Journal of Caribbean Ornithology

RESEARCH ARTICLE

Vol. 36:36-44. 2023

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Joshua B. LaPergola C. Justin Proctor Hodali Almonte Kate J. Wallace





Research Article Vol. 36:36–44. 2023

jco.birdscaribbean.org ISSN 1544-4953 https://doi.org/10.55431/jco.2023.36.36-44



Mortality of an adult Antillean Palm Swift (*Tachornis phoenicobia*) associated with *Philornis* sp. parasitism in the Sierra De Bahoruco, Dominican Republic

Joshua B. LaPergola^{*1,2,3}, C. Justin Proctor^{2,4,5}, Hodali Almonte⁶, Kate J. Wallace⁷

Associate Editor: Floyd Hayes

Cover Page: Adult Antillean Palm Swift (*Tachornis phoenicobia*) captured near Jarabacoa, Dominican Republic, on 25 June 2017 by Josh La-Pergola. This bird was caught incidentally while targeting Hispaniolan Woodpeckers (*Melanerpes striatus*) and Palmchats (*Dulus dominicus*) for focal studies on these enigmatic endemic species. Photo by Josh LaPergola.

Published: 17 April 2023

*Corresponding author: e-mail: jbl96@cornell. edu

¹Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA

²Cornell Lab of Ornithology, Ithaca, NY 14853, USA

³Current address: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA; e-mail: jl101@princeton.edu

⁴Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA; e-mail: ProctorCJ@si.edu

⁵Current address: Virginia Working Landscapes, Smithsonian National Zoo and Conservation Biology Institute, Front Royal, VA 22630, USA

⁶Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic; e-mail: almontehodali@hotmail.com

⁷Tody Tours, Rabo de Gato, Provincia de Independencia, Dominican Republic; e-mail: katetody@gmail.com

Cite this article as:

LaPergola, J.B, C.J. Proctor, H. Almonte, and K.J. Wallace. 2023. Mortality of an adult Antillean Palm Swift (*Tachornis phoenicobia*) associated with *Philornis* sp. parasitism in the Sierra De Bahoruco, Dominican Republic. Journal of Caribbean Ornithology 36:36–44. https://doi. org/10.55431/jco.2023.36.36-44

Abstract

The ecological importance of avian myiasis caused by fly (Diptera) larvae, especially in the genus *Philornis*, remains poorly understood. One major gap in our knowledge is which bird species experience such parasitism. We present here the first report of *Philornis* parasitism on an adult Antillean Palm Swift (*Tachornis phoenicobia*) from the Dominican Republic, representing the first documented record of *Philornis* parasitism of a swift species (Apodidae). The host bird was found dead shortly after being observed alive with clear evidence of myiasis, and we suggest the bird's death was due to the detected fly larvae. We also propose that this parasite-associated adult mortality implicates *Philornis* as another potential factor contributing to observed aerial insectivore declines, and highlights the pressing need for more comprehensive studies investigating the occurrence of parasitism in other Caribbean avian species.

Keywords

aerial insectivores, Antillean Palm Swift, *Philornis*, Sierra de Bahoruco, *Tachornis phoenicobia*

Resumen

Mortalidad de un *Tachornis phoenicobia* adulto asociado on el parasitismo por *Philornis* sp. en la Sierra de Bahoruco, Republica Dominicana • La importancia ecológica de la miasis en aves causada por las larvas de moscas del género *Philornis* ha sido poco estudiada en el pasado. Un vacío importante en nuestro conocimiento es la distribución taxonómica de las especies hospederas. Reportamos el primer registro de parasitismo por la mosca del género *Philornis* en un individuo de *Tachornis phoenicobia* de República Dominicana, lo que representa el primer registro documentado de parasitismo por *Philornis* en una especie de vencejo (Apodidae). El hospedero fue un espécimen adulto encontrado muerto poco después de haber sido observado vivo con claras evidencias de parasitismo por *Philornis*, por lo que atribuimos su muerte a las larvas de mosca detectadas. Sugerimos que la mortalidad de aves adultas inducida por parasitismo de *Philornis* sea considerada como otro factor potencial que contribuye a la disminución de los insectívoros aéreos y destacamos la necesidad urgente de estudios más completos que investiguen la aparición de parasitismo en otras especies de aves del Caribe.

