Reproductive biology of the Sapayoa (Sapayoa aenigma), the “Old World suboscine” of the New World

Authors: Dzielski, Sarah A., Van Doren, Benjamin M., Hruska, Jack P., and Hite, Justin M.

Source: The Auk, 133(3) : 347-363

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-16-5.1

The Auk
Ornithological Advances

AmericanOrnithology.org

Volume 133, 2016, pp. 347–363
DOI: 10.1642/AUK-16-5.1

RESEARCH ARTICLE

Reproductive biology of the Sapayoa (*Sapayoa aenigma*), the "Old World suboscine" of the New World

Sarah A. Dzielski,[1#*] **Benjamin M. Van Doren,**[1#*] **Jack P. Hruska,**[1a] **and Justin M. Hite**[1b]

[1] Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York, USA
[a] Current address: Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas, USA
[b] Current address: Kauai Forest Bird Recovery Project, Hanapepe, Hawaii, USA
* Corresponding authors: Sarah A. Dzielski, sad88@cornell.edu; Benjamin M. Van Doren, bmv25@cornell.edu
[#] These authors contributed equally to the paper.

Submitted January 8, 2016; Accepted February 17, 2016; Published April 27, 2016

ABSTRACT

The Sapayoa (*Sapayoa aenigma*), a low-density resident of Chocó rainforests from Panama to Ecuador, has long perplexed ornithologists. It was originally described as a manakin (Pipridae), but molecular work has revealed its closest living relatives to be Old World suboscines (Eurylaimides) and supported its placement in the monotypic family of Sapayoidae. Despite such phylogenetic intrigue, little is known about the Sapayoa's general life history or reproductive biology; only one nest has been described. We present information on 2 actively attended and 13 inactive Sapayoa nests in Darién National Park, Panama. We provide the first detailed description of individual effort at an active nest, family group dynamics during the nesting period, the plumage of immature birds, and the range of vocalizations produced. We also present the first documentation of cooperative breeding and compile several recent nesting observations, extending the published Sapayoa breeding period by several months. Furthermore, we describe unusual behaviors among provisioning birds, including mounting between individuals of the same sex and mounting of a female by immature male helpers during chick provisioning. The receiving individual gave a conspicuous solicitation display before each mounting. Finally, we highlight elements of the Sapayoa's natural history that echo its Old World relatives and contrast with members of the New World Tyranni. For example, the Sapayoa resembles the eurylaimid broadbills—and differs starkly from the manakins—in diet, nest structure, breeding system, and mode of parental care.

Keywords: cooperative breeding, helpers, mounting, Old World suboscines, *Sapayoa aenigma*, Sapayoidae

Biología reproductiva de *Sapayoa aenigma*, el "suboscín del Viejo Mundo" que habita el Nuevo Mundo

RESUMEN

Sapayoa aenigma, un ave residente en bajas densidades en los bosques húmedos del Chocó desde Panamá hasta Ecuador, ha confundido a los ornitólogos por bastante tiempo. Aunque la especie originalmente fue descrita como un saltarín (Pipridae), estudios moleculares recientes revelaron que sus parientes más cercanos son los suboscinos del viejo mundo (Eurylaimides) y sustentan su ubicación en la familia monotípica Sapayoidae. A pesar de esta intriga filogenética se sabe muy poco sobre la historia de vida o la biología reproductiva de *Sapayoa*; sólo se ha descrito un nido. En este trabajo presentamos información de 2 nidos activos y 13 nidos inactivos de *Sapayoa* encontrados en el Parque Nacional Darién, Panamá. Presentamos la primera descripción detallada del esfuerzo individual en un nido activo, la dinámica del grupo familiar durante el periodo de anidación, el plumaje de las aves inmaduras y el repertorio de vocalizaciones. También presentamos la primera evidencia de cría cooperativa y recopilamos varias observaciones recientes de anidación que extienden el periodo reproductivo conocido de *Sapayoa* en varios meses. Además describimos comportamientos inusuales entre las aves que proveen alimento a sus crías, incluyendo la monta entre individuos del mismo sexo y entre un individuo joven y una hembra adulta durante la alimentación de los polluelos. El individuo que recibía la monta ejecutaba antes un despliegue para solicitarla. Finalmente, resaltamos elementos de la historia natural de *Sapayoa* que se asemejan a las de sus parientes del Viejo Mundo y contrastan con las de miembros de Tyranni en el Nuevo Mundo. Por ejemplo, *Sapayoa* se asemeja a los Eurylaimidae (y difiere drásticamente de los Pipridae) en dieta, estructura de los nidos, sistema reproductivo y modo de cuidado parental.

Palabras clave: ayudantes del nido, cría cooperativa, monta, *Sapayoa aenigma*, Sapayoidae, suboscines del viejo mundo

INTRODUCTION

The Sapayoa (*Sapayoa aenigma*) is an olive-colored interior rainforest bird restricted to the Chocó bioregion of eastern Panama to northeastern Ecuador. Although it is rather unremarkable in appearance, its taxonomic status has long been debated. *Sapayoa* (a monotypic genus) was originally placed with the Pipridae (manakins) on the basis of similarities in plumage and toe morphology (Hartert 1903). However, Karr (1971) found that its behavior and ecology grouped it with the tyrannid flatbills, and Prum and Lanyon (1989) argued that syringeal and femoral artery morphology also placed it among the tyrannids. Yet there were indications that *Sapayoa* belonged to a more distant group: Warter (1965) had already noted that its cranial morphology recalls that of the eurylaimid broadbills of Asia, and allozyme-based reconstructions by Lanyon (1985) supported placement of *Sapayoa* outside of the current-day Tyrannidae, Tityridae, Pipridae, and Cotingidae. Sibley and Ahlquist (1990) left *Sapayoa*'s placement undetermined but noted that its DNA–DNA hybridization melting curve closely resembled those of Old World suboscine genera *Pitta* and *Calyptomena*. Given the evidence that *Sapayoa* was distantly related to all other Neotropical suboscines, Sibley and Monroe (1990) placed it in its own infraorder, *incertae sedis*, but they noted that *Sapayoa* may indeed belong among the Old World suboscines (Infraorder Eurylaimides); recent genetic work has strongly supported this hypothesis (Fjeldså et al. 2003, Irestedt et al. 2006, Moyle et al. 2006, Ericson et al. 2014, Claramunt and Cracraft 2015). Today, this denizen of wet Neotropical rainforests represents the monotypic family of Sapayoidae (Winkler et al. 2015) within the Old World suboscine clade, a biogeographic paradox given its New World range. Its closest living relatives may be the eurylaimid broadbills and asities (Moyle et al. 2006), the pittas (Claramunt and Cracraft 2015), or the calyptomenid (green) broadbills (Irestedt et al. 2006); or *Sapayoa* may be sister to all other Old World suboscines (Ericson et al. 2014). This makes the species an interesting subject for comparative study, and it begs the question: How does the Sapayoa's natural history link it to its Old World relatives?

Very little is known about the Sapayoa's reproductive biology, social behavior, or general life history. Prior to this study, published data from one nest indicated that the nesting period spans at least May and early June (Christian 2001). Here, we document 2 actively attended and 13 inactive Sapayoa nests in Darién National Park, Panama, and describe in detail the breeding behavior of a family group of 6 Sapayoas (4 adults and 2 chicks). We describe several elements of the species' social and reproductive biology for the first time, including individual effort and group dynamics at the nest. We also document helpers at the nest, which are not known from the Pipridae and rarely encountered in the Tyrannidae, but reported from several eurylaimid broadbills (Phillipps 1970, Lambert and Woodcock 1996, Zubkova 2013, E. Gulson-Castillo and T. Pegan personal communication). We also describe social and breeding behaviors rarely reported in avian systems. These unusual behaviors include same-sex mounting events, mounting of the female by multiple males after the chicks have hatched, and possible feeding deception by immature helpers. Finally, we discuss the Sapayoa's natural history in the context of its phylogenetic relationships.

METHODS

In June and July 2014, we conducted an expedition to Darién National Park, Panama, specifically to rainforest near the Autoridad Nacional del Ambiente de Panamá (ANAM) station on the Pacific slope of the northern Serranía de Pirre (N 8.01735°, W 77.730917°). From June 4 to July 8, 2014, we searched for Sapayoas within 2 km of Pirre Station (N 8.01397°, W 77.72857°; elevation 125 m; known colloquially as "Rancho Frío"). This area consists of the lower foothills of Cerro Pirre (100–330 m above sea level) and contains many forested ravines with small streams. We detected Sapayoas almost exclusively in these areas, and we found that traveling along ravine-bottom streams was an efficient nest-searching strategy. We still spent significant time outside of ravines because the park's trail system favored ridges, so we do not believe that this alone introduced substantial detection bias.

We discovered 2 active Sapayoa nests, as well as 13 inactive presumed Sapayoa nests (detailed below). We located the first active nest on the morning of June 12, 2014, after capturing a pair of foraging Sapayoas in a mist net, close to a small, meandering stream at the bottom of a heavily forested ravine. The captured birds had been associating with a mixed-species foraging flock and perching above the height of our mist nets (~2.6 m). To aid in the capture effort, we used an "iMainGo X" portable speaker to broadcast Sapayoa songs and calls (recorded in Nusagandi, Panama, and archived on xeno-canto.org by Andrew Spencer: XC127918-21). Although they did not respond aggressively to the recordings, the pair approached and became caught while performing steep diving sallies for insects. After capture, we handled the birds for several minutes, during which we took measurements and applied identification bands (colored and aluminum) to the legs of each (Table 1). We did not take blood samples, in order to minimize intrusiveness, because the female had a brood patch. After release, a thorough search of the vicinity of the capture site revealed a nest hanging ~2.75 m directly over a bend in the stream; its contents were 2 white eggs. We monitored the nest from a blind ~20 m from the site, and the birds did not return. During a follow-up visit hours later, one Sapayoa flushed

TABLE 1. Measurements of 8 Sapayoas from Darién National Park, Panama. The first 6 individuals, from our focal nest, were captured and measured on July 1, 2014 (N 8.01593°, W 77.71685°, elevation 275 m); specimens are currently housed at Cornell University Museum of Vertebrates (CUMV) and Museo de Vertebrados de la Universidad de Panamá. The last 2 individuals were captured and released on June 12, 2014 (N 8.01335°, W 77.72832°). A dash indicates that data were not recorded.

