

PREDATORS OF BIRD NESTS IN THE ATLANTIC FOREST OF ARGENTINA AND PARAGUAY

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ABSTRACT.—Predation is the major cause of avian nest failure, and an important source of natural selection on life history traits and reproductive behavior. However, little is known about the identity of nest predators in much of the world, including the Neotropics. To identify some of the nest predators exerting selection pressure on birds of the subtropical Atlantic forest, we present observations of animals depredating bird nests in Argentina and Paraguay. We recorded depredations (destruction or removal of eggs or nestlings) at 33 nests of 25 species of birds, confirming as predators ten species of birds (Squirrel Cuckoo *Piaya cayana*, White-eared Puffbird *Nystalus chacuru*, Toco Toucan *Ramphastos toco*, Red-breasted Toucan *Ramphastos dicolorus*, Saffron Toucanet *Pteroglossus bailloni*, Chestnut-eared Aracari *Pteroglossus castanotis*, Planalto Woodcreeper *Dendrocolaptes platyrostris*, White-throated Woodcreeper *Xiphocolaptes albicollis*, Buff-browed Foliage-gleaner *Syndactyla rufosuperciliata*, and Plush-crested Jay *Cyanocorax chrysops*) and two species of medium-sized mammals (White-eared Opossum *Didelphis albiventris* and Crab-eating Fox *Cerdocyon thous*), and inferring two additional mammal species (Black Capuchin Monkey *Sapajus nigritus* and Southern Tigrina *Leopardus guttulus*). Fifty-five percent of these nests were depredated by toucans or aracarís (Ramphastidae), which destroyed eggs and nestlings at cup-, closed- and cavity-nests. Red-breasted Toucans destroyed nests 1.6–22 m high, in habitats ranging from primary forest to a backyard. Mammals and jays depredated nests from ground-level to midstory, whereas woodcreepers and aracarís depredated nests from the midstory to canopy. We did not record snakes at any bird nests, in strong contrast to studies from other Neotropical forests. Further studies should examine trade-offs among nest concealment, physical protection, and parental defense behavior as means of reducing nest predation, and use camera traps to quantify nest predation rates by predator species. Received 8 January 2015. Accepted 30 May 2015.

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Predation is the major cause of nest failure among birds (Ricklefs 1969). As such, it is an important source of natural selection on life history traits and reproductive behaviors such as nest construction and attentiveness (Lack 1948; Martin 1993, 1995; Fontaine and Martin 2006). These selection pressures are likely to vary according to nest predator taxon; however, nest predation is difficult to observe, and little is known about the identity of nest predators in many parts of the world.

Skutch (1985) considered snakes to destroy more bird nests in tropical America than all other

predators together. His idea was supported by videos of understory nests in Central America, where snakes were responsible for >80% of predations (Robinson et al. 2005, Visco and Sherry 2015). Likewise, studies from Jamaica and Argentina (Chaco) revealed snakes to be major predators of nestling parrots in tree cavities (Koenig et al. 2007, Berkunsky et al. 2011). Snakes, birds, mammals, and fire ants preyed on nests in northwestern Argentina, Panama and Costa Rica (mostly cup nests in the understory; Robinson and Robinson 2001, Auer et al. 2007, Tarwater 2008, Visco and Sherry 2015). Within regions, predator-specific predation risk varies according to habitat, nest type, and nest placement (Thompson and Burhans 2003, Benson et al. 2010, Chiavacci et al. 2014, Visco and Sherry 2015). Here we contribute to the identification of nest predators in the Neotropics by presenting observations of nest predations in the subtropical Atlantic forest of Argentina and Paraguay.

METHODS

We observed predation of bird nests in the Atlantic forest in the course of bird surveys in Argentina (1997, 2000, 2003–2014) and Paraguay (2000–2002), and as part of our studies of tree-cavity nests

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TABLE 1. Number of predations of bird nests we observed in the Atlantic forest by predator identity and nest type.

Predator/usurper	Simple unlined or cup on ground	Cup in shrub or tree	Closed in shrub or tree	Cavity in tree, bank, or termitarium	Total
Squirrel Cuckoo			1		1
White-eared Puffbird				1	1
Toco Toucan				1	1
Red-breasted Toucan		6	4	2	12
Saffron Toucanet			1		1
Chestnut-eared Aracari			1	3	4
Planalto Woodcreeper				1	1
White-throated Woodcreeper		1	1	1	3
Buff-browed Foliage-gleaner				1	1
Plush-crested Jay	1		2		3
White-eared Opossum				1	1
Black Capuchin Monkey				2	2
Crab-eating Fox	1				1
Southern Tigrina				1	1
Total	2	7	10	14	33

(2006–2014) and woodpecker biology (2011–2014) in Argentina. Although our study sites were south of the Tropic of Capricorn, floristics and physiognomy unite these southern forests with the northern Atlantic forests and they are often included under the broader category of tropical moist forests (Oliveira-Filho and Fontes 2000, Negrelle 2002). The Atlantic forest is among the top five biodiversity hotspots in the world, characterized by high levels of endemism, but with extensive habitat loss and high numbers of threatened species (Myers et al. 2000, Ribeiro et al. 2009).