Palabras clave

insectívoros aéreos, Philornis, Sierra de Bahoruco, Tachornis phoenicobia

Résumé

Mortalité d'un Martinet petit-rollé (*Tachornis phoenicobia*) adulte associée au parasitisme par *Philornis* sp. dans la Sierra de Bahoruco en République dominicaine • L'importance écologique de la myiase aviaire causée par des larves de mouches (diptères), notamment du genre *Philornis*, reste mal connue. Une lacune importante dans nos connaissances est de savoir quelles espèces d'oiseaux sont affectées par ce type de parasitisme. Nous présentons ici la première mention de parasitisme d'un Martinet petit-rollé (*Tachornis phoenicobia*) adulte par *Philornis* en République dominicaine, ce qui constitue la première mention documentée de parasitisme d'une espèce de martinet (Apodidae) par cette mouche. L'oiseau hôte a été retrouvé mort peu de temps après avoir été observé vivant avec des preuves évidentes de myiase, et nous attribuons donc la mort de l'oiseau aux larves de

© 2023 LaPergola *et al.*; licensee BirdsCaribbean. Open Access article distributed under the Creative Commons Attribution License (creativecommons.org/licenses/ by/3.o/), which permits unrestricted use, distribution, and reproduction, provided the original work is properly cited. mouche détectées. Nous suggérons également que la mortalité à l'âge adulte induite par le parasitisme par *Philornis* soit considérée comme un autre facteur pouvant contribuer au déclin observé des insectivores aériens, et nous soulignons le besoin urgent d'études plus complètes sur l'occurrence du parasitisme chez d'autres espèces d'oiseaux de la Caraïbe.

Mots clés

insectivores aériens, Martinet petit-rollé, Philornis, Sierra de Bahoruco, Tachornis phoenicobia

An important question in avian parasitology is how many species—and which—act as hosts for a given species or clade of parasites. This question is especially relevant for the study of avian myiasis, defined as "the infestation of healthy or necrotic tissue of living vertebrate animals by dipteran larva" (Little 2009:546). For the Neotropics, a growing literature suggests that myiasis caused by larvae of the fly genus Philornis (Diptera: Muscidae) is an ecologically important phenomenon (Couri 1999, Teixeira 1999, Dudaniec and Kleindorfer 2006). Unfortunately, the biology of these flies and which hosts they choose remains poorly understood. Philornis comprises ~50 recognized species restricted to parts of the southern United States and the New World tropics, including the West Indies (Dodge 1955, Skidmore 1985, Carvalho et al. 2005, Couri et al. 2009). Of the described species, 28 have larvae with known habits, including three species that are free-living coprophagous commensals that subsist on bird feces in nests. The remaining sufficiently known Philornis species have larvae that are either free-living (2 species) or subcutaneous (23 species) hematophagous parasites primarily on nestling and occasionally on adult birds (Couri 1999, Teixeira 1999, reviewed in Common et al. 2019). At least some Philornis species (e.g., P. downsi and P. sequyi) can have substantial negative effects on host reproductive success and nestling survival (Arendt 1985a, 1985b, Young 1993, Dudaniec et al. 2007, Rabuffetti and Reboreda 2007, Segura and Reboreda 2011), but large gaps remain in understanding the general impacts and host specificity of these parasitic species.

