First breeding record, vocalisations and morphology of Stripe-cheeked Woodpecker *Piculus callopterus*, a Panamanian endemic

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Se documenta el primer registro de anidación del Carpintero Carirrayado *Piculus callopterus*, una especie endémica de la República de Panamá. Se trata de un nido observado durante 41 días, desde el 13 de abril hasta el 23 de mayo de 2013. El nido fue excavado por ambos adultos en el tronco muerto de *Cecropia* sp. en proceso de descomposición. La localidad estaba situada a 800 m, en el Parque Nacional Chagres, en la parte centro-oriental del país. Se hicieron observaciones tanto del nido como de los hábitos reproductivos de la pareja, incluyendo la incubación, nacimiento de los pichones y muerte de los mismos. Las observaciones adicionales incluyen a adultos buscando sitios para la anidación y la alimentación de pichones maduros. Se compara el proceso de anidación con el del Carpintero Alirrufo *P. simplex*, que en el pasado ha sido considerado coespecífico con el Carpintero Carirrayado, y se hacen observaciones sobre la depredación del nido. Se documentan vocalizaciones, se comparan con otras tres especies que en el pasado han sido consideradas coespecíficas con el Carpintero Carirrayado y se hacen observaciones sobre algunos aspectos de morfología.

Stripe-cheeked Woodpecker *Piculus callopterus* occurs in forest and small adjacent clearings in foothills at 300–900 m on both the Pacific and Caribbean (Atlantic) slopes of Panama, to which country it is endemic. Its range extends from the provinces of Coclé (and perhaps Veraguas—one old record) in mid-west Panama, east to the province of Darién near the Colombian border^{2,3,4,9,20,21}. There are old sightings from the Caribbean lowlands⁹ and recently a female (or immature) was photographed in the Pacific lowlands (I. Quiroz pers. comm.; Fig. 6). Such individuals are thought to be wanderers from adjacent foothill forests⁹.

The species generally is found in the midstorey to upper levels of live or dead trees, where it forages by pecking at knot holes or prying loose bark on trunks and branches, or occasionally by searching epiphytic plants. Its diet consists mostly or entirely of ants^{20,21}. This woodpecker forages either alone, in pairs or with mixed-species flocks including tanagers and midstorey birds (antwrens, etc.), is typically unobtrusive (blending remarkably well with trunks and branches) and can easily go unnoticed unless vocalising (pers. obs.).

Taxonomy

Opinions have varied over the years concerning the status of Stripe-cheeked Woodpecker within the genus *Piculus*. Sibley & Monroe¹³ considered White-throated Woodpecker *P. leucolaemus* (then including the now split Lita Woodpecker *P. litae*) to form a superspecies with Middle American Rufous-winged *P. simplex* and Stripe-cheeked Woodpeckers, while some authors (e.g. Short¹² and—formerly—AOU¹) have considered them all to be conspecific, and Peters⁷ treated *callopterus* as a subspecies of White-throated Woodpecker. On the other hand, Wetmore²⁰, Stiles & Skutch¹⁹ and Ridgely & Gwynne⁹ presented rationale for treating them as separate species; thereafter, Winkler & Christie²¹, Angehr & Dean² and Gorman⁴, among others, followed suit.

The breeding biology of Stripe-cheeked Woodpecker is unknown²¹ and the voice, although known since the 1980s, was not formally described until 2014⁴. With respect to the three putative relatives of Stripe-cheeked Woodpecker (Whitethroated, Lita and Rufous-winged Woodpeckers), detailed breeding data are available only for the last-named¹⁷, whereas vocalisations have been documented for all three²¹.

Breeding of Stripe-cheeked Woodpecker

We observed a Stripe-cheeked Woodpecker nest in April-May 2013, in a decaying 6 m-tall *Cecropia* sp. stump at the forest edge, in Altos del Torreón, a subdivision of Los Altos de Cerro Azul private residential development in eastern Panamá prov. (09°12.672'N 79°24.899'W; 800 m). The site is in the Caribbean slope foothills, in Chagres National Park.