	Focal nest						First pair captured	
	Adult male	Adult female	Chick 1	Chick 2	Immature 1	Immature 2	Adult male	Adult female
Sex by DNA	Male	Female	Female	Male	Male	Male	–	–
Mass (g)	19.0	18.8	15.4	15.75	19.75	19.0	–	–
Total length (mm)	157	158	66	70	165	151	–	–
Spread wing (mm)	244	258	143	156	252	236	–	–
Molt	P9 & P10 old, P8 growing, R3–R6 growing	None; feathers tattered and worn	All pin feathers	All pin feathers	Moderate body	Light body	One P and one R on both sides; moderate body	None
Fat	–	Trace	Some	Some	Trace	Trace	Trace	Trace
Skull ossification	–	Complete	None	None	30%	30%	–	–
Tail (mm)	60.9	54.3	5.2	5.8	60.2	57.0	60	55
Tarsus (mm)	15.3	15.3	14.8	15.2	15.0	15.4	14.4	15.6
Wing chord (mm)	82	80.0	32	36	81	75	82	81.5
Culmen (mm)	14.9	15.9	7.2	7.8	15.4	14.3	14.5	13.9
Bill depth (mm)	5.1	5.4	4.3	4.5	5.1	5.3	5.2	5.2
Bill width (mm)	7.3	8.3	4.3	4.6	8.1	8.0	7.8	8.9
Head and bill (mm)	35.0	37.3	25.0	25.1	36.4	36.0	36.8	36.4
CUMV catalog number	55871	55868	55869	55870	55971	55972	–	–
Specimen type	Spread wing, whole body, blood, tissue	Flat skin, pickled carcass, blood, tissue	Spread wing, whole body pickle, blood, tissue	Spread wing, whole body pickle, blood, tissue	Study skin, carcass, blood, tissue	Study skin, carcass, blood, tissue	–	–

from the nest. However, several hours of monitoring on the following day yielded no additional sightings, and we did not detect the birds in the area during brief visits in subsequent days. We concluded that the birds may have abandoned their nest as a result of disturbance (but see Discussion).

In the following week, we continued to survey ravine-bottom streams in the vicinity of Pirre Station and detected a number of Sapayoas. We attempted to capture these birds for marking and measurement using the approach described above, but they did not respond aggressively to the recordings and these efforts failed.

On June 19, 2014, we found another active Sapayoa nest containing 2 white eggs. Both eggs hatched by the afternoon of the following day. After our experience with the first pair, we did not attempt to capture these birds and made every effort to minimize disturbance. We observed this nest (hereafter "focal nest") for several hours daily from June 20 to 30, with the exception of June 28 (total 76.05 hr). Observers sat behind a camouflaged blind located ~20 m away while operating Canon EOS 7D and 5D Mark II cameras with 70–200 mm, and occasionally 500 mm, lenses. We filmed the nest during shifts lasting 2–4 hr and recorded observations of behaviors in a notebook. Observers noted interactions among 4 provisioning Sapayoas both at the nest and on a favored perching branch located ~2 m away; we observed various activities on this branch, including perching, sallying, preening, wing flitting, tail wagging, mounting, and other social interactions.

Later, we reviewed all footage retained in the field and compiled a record of events exclusively from video recordings. This allowed us to more confidently identify individuals and accurately time events. We recorded nest arrivals, departures, food deliveries, displays, and mounting events. We identified individuals whenever possible, using the phenotypic differences discussed below (see "Description of Individuals"). From review of video footage, we identified individuals as adult female, adult male, or immature.

These active nests also allowed us to confidently assign several unused nests to *Sapayoa*. We used location (hanging over a ravine-bottom stream in dense rainforest) and structure (pear-shaped, thin strands, long "tail," covered opening) as primary identification criteria (see "Nest Descriptions"). We also found that Sapayoa nests were clustered in space; for example, 4 inactive nests were within 140 m of the focal nest, with the closest ~30 m away (Supplemental Material Table S1). Among the other species at this site with similar nests, Olivaceous Flatbills (*Rhynchocyclus olivaceus*) build a nest that has a less tapered shape (i.e. no "tail") and is smaller than that of Sapayoas (see Skutch 1960:513), only 15 cm long (Bates 2015). We found one active flatbill nest hanging above a sloping ridge and noted many similarly shaped nests above other ridges and slopes, but not above water. A Sulphur-rumped Flycatcher (*Myiobius sulphureipygius*) nest placed above a stream in the lowlands had a nest that recalled *Sapayoa* but was narrower, less bulbous, less tapered (no "tail"), and less robust overall (see Skutch 1960:543–544).

Physical and Media Specimens

We collected the 4 Sapayoas provisioning the focal nest and the 2 chicks on July 1, 2014. Placing mist nets around the nest allowed us to capture the 4 birds without relying on playback. We took photographs, morphometrics (Table 1), and blood samples. These 6 birds were euthanized by thoracic compression, prepared as specimens, and deposited in the collections of the University of Panama (Museo de Vertebrados de la Universidad de Panamá) and the Cornell University Museum of Vertebrates. During the 11-day period of nest observation, we occasionally observed all 4 older individuals visiting the nest simultaneously, and we concluded that these 6 birds composed a complete family group. However, we heard an additional Sapayoa in the vicinity of the nest on July 2, which may have been a bird from a neighboring territory or an additional undetected member of the focal group.

Audio and video recordings collected during this study are archived with the Macaulay Library at the Cornell Lab of Ornithology and can be accessed via the library website (macaulaylibrary.org). We provide catalog numbers for specific recordings in the Results as "ML" followed by a number.

Sexing

We determined the sex of all 6 individuals (2 adults, 2 immatures, and 2 chicks) by amplification of W- and Z-specific alleles using a 2550F/2718R sexing protocol (Fridolfsson and Ellegren 1999). The sex indicated by the polymerase-chain-reaction products of the 2 adults corresponded to their expected sex based on plumage, and these served as positive controls. Both immatures were male. One chick was male and the other female.

Statistical Analyses

To compare mean visit duration and mean daily visitation rate among individuals, we used one-way analyses of variance and corrected for multiple comparisons by calculating Tukey's HSD in the R statistical programming environment (functions "anova" and "TukeyHSD"; R Foundation for Statistical Computing, Vienna, Austria). We log transformed visit duration to satisfy assumptions of homoscedasticity and normality. We also tested for an effect of time of day and of chick age on visit duration and visitation rate using linear models; here, we included bird identity (male, female, or immature) as an additional categorical predictor.

FIGURE 1. Images of right wing, tail, and belly of adult and immature Sapayoas. Note the worn primaries and secondaries on the wing of the adult female, as well as the molt limit in the primaries of the adult male. In addition, note the worn edges to the rectrices of the adult female, the pointed tips to the rectrices of the immature males, and the growing outer rectrices of the adult male, giving a graduated appearance. Finally, note the worn belly feathers and brood patch of the female compared to the intact feathers and lack of brood patch on the males.

RESULTS

Description of Individuals

From our focal nest, the adult female was the only feathered individual lacking a yellow crown patch, consistent with previous evidence that Sapayoas are sexually dimorphic (Angehr and Dean 2010). This bird's tail, belly, and wing feathers were clearly abraded (Figure 1). This wear caused the belly feathers to appear noticeably gray from a distance, making the bird easily identifiable. The female's gape was not overly prominent, her irides were dark brown (Figure 2), and her rectrices were round-tipped. We captured one adult male with an extensive yellow crown patch, which was visible even when the crown feathers were not parted. The male also had dark irides (Figure 2), round-tipped rectrices, and an indistinct gape. Rectrices 3–6 were still growing in, resulting in a graduated or fan-shaped tail (Figure 1). This tail shape was noticeable from a distance. Primary 8 was also growing in on both wings, leaving old primaries 9 and 10 not yet molted. We did not notice any obvious change in these feathers during the 11-day observation period, so molt could have been suspended during breeding.