While parasitism in Caribbean birds remains insufficiently studied in general (Latta 2012; but see Latta and Ricklefs 2010), one notable exception has been work on Philornis parasitism in Puerto Rico (Arendt 1985a, 1985b, Snyder et al. 1987). However, on the neighboring island of Hispaniola, especially within the Dominican Republic, *Philornis* has a long yet incomplete history. The first described species of this genus, P. pici (originally named Aricia pici), was collected on, and derived its name from, an adult Hispaniolan Woodpecker (Melanerpes striatus) (Macquart 1853, Pont 2012). On Hispaniola, Philornis is currently known to parasitize the following resident breeding species: Ridgway's Hawk (Buteo ridgwayi; Woolaver et al. 2015, Hayes et al. 2019), Hispaniolan Trogon (Priotelus roseigaster; S. Guerrero pers. comm.), Hispaniolan Woodpecker (Macquart 1853, LaPergola 2021), White-necked Crow (Corvus leucognaphalus; Wiley 2006), Redlegged Thrush (Turdus plumbeus; Quiroga et al. 2020), Eastern Chat-Tanager (Calyptophilus frugivorus; Quiroga et al. 2020), Black-crowned Palm-Tanager (Phaenicophilus palmarum; Quiroga et al. 2020), and Palmchat (Dulus dominicus; Teixeirra 1999, JBL unpubl. data). Meanwhile, no signs of parasitism from Philornis have been found in Black-capped Petrels (Pterodroma hasitata, E. Rupp pers. comm.) nor in the well-studied Hispaniolan

Golden Swallow (*Tachycineta euchrysea sclateri*; Proctor 2016), despite other *Tachycineta* swallows being parasitized by *Philornis* elsewhere (Stager *et al.* 2012).

Philornis utilizes a wide diversity of host bird families and orders, but one group for which the incidence of Philornis remains uncertain is the swift family, Apodidae. The two previous accounts of Philornis associated with an apodid species of which we are aware must be treated skeptically regarding the identity of the reported parasites. The first record is from Sick (1958), who observed two empty dipteran cocoons in old nests of the Lesser Swallow-tailed Swift (Panyptila cayennensis) in Brazil. Sick suggested these cocoons belonged to Philornis angustifrons, a species with subcutaneous larvae, but never provided specific evidence (e.g., descriptions of cocoon morphology) to support this claim. Furthermore, Sick never documented nestling or adult Lesser Swallow-tailed Swifts with current or recent myiasis. The second account by Marín (1999) reported "5 botfly larvae on the nape, upper back, chest, underwing, and anal area" on one of two Black Swift (Cypseloides niger) nestlings in Costa Rica, but provided no taxonomic assignment nor any descriptions of the larvae. To the best of our knowledge, though, Philornis is the only dipteran genus present in Costa Rica known to parasitize birds. Lowther and Collins (2002; revised in Gunn et al. 2021) cited Marín's observation of the "botfly" larvae as belonging to *Philornis*, but they provided no justification for this taxonomic assignment. Subsequent references (Wiggins 2004, Di Iorio and Turienzo 2009) perpetuated Lowther and Collins' (2002) reporting. Thus, the incidence of Philornis in Apodidae has so far been questionable at best.

Here we describe the first documented record of Philornis in the swift family Apodidae as provided by a case of *Philornis* parasitizing an adult Antillean Palm Swift (Tachornis phoenicobia; hereafter ANPS) in the Dominican Republic. ANPS is a breeding resident known exclusively to the Greater Antilles, including the islands of Hispaniola, Jamaica, Cuba, and the Isle of Pines (Raffaele et al. 1998). Vagrants have been observed in western Puerto Rico on rare occasion (1969, 2008, and 2011), but there have been no breeding colonies established (Kepler 1971, eBird 2015, A.L. Morales pers. comm.). ANPS is currently considered a species of Least Concern with a stable population trend (BirdLife International 2016), yet its natural history and breeding biology remain poorly known (Raffaele et al. 1998, Kirwan et al. 2019, Damaj 2020). This paucity of data is more striking given that the foraging and nesting behaviors of the species are conspicuous where it is common. The species nests colonially, constructing nests on the undersides of hanging (usually dead) fronds of Roystonea and Sabal palm trees (Raffaele et al. 1998, Kirwan et al. 2019, Damaj 2020); within dead fronds that have been harvested and used for thatched roofs (CJP and JBL pers. obs.); and less