Cecropia trunks comprise many hollow internodes divided by hard, thin septa that create individual cylindrical capsules one above the other. Many of these frequently become hollow ant domatia, most commonly occupied by *Azteca* sp. ants that have a symbiotic relationship with the tree during its lifetime⁶. When the tree dies the domatia cease to be used. The woodpeckers excavated an entrance tunnel until they reached a hollow domatium, then enlarged the nest cavity, heightening it by removing septa and incorporating more domatia, and widening it by pecking out the domatia lining and soft wood on the entrance side of the cavity. The hard domatia lining opposite the entrance became the back wall of the nest.

A total of seven widened domatia formed the nest cavity, one above the entrance, one at entrance level and five below it. The cavity was slightly wider at the base than at the entrance, and at the top it narrowed considerably until it was barely wider than the original domatium. The nest's dimensions are shown in Fig. 1.

Methods

The nest was observed from 13 April until 25 May 2013. Initial observations were sporadic but sufficient to document nest building and behaviour that indicated eggs had been laid. On 28 April we set up a time-lapse video camera (one frame per 1.08 seconds) in WJA's house, from which the nest—c.30 m away—was visible. From then until 23 May, almost daily, the time-lapse camera recorded 12 hours of activity at the nest (06h30–18h30), capturing most events, except on a few occasions with bad light, heavy rain, waving branches or due to equipment failure. Conditions deteriorated dramatically in the final days of observation (when the wet season began in earnest). Also a few splitsecond events were missed by the camera.

Additionally, on several occasions from 13 April, we used an SLR camera with video capability within 10 m of the nest, to photograph and video-record some adult behaviours, and made sound-recordings of calls and mechanical noises made by adults and begging young. Videos and photographs are posted at the Internet Bird Collection (IBC) (http://ibc. lynxeds.com) and sound-recordings on Xeno-canto (www.xeno-canto.org); a full list of web links can be provided on request. We decided not to try to observe the nest internally.

Results

Nest site and construction.—On 12 April 2013, WJA heard two Stripe-cheeked Woodpeckers duetting at the forest edge by his house. One uttered a short burst of song, the typical *heew-whéet* vocalisation rapidly repeated 4–5 times. The other immediately responded (on a slightly different pitch), and the sequence was repeated at least ten times. WJA was unable to reach the location immediately, but by the time he did so the birds had ceased vocalising and could not be seen.

Suspecting that the unusually intensive exchange was related to breeding, he returned next day (13 April) and found a female excavating in a decayed *Cecropia* stump. She left the shallow round hole and perched slightly above it (Fig. 2). WJA visited again on 18 April, when the hole had been excavated horizontally well into the trunk and

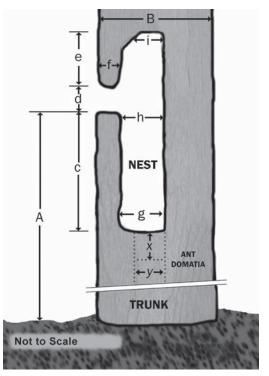


Figure 1. Cross-section of nest and stump (not to scale). A: height of nest above ground (to lower lip of nest entrance) 3.4 m; B: diameter of stump at nest level 20.4 cm; c: depth of nest cavity below entrance tunnel 25.0 cm; d: height of entrance tunnel 5.5 cm; e: height of nest cavity above entrance tunnel 12 cm (total height of nest cavity 42.5 cm); f: length of entrance tunnel 4.5 cm; g: diameter of nest cavity at floor 9.0 cm; h: diameter of nest cavity at entrance 8.5 cm; i: diameter of nest at ceiling 5.5 cm; ant domatia: x—height (of each) 7.0 cm; y—diameter 4.5 cm.

there appeared to be a downward-slanting chamber at its end. The hole was unoccupied and, despite a long wait, no bird appeared.