Nests were found by flushing or following adult birds (including radio-tagged *Dryocopus* woodpeckers), and, when possible, monitored every 1–15 days using direct observations, tree climbing, or a pole-mounted video camera to view nest contents (see Cockle et al. 2015). Several nests were discovered just as they were being depredated. We observed nests during >1000 daylight hours (mostly nests in tree cavities) and about 40 hours on moonlit nights (mostly nests of owls and nightjars), using binoculars or telescope, sometimes from a blind. We confirmed nesting by observing nest contents (eggs or nestlings), or by adult behavior (long periods in nest, apparently incubating; taking food to nest). We defined predation to include any removal or destruction of eggs or nestlings (regardless of whether they were consumed). In most cases, predator identity was determined from direct observations of predators removing nest contents. In a few cases, we inferred predator identity from observations of known predator species inspecting nests around the time their

contents disappeared. We included these unconfirmed cases to reduce bias against mammals. Wary of observers and often nocturnal, Atlantic forest mammals are extremely difficult to observe in the act of predation. Two predation events were recorded by camera traps, which were mounted ca. 5 m from nests and took a photo every 5 sec during daylight hours. We took the following measurements of tree cavities at the end of the nesting cycle: diameter (horizontal \times vertical) of each entrance, cavity depth, height above ground (from bottom lip of lowest cavity entrance to the ground). For non-cavity nests, heights were estimated visually. Nest descriptions conform to Simon and Pacheco (2005).

RESULTS

We identified or inferred 10 species of birds and 4 species of medium-sized mammal to be the predators at 33 depredated nests of 25 species of birds (Table 1). Toucans and aracarids (Ramphastidae) were responsible for 55% of these depredations, destroying both eggs and nestlings at cup-, closed- and cavity-nests, at heights from 1.6 to 22 m, in habitats ranging from primary forest to a backyard (Table 1, Fig. 1).

Squirrel Cuckoo (*Piaya cayana*)

On 14 November 2010, KC and AB observed a Squirrel Cuckoo hopping among approximately 40 closed/long/pensile Red-rumped Cacique (*Cacicus haemorrhous*) nests, which hung from three *Syagrus romanzoffiana* palms in a 0.2 ha clearing beside the ranger station at Parque Provincial (PP)

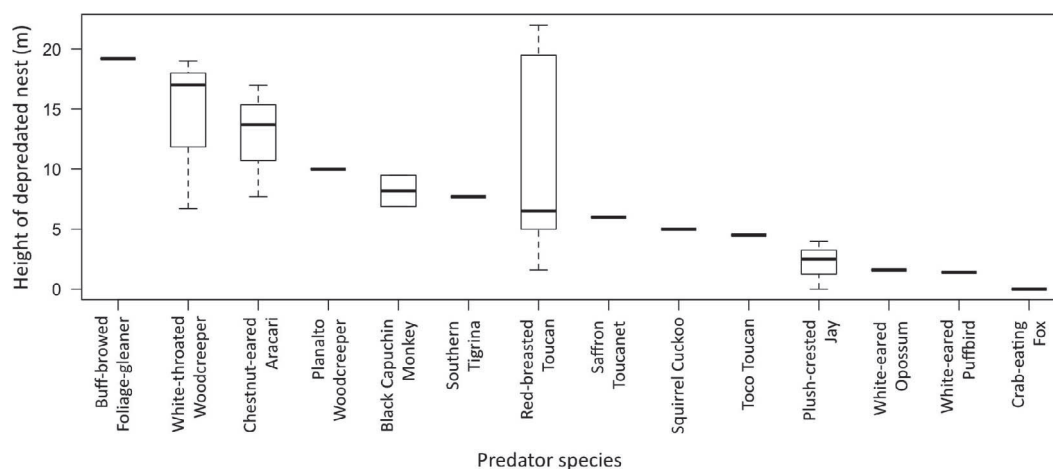


FIG. 1. Box-and-whisker plot of the heights of nests confirmed or inferred to have been depredated by 14 species of birds and mammals in the Atlantic forest of Argentina and Paraguay. Thick horizontal bars indicate median nest height, boxes indicate first and third quartiles, and whiskers indicate range.

Cruce Caballero in Misiones, Argentina (26° 31' S, 53° 59' W). Piratic Flycatchers (*Legatus leucophaius*) had usurped, from the caciques, a nest about 5 m high, which now contained nestlings. The cuckoo inserted its head into this nest, and over the course of several minutes apparently consumed the nestlings, while the flycatchers fluttered nearby and the caciques vocalized insistently from a distance. On following days, the Piratic Flycatchers no longer attended the nest, although the structure remained intact.

White-eared Puffbird (*Nystalus chacuru*)

In October 2005, AB observed a White-eared Puffbird emerge from a tunnel at a height of about 1.4 m in the 2-m high embankment of a dirt road at the edge of the town of San Pedro in Misiones, Argentina (26° 38' S, 54° 07' W). Southern Rough-winged Swallows (*Stelgidopteryx ruficollis*) had been seen exiting the tunnel on previous days. Now, they swooped at the puffbird, which flew away with an egg.