frequently in seaside caves (Kirwan et al. 2002). The swift's colonial nesting habits might increase its susceptibility to Philornis, as increased risk of parasitism is considered a major cost of group living, especially in avian species (Hoogland and Sherman 1976, Brown and Brown 1996). However, the available literature pertaining to ANPS natural history (Gosse 1847, Verrill and Verrill 1909, Bond 1928, Wetmore and Swales 1931, Wetmore and Lincoln 1933, Barbour 1943, Raffaele et al. 1998, Chantler 1999, Chantler and Driessens 2000, Kirwan et al. 2002, Kirwan et al. 2019, Damaj 2020) does not mention Philornis parasitizing the species. We use a combination of morphological evidence and distribution records to support our identification of the larva as belonging to *Philornis*. Our observations suggest that more work is needed on Philornis generally and on the breeding biology of ANPS specifically, as our findings would constitute a new bird family being exploited by this genus of parasitic fly. We also suggest that avian myiasis might be a potentially relevant addition to the amalgam of factors contributing to the aerial insectivore population declines observed throughout much of North America (Nebel et al. 2010, Spiller and Dettmers 2019).

Methods

Study Site.—Rabo de Gato (18°19'04"N, 71°34'31"W; Fig. 1) is a trail system located near the village of Puerto Escondido at ~400 m above sea level (asl) on the north slope of the Sierra de Bahoruco, above the town of Duverge, Provincia de Independen-

cia, Dominican Republic. The area is known for its abundance of freshwater springs that support extensive agricultural activity, generating streams with narrow riparian habitat and dry thorn forest on one side and plantations of vegetables and avocados on the other. Tall fig (*Ficus*) trees are common along the land-scape's walking trails. ANPS are regularly observed foraging in the Rabo de Gato area year-round, but no confirmed observations of nesting colonies exist for the area.

On 16 July 2015 at 1800, KJW observed an ANPS (Fig. 2A–C) falling from the sky at Villa Barrancolí, the basecamp for the Rabo de Gato trail. Still alive, the swift was retrieved from the ground, briefly visually inspected, and photographed by KJW before being placed upon a nearby low-hanging branch to recuperate. Although the individual made some weak attempts to fly, it was found dead shortly afterwards on the ground (at 1900). The specimen, with embedded parasites (see below), was immediately frozen and ultimately deposited at the Museo Nacional de Historia Natural (MNHN) in Santo Domingo (MNHNSD. 24. 1092). We collected all morphometric measurements and documentation of the ANPS specimen and associated parasites post-mortem.

Measurements.—We made all ANPS measurements with a wing ruler (flat wing, wing chord, and tail length), digital calipers (exposed culmen, culmen at nares, bill width, and bill depth), or manual calipers (tarsus). We scored fat and feather wear based on standard ornithological metrics using the numeric scales pre-



Fig. 1. Map of eastern Hispaniola, Greater Antilles, depicting the location of Rabo de Gato on the northern slopes of the Sierra de Bahoruco. Darker shading denotes elevations > 475 m asl.



Fig. 2. Photos depicting *Philornis* wounds on the collected Antillean Palm Swift, *Tachornis phoenicobia* (A–C). (A) Two botfly wounds are visible on the throat (indicated by white arrows). The wound closest to the left eye contained the larva (B), shown with the swift specimen for scale. (C) The swift's knee exhibited two old larval wounds (the more laterally located wound is indicated by a white arrow), one of which is more medially located and thus more difficult to see in the photo.

sented by Ralph *et al.* (1993). In this reference, fat class ranges from o–7, with a score of o indicating no visible accumulated fat and 7 indicating "very large fat pads of furculum and abdomen" (Ralph *et al.* 1993:20). Similarly, feather wear ranges from o–5, with a score of o indicating no visible wear on the outer four or five primaries and 5 indicating "excessive wear" (Ralph *et al.* 1993:20). We used ImageJ version 1.46r (Abràmoff *et al.* 2004) to estimate measurements of the extracted larva from a digital photo that had a metric ruler in frame for reference.