Incubation.-On 23 April at midday, WJA observed a male woodpecker peering from the hole (Fig. 5). After a few seconds it retreated from view. In light of subsequent observations, the bird was clearly incubating. Continuous daytime monitoring using a time-lapse video camera commenced on 28 April. From then until 3 May, there was always one bird incubating and the pair maintained a routine of four changeovers per day: early morningfemale arrived, male departed (earliest 06h52; latest 07h30); mid-morning-male arrived, female departed (09h57; 10h30); early to mid-afternoonfemale arrived, male departed (14h07; 15h14); late afternoon-male arrived, female departed (17h43; 18h16); night—the male occupied the nest. Changeovers occurred with little or no ceremony.

The arriving bird would sometimes signal its presence with a short soft 'murmuring' call, which differed between the sexes. Generally, the changeover was performed within a few seconds, but sometimes the arriving bird waited >1 minute for the other to vacate the nest.

Occasionally, the incubating bird pecked wood flakes inside the cavity (but not the entrance hole), either throwing them out immediately or removing them on changeover. Additionally, the bird sometimes peered from the entrance, especially in response to some outside disturbance or when the other was late for changeover.

Hatching and brooding.—On 4 May the adults' routine changed, with usually six changeovers at regular intervals during the day. The male again stayed in the nest overnight, being relieved by the female usually before 07h15. The final changeover usually occurred after 18h00. One bird was always present in the nest. On 6 May, due to equipment failure, the time-lapse recording covered only the morning and on 7 May nothing at all. However, some SLR video was made of changeovers on those days, and of the male pecking flakes in the nest above the entrance. On 6 May the female was filmed entering the nest at 17h09 and she was not relieved by the male before nightfall. Apparently she spent the night in the nest, to our knowledge the only time this occurred. On 8 May time-lapse video recording resumed and the female was observed removing a piece of white eggshell at 14h08, dropping it outside the entrance. She then left the nest, returning at 14h14. Shortly thereafter, we searched the base of the trunk, but the eggshell could not be found. Presumably the bird had carried it further away, or consumed it. Evidently, at least one egg had recently hatched. We saw no more eggshell removed from the nest; if any parts were ejected, it happened on 6-7 May when the camera was not working.

Provisioning the young.-From 11 May the routine changed again. As they fed the young more intensively, the adults made more and briefer nest visits and, between visits, the chicks were left alone, occasionally for two hours or more. The male generally made more visits than the female. On arriving, food was never visible in the adults' bills, suggesting that the young were fed by regurgitation. While in the nest each adult spent time pecking wood flakes from the walls, and removed these, occasionally together with faecal sacs. The young could be heard begging whenever an adult arrived. When the incoming bird arrived before the other had left, behaviour varied; sometimes there was no apparent communication between them, on other occasions there was face-to-face contact at the entrance, accompanied by odd head movements that may have involved very brief bill touching. Occasionally, the arriving bird entered the nest before the other had departed, and the two adults were in the nest together for a brief period.

The log of a typical day (17 May) reads as follows; at each arrival, the adult fully entered the cavity: 06h40 male departed; 07h53 female arrived, departed 08h07; 08h16 male arrived, departed 08h55; 10h08 male arrived, departed 10h20; 10h36 female arrived, departed 10h38; 12h30 male arrived, departed 12h32; 13h52 male arrived, departed 14h11; 16h01 male arrived, departed 16h02; 16h25 female arrived, departed 16h53; 17h31 male arrived and remained overnight. The male made six visits, the female just three. The shortest visit was one minute and the longest (apart from the overnight shift) lasted 39 minutes (in both cases the male). This pattern continued with tiny variations until late afternoon on 19 May.

Army ant attack.—On 19 May, the female entered the nest at 17h29. At 17h36 a column of army ants climbed the trunk. The first ants passed the nest without entering, but a few went inside, shortly followed by large numbers. The female was visible inside 15 seconds after the ants entered. The swarm left the nest at 17h42 forming a large dark stain that virtually covered the trunk around the hole for several seconds. The camera missed the female's departure, so we do not know if she left while the ants were inside, or subsequently. At 17h53 the male arrived and was seen in the entrance with an unidentified white object in its bill, perhaps a burst faecal sac. At 18h03, the male hopped out and pecked at the rim of the entrance (which had not occurred previously) before re-entering and apparently spending the night inside.

On 20 May the male's departure in early morning was not recorded. No activity was seen at the nest until 09h32 when the male arrived and left at 10h00. During this visit the male pecked vigorously at the interior walls and removed more wood flakes than usual. The female arrived at 10h42, left at 10h44 and was not seen again that day. The male returned at 12h16 and 15h30 for 15 and four minutes, respectively. Light conditions were very poor thereafter. At 16h46 and 17h02 there was an unidentified movement at the nest entrance. Nevertheless, at 17h08 the male was visible inside the nest entrance looking out.

On 21 May no bird was seen to leave the nest in early morning. The male arrived at 08h25 and removed waste material. At 11h07 the male arrived and entered the nest. At 11h25 the female arrived, the male came out and joined her on the trunk, then both departed. At 11h29 the female reappeared and entered the nest. No further activity was noted that day, and the time-lapse camera did not record the female's departure.

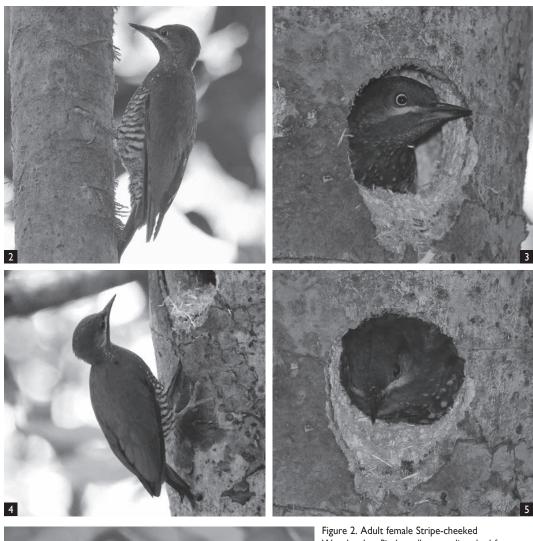




Figure 2. Adult female Stripe-cheeked Woodpecker *Piculus callopterus* disturbed from nest construction; note narrow sky-blue iris and red on nape extending to hindcrown, forecrown and moustachial brown (W. J. Adsett) Figure 3. Adult female Stripe-cheeked Woodpecker *Piculus callopterus* in nest (W. J. Adsett)

Figure 4. Adult male Stripe-cheeked Woodpecker *Piculus callopterus* arriving at nest; note long white stripe on head-sides from base of bill to neck-sides (W. J. Adsett)

Figure 5. Adult male Stripe-cheeked Woodpecker Piculus callopterus in nest (W. J. Adsett) Figure 6. First photographic record from Pacific slope lowlands (100 m): female (or immature) Stripe-cheeked Woodpecker Piculus callopterus, San Francisco Private Reserve, Tortí, eastern Panamá prov., 31 January 2015 (I. Quiroz) On 22 May the male arrived at 09h10 and left at 09h12 carrying an unusually large and odd-shaped pale object, which could not be identified. Subsequently, there was no activity until 16h39 when first the male and then the female arrived. Both entered the nest, but the female left almost immediately, followed within one minute by the male. On 23 May and subsequently there was no activity at the nest. On 25 May one of the adults vocalised briefly nearby, but did not visit the nest. On 26 May we inspected the nest and found it empty.

Other visitors

On 30 April a White-faced Capuchin Cebus capucinus visited the stump at 15h39. The male woodpecker departed and the monkey peered into the nest, then placed its hand inside for c.5 seconds, without removing anything. The male re-entered the nest at 16h03. On the following days several capuchins fed on the seed pods of an *Inga* sp. tree nearby, but did not visit the nest. On 11 May a Black-throated Trogon *Trogon rufus* inspected the nest hole; possibly, it was searching for a vacant hole in which to nest. On 20 May a Red-tailed Squirrel *Sciurus granatensis* inspected the entrance for c.5 seconds then left.