Toco Toucan (*Ramphastos toco*)

In October 2001, AB observed a Toco Toucan fly to the cavity nest of a Buff-bellied Puffbird (*Notharchus swainsonii*), excavated in an arboreal termitarium about 4.5 m high, within a plantation of shade-grown yerba mate (*Ilex paraguariensis*) at Itabó Private Nature Reserve in Canindeyú, Paraguay (24° 30' S, 54° 38' W). The puffbird flushed from the nest and perched on a nearby

tree, emitting alarm calls. The toucan spent about 5 mins pulling the (unidentified) contents out of the cavity, and then flew away. The puffbird returned quickly, but on following days the nest was not active.

Red-breasted Toucan (*Ramphastos dicolorus*)

Toward the end of November 2011, AB and J. M. Klavins heard a commotion from a nest of Squirrel Cuckoos, which contained nestlings. The nest was a cup, placed about 6 m high in a vine tangle in a young *Araucaria angustifolia*, in primary forest at the edge of the 0.2-ha clearing around the ranger station at PP Cruce Caballero. On approaching, the observers saw a Red-breasted Toucan exit the nest. One of the cuckoos attempted to chase away the toucan, but was unsuccessful. The nest was abandoned that afternoon and not used again.

On 23 November 2011, AB and J. M. Klavins saw a Red-breasted Toucan flush a Pearly-breasted Cuckoo (*Coccyx euleri*) from its cup nest, about 20 m high in a living *Cedrella fissilis* in primary forest at PP Cruce Caballero. The cuckoo fluttered around the toucan and then perched a few meters from the nest while the toucan consumed at least one egg. The toucan quickly flew away and the cuckoo returned to its nest a few seconds later.

On the evening of 14 October 2014, AB heard a Lineated Woodpecker (*Dryocopus lineatus*) vocalizing in alarm, and drumming insistently, near its nest cavity, which was excavated 22 m high in a dead tree, in primary forest at PP Cruce

Caballero. Its mate answered with calls and drumming, and then flew in. A Red-breasted Toucan flew to the cavity and introduced its bill, head, and body, leaving only the tail visible. One of the woodpeckers fluttered around the toucan but did not fly at it directly. The toucan pulled its head out and held a white egg in its bill. It flew away and the observer left 5 mins later. The next morning, CF observed the toucan again clinging to the cavity. On following days, the nest appeared inactive. A pair of Red-breasted Toucans was incubating eggs in another cavity, about 20 m away.

Near the end of September 2011, CF and M. R. Gómez heard a commotion from a yard in the town of San Pedro, and observed a Red-breasted Toucan descending toward the closed/globular nest of a pair of Great Kiskadees (*Pitangus sulphuratus*), about 7 m high in a nearly leafless *Melia azedarach*. The toucan removed and consumed an egg and apparently a small nestling, ripping a piece of the nest in the process. The kiskadees swooped at the toucan but did not touch it. A second toucan was present but did not approach the nest.

On 3 November 2010, AB observed a Red-breasted Toucan consuming at least one nestling from a Boat-billed Flycatcher (*Megarynchus pitangua*) nest at PP Cruce Caballero. The nest was a cup placed about 6 m above the ground in the same *Araucaria angustifolia* as the Squirrel Cuckoo nest. The adult flycatchers swooped at the toucan repeatedly, hitting it audibly, and the toucan quickly left the area. That afternoon, and on following days, the nest was no longer active.

On 15 November 2008, J. M. Segovia was watching a Black-tailed Tityra (*Tityra cayana*) nest in a tree cavity above a road in primary forest at PP Cruce Caballero, when a Red-breasted Toucan arrived and consumed the contents (probably young nestlings). The cavity was 21 m high in a branch of a dead *Apuleia leiocarpa*. It had been excavated by Yellow-fronted Woodpeckers (*Melanerpes flavifrons*), and then a piece of the wall had broken, enlarging the entrance before the tityras used it.

On 4 November 2011, AB heard a commotion from a cup nest of Plush-crested Jays (*Cyanocorax chrysops*), about 8 m high in an *Araucaria angustifolia* in primary forest near the ranger station at PP Cruce Caballero. He approached the nest and observed two or three jays chasing away a Red-breasted Toucan, which escaped with an egg. Apparently the toucan did not remove all the

contents because on following days the nest remained active.

On 26 October 2010, AB observed a Red-breasted Toucan depredating the cup nest of a Pale-breasted Thrush (*Turdus leucomelas*) at PP Cruce Caballero. The nest was placed 2.7 m above the ground on epiphytes on the trunk of a *Cabralea canjerana* in primary forest at the edge of the 0.2-ha clearing beside the ranger station. The adult thrushes scolded the toucan and attempted to chase it away, but it consumed their three eggs. The same toucan, or its mate, likely depredated the Boat-billed Flycatcher nest (see above).