Exemplar Larva for Comparison.—As part of a separate study on the breeding biology of the endemic Hispaniolan Woodpecker (*Melanerpes striatus*; LaPergola 2021, LaPergola and Riehl 2022) near Jarabacoa, Provincia de La Vega, JBL collected a *Philornis* larva from a nestling woodpecker on 28 April 2014. This larva fell out of a wound on the nestling woodpecker during processing and was opportunistically collected and photographed. We include a photograph of this larva to allow visual comparison with the larva extracted from the ANPS specimen.

Results

Characteristics of Host Bird.—A close analysis of the plumage of the ANPS individual, along with comparison against other ANPS specimens in the MNHN ornithological collection, suggested that it was an adult. The specimen had dark brown plumage of the wings, crown, nape, back, and tail, and dull white plumage on the chin, throat, and chest (Fig. 2A–C). In contrast to adults, juvenile ANPSs have paler brown plumage, especially along the sides and undertail coverts, and buffy (instead of white) throat and breast (see Raffaele *et al.* 1998 and Damaj 2020 for description). The specimen also had rounded rectrices. In comparison, juvenile ANPS specimens in the MNHN collection had more pointed rectrices. These differences in the shape of rectrices are commonly used to age North American swifts (e.g., *Cypseloides niger, Chaetura pelagica*, and *Ch. vauxi*; Pyle 1997).

The individual had the following measurements and attributes: wing chord, 102 mm; flat wing, 104 mm; weight, 8.0 g; tail

length, 37 mm; exposed culmen, 5.46 mm; culmen at nares, 2.73 mm; bill width, 2.4 mm; bill depth, 3.2 mm; and tarsus, 4.9 mm. The specimen had a fat score of 2 and feather wear of 0. The bird exhibited symmetrical molt in the wings with left primary 1 ~90% replaced and right primary 1 growing. Additionally, the individual had an internal fracture at the bottom of the ribcage and a broken neck, injuries likely sustained when the bird fell from the sky and impacted the ground.

Parasites.—Brief visual inspection of the live bird on 16 July 2015 revealed evidence of ectoparasite-induced wounds on the throat. After field collection, the specimen was temporarily frozen and stored until a more detailed visual inspection was carried out on 24 July 2015, which revealed \geq 4 wounds that we ascribed to *Philornis* myiasis (Fig. 2A–C).

Two older (empty) wounds were present on the left leg (one on the knee and one immediately adjacent to the knee but more medially positioned; Fig. 2B, C). Two wounds were present on the throat, both containing larvae (Fig. 2A). We removed an intact larva (Fig. 2B, Fig. 3A, B, D–F) from the left-most wound and preserved it in an alcohol solution. This larva is archived with the ANPS specimen in the ornithological collection at MNHN under the same catalog number (MNHNSD. 24. 1092).

The collected larva (Fig. 2B, Fig. 3A, B, D–F) was discolored relative to typical live *Philornis* larvae (Fig. 3C), likely a result of tissue damage caused by the freezing process. We estimated the length and width of the larva as 16.1 mm and 6.5 mm, respectively. The larva was thus large and similar in size to *Philornis* larvae parasitizing Hispaniolan Woodpecker nestlings (JBL pers. obs.). We were unable to assign the specimen to species.