Other breeding data

The following observations (in order of breeding chronology) also made at Los Altos de Cerro Azul complement the above. On 26 January 2014, we observed a female for >30 minutes, flying to and fro between several tall (up to 25 m) dead trunks, on each one climbing up and down, drumming infrequently and investigating holes, without feeding, calling loudly and repeatedly. In February 1999, WJA observed a female alight on a decaying stump c.1 m above ground, where she was quickly joined by a male. They called excitedly to each other (like the breeding pair on 12 April 2013), examined the trunk and departed, but did not use the site to nest. On 28 March 2009 WJA observed a pair and two young being fed by regurgitation. Begging and other calls were sound-recorded. The young flew strongly and were similar to the adult female in plumage.

Voice

In 1989, Ridgley and Gwynne⁹ stated that the voice of Stripe-cheeked Woodpecker was known but did not describe it. In 1992, the first publicly available audio recordings of the voice were made by P. Coopmans at Cana, Darién (Pacific slope of easternmost Panama), archived at the Macaulay Library (http://macaulaylibrary.org/). Since then many recordings of what may constitute the species' entire repertoire have been deposited at the Macaulay Library and Xeno-canto. However, it was not until 2014 that some details of the voice were formally described in print⁴.

The main vocalisation is a sharp, high-pitched and loud heew-whéet uttered by both adults and juveniles. The first syllable ascends very briefly, then drops; the second ascends sharply. The accent is on the second. This call may be given singly, but more frequently it is repeated several times with little or no interval between each call. There are two versions; a fast one, in which 1.5 or more heew-whéet calls are given per second and a slower one (rate c.1 per second). It is unclear what circumstances prompt one or the other version to be used. When males and females call to each other, there is usually a gap of a few seconds between the first to call and the reply, but occasionally the male and female duet, with one issuing a series of 4-5 rapid calls, and the other following immediately with a similar number on a slightly different pitch, with the sequence repeated several times. This duet may be related to the start of breeding. Overall, the number of times this call is repeated in a series appears completely random.

Recordings posted online also include an infrequently heard single-note call, similar to the first note in the double call; scolds; various soft chatters by adults; and young begging for food both in the nest and post-fledging. Figs. 7–8 depict the principal Stripe-cheeked Woodpecker vocalisations and, for comparison, equivalent calls of its putative relatives.

Bare parts and plumage

Male, female and juvenile plumages have been described and / or illustrated previously^{2,3,4,9,20,21}, but our observations have revealed several errors and omissions. We list the most important as follows, and illustrate them in Figs. 2-6. (1) As Gorman pointed out⁴, the eye is not all dark, as was generally described and illustrated in the past. In fact, both sexes have narrow irides, usually visible, sky-blue or pale grey in colour, depending on light conditions, rather than individual variation. (This feature is not obvious in Figs. 4-5 of the male, but can be seen at http://ibc.lynxeds.com/node/240482.) (2) The pale, slightly wavy stripe on the head-sides of males does not fade below the eye, usually being well defined from the bill base to well back on the neck, and its colour is not yellow, as has often been stated, but white or off-white. (3) Red-tipped feathers on the female's head are not confined to the nape (as usually depicted), but extend onto the hindcrown. (4) The rest of the female's crown, forehead and moustachial area is not dark grey but rather dark brown or olive-brown. This is true, at least, of all individuals we have seen in life or in photographs.

Discussion

Breeding.—As we did not observe all facets of the breeding process, and there are no other reproductive data for Stripe-cheeked Woodpecker²¹,

we searched for well-documented records of a relative. There are detailed records for the closely related Rufous-winged Woodpecker in Costa Rica¹⁷. Skutch¹⁷ witnessed three aspects of behaviour not seen by us: courtship display, views inside the nest cavity, and fledging of young. He was able to correlate changes in adult behaviour to events in the nest.