On 3 November 2010, AB observed a Red-breasted Toucan at a nest of Rufous-bellied Thrush (*Turdus rufiventris*) at PP Cruce Caballero. The nest was a cup placed 1.6 m high in an *Ocotea diospyrifolia* in primary forest at the edge of the 0.2-ha clearing beside the ranger station. It had contained an egg and two unfeathered nestlings earlier in the day. The adult thrushes scolded and chased the toucan, hitting its wing as it flew, but the nest was now empty. The same toucan, or its mate, likely depredated the Boat-billed Flycatcher and Pale-breasted Thrush nests (see above).

On 18 October 2005, AB observed a Red-breasted Toucan entering the closed/long/pensile nest of a Red-rumped Cacique at PP Moconá in Misiones, Argentina (27° 09' S, 53° 54' W). The nest was about 5 m high, part of a colony in a *Syagrus romanzoffiana* palm. The palm was in a clearing beside the ranger station, adjoining an abandoned air strip, surrounded by well-conserved native forest. The nest swung as the toucan landed. Clinging to the entrance, the toucan inserted its bill, head, and neck. It consumed part of the nest contents and emerged with one egg, which it consumed quickly. The caciques vocalized and fluttered at a safe distance, but did not approach the toucan.

On 3 November 2010, AB observed a Red-breasted Toucan entering the 5-m high closed/long/pensile nest of a Red-rumped Cacique in the colony next to the ranger station at PP Cruce Caballero (habitat described above). The toucan removed and consumed at least one unfeathered nestling. The caciques vocalized and fluttered around the toucan, but did not approach it. On following days, the nest was no longer attended, and soon fell to the ground. The same toucan, or

its mate, likely depredated the nests of the Boat-billed Flycatcher and two thrushes (see above).

On 27 October 2010, AB observed a Blue-naped Chlorophonia (*Chlorophonia cyanea*) flush from its closed/globular/lateral nest, about 19 m high, on the trunk of an *Araucaria angustifolia* in primary forest at PP Cruce Caballero. A Red-breasted Toucan was hopping along a branch toward the nest. It opened the nest and consumed the (unidentified) contents. A chlorophonia vocalized from higher in the nest tree, but did not approach the toucan.

Saffron Toucanet (*Pteroglossus bailloni*)

On 23 October 2010, AB observed a Saffron Toucanet enter one of the closed/long/pensile Red-rumped Cacique nests in the colony next to the ranger station at PP Cruce Caballero (mentioned by Fraga 2011). The nest was about 6 m above ground and contained nestlings. The toucanet removed the nest contents, swallowed, and flew away, all within about 30 seconds. It was much more efficient than the Red-breasted Toucan, presumably because its smaller body size allowed it to perch on the nest, enter and exit quickly. The caciques vocalized loudly but perched and watched the toucanet rather than attempting to chase it away.

Chestnut-eared Aracari (*Pteroglossus castanotis*)

A Green-barred Woodpecker (*Colaptes melanochloros*) nest in a *Cedrela fissilis* was depredated in stages, possibly by Chestnut-eared Aracari. The cavity was excavated by the Green-barred Woodpeckers, 13.7 m high in a broken branch. It had one entrance, 6.4 × 12.1 cm in diameter, and the interior was 31.9 cm deep vertically. The tree was at the edge of primary forest, beside the ranger station at PP Cruce Caballero. On 4 November 2008 the cavity contained four eggs, which were expected to hatch between 8 and 10 November. On 11 November it contained at least one egg and an incubating/brooding female (which covered the rest of the contents, probably young nestlings). On 12 November, S. A. Fernández observed a Chestnut-eared Aracari with its head inside the cavity. The adult woodpeckers chased away the aracari. The cavity, checked immediately, contained one egg and one eggshell. On 18 November it was empty. Although it is possible that another predator was responsible, we infer that Chestnut-eared Aracari was the most likely predator.

On 18 October 2014, EBB witnessed a Chestnut-eared Aracari depredating a Green-barred Woodpecker nest in a tree cavity, 17 m high, in a dead branch of a *Nectandra lanceolata* at the edge of PP Cruce Caballero, in degraded forest beside a dirt road. The female woodpecker was inside the cavity, apparently incubating. A Chestnut-eared Aracari flew to the tree, and approached the cavity. The female woodpecker flushed and joined the male in chasing away the intruder. When the woodpeckers had disappeared from sight, two or three other Chestnut-eared Aracaris flew in. One stayed on a branch near the nest, while another entered the cavity, emerging with an egg in the tip of its bill. Lifting its head, it tossed the egg down to the base of its bill, without swallowing it, then flew away with two other aracaris. After ~1 min, a Red-breasted Toucan flew to the cavity, inserted its head several times, and flew away. The pair of woodpeckers returned 5 mins later and entered the cavity. The female disappeared into the nest chamber, and the male remained in the entrance, looking out for 30 mins before flying away. Julieta Benítez observed the cavity on 20 October. An adult Green-barred Woodpecker spent 1 hr 50 mins in the cavity (apparently incubating), then emerged and disappeared from view. Two Chestnut-eared Aracaris flew to the cavity 13 mins later. One of the adult woodpeckers vocalized insistently and attempted to chase them away, but they entered the cavity several times, appearing to remove and eat some nest contents. The adult woodpeckers did not return within the next 40 mins, but one was seen looking out of the cavity on two separate occasions the following day. By 2 November the nest appeared inactive.