We posit that the larvae belonged to a species of *Philornis*. The only other dipteran family known to regularly infest birds in the Americas is Calliphoridae (genera *Trypocalliphora* and *Protocalliphora*), which we exclude as a possible taxonomic assignment based on the following evidence. (1) *Trypocalliphora* and *Protocalliphora* are Holarctic in distribution, and as far as is known, there are no records from Hispaniola, let alone the Greater Antilles, for either genus. (2) The only calliphorid species known to

exhibit obligate subcutaneous parasitism is *T. braueri*, which is thought to be "widespread throughout North America" (Whitworth 2003:1022). However, the closest geographic record to Hispaniola is from northern Georgia, United States, with most other records from farther north (Sabrosky *et al.* 1989), reducing the probability of the present specimens being extra-limital *T. braueri*. Furthermore, the empty wounds observed on the swift were consistent in appearance to those caused by subcutaneous *Philornis* larvae infesting Hispaniolan Woodpeckers. (3) The present larval specimen lacks a prothoracic fringe, de-



Fig. 3. Photos depicting the putative Philornis larva (A, B, D-F) extracted from the Antillean Palm Swift, and (C) a Philornis larva extracted from a Hispaniolan Woodpecker, Melanerpes striatus, for comparison. (A) The larva shown within minutes of extraction from the dead palm swift, also pictured. Note the contrast in colors between the anterior and posterior regions of the larva. (B) Larva with metric ruler for scale. This photo, taken shortly after (A), shows discoloration has spread across the whole specimen. The extracted, dead larva is shown with a ruler for scale. (C) The live Philornis larva, on a metric wing ruler, exhibits the typical coloration in contrast to that of the dead larva (B, D-F). (D) Higher resolution photo of the larva in ventral aspect. (E) Larva in posterior aspect showing the posterior spiracles. (F) Larva in anterior aspect showing the head, thorax, and first few abdominal segments. Photographs A-C by Joshua B. LaPergola, and photographs D–F by Eladio M. Fernández.

scribed as "a band of long spines on the anterior margin of the prothoracic segment" (Whitworth 2003:1001-1002). Nearly all North American Protocalliphora larvae are recognized by the presence of a prothoracic fringe, which aids in attachment to avian hosts (Whitworth 2003, T.L. Whitworth pers. comm.), whereas Philornis larvae lack this morphological feature (Skidmore 1985, Couri 1999). Trypocalliphora braueri also lacks a prothoracic fringe (Rognes 1984, Whitworth 2003), but as mentioned above, this species' current known geographic distribution excludes Hispaniola. (4) The larval specimens examined here lacked cuticular spines (Fig. 3E-F), which are a common feature of some, though not all, Protocalliphora larvae. (5) The third stage larva of T. braueri, the only likely contender for alternative identification, range in length from 6-12 mm and width up to 6 mm (Rognes 1984). The measured length of our larva (16.1 mm) either further excludes T. braueri as a possibility or would otherwise represent a new maximum length record T. braueri larva at ~34% greater than the previously recorded maximum length. (6) The posterior spiracles (Fig. 3E) are very close together, which is typical for Philornis (Dodge and Aitken 1968, Skidmore 1985, Bulgarella et al. 2015) but not for Proto*calliphora* nor *Trypocalliphora*, which typically have more widely spaced posterior spiracles (Sabrosky et al. 1989, Iwasa and Hori 1990). (7) Lastly, the spiracular slits appear horseshoe-shaped (Fig. 3E), which is typical of other muscid flies (e.g., Bulgarella et al. 2015, M. Bertone pers. comm). In contrast, calliphorid larva typically have more linear and parallel spiracular slits (Rognes 1984, Whitworth 2003, M. Bertone pers. comm.). Unfortunately, we were unable to obtain a clearer photograph of the spiracular slits when the specimen was of fresher condition.

Discussion

Based on the morphological evidence and distribution records, our observations provide the first unequivocal case of Philornis parasitizing a swift species. Although we were unable to identify the *Philornis* specimen to species, we suggest it was likely P. pici. Host specificity of different Philornis species varies and is incompletely known (Löwenberg-Neto 2008). On Hispaniola, P. pici is known to impact at least two other resident bird species, Hispaniolan Woodpecker (Macquart 1853) and Ridgway's Hawk (Hayes et al. 2019), and until recently, this species was the only Philornis documented on Hispaniola (Carvalho et al. 2005). Other Philornