellus*, Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), *Campylorhamphus falcularius*, Red-billed Scythebill (*Campylorhamphus trochilirostris*), and Scimitar-billed Woodcreeper (*Drymornis*

bridgesii; Bodrati 2003; Cockle and Bodrati 2009, 2013; Bodrati and Cockle 2011; Bodrati et al. 2015; AB, unpubl. data). Stealthy behavior and egg-concealment may reduce the risk of detection by predators.

The 2-egg clutch of *D. turdina* in the Atlantic Forest is smaller than expected given that our nests were at a higher latitude than any other *Dendrocincla* nest that has been studied. In general, avian clutch size increases with latitude (a pattern that is, nevertheless, most pronounced in the northern hemisphere; Lack 1948, Jetz et al. 2008). One-egg clutches were reported for 2 *Dendrocincla* nests (*D. tyrannina* Greeney et al. 2009; and *D. fuliginosa* Pinto 1953), and 3-egg clutches are mentioned for *D. homochroa* (Stiles and Skutch 1989), but all other *Dendrocincla* clutches comprised 2 eggs (*D. turdina*, Willis 1983; *D. fuliginosa*, Snow and Snow in Willis 1972, French 1973; *D. homochroa*, Stiles and Skutch 1989; *D. anabatina*, Skutch 1969). In our study area, biparental *Dendrocolaptes platyrostris*, *Lepidocolaptes falcinellus*, and *Xiphocolaptes albicollis* typically lay 3 or even 4 eggs (Cockle and Bodrati 2009, 2013; Bodrati and Cockle 2011; KLC, unpubl. data). *Dendrocincla turdina* may be constrained to a 2-egg clutch by the single parent's ability to care for the young.

The nestling period we found for *D. turdina* (26–27 d) falls within the typical range for *Dendrocincla* but is longer than that of woodcreepers with biparental care. Skutch (1969) characterized the 24 d nestling period of *D. anabatina* as “surprisingly long,” and Greeney et al. (2009) found an even longer nestling period of at least 29 d for *D. tyrannina*. In our study area, biparental *Dendrocolaptes platyrostris*, *Lepidocolaptes falcinellus*, and *Xiphocolaptes albicollis* have nestling periods of 16–18, 18–19, and 18–22 d, respectively (Cockle and Bodrati 2009, 2013; Bodrati and Cockle 2011).

Nestling development was slower in *D. turdina* than in biparental woodcreepers in our study area (Cockle and Bodrati 2009, 2013; Bodrati and Cockle 2011). Recently hatched nestlings of *Dendrocincla turdina* appeared very similar to those of *Dendrocolaptes platyrostris*, *L. falcinellus* and *X. albicollis*. In *Dendrocincla turdina*, pin feathers emerged between days 6 and 10, and the eyes opened between days 10 and 15. In *Dendrocolaptes platyrostris*, *L. falcinellus*, and *X.*

albicollis, pin feathers were projecting from the skin by day 4–5 and eyes were open by day 5–7. By day 15, when the pin feathers on *Dendrocincla turdina* nestlings were just starting to open, these other birds were fully feathered and nearly ready to fledge. Rate of food delivery by *Dendrocincla turdina* was similar to that of *X. albicollis* but generally lower than that of *Dendrocolaptes platyrostris* and *L. falcinellus*. The adult *Dendrocincla turdina* was on the nest only 45% of the time between days 1 and 5 and stopped brooding by day 9, similar to *D. anabatina* (Skutch 1969), whereas *X. albicollis* and *L. falcinellus* adults in our study area were in the nest 65% and 88% of the time, respectively, over the first 5 days (Bodrati and Cockle 2011; KLC, unpubl. data). When nestling birds experience cooler temperatures they must sacrifice growth to invest more energy in thermoregulation (Dawson et al. 2005). We suggest that adults in the genus *Dendrocincla*, working alone, face a trade-off between brooding time and food delivery, resulting in slower nestling growth and a longer nestling period compared to sympatric woodcreepers with biparental care.

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