On 13 October 2014, a camera trap recorded a Chestnut-eared Aracari depredating the nest of a banded pair of Lineated Woodpeckers over the main trail in primary forest at PP Cruce Caballero (Fig. 2). The cavity was excavated by the same pair of woodpeckers in 2013. It was 7.7 m high in the trunk of a dead *Solanum granuloso-leprosum*; it had one entrance, 8 × 7 cm in diameter; and the interior was 31 cm deep vertically. Prior to the arrival of the aracari, the nest contained an unfeathered, 7-day old nestling and one or two non-viable eggs. The female woodpecker was brooding, and looked from the cavity with open bill from 1052 to 1100, presumably warily watching the aracari approach. At 1101 the aracari landed in front of the cavity, the woodpecker apparently having fled. Over the next 2 mins, the aracari entered the cavity three



FIG. 2. Sequence of images registered by camera trap, showing a Chestnut-eared Aracari (*Pteroglossus castanotis*) depredating a nest of Lineated Woodpecker (*Dryocopus lineatus*) in a tree cavity at PP Cruce Caballero, 13 October 2014. At 10:55:10 the brooding female woodpecker looks from the cavity entrance with open bill; 11:01:30 and 11:01:35 the aracari clings to the cavity; 11:01:50 the aracari emerges from the cavity; 11:02:00 the aracari reaches in to the cavity; 11:02:05 the aracari removes the 7-day old woodpecker nestling; 11:02:10 the aracari drops the nestling, 11:02:20 the aracari climbs into the cavity (tip of tail visible); 11:02:25 the aracari holds an egg or egg shell in its bill.

times, removed the nestling and dropped it on the ground (it appeared too large for an aracari to swallow), and removed an egg or egg shell (Fig. 2). At 1115 the nestling was found dead on the ground below the cavity, with small wounds to the skin, and the cavity contained the remains of an egg (M. Cenizo, pers. comm.).

On 5 February 2000, AB observed a Chestnut-eared Aracari inside a closed/long/pensile nest of Red-rumped Caciques, where nestlings had been heard vocalizing, at Parque Nacional Iguazú in Misiones, Argentina (25° 41' S, 54° 27' W). The nest was part of a colony in a *Syagrus romanzoffiana* palm, in a clearing beside a house, surrounded mostly by secondary forest. As it was late in the season, few of

the other nests remained active. The aracari consumed the nest contents and flew away, leaving the nest empty, with light visible through the woven fibers.

Planalto Woodcreeper (*Dendrocolaptes platyrostris*)

On 5 October 2005, AB discovered a group of Yellow-fronted Woodpeckers (*Melanerpes flavifrons*) displaying loudly near an excavated cavity about 10 m high in a dead tree within a small natural clearing in well-conserved forest at Área Experimental Guaraní in Misiones, Argentina (26° 56' S, 54° 13' W). A Planalto Woodcreeper entered the cavity, emerged with something in its bill, and flew away. One of the woodpeckers

swooped down to give chase, and three or four stayed calling on the nest tree.

White-throated Woodcreeper
(*Xiphocolaptes albicollis*)

On 26 September 2014, CF saw a White-throated Woodcreeper flush a Short-tailed Antthrush (*Chamaeza campanisona*) from a cavity in primary forest at PP Cruce Caballero (Bodrati et al. 2014). The cavity was produced by natural decay, 6.7 m high, in the main trunk of a living tree. It had one entrance, 9.1 × 11.6 cm in diameter, facing upward, and was 145 cm deep vertically. The woodcreeper descended the branch and entered the cavity backwards, then exited with an egg and flew away. About an hour later, on returning to the tree, CF observed a Short-tailed Antthrush holding a brown leaf, on a branch near the cavity. We returned to the tree on 1 October and found eggshells on the ground, but the cavity contained only leaves.

On 25 October 2014, AB was watching a White-throated Woodcreeper about 80 m from its nest tree in primary forest at PP Cruce Caballero. It hitched up a large branch covered in lichens, about 19 m high in a living tree. Suddenly, it was attacked by a Red-eyed Vireo (*Vireo olivaceus*). It continued to hitch up the branch, then moved easily to the vireo's cup nest, which was attached laterally to twigs about 50 cm away. It removed and consumed a nestling, then flew downward with an empty bill, leaving the nest structure destroyed. The vireo continued to swoop at the woodcreeper, which seemed unperturbed.

On 28 October 2010, J. M. Segovia and L. G. Pagano observed a White-throated Woodcreeper destroying the nest of a Blue-naped Chlorophonia at the edge of primary forest beside the ranger station at PP Cruce Caballero (Bodrati and Cockle 2011). The nest was closed/globular/lateral, attached to a *Cabrlea canjerana* branch about 17 m high. The woodcreeper carried away an egg, flying in the direction of its own nest.

Buff-browed Foliage-gleaner
(*Syndactyla rufosuperciliata*)

On 23 November 2013, Kirsten Wilcox saw a Buff-browed Foliage-gleaner destroy a Black-crowned Tityra (*Tityra inquisitor*) egg at PP Cruce Caballero. The tityra nest was in an excavated cavity 17 cm deep, 4.5 × 3.5 cm in entrance diameter, 19.2 m high in a live branch of

a *Cedrela fissilis* at the edge of primary forest. During an incubation off-bout, two Buff-browed Foliage-gleaners flew to the cavity. One entered and removed an egg, which it crushed in its bill and let drop to the ground. The two foliage-gleaners flew away, and later the female tityra returned to the cavity. The foliage-gleaners returned but the male tityra chased them from the tree. The foliage-gleaner apparently did not remove all the tityra nest contents, because the tityras were observed feeding nestlings on four occasions between 8 and 21 December. We interpret the egg-crushing incident as interference competition. Buff-browed Foliage-gleaners had nested in this cavity in 2012, and in another cavity in the same tree in 2013, until their nest failed, about 8 days earlier.

Plush-crested Jay (*Cyanocorax chrysops*)

On 25 October 2013, AB heard a group of Plush-crested Jays vocalizing near the nest of a Yellow-olive Flycatcher (*Tolmomyias sulphurescens*), in primary forest at PP Cruce Caballero. The nest was closed/retort/pensile and hung about 4 m above a stream. On approaching, the observer saw that a jay was hanging from the entrance. It inserted its head and extracted an egg. One of the flycatchers swooped near the jay, without much effect. When the jays left, the nest hung lopsided and empty, with the entrance deformed. Salvador and Bodrati (2013) reported this predation event without details.

On 28 September 2008, AB observed Plush-crested Jays depredating a cup nest of Rufous-collared Sparrows (*Zonotrichia capensis*) on the ground amid grass in a pasture at the edge of PP Cruce Caballero. Two jays were on the ground, and at least one of them consumed an egg. The sparrows vocalized in alarm but did not approach the jays. The nest structure was left empty but intact.

On 12 November 2011, AB approached the nest of a Golden-winged Cacique (*Cacicus chrysopterus*) at PP Cruce Caballero, and saw that it was moving. It was a closed/long/pensile nest, suspended 2.5 m above an artificial pond in primary forest. One Plush-crested Jay flew from the nest area, and another hung from the nest. It removed a nestling with newly opened pin feathers, and flew away with it. The caciques vocalized insistently nearby but did not approach the jays. The nest entrance was left enlarged, and the nest



FIG. 3. Sequence of images taken from a blind, showing a Black Capuchin Monkey (*Sapajus nigritus*) attempting to depredate a nest of Helmeted Woodpecker (*Dryocopus galeatus*) in PP Cruce Caballero on 15 October 2013. At 17:56:44, the male Helmeted Woodpecker looks from the nest cavity as a group of monkeys approaches; 18:03:14 the monkey peeks into the nest cavity; 18:03:17 it looks at the camera presumably because of hearing the mirror slap; 18:03:40 it inserts a hand in the cavity, then leaves without taking an egg; 18:12:16 the male woodpecker returns to the nest. Photos: M. Lammertink.

was no longer active that afternoon or on following days.

White-eared Opossum (*Didelphis albiventris*)

On 23 October 2014, AB heard a commotion of Black-throated Trogons (*Trogon rufus*) and observed a White-eared Opossum with the front half of its body inside a non-excavated cavity (produced by natural decay) in primary forest at PP Cruce Caballero. The cavity was 26 cm deep vertically, 1.6 m high in the main trunk of a living *Alchornea triplinervia*, and had one entrance, 6.3×12.5 cm. The opossum entered the cavity farther, and then, perhaps on hearing the observer, exited with part of a nestling, which had open pin feathers. The male trogon was most active in nest defense, fluttering close to the opossum; the female swooped at the opossum once but was not as persistent. On inspection the next day, there were feathers inside the cavity, at the cavity entrance, and on the ground below the cavity.

Black Capuchin Monkey (*Sapajus nigritus*)

A cavity-nest of Helmeted Woodpecker (*Dryocopus galeatus*) in primary forest at PP Cruce Caballero was partially depredated between 22 October 2013, when it contained four newly hatched nestlings, and 27 October when only one nestling remained. The cavity was excavated 9.5 m high in a dead branch of a living *Nectandra lanceolata*. It had one entrance 7×7.5 cm and was approximately 30 cm deep. On 15 October 2013 while a male Helmeted Woodpecker was incubating, a group of Black Capuchin Monkeys

approached the nest tree, with the male woodpecker watching warily from the nest entrance. One monkey descended to the top of the nest branch and the male woodpecker fled. The monkey peeked into the cavity and inserted its hand, but was apparently startled by the mirror slap sound of ML's camera from a blind and did not take an egg (Fig. 3). Black Capuchin Monkeys were seen within 50 m of the nest nearly daily between 15 and 27 October. They were the only potential predators seen approaching the nest during 92 observation hours. Capuchin monkeys are known predators of birds' nests (Fedigan 1990, Robinson et al. 2005, Tarwater 2008) and we regard Black Capuchin Monkey as an unconfirmed, but likely, predator of the three nestlings.