We also captured 2 immature males with small yellow crown patches, light brown irides, lighter and more exposed gapes, and point-tipped rectrices (Figures 1 and 2). They showed much-reduced yellow crown patches that were not always visible in the field. We identified these birds as immature, possibly juvenile, on the basis of this plumage characteristic, incomplete skull ossification (following capture), and iris color. These 2 birds did not display any tail-feather molt; the combination of square tail and uniform green underside separated them from both adult individuals in the field, but they could not be distinguished from one another at a distance. The brood comprised 2 chicks, which hatched on June 19 or 20. The

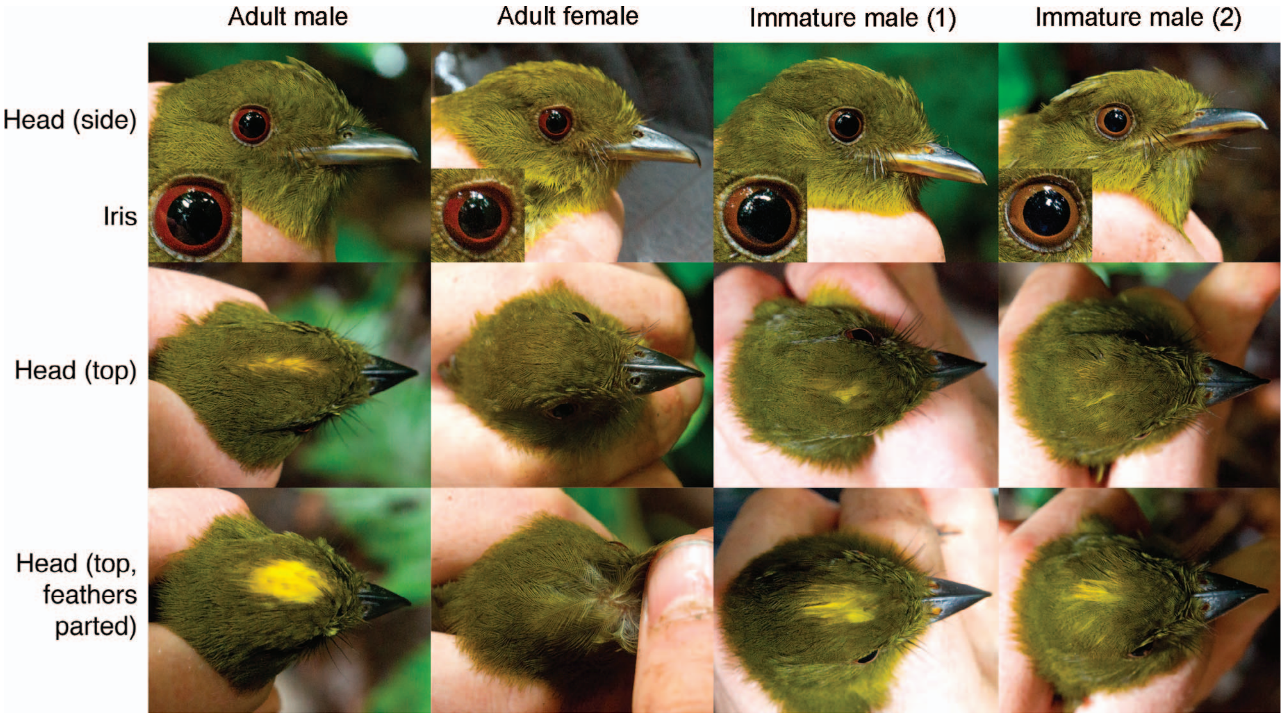

FIGURE 2. Images of the heads of adult and immature Sapayoas. Note the burnt-orange iris color of the immature birds in contrast to the deep-red iris color of the adults. Also note that the immature male birds showed reduced yellow coloration in the crown, but the amount of visible color depends on how the feathers are laid.

chicks were ~11 days old at the time of collection. The male chick was the larger of the 2 and had feather tips protruding from their sheaths, while the female chick's feathers were still pins. Measurements and further description are provided in Table 1.

Measurements of our first-captured pair—which may have abandoned their nest—were similar to those of the adults described above (see Table 1). Notably, the male of this pair also showed molt in the primaries and rectrices; the female did not. Again, only the female had a brood patch.

Nest Descriptions

The first and only other published description of a Sapayoa nest stated that "the nest was suspended from a lower branch of a 8 m-tall tree (*Perebea* sp.; Moraceae), 2 m above the surface of a permanent stream flowing through a deep ravine, forested on both slopes" (Christian 2001:331). Our experience was similar: Although we initially searched for Sapayoas on ridges, slopes, and ravines, we found Sapayoa nests only along ravine-bottom streams. Our monitored nest (Figure 3) hung directly above a very small stream in a tree 2.5 m tall. It was pear-shaped, with long strands of fibrous material dangling from the bottom. A strap of long, thicker material secured the top of the nest to a branch over the stream. Live leaves at the end of the branch fell over the nest entrance: a hole in the side of the nest, with overhanging nest material shielding it from above. The dimensions of the main "body" of the nest were 230 mm high × 120 mm wide × 110 mm deep; longer thin fibers that made up the "tail" of the nest generally extended an additional 500 mm, with the longest strands extending 950 mm. Later analysis by a botanist at the Smithsonian Tropical Research Institute revealed that the nest was primarily composed of palm fibers (Arecaceae), tree bark fibers, and leaf fibers possibly from Cyclanthaceae, Poaceae, and/or Cyperaceae (A. Ibañez personal communication). Analysis of photographs of the nest tree by another botanist at the institute indicated that the tree was of the genus *Tovomita* in the family Clusiaceae (R. Flores personal communication).

Overall, we found 2 confirmed active and 13 inactive presumed Sapayoa nests. Both active nests were hung from a tree branch, directly over a stream; this was the case for all nests we documented (with the exception of one hanging 0.5 m away from a stream edge). The trees from which nests were hung were young and sapling-like, with diameters at breast height typically <50 mm (maximum = 95 mm) and overall heights typically <5 m (with 2 exceptions: 9 m and 18 m). Nests were generally placed 2–3 m above the ground or water (minimum = 1 m, maximum about 5–6 m). The leaves on the branches to which nests were attached grew directly over the entrance in both active nests, and there was at least one leaf (and

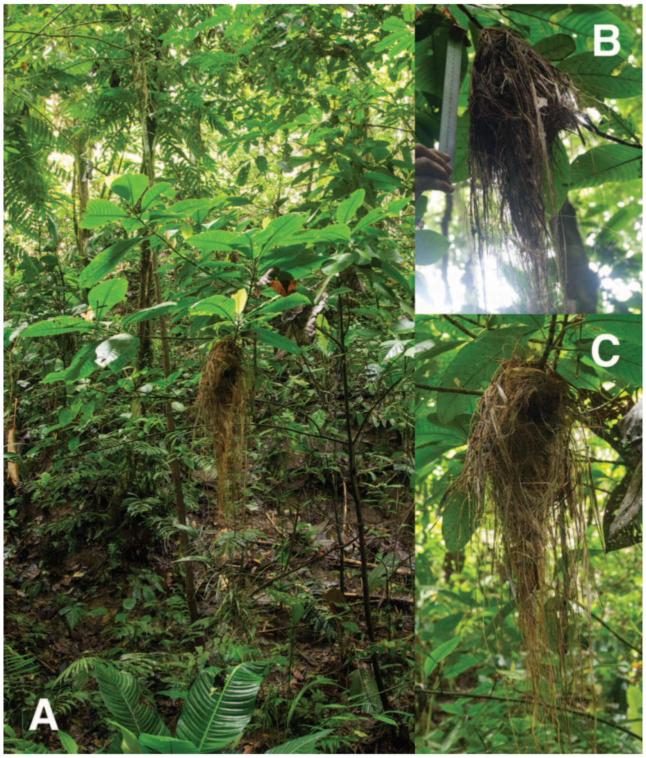

FIGURE 3. The active Sapayoa nest we observed in Darién National Park, Panama, photographed on July 1, 2014, about 11 days after hatch. (**A**) The nest as photographed from the opposite bank of the small stream over which it is placed. The nest entrance faces the camera. (**B**) The nest photographed from upstream (left side of A), with a 300 mm ruler placed for scale. (**C**) A closer image of the nest, taken from the stream itself. Note the "roof" of material over the nest entrance.

typically >2) positioned over the nest entrance for all nests at which we noted this. The entrance size for both nests was 40 × 40 mm. The average length of the nest's "roof," the extended covering over the nest entrance, was 40 mm (for additional measurements, see Supplemental Material Table S1). The condition of inactive nests ranged from seemingly recently abandoned to largely fallen apart; thus, measurements of inactive nests varied greatly because of age and wear.

Brooding and Female Care

Only the female brooded the 2 chicks. During nest observations, the female brooded for a total of 20.12 hr (26% of total observation time). The percentage of total observation time that the female spent brooding in the nest per day decreased significantly as the chicks aged (linear model: slope = –0.051 day^{-1}, $t = -3.38$, $P = 0.01$; Figure 4A). Nest watches did not start earlier than 0745 hours or end later than 1735 hours, so we cannot estimate the total number of hours that the female brooded outside of that period. However, the female emerged from the nest at the beginning of some early nest watches, so it is likely that she regularly brooded chicks overnight.

On June 21 at 1040 hours, the female removed a large white fecal sac from the nest. This is the only recorded instance during the 11-day period of any older bird removing a fecal sac. On other occasions, nestlings, on their own, expelled droppings from the nest into the stream below.

Nest Visitation

Four individuals—an adult female, an adult male, and 2 immature males—attended the nest from June 20 to 30, 2014. All 4 individuals brought food to the nest during the observation period. We observed Sapayoas both sally-gleaning prey from leaves (e.g., in ML 484055 at 1:23, a Sapayoa catches a wingless insect) and flycatching aerially (e.g., ML 484051 at 0:31). Conclusively identified food items included katydids (Tettigoniidae; e.g., ML 484032, 484036, 484056), lepidopterans (e.g., ML 484025, 484034, 484052, 483799, 483804, 483809, 483810, 483811), and one hymenopteran (likely a wasp: ML 484043) (G. Montgomery personal communication). In one instance, we observed a bird carrying a blue, spherical food item that may have been a berry. Sapayoas also carried smaller prey items, but they were generally difficult to spot and identify. Therefore, we recorded all nest visits, regardless of whether food was visible. All descriptions of "nest visits" in this article refer to a bird landing at the nest entrance.

The typical pattern we observed was large periods of silence punctuated by the arrival of multiple birds: The median interval between visits was 3.1 min, but 81.9% of total watch time was spent waiting during intervals of ≥20 min. The average visit interval for these longer waits was 46.5 min. During long absences, Sapayoas were typically out of earshot (or silent), likely foraging with a mixed-species flock.