Nest site selection.—The behaviour we witnessed on 26 January 2014 and in March 1999 has also been noted for Rufous-winged Woodpecker¹⁷. By selecting a decaying *Cecropia*, the Stripe-cheeked Woodpecker pair significantly reduced the labour of excavating the nest. Firstly, the wood was soft, and secondly, once the entrance tunnel was made, the birds only had to expand the existing domatia. It is unlikely that Stripe-cheeked Woodpeckers always use Cecropia trunks. Probably any dead trunk of the right size and softness suits their purpose, as it does other similar-sized species^{15,17}. Given our 2014 sighting, perhaps the birds also consider using an existing hole in harder wood, as Skutch¹⁶ observed for Golden-olive Woodpecker Colaptes rubiginosus.

Nest chronology.—Based on our observations and Skutch¹⁷, we constructed the chronology of Stripe-cheeked Woodpecker to an accuracy of \pm 1–2 days: (1) nest building to egg laying 9–10 days; (2) incubation 12–13 days; (3) brooding period 7–8 days; (4) young died 17–18 days after hatching; (5) fledging period unknown, but for Rufous-winged Woodpecker it is 23–24 days¹⁷.

The habits of nesting Stripe-cheeked and Rufous-winged Woodpeckers are very similarfor example, nest size, changeover patterns and protocol, feeding the young and nesting chronology. In both species the male stayed in the nest overnight. Skutch^{14–16} noted that this trait is true of all woodpeckers that typically roost alone. He also noted that after Rufous-winged Woodpecker chicks hatched, eggshells remained in the nest at least three days before disappearing¹⁷. This supports our own hypothesis (based on changes in parental behaviour) that at least one Stripecheeked Woodpecker egg hatched on 4 May, four days before the female was observed removing a piece of shell. Sanitation by way of adults removing faecal sacs and wood flakes is common to both species.

Breeding failure and nest predation.— All evidence points to predation as the cause of nest failure. Robinson & Robinson¹⁰ noted that approximately two-thirds of tropical bird nests fail for that reason, although this figure may be reduced for cavity-nesting species. Skutch¹⁸ noted that while snakes are the commonest (or most commonly detected) predators, others include mammals such as White-faced Capuchin, the same species that made an unsuccessful presumed

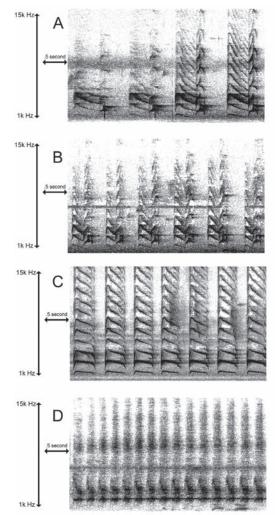


Figure 7. Comparative sonograms of typical repeated calls (four-second cuts): A. Stripe-cheeked Woodpecker *Piculus callopterus*, slow version, Altos del Torreón, Chagres National Park, Panama, 16 January 2011 (W. J. Adsett; XC82932). B. Stripe-cheeked Woodpecker, fast version, Las Minas, Coclé, Panama, 17 October 2008 (K. Allaire; XC24235). C. Rufous-winged Woodpecker *P. simplex*, Braulio Carrillo National Park, Limón, Costa Rica, 10 February 2011 (A. Spencer; XC71544). D. White-throated Woodpecker *P. leucolaemus*, Mishquiyacu, San Martín, Peru, 14 December 2008 (D. Geale; XC28106). (Comparable recording of Lita Woodpecker *P. litae* not available.)

attempt on the Stripe-cheeked Woodpecker nest. Skutch¹⁸ stated that *Eciton* and *Labidus* army ants rarely attack nests in forests; when scouts locate one, they usually ignore it. However, a handful of exceptions are known, when army ants attacked and even killed nestlings. Robinson & Robinson¹⁰

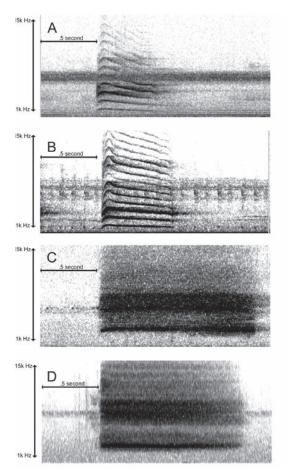


Figure 8. Comparative sonograms of single-note calls (two-second cuts): A. Stripe-cheeked Woodpecker *Piculus callopterus*, Cana, Darién, Panama, 7 February 1992 (P. Coopmans; ML 60344). B. Rufous-winged Woodpecker *P. simplex*, Osa Biodiversity Center, Piro, Costa Rica, 19 April 2010 (L. E. Vargas; XC50682). C. White-throated Woodpecker *P. leucolaemus*, Mirador de Lumbaqui, Sucumbíos, Ecuador, 25 July 2011 (A. Spencer; XC84186). D. Lita Woodpecker *P. litae*, Playa del Oro, Esmeraldas, Ecuador, 6 November 2011 (A. Spencer; XC65406).

recorded that J. Nesbitt observed army ants in Panama swarming over and attacking a 'screaming' Black-crowned Antshrike *Thamnophilus atrinucha* nestling. Pizo⁸ reported *Labidus praedator* killing Chestnut-bellied Euphonia *Euphonia pectoralis* chicks in Brazil and Greeney⁵ described an unsuccessful attack on a Blue-crowned Manakin *Lepidothrix coronata* nest in Ecuador. Schneirla¹¹, referring to *Eciton burchelli* army ants, stated that in Panama he 'had seen snakes, lizards and nestling birds killed [by the ants] on various occasions; undoubtedly a larger vertebrate ... would be killed by stinging or asphyxiation. But lacking a cutting or shearing edge on their mandibles ... these tropical American swarmers cannot tear down their occasional vertebrate victims'.

The video from the time-lapse camera did not permit identification of the species of army ant that attacked the Stripe-cheeked Woodpecker nest. Neither can we be sure that ants caused the death of the chick(s), but it is probably significant that the adults changed their visits immediately afterwards. Given the large number of ants that swarmed into the nest, and the time spent there (six minutes), there can be little doubt that the chicks were harmed. Possibly one or more did survive for a few days before succumbing, which would explain the adults not abandoning the nest immediately.

The fate of the chick(s) thereafter is unknown. The large object removed from the nest by the male on 22 May was not the body of a chick. Possibly a nocturnal predator was responsible for taking the nestlings, dead or still alive, after the ants' visit. Certainly, by 23 May the adults had abandoned the nest and it can be assumed that the nestlings were dead.

Breeding season.—Our observations demonstrate that the breeding season lasts at least from late January to late May, i.e. the entire dry season and onset of the wet season in the foothills of eastern Panama.

Voice.—Stripe-cheeked Woodpecker vocalisations are now well known. The principal two-syllable call is quite unlike that of any other *Piculus*. With respect to former conspecifics, Figs. 7–8 show that the principal vocalisations of White-throated and Lita Woodpeckers bear no resemblance to those of Stripe-cheeked Woodpecker. Rufous-winged Woodpecker lacks a two-syllable vocalisation, but its single-syllable call is very similar to the first syllable of Stripe-cheeked (Fig. 7). The similarity is even more noticeable when Rufous-winged Woodpecker's call is compared to the infrequent single-note call of Stripe-cheeked Woodpecker (Fig. 8).

Morphology.—The pale iris of Stripecheeked Woodpecker is shared by Rufous-winged Woodpecker (although the latter's is generally wider) but not by White-throated and Lita Woodpeckers. The stripes on the head-sides of Stripe-cheeked Woodpecker are white or off-white. Rufous-winged Woodpecker lacks such a stripe, while White-throated and Lita Woodpeckers do possess stripes but they are yellow^{4,21}.

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winged Woodpecker nest; David Ascanio for checking the Spanish summary and reviewing a draft of the paper; and Kent Livezey, Thomas Donegan and George Angehr for helpful recommendations. We are especially grateful to our referee, Harold F. Greeney, for his in-depth analysis, advice and encouragement. We also thank various recordists for sharing audio material, notably the late and sorely missed Ken Allaire; and Ismael Quiroz for his recent report from the Pacific slope lowlands.

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