A cavity-nest of Lineated Woodpecker at PP Cruce Caballero was partially depredated between 25 October 2014, when it contained three recently hatched nestlings, and 6 November when it contained only one nestling. The cavity was excavated 6.9 m high in a dead tree in a small canopy gap within forest that had likely been subject to some selective logging. It had one entrance of 8.1×7.4 cm and was 34 cm deep vertically. On 27 October 2014 a camera trap photographed a group of four Black Capuchin Monkeys climbing up to the nest from the bamboo understory (Fig. 4). One to four monkeys were at the cavity entrance from 1114–1139 hrs (i.e., a period of 25 mins), and postures captured in the photos include a monkey sitting on its haunches examining an item between its front paws, and



FIG. 4. Sequence of images, registered by a camera trap, of Black Capuchin Monkeys (*Sapajus nigritus*) at a nest of Lineated Woodpecker (*Dryocopus lineatus*) with three 4-day old nestlings in PP Cruce Caballero, on 27 October 2014. At 11:16:24 a monkey climbs up the nest snag. Red arrow indicates the cavity entrance. By 11:23:59, three other monkeys have joined it near the nest cavity. The left middle monkey sits on its haunches and seems to be inspecting something in its front paws, while the monkey on the right leans over into the cavity entrance. 11:24:39 the monkey on the right puts its hand into the cavity entrance. 12:08:09 adult woodpecker returns to the cavity entrance after the monkeys leave.

another monkey peeking into and reaching into the cavity (Fig. 4). The resolution of the photos is too poor to see an item the size of a 4-day old woodpecker nestling. The camera trap did not document another potential predator approach the nest during 322 (daylight) monitoring hours. Although we cannot rule out the possibility of a nocturnal predator, we consider the Black Capuchin Monkeys documented on 27 October as the most probable predators of the two nestlings.

Crab-eating Fox (*Cerdocyon thous*)

Common Pauraques (*Nyctidromus albicollis*) had a simple/unlined nest on the ground, in old secondary forest at PP Cruce Caballero in November 2009. The eggs hatched between 6 and 8 November, and two nestlings were present on the evening of 11 November. When AB approached on 12 November, he saw a Crab-eating Fox crouched at the nest. The fox turned its head, and was seen to be chewing. It moved away, leaving open pin feathers on the ground. The area was searched, but no nestling or adult Pauraques could be found.

Southern Tigrina (*Leopardus guttulus*)

A Southern Tigrina may have depredated the first nest of the banded pair of Lineated Woodpeckers in the cavity over the wide main trail in primary forest at PP Cruce Caballero in 2013. The same cavity was also used by the

banded pair in 2014, when it was depredated by a Chestnut-eared Aracari (see above). The cavity was 7.7 m high, at the top of an isolated snag within a natural clearing. The bottom half of the snag emerged diagonally from the underbrush, and the top half extended vertically above the middle of the trail (an internal road with grass cut short). The ground below the cavity was worn from our nest checks and frequent passing. On 2 October 2013 the cavity contained four feathered nestlings. On 5 October, EBB, FGDS, and Kirsten Wilcox passed under the nest twice between 1000 and 1100, observing live nestlings at the cavity entrance both times, and flushing the female from the nest tree the second time. At 1505, ML and CF found two dead nestlings in the middle of the trail, directly below the cavity, which had not been present when the other team passed. One of the dead nestlings had a broken wing, and one had a wet head with ruffled and plastered feathers, but neither was obviously crushed or bitten. The other two nestlings could be heard vocalizing inside the cavity, and at 15:33 they were fed by the adult male. We did not visit the nest on 6 October. On the morning of 7 October, AB observed a Southern Tigrina approach the nest tree and sniff the trunk. It climbed about 2 m up the tree, leapt to the trail, sniffed the air, and ran off into the forest. At 1200, ML and CF observed pin feathers on the ground directly below the cavity. There was no activity at the nest from 1200 to 1315, although the (radio-

tagged) male was within 30 m the entire time. At 1603 we found the remaining two nestlings dead inside the cavity, with ants and flies. On the morning of 8 October, AB again surprised a Southern Tigrina, this time backing down the nest snag about 1.5 m below the cavity. When it reached a height of about 3.5 m, it jumped to the ground and ran into the forest. There was nothing unusual on the trail below the cavity. On 9 October at 1603 the cavity contained only feathers, ants and flies. On the trail, directly below the cavity, were feathers, and feces of a small felid. We cannot be certain that the tigrina was the predator; however, this seems the most parsimonious explanation for our observations. Their diet is known to include birds and arboreal mammals, but tigrinas are mainly terrestrial (Wang 2002, Rocha-Mendes et al. 2010, Campos Trigo et al. 2013). In our years working in the Atlantic forest, we have not otherwise seen a tigrina off the ground. The style of killing is also consistent with a cat: Southern Tigrina and other cats are known to engage in surplus killing, i.e., killing prey they cannot immediately consume, and sometimes returning to retrieve it at a later date (Kruuk 1972; Tortato et al. 2013; AB and KLC, pers. obs.). Southern Tigrinas, congeneric Ocelots (*Leopardus pardalis*) and Guiña (*Leopardus guigna*) have also been recorded returning repeatedly to specific prey locations (Tortato et al. 2013; Emsens et al. 2014; AB and KLC, pers. obs.; T. Altamirano, pers. comm.). In the case of the Guiña, these locations were nest boxes with nestling birds, one of which was depredated (Altamirano et al. 2013). Feces of Geoffroy's Cat (*Leopardus geoffroyi*) were also found numerous times in depredated raptor nests or a fork of the nest tree (Liébana 2015; M. S. Liébana, pers. comm.). We believe the tigrina was the most likely predator of the woodpecker nest, and probably returned at least twice to retrieve the dead nestlings.