From review of video footage, we recorded 253 nest visits of the 4 attending individuals. The female visited 80 times, including 22 daytime brooding visits. Because we could not distinguish between the 2 immature males on camera, behaviors such as nest visits, mounting events, and other actions could only be identified to age for male birds. The 2 immature males visited the nest a combined total of 66 times. The adult male visited the nest the most frequently, totaling 107 visits in the observation period. Mean visitation rate increased during the 11-day period for all individuals by 0.16 visits hr^{-1} day^{-1} ($t = 5.099$, $P < 0.001$; Figure 4B); the baseline visitation rate (i.e. the intercept term) was significantly higher for the adult male than for the other individuals ($t = 2.146$, $P = 0.0414$) but did not significantly differ between the adult female and the collective pair of immature birds ($t = 0.330$, $P = 0.7441$). Over the course of the day, mean visitation rate increased for all individuals at a rate of 0.15 visits hr^{-2} ($t = 3.865$, $P < 0.001$; Figure 4C); here,

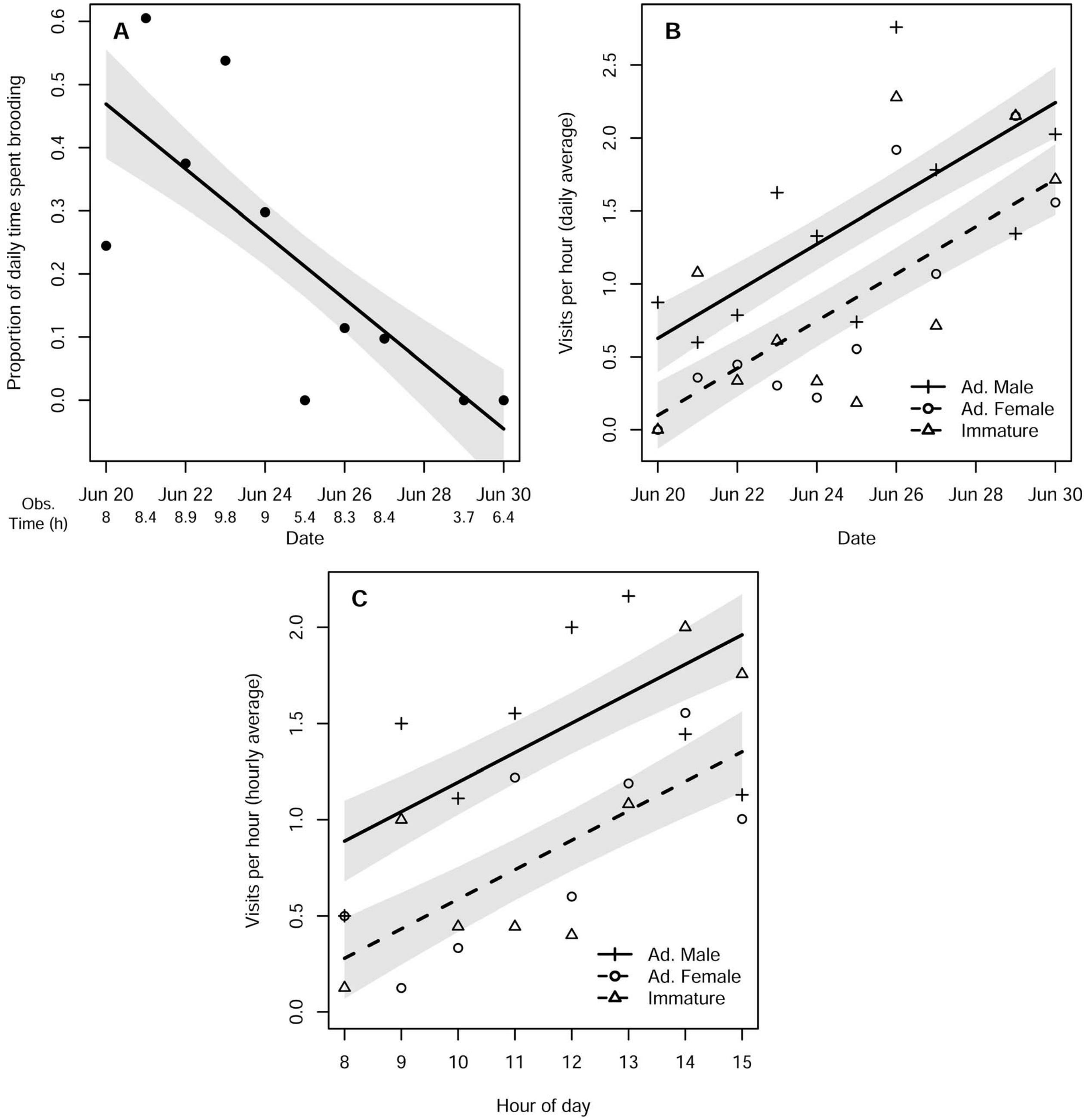

FIGURE 4. (**A**) Proportion of total observation time that the female spent brooding each day in the Sapayoa nest we observed in Darién National Park, Panama. Time spent brooding significantly decreased as the chicks aged. Total observation time per day is shown below the *x*-axis. (**B**) Visitation rates during the observation period for the adult and immature birds. The dashed line corresponds to visitation rates of the female and the immature males (combined effort), which did not significantly differ. The solid line corresponds to those of the adult male, which showed a significantly higher intercept term but the same slope. Visitation rate increased significantly for all birds as the chicks grew older. Only visits to the nest entrance are included (with or without visible food). (**C**) Visitation rate by time of day for the adult and immature birds. The dashed line corresponds to visitation rates of the female and the immature males; the solid line corresponds to those of the adult male. The visitation rate in visits per hour significantly increased over the course of the day. The adult male had a higher visitation rate than the female and the immature males for the majority of the watch periods. Shading above and below the mean line in A, B, and C represents SE.

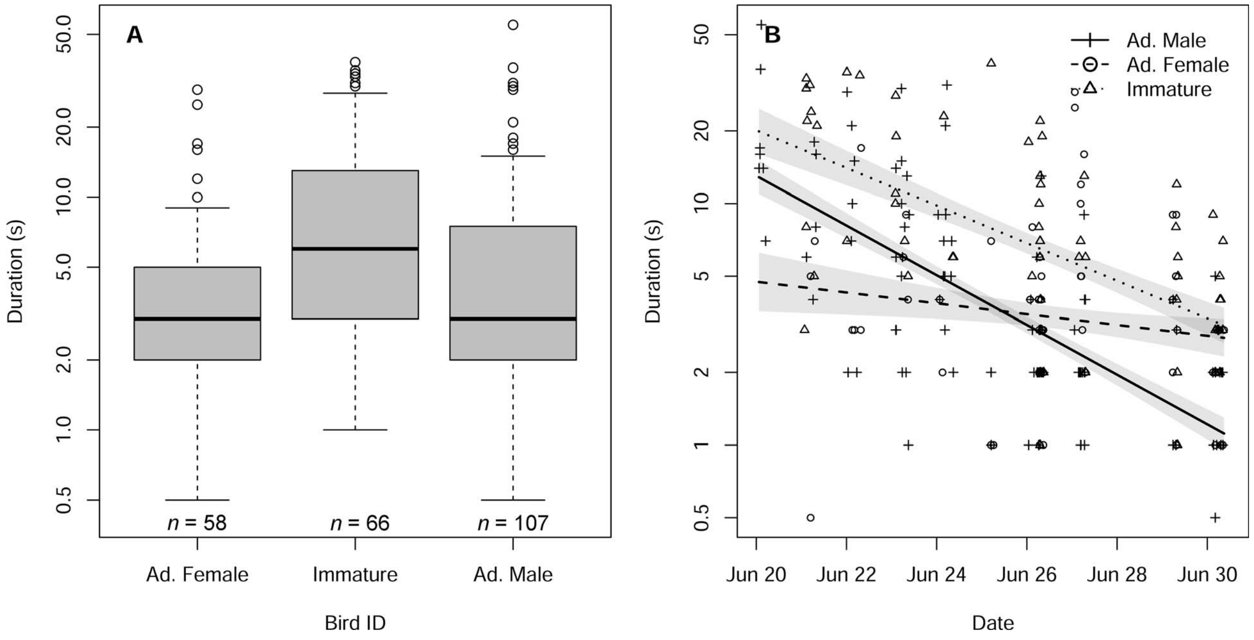

FIGURE 5. (**A**) Visit length over time at the Sapayoa nest we observed in Darién National Park, Panama, with *y*-axis plotted on a log scale. For the adult male and the immature males, visit length became significantly shorter as the chicks matured, but this was not true for the adult female. (**B**) Nest-visit duration for adult male, adult female, and immature males, plotted in log scale. A nest visit includes feeding visits and visits during which an individual arrived at the nest entrance but did not enter (i.e. excluding brooding periods). Mean visit duration of immature birds was significantly greater than that of both adults. Shading above and below the mean line represents SE.

too, the intercept term for the adult male was significantly higher than that of the other 3 individuals ($t = 2.735$, $P = 0.012$). Over the entire 11-day observation period, the female, immature males (combined), and adult male spent 1,212.1, 11.3, and 11.4 min at the nest, respectively. For the adult and immature males, visit length became significantly shorter as the chicks matured, but this was not true for nonbrooding visits of the adult female ($t_{\mathrm{Male}} = -3.935$, $P_{\mathrm{Male}} < 0.001$; $t_{\mathrm{Immature}} = -2.534$, $P_{\mathrm{Immature}} = 0.01$; $t_{\mathrm{Female}} = -1.317$, $P_{\mathrm{Female}} = 0.19$; Figure 5B). When brooding periods are excluded, the mean and median nest-visit duration was comparable between the adult male and female (Figure 5A). However, the immature birds spent significantly more time at the nest during their visits than either adult (Tukey's HSD: $P_{\mathrm{Immature-Female}} < 0.001$, $P_{\mathrm{Immature-Male}} < 0.001$, $P_{\mathrm{Male-Female}} = 0.87$; Figure 5A). Mean nest-visit duration was 5 s, 6.4 s, and 10.3 s for the female, adult male, and immature males, respectively.

In addition to this difference in visit duration, the immature males exhibited a number of behaviors distinct from those of the adult male and female. As described above, the nest was pear-shaped and hung by a thick belt of material woven over the top of a branch. The end of the branch protruded from the belt of material, and the leaves at its tip fanned over the nest entrance. Immature males were the only individuals to use this branch as a perch, and they did so only during the first 4 days of the 11-day observation period. They landed on the branch somewhat clumsily during 4 different instances. During the second day of nest watching (June 21), an immature bird approached the side of the nest, bumped it in flight, and perched on the branch from which the nest hung (ML 483799). Four hours later, an immature bird again bumped the back of the nest and landed on this branch while the other immature successfully arrived at and left the actual nest entrance. Two days later (June 23), at 0703 hours, a lone immature flew back and forth to the nest branch and a nearby tree branch twice. It did not bump or enter the nest. We observed similar behaviors on June 25, when an immature male made multiple apparent attempts to visit the nest, including perching on the side (ML 483803). Why the immature birds used these alternate perches or bumped the nest is unknown but may have been due to inexperience. Alternatively, it is possible that they were attempting to fix or modify the exterior of the nest in some way. Neither the female nor the adult male performed these actions.

Immature males were also the only individuals to arrive at the nest with food and depart without feeding the chicks. Although it was often difficult to see whether food was delivered to the nest, in these instances the immature birds would bring food to the nest and land on a nearby perch while visibly still holding food. On June 21, at 1213 hours, an immature male landed on the branch above the

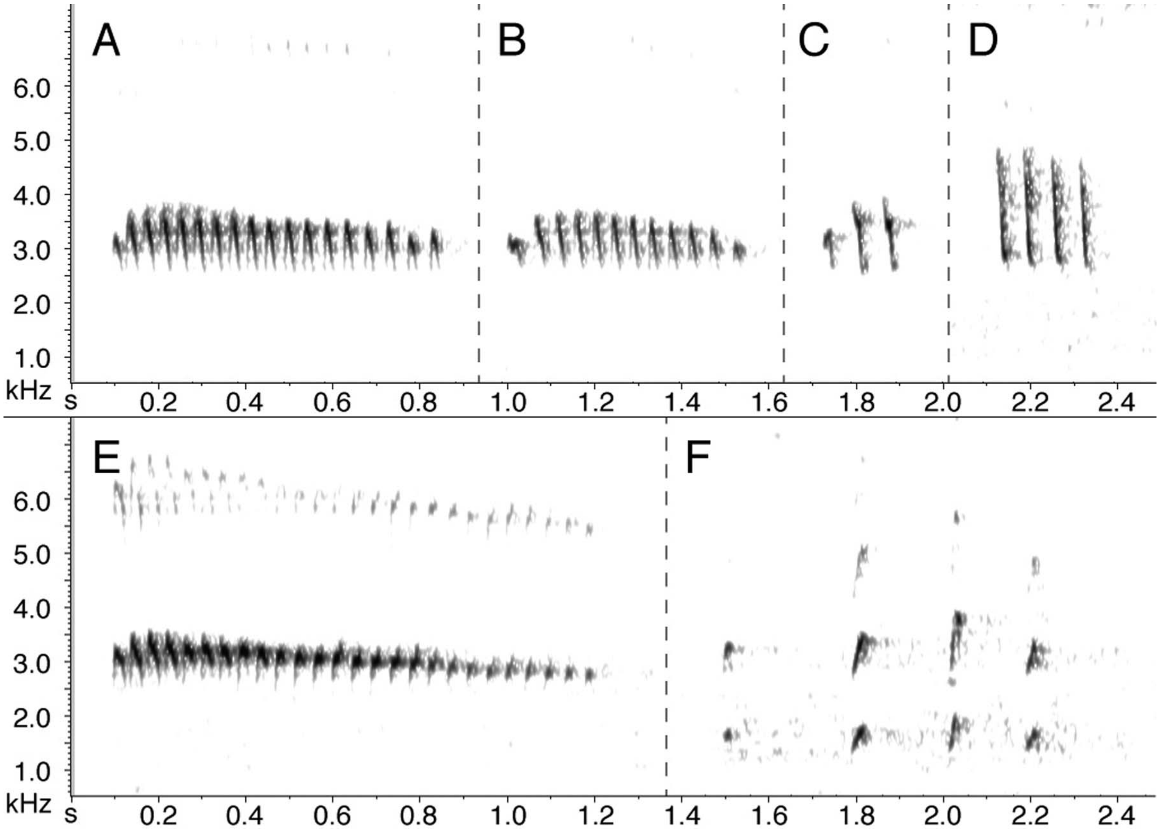

FIGURE 6. Examples of vocalizations recorded at the Sapayoa nest we observed in Darién National Park, Panama. The birds gave trills and twitters of varying lengths near the nest (**A**, **B**) and often uttered emphatic twittered calls when taking flight (**C**, **D**). Longer trilled "songs" were also given (**E**), usually when farther from the nest. When very close to the nest, the birds gave single-note calls (**F**). All clips are from ML 214702. Spectrogram parameters: Hann windows; window size = 600 samples; overlap = 75%; hop size = 151 samples; DFT size = 1024 samples.

nest entrance with food, flew to a nearby perch, to the nest, and then back to the perch, and proceeded to eat the food it had been carrying (ML 483799). That same day, at 1359 hours, an immature bird flew back and forth from the side of the nest to a nearby branch with food 4 times and never delivered the item to the nest. The female was present in the nest during this event. The following day, at 0713 hours, an immature flew to the nest entrance with food, flew to a nearby branch with the same food item, and then returned 5 min later to feed the chicks with the original food item. We never documented either adult leaving the nest with food, although difficulties in viewing smaller food items prevent us from being certain.

During trips to and from the nest, Sapayoas would typically take flight and then hover for a brief moment, sometimes more than a second, before continuing on (e.g., ML 484041, 484052, 484055, 484060). Hovering shortly after taking flight is unusual and would appear to incur unnecessary energetic costs. In addition, hovering shortly after departing from the nest entrance (ML 484041) would seem to increase the risk of drawing attention to the nest area. This behavior lacks explanation.

Vocalizations at the Nest

We could often predict an upcoming nest visit because the approaching birds gave long, descending trills in the minutes preceding a visit (Figure 6E; ML 516296: 0:00–2:00 in the recording; see also ML 186853, but this recording was not taken near a known nest). Birds near the nest would typically give shorter trills and twitters (Figure 6A–D, F; see ML 516296, 483812, 515023). Very short twittered calls were often given as birds flew from a perch (Figure 6C–D; e.g., ML 199614). During feedings, chicks would answer with begging calls (ML 483812, 516296) (for more examples of vocalizations near the nest, see ML 214700, 214701, 214702, and 214703). When foraging among a flock, Sapayoas typically gave single-note calls and short trills and twitters (e.g., ML 199673 and 199674). On one occasion, we recorded a Sapayoa making a snap-like mechanical noise in flight (ML 186853).

Cooperative Breeding Dynamics

We observed unconventional reproductive behaviors, such as mounting between individuals of the same sex, mounting of the female by more than one male, and multiple mounting events per day. We captured 15 mounting events on film, involving pairings of the 2 immature males, the adult male, and the female. These events each involved one bird mounting the other, but we could not determine whether sperm was transferred. All mounting events we describe occurred on branches ~2 m from the nest.

Of these 15 mounting events, 8 involved an immature male mounting the adult female, 5 involved the adult male mounting the female, 1 involved the adult male mounting the immature male, and 1 occurred between the 2 immature males. In all events involving the female and a male individual, the male was on top. During the 5 mounting events involving the adult male mounting the female (e.g., ML 483802, 483804, 484060, 483808, 483810, 484026), the male visited the nest just before mounting her and no immature birds were present. Mounting events were always preceded by a visual solicitation display given by the receiving individual. Only the immature males and the adult female performed this display; it typically involved the receiving bird assuming a horizontal posture and initiating some combination of calling, wing fluttering, tail wagging, crown flaring (for males), and/or rapid shaking. Solicitation displays performed by immature males often emphasized tail wagging; displays performed by the adult female often began with exaggerated wing movements and ended with similar tail wagging and quivering. The likelihood of cloacal contact was difficult to determine, but tail positioning suggested that it may have occurred in at least some cases, especially those involving the adult male and female. Solicitation displays were not always followed by a mounting event (e.g., ML 484030, 484042, 484055, 484058).

An immature male mounted the female a total of 8 times, all in response to displays by the female (primarily tail quivering); 6 of the 8 events occurred while the other immature was present. Three events occurred within minutes of each other on June 26 at 1315 hours (ML 483805). The other events occurred on June 21 (ML 483800), June 25 (ML 484059), June 27 (ML 483807), June 29 (ML 483809), and June 30 (ML 483811). The adult male was present in the area during only one of the events (25 June; ML 484059). In some events, immature males responded to the female's solicitation displays with actions of their own (e.g., wing flicks).

Two mounting events between males also occurred. On June 23, the adult and 2 immature males perched on the nearby branch shortly after the female had entered the nest, presumably to brood. One immature bird performed a solicitation display, quivering its tail and flaring its crown feathers, after which the adult male mounted it and flew out of frame (ML 483801). Later on in the clip, the first immature male quivered its tail repeatedly in the presence of the second, but no mounting occurred. A similar behavior occurred on June 25: One immature male displayed to the other but with no associated mounting (ML 483803). The second male–male mounting event occurred on June 27 after one immature male had mounted the female in the presence of the other (described above). After the female left the area, the first immature bird performed a solicitation display and the second immature then mounted the displaying bird (ML 484054, 483807).