DISCUSSION

We identified or inferred 14 species of nest predators, all birds and mammals. Other observations from the Atlantic forest suggest a similar pattern. Circumstantial evidence links White-eared Opossums, Red-breasted Toucans, and Maroon-bellied Parakeets to the predation and usurpation of eight additional cavity-nests in our study area in Argentina (Segovia and Cockle 2012; KLC, unpubl. data). Additionally, we observed White-throated

Woodcreeper, Planalto Woodcreeper, and Plush-crested Jays carrying bird eggs or nestlings, without being able to identify the victim species (Cockle and Bodrati 2013; KLC, unpubl. data). Only birds were observed preying on nests of Red-rumped Cacique (Duca and Marini 2004, Fraga 2011). White-eared Opossums were considered to have taken eggs, nestlings, and an adult female of Red-spectacled Parrot (*Amazona pretrei*; Martinez et al. 2008). Big-eared Opossums (*Didelphis aurita*), Agoutis (*Dasyprocta neoprina*), Coatis (*Nasua nasua*), and Tegú Lizard (*Tupinambis marianae*) preyed on artificial nests on an Atlantic forest island (Galetti et al. 2009). Additionally, López-Lanús and Goñi (2004) saw a Saffron Toucanet attempting (unsuccessfully) to depredate a nest of White-spotted Woodpecker (*Veniliornis spilogaster*). We have not observed raptors preying on bird nests in the Atlantic forest, in contrast to Duca and Marini (2004).

Snakes are present at our study sites, but we never observed them at bird nests, and rarely in trees or shrubs. Most snakes in the interior Atlantic forest (Argentina and Paraguay) have terrestrial habits (Cacciali 2009) and may be more likely to consume nests on the ground. Although our methods were not always quantitative or standardized, they were similar to those of Skutch (1985), Robinson and Robinson (2001), Koenig et al. (2007), and Berkunsky et al. (2011), all of whom identified snakes as key nest predators in Neotropical forests. We did not find snakes in tree cavities, although in other regions they often remain for several days after consuming eggs or nestlings (e.g., Robinson and Robinson 2001). We surmise that snakes are not a major cause of nest failure in the Atlantic forest, at least for nests in trees.

Our observations suggest that birds in the Atlantic forest face a series of trade-offs in placing their nests. Whereas low nests were vulnerable to mammals and jays, nests in the canopy were depredated by woodcreepers and Chestnut-billed Aracaris (Fig. 1). Despite many attempts, Red-breasted Toucans were unable to depredate two cavities 5–6 cm in diameter (Bodrati and Cockle 2011), suggesting that small cavity-nesting birds may be able to protect their offspring from Red-breasted Toucans by selecting small cavities. However, Saffron Toucanets and White-throated Woodcreepers routinely access cavities as small as 4.3 and 3.3 cm in diameter, respectively (Cockle and Bodrati 2013; KLC, unpubl. data). Deep cavities, likewise, may protect nests from depredation by monkeys and cats, but remain vulnerable to woodcreepers. In a recent study

of cavity-nesters in the Atlantic forest, the only significant predictors of daily nest survival were height, entrance diameter and tree condition (Cockle et al. 2015).

Birds nesting in the Atlantic forest also face apparent trade-offs in terms of nest concealment and defensive behavior. Foraging toucans and aracarís usually move among the tree tops, from which they appear to search for nests (and other food) from a distance (Skutch 1971). They presumably find nests using visual and auditory clues including the nest structure itself, nestling vocalizations, and movements of adult birds. Potential victims might thus protect their offspring from toucans by concealing their nest (e.g., within foliage) and reducing adult and nestling activity. In contrast to toucans, woodcreepers appear to hunt opportunistically and at short range, probing into cavities, epiphytes, and vine tangles as they hitch up trees in search of (mostly arthropod) prey (Marantz et al. 2003). Thus, secrecy is not likely to have a substantial influence on risk of predation by woodcreepers. Adult birds can also save part or all of their nest contents by attacking intruders, and survival of cavity nests is highest for species that tend to show aggressive nest defense (Cockle et al. 2015). However, in the present study, Red-breasted Toucans sometimes took whole broods while under attack from parents. Aracarís, jays and monkeys visited nests in groups of three or more, and returned repeatedly on successive days, which may be strategies to overcome and wear down the nest owners. Further studies should examine trade-offs among nest placement, concealment, and defense behavior as strategies to reduce nest predation and usurpation. We recommend placing video or time-lapse cameras at nests, especially cameras with infrared capability, to provide quantitative and standardized information about the identity and *modus operandi* of nest predators in Neotropical forests.

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