DISCUSSION

Nesting Season

Like other Neotropical forest birds (Skutch 1950), especially those that breed cooperatively (Russell et al. 2004), the Sapayoa appears to have an extended nesting season. The nest found in 1996 in the Nusagandi reserve in Guna Yala, Panama, was active in May and likely into early June (Christian 2001); we found egg-laying birds in the Darién during June and chicks into July. Other observers in Nusagandi have recently noted active Sapayoa nests on the following dates: March 25, 2014 (one bird near a completed nest; G. Bieber personal communication); March 29, 2013 (pair attending a nest; G. Bieber personal communication); early June 2013 (female attending a nest; S. Gladstone personal communication); and September 2, 2014 (pair provisioning food for nest ~1 m over a stream; J. Sinasac personal communication). Patterns of nest placement at Nusagandi appear to be nearly identical to those we observed, with nests hanging directly above streams in steep, forested ravines (G. Bieber personal communication). These areas have similar relative rainfall patterns, with nearby meteorological stations (Corti, 4 km from Nusagandi; and Tucuti, 23 km from Pirre Station) both receiving the least amount of rain from December through March, followed by a sharp increase in April and May (Hidrometeorología de ETESA, 2015). The Corti station near Nusagandi receives a monthly average of 291.6 mm of rain, whereas the Tucuti station near Pirre Station receives a monthly average of 252.0 mm.

Possible Nest Desertion

We concluded that the first pair of captured Sapayoas likely abandoned their nest after disturbance. However, there is little information on clutch size in Sapayoas (2 nestlings described here and in Christian 2001) and no information on behavior before or during incubation; furthermore, we do not know whether this pair had begun incubating at the time of capture. Therefore, multiple alternative explanations are possible. For example, the clutch of 2 eggs may not have been complete, or the pair may have returned to continue incubation after an extended absence. Incubation could also be intermittent in this species. For example, the Spotted Barbtail (*Premnoplex brunnescens*), a New World suboscine, leaves its nest for several hours each day during the incubation period (Greeney 2009).

Cooperative Breeding

In many cooperatively breeding species, a dominant breeding pair is accompanied by younger helpers of varying ages (Brown 1978, Skutch 1999, Ekman et al. 2004, Cockburn 2006); based on our observations of the birds attending one nest, this appears to be true for *Sapayoa*. Relations in this small group of Sapayoas have not yet been determined by genetic testing, but the group clearly consisted of an adult male and female and 2 immature male birds. Although we were able to observe only one active Sapayoa nest for an extended period, the fact that we observed helpers suggests that cooperative breeding is probably not uncommon in this species.

In other bird species, the presence of helpers can increase breeding success and parental survival while increasing helpers' inclusive fitness (Langen 2000, Doerr and Doerr 2007, Russell et al. 2007, Meade et al. 2010, Nam et al. 2010). Young may be compelled to stay and help with nesting when natal territories are resource rich (Koenig et al. 1992, Dickinson and McGowan 2005, Baglione et al. 2006). We found Sapayoas to be present at low densities and restricted to stream-lined ravines, which suggests that food availability or habitat quality may constrain dispersal. When surveying forested streams, we noted stretches of hundreds of meters without any visible Sapayoa nests (new or old), punctuated by small areas with multiple nests of varying condition. Specific territory requirements could contribute to low population densities in this species.

Among *Sapayoa*'s closest relatives in the Old World, Dusky Broadbills (*Corydon sumatranus*) breed cooperatively; nest helpers have been reported in Long-tailed Broadbills (*Psarisomus dalhousiae*) and Silver-breasted Broadbills (*Serilophus lunatus*) (Lambert and Woodcock 1996, Bruce 2015a, 2015c); and Black-and-red Broadbills (*Cymbirhynchus macrorhynchos*) may at least nest-build cooperatively on occasion (Zubkova 2013, G. Montgomery personal communication, E. Zubkova personal communication). Cooperative breeding in the Eurylaimidae may be underreported given the paucity of detailed natural history data for many taxa. There is also some indication of cooperative reproductive behaviors in the Philepittidae: Nest construction in the lek-mating Velvet Asity (*Philepitta castanea*) can involve the efforts of 2 female-plumaged birds (Prum and Razafindratsita 1997, Rakotomanana and René de Roland 2007). By contrast, there have been no records of cooperative breeding species in the Pipridae and only 6 (<2%) in the speciose Tyrannidae (Cockburn 2006).

Climatic variability has been strongly linked to the incidence of cooperative breeding in birds (Rubenstein and Lovette 2007, Jetz and Rubenstein 2011). Temperatures show little variation close to the Equator, and the Chocó bioregion is the wettest place in the Americas. However, rainfall varies considerably with the El Niño–Southern Oscillation: El Niño years are strongly associated with dry conditions (Poveda et al. 2006). It is not clear to what extent this may influence annual variability in food abundance for Sapayoas.

Various behaviors exhibited by immature male Sapayoas suggest inexperience with breeding. These include longer visitation time per visit to the nest, flights to and from the nest with food, repeated flights to the back or side of the nest instead of to the entrance, and initial failed attempts to mount the female before succeeding (in contrast to the adult male's behavior). Deception is one possible explanation for the immature birds' failed food deliveries; in White-winged Choughs (*Corcorax melanorhamphos*), helpers bring food to the nest and appear to feed young while actually consuming the food themselves (Boland et al. 1997). However, no other individuals were visible in frame during all 3 possible fake-feeding events (in one, the female was in the nest). This suggests that this behavior is not a signal to other members of the group and instead could simply occur when the chicks are satiated and/or the helpers are particularly hungry (McDonald et al. 2007, Canestrari et al. 2010). Our camera view was limited to the area immediately around the nest, so it is possible that unseen birds were present during these events. The adult male and female never exhibited this behavior.

Given our observations of apparent inexperience in the immature males, their assistance at the nest may simultaneously train the young birds while allowing the adults to raise more offspring. This would make particular sense if the immature birds were too young, or it was too late in the season, for them to nest themselves. This hypothesis is supported by studies showing that younger birds are less successful at reproduction (Tøttrup Nielsen and Drachmann 2003, Förschler and Kalko 2006, Balbontín et al. 2007) and by evidence that helpers can benefit from "practice" with enhanced reproductive success later in life (Komdeur 1996). Molting during the breeding season, as we observed for both captured adult males, may be an additional adaptation for maximizing productivity; this behavior has been explained as a way for tropical birds to extend breeding (Foster 1974, 1975).

The adult female Sapayoa was the only bird to brood the chicks and showed distinct whitish belly feathers due to feather wear, in addition to having a brood patch. By contrast, the adult male showed no such wear and did not have a brood patch. The male therefore does not appear to incubate the eggs or brood the chicks. Although our observation of only one nest prevents us from assessing the generality of the pattern of feather wear, we did note at least one other Sapayoa that showed distinctive whitish belly feathers (see ML 476249).

Mounting Events during Nest Provisioning

We documented 15 mounting events between members of the Sapayoa group, all after the chicks had hatched. In all cases, the receiving bird performed a solicitation display that involved horizontal posture, tail quivering or wagging, and wing quivering or flicking.

The majority of observed mounting events involved an immature bird mounting the adult female. Male Pale-winged Trumpeters (*Psophia leucoptera*) copulate with a female according to a dominance hierarchy, and subordinate males engage in various strategies to achieve copulations and sire offspring (Eason and Sherman 1995). In Smith's Longspur (*Calcarius pictus*), males copulate with females at very high rates according to a dominance hierarchy, but copulations cease after egg laying (Briskie 1992). However, the mounting events we observed occurred after the chicks had hatched, which appears to be inconsistent with competition to sire offspring. Furthermore, if the immature male helpers were indeed the offspring of the adult pair—a typical scenario in cooperative breeding systems (Skutch 1999, Cockburn 2006)—such behavior would be incestuous (see Cockburn 1998). Therefore, this behavior may not serve an explicitly reproductive function, although this possibility is not ruled out.

We also documented male Sapayoas engaging in same-sex mounting behaviors, which included the adult male mounting an immature male as well as an immature male mounting an immature male. In other birds, male–male mounting is used to demonstrate dominance between males in a social group. For example, in the Pukeko (*Porphyrio p. melanotus*), most mounting events involve a male and a female, but male–male and female–female mounting events also occur at lower frequency, likely to establish social status within a cooperative breeding group (Craig 1980). These dominance hierarchies help maintain order within breeding groups and determine the division of labor and interactions among individuals (Craig 1980). In the one event involving the adult male Sapayoa and an immature male, the adult was on top.

One possible function of this collection of mounting events, especially those involving the adult female, is to maintain social cohesion of the breeding group and secure assistance in provisioning the nest. The female was involved in 13 of 15 observed events, and she expended a great deal of effort in soliciting male attention (e.g., exaggerated wing-flicking and prolonged displaying). Clearly, it would benefit her to reinforce group bonds and maintain provisioning effort at the nest, given that males made three-fourths of nest visits. This hypothesis of group cohesion could also explain why other group members (i.e. immature male helpers) also solicited mountings. Acorn Woodpeckers (*Melanerpes formicivorus*), which breed cooperatively, engage in mounting behaviors among all members of the cooperative group (MacRoberts and MacRoberts 1976); these appear to be unrelated to copulation, but their function has not yet been determined (Koenig and Walters 2014). In Sapayoas, an alternative explanation could be "training" or experimenting by inexperienced immature birds; we have already described how immature males engaged in other behaviors that suggest inexperience or incompetence. Finally, we cannot rule out the possibility that mounting behaviors are indeed related to reproduction. Many mountings, including those involving the adult female and an immature male, could have involved cloacal contact. If these behaviors involve sperm transfer, the immature males could be cobreeders unrelated to the adult female. Clearly, future research on Sapayoa behavior holds promise; these hypotheses could be investigated with information on the social behavior of Sapayoas during nest building and incubation or outside of the breeding season, and with information on the relatedness of chicks, helpers, and adults.

Sapayoa in a Phylogenetic Context

Sapayoa aenigma is currently considered an Old World suboscine, with evidence supporting a number of different hypotheses: that *Sapayoa* is sister to the clade comprising the eurylaimid broadbills (Eurylaimidae) and asities (Philepittidae) (Moyle et al. 2006), sister to the African Broadbill (*Smithornis capensis*) and Green Broadbill (*Calyptomena viridis*) (Irestedt et al. 2006), sister to the pittas (Claramunt and Cracraft 2015), or sister to all other Old World suboscines (Ericson et al. 2014). *Sapayoa*'s exact position among the Old World suboscines is clearly unresolved. In Table 2, we compare *Sapayoa* to representative species from closely related or morphologically similar suboscine families. This table is not meant to be exhaustive.

We can conclude that much of the morphological similarity between *Sapayoa* and the New World suboscines arose independently. For example, *Sapayoa* shares toe morphology with all members of the Pipridae, and it shares a largely sexually monomorphic olive-brown-green complexion with many New World suboscines—including but not limited to the Green Manakin (*Xenopipo holochlora*), Thrush-like Schiffornis (*Schiffornis turdina*), and Olivaceous Flatbill (see Table 2). However, with respect to breeding biology, Sapayoa is less similar to these families: Relatively few genera of New World suboscines construct

TABLE 2. A comparison of morphological and life history traits of *Sapayoa* and 6 similar species: 2 species from the families in which *Sapayoa* was previously grouped (Pipridae and Tyrannidae), 3 of its phylogenetically most closely related species (from Eurylaimidae, Calyptomenidae, and Philepittidae), and a morphologically similar species (*Schiffornis*). Scientific names of species are given in the text. Information is from Rakotomanana and René de Roland (2007); Bates (2015); Bates and de Juana (2015); Bruce (2015a, 2015b); Hawkins (2015); Snow (2015a, 2015b, 2015c); Winkler et al. (2015).

Clade	Old World				New World		
Family	Sapayoidae	Eurylaimidae	Calyptomenidae	Philepittidae	Tyrannidae	Pipridae	Tityridae
Species	Sapayoa	Dusky Broadbill	Green Broadbill	Velvet Asity	Olivaceous Flatbill	Green Manakin	Thrush-like Schiffornis
Bill size	Large, flat, base wide	Large, inflated, base wide	Small, wide gape	Small, decurved, base narrow	Large, flat, base wide	Small, base narrow	Medium-sized
Color	Olive, male yellow crown	Sexes similar	Green, female duller	Males colorful; females drabber	Olive-green, sexes similar	Greenish, sexes similar	Brown-olive, sexes similar
Nest shape	Woven, pear-shaped, hanging	Woven, pear-shaped, hanging	Woven, pear-shaped, hanging	Woven, pear-shaped, hanging	Woven, pear-shaped, hanging	Cup	Cup
Nest location	Hung over streams in ravines	Hung over clearings, streams, etc.	Hung over ground or water	Hung over small brooks or clearings	Hung from tree	Usually fork of tree	Palm or epiphyte supported from below
Diet	Largely insects	Largely insects	Largely fruit	Largely fruit	Insects	Largely fruit	Fruit and insects
Biparental provisioning?	Yes	Yes	Yes	Female only; lekking	Unknown; yes in congener (*R. fulvipectus*)	Female only; no lekking	Unknown
Cooperative?	Yes	Yes	No evidence	Likely (nest building)	Unknown; no evidence in congener	No evidence	Unknown

hanging nests (Fitzpatrick 2016) and only 1% breed cooperatively (Cockburn 2006). One exception among the tyrannids are the flatbills, which are among the few groups that build hanging nests; sympatric Olivaceous Flatbills also have similarly wide and compressed bills.

Although the plumages of the Eurylaimidae, Calyptomenidae, and Philepittidae are very different from that of *Sapayoa*, they share certain aspects of morphology and behavior. Most consistent among Old World suboscines is the pear-shaped hanging nest. The solicitation displays we observed are also reminiscent of the closely related Black-and-yellow Broadbill's (*Eurylaimus ochromalus*) precopulation displays, which involve birds spreading their wings, opening their bills, and, at least occasionally, tail wagging (Prentice 1988, Lambert and Woodcock 1996, E. Gulson-Castillo and T. Pegan personal communication; video: ML 471162).

Sapayoa's simple trilled and twittered vocalizations are distinct from those of other Old World suboscines, although the calls of some broadbills, such as the Banded Broadbill (*E. javanicus*), have been described as "cicada-like trills" (Lambert and Woodcock 1996). Mechanical noises are produced by other Old World suboscines, for example *Pitta ussheri* (Pegan et al. 2013), *Philepitta castanea* (Hawkins 2016), and broadbills in the genus *Smithornis* (Bruce 2016). We considered the possibility that some of our recorded vocalizations (see Figure 6D) were actually produced mechanically, but we think they are most likely vocal.

Overall, *Sapayoa* most closely resembles the Eurylaimidae: Both have broad-based bills and extensively fused outer toes (Hartert 1903, Sibley and Ahlquist 1990); both are predominantly insectivorous; several eurylaimids exhibit cooperative reproductive behaviors and biparental care; and a solicitation display similar to that of Sapayoa is given by females in at least one eurylaimid (described above). Many of the shared characteristics between Sapayoidae and Eurylaimidae are not exhibited by the Philepittidae or Calyptomenidae: These families have small bills and marked sexual dimorphism, and they are largely frugivorous. Although there is no documentation of cooperative breeding in calyptomenids, there is some evidence in one philepittid (Prum and Razafindratsita 1997, Rakotomanana and René de Roland 2007). The large number of morphological and behavioral similarities between *Sapayoa* and the Eurylaimidae is more consistent with the topology presented by Moyle et al. (2006); clearly, however, detailed conclusions regarding the comparative biology of the Old World suboscine clade will require both a better-resolved phylogeny and more information about the natural histories of its species. Nonetheless, our study better informs the relationship between *Sapayoa*, the only Old World suboscine in the Americas, and its closest relatives on the other side of the world. We now see that certain elements of *Sapayoa*'s reproductive biology (e.g., cooperative behavior, displays, nest placement, and nest structure) closely resemble those of its Old World relatives, especially the eurylaimid broadbills.

ACKNOWLEDGMENTS

The Cornell Lab of Ornithology generously supported our research from the Ivy Expeditions Fund and other sources, with additional support from K. McMahon, the Macaulay Library, and the Hunter R. Rawlings III Cornell Presidential Research Scholars Program. We especially thank D. Winkler, I. Lovette, C. Dardia, D. Bonter, M. Webster, A. Dalziell, D. Christian, J. Perez, J. Sinasac, G. Angehr, and members of the Ivy Expeditions team for their support and advice. We thank S. Gladstone and C. Hruska for their help and hospitality in Panama, as well as I. Pissaro and P. L. Castillo Caballero for their help in the field. We thank T. Pegan and K. Hallinger for DNA sexing of the Sapayoa specimens. We thank the staff of the Smithsonian Tropical Research Institute for their extensive assistance, especially M. Miller, L. Camacho, and D. Buitrago; and botanists A. Ibáñez and R. Flores. We greatly appreciate the kindness of the Pirre Station staff, especially Cholo, Teresa, and her family; and we thank the Autoridad Nacional del Ambiente de Panamá for their efforts and logistical support. We thank T. Pegan, E. Gulson-Castillo, and one anonymous reviewer for valuable comments on the manuscript.

Funding statement: This work was financially supported by a generous donation to the Ivy Expeditions Fund at the Cornell Lab of Ornithology. The donor did not have any influence on the content of the submitted or published manuscript. The donor did not require approval of the final manuscript to be published.

Ethics statement: All work was conducted under an approved Cornell Institutional Animal Care and Use (IACUC) protocol (no. 2001-051) to D. Winkler. Specimens were collected under permit no. SE/A-54-14 and IACUC protocol no. 2014-0601-2017-5, issued by the Smithsonian Tropical Research Institute.

Author contributions: All the authors conceived the idea and design of the research; all authors performed the research (conducted fieldwork, collected and processed data); S.A.D. and B.M.V.D. wrote the paper; B.M.V.D. and S.A.D. analyzed the data.

LITERATURE CITED

Angehr, G. R., and R. Dean (2010). The Birds of Panama: A Field Guide. Comstock, Ithaca, NY, USA.

Baglione, V., D. Canestrari, J. M. Marcos, and J. Ekman (2006). Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding Carrion Crows. Proceedings of the Royal Society of London, Series B 273:1529–1535.

Balbontín, J., I. G. Hermosell, A. Marzal, M. Reviriego, F. De Lope, and A. P. Møller (2007). Age-related change in breeding performance in early life is associated with an increase in competence in the migratory Barn Swallow *Hirundo rustica*. Journal of Animal Ecology 76:915–925.

Bates, J. (2015). Olivaceous Flatbill (*Rhynchocyclus olivaceus*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/57307.

Bates, J., and E. de Juana (2015). Fulvous-breasted Flatbill (*Rhynchocyclus fulvipectus*) in Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/57309.

Boland, C. R. J., R. Heinsohn, and A. Cockburn (1997). Deception by helpers in cooperatively breeding White-winged Choughs and its experimental manipulation. Behavioral Ecology and Sociobiology 41:251–256.

Briskie, J. V. (1992). Copulation patterns and sperm competition in the polygynandrous Smith's Longspur. The Auk 109:563–575.

Brown, J. L. (1978). Avian communal breeding systems. Annual Review of Ecology and Systematics 9:123–155.

Bruce, M. D. (2015a). Dusky Broadbill (*Corydon sumatranus*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/56350.

Bruce, M. D. (2015b). Green Broadbill (*Calyptomena viridis*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/56340.

Bruce, M. D. (2015c). Long-tailed Broadbill (*Psarisomus dalhousiae*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/56344.

Bruce, M. D. (2016). Broadbills (Eurylaimidae). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/52287.

Canestrari, D., R. Vera, E. Chiarati, J. M. Marcos, M. Vila, and V. Baglione (2010). False feeding: The trade-off between chick hunger and caregivers needs in cooperative crows. Behavioral Ecology 21:233–241.

Christian, D. G. (2001). Nests and nesting behavior of some little known Panamanian birds. Ornitologia Neotropical 12:327–336.

Claramunt, S., and J. Cracraft (2015). A new time tree reveals Earth history's imprint on the evolution of modern birds. Science Advances 1:e1501005.

Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. Annual Review of Ecology and Systematics 29:141–177.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. Proceedings of the Royal Society of London, Series B 273:1375–1383.

Craig, J. L. (1980). Pair and group breeding behaviour of a communal gallinule, the Pukeko, *Porphyrio p. melanotus*. Animal Behaviour 28:593–603.

Dickinson, J. L., and A. McGowan (2005). Winter resource wealth drives delayed dispersal and family-group living in Western Bluebirds. Proceedings of the Royal Society of London, Series B 272:2423–2428.

Doerr, E. D., and V. A. J. Doerr (2007). Positive effects of helpers on reproductive success in the Brown Treecreeper and the general importance of future benefits. Journal of Animal Ecology 76:966–976.

Eason, P. K., and P. T. Sherman (1995). Dominance status, mating strategies and copulation success in cooperatively polyandrous White-winged Trumpeters, *Psophia leucoptera* (Aves: Psophiidae). Animal Behaviour 49:725–736.

Ekman, J., J. L. Dickinson, B. J. Hatchwell, and M. Griesser (2004). Delayed dispersal. In Ecology and Evolution of Cooperative Breeding in Birds (W. D. Koenig and J. L. Dickinson, Editors). Cambridge University Press, Cambridge, UK. pp. 35–47.

Ericson, P. G. P., S. Klopfstein, M. Irestedt, J. M. T. Nguyen, and J. A. A. Nylander (2014). Dating the diversification of the major lineages of Passeriformes (Aves). BMC Evolutionary Biology 14:8.

Fitzpatrick, J. (2016). Tyrant-flycatchers (Tyrannidae). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/52297.

Fjeldså, J., D. Zuccon, M. Irestedt, U. S. Johansson, and P. G. P. Ericson (2003). *Sapayoa aenigma*: A New World representative of 'Old World suboscines'. Proceedings of the Royal Society of London, Series B 270:S238–S241.

Förschler, M. I., and E. K. V. Kalko (2006). Age-specific reproductive performance in citril finches *Carduelis* [*citrinella*]. Ardea 94:275–279.

Foster, M. S. (1974). A model to explain molt-breeding overlap and clutch size in some tropical birds. Evolution 28:182–190.

Foster, M. S. (1975). The overlap of molting and breeding in some tropical birds. The Condor 77:304–314.

Fridolfsson, A.-K., and H. Ellegren (1999). A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Biology 30:116–121.

Greeney, H. F. (2009). Unusual incubation rhythms of the Spotted Barbtail, *Premnoplex brunnescens*. Journal of Ornithology 150:529–535.

Hartert, E. (1903). On a remarkable new oligomyodian genus and species from Ecuador. Novitates Zoologicae 10:117–118.

Hawkins, F. (2015). Velvet Asity (*Philepitta castanea*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/56352.

Hawkins, F. (2016). Asities (Philepittidae). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/52288.

Irestedt, M., J. I. Ohlson, D. Zuccon, M. Källersjö, and P. G. P. Ericson (2006). Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). Zoologica Scripta 35:567–580.

Jetz, W., and D. R. Rubenstein (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology 21:72–78.

Karr, J. R. (1971). Ecological, behavioral, and distributional notes on some central Panama birds. The Condor 73:107–111.

Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback (1992). The evolution of delayed dispersal in cooperative breeders. Quarterly Review of Biology 67:111–150.

Koenig, W. D., and E. L. Walters (2014). What we don't know, and what needs to be known, about the cooperatively breeding Acorn Woodpecker *Melanerpes formicivorus*. Acta Ornithologica 49:221–223.

Komdeur, J. (1996). Influence of age on reproductive performance in the Seychelles Warbler. Behavioral Ecology 7:417–425.

Lambert, F. R., and M. Woodcock (1996). Pittas, Broadbills and Asities. Pica Press, Robertsbridge, UK.

Langen, T. A. (2000). Prolonged offspring dependence and cooperative breeding in birds. Behavioral Ecology 11:367–377.

Lanyon, S. M. (1985). Molecular perspective on higher-level relationships in the Tyrannoidea (Aves). Systematic Biology 34:404–418.

MacRoberts, M. H., and B. R. MacRoberts (1976). Social organization and behavior of the Acorn Woodpecker in Central Coastal California. Ornithological Monographs 21.

McDonald, P. G., A. J. N. Kazem, and J. Wright (2007). A critical analysis of 'false-feeding' behavior in a cooperatively breeding bird: Disturbance effects, satiated nestlings or deception? Behavioral Ecology and Sociobiology 61:1623–1635.

Meade, J., K.-B. Nam, A. P. Beckerman, and B. J. Hatchwell (2010). Consequences of 'load-lightening' for future indirect fitness gains by helpers in a cooperatively breeding bird. Journal of Animal Ecology 79:529–537.

Moyle, R. G., R. T. Chesser, R. O. Prum, P. Schikler, and J. Cracraft (2006). Phylogeny and evolutionary history of Old World suboscine birds (Aves: Eurylaimides). American Museum Novitates 3544:1–22.

Nam, K.-B., M. Simeoni, S. P. Sharp, and B. J. Hatchwell (2010). Kinship affects investment by helpers in a cooperatively breeding bird. Proceedings of the Royal Society of London, Series B 277:3299–3306.

Pegan, T. M., J. P. Hruska, and J. M. Hite (2013). A newly described call and mechanical noise produced by the Black-and-crimson Pitta *Pitta ussheri*. Forktail 29:160–162.

Phillipps, Q. (1970). Some important nesting notes from Sabah. Sabah Society Journal 5:141–144.

Poveda, G., P. R. Waylen, and R. S. Pulwarty (2006). Annual and inter-annual variability of the present climate in northern South America and southern Mesoamerica. Palaeogeography, Palaeoclimatology, Palaeoecology 234:3–27.

Prentice, C. (1988). Observations of the nuptial behaviour of Black-and-yellow Broadbill *Eurylaimus ochromalus*. Enggang 1(4):8.

Prum, R. O., and W. E. Lanyon (1989). Monophyly and phylogeny of the *Schiffornis* group (Tyrannoidea). The Condor 91:444–461.

Prum, R. O., and V. R. Razafindratsita (1997). Lek behavior and natural history of the Velvet Asity (*Philepitta castanea*: Eurylaimidae). The Wilson Bulletin 109:371–392.

Rakotomanana, H., and L.-A. René de Roland (2007). Breeding ecology of the endemic, Madagascan, Velvet Asity *Philepitta castanea*. Ornithological Science 6:79–85.

Rubenstein, D. R., and I. J. Lovette (2007). Temporal environmental variability drives the evolution of cooperative breeding in birds. Current Biology 17:1414–1419.

Russell, A. F., N. E. Langmore, A. Cockburn, L. B. Astheimer, and R. M. Kilner (2007). Reduced egg investment can conceal helper effects in cooperatively breeding birds. Science 317:941–944.

Russell, E. M., Y. Yom-Tov, and E. Geffen (2004). Extended parental care and delayed dispersal: Northern, tropical, and southern passerines compared. Behavioral Ecology 15:831–838.

Sibley, C. G., and J. E. Ahlquist (1990). Phylogeny and Classification of Birds: A Study in Molecular Evolution. Yale University Press, New Haven, CT, USA.

Sibley, C. G., and B. L. Monroe (1990). Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, CT, USA.

Skutch, A. F. (1950). The nesting seasons of Central American birds in relation to climate and food supply. Ibis 92:185–222.

Skutch, A. F. (1960). Life Histories of Central American Birds II: Families Vireonidae, Sylviidae, Turdidae, Troglodytidae, Paridae, Corvidae, Hirundinidae and Tyrannidae. Pacific Coast Avifauna 34.

Skutch, A. F. (1999). Helpers at Birds' Nests: A Worldwide Survey of Cooperative Breeding and Related Behavior. University of Iowa Press, Iowa City, IA, USA.

Snow, D. (2015a). Broad-billed Sapayoa (*Sapayoa aenigma*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/57116.

Snow, D. (2015b). Green Manakin (*Chloropipo holochlora*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/57101.

Snow, D. (2015c). Thrush-like Mourner (*Schiffornis turdina*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/57118.

Tøttrup Nielsen, J., and J. Drachmann (2003). Age-dependent reproductive performance in Northern Goshawks *Accipiter gentilis*. Ibis 145:1–8.

Warter, S. L. (1965). The cranial osteology of the New World Tyrannoidea and its taxonomic implications. Ph.D. dissertation, Louisiana State University, Baton Rouge, LA, USA.

Winkler, D. W., S. M. Billerman, and I. J. Lovette (2015). Bird Families of the World. Lynx Edicions, Barcelona, Spain.

Zubkova, E. N. (2013). Nest and nest-building in two species of broadbills from south Vietnam (Eurylaimides: *Cymbirhynchus macrorhynchos*, *Corydon sumatranus*). Poster 128. 9th Conference of the European Ornithologists' Union, Norwich, UK. http://eounion.org/wp-content/uploads/2015/07/EOU_Norwich_2013_Abstract.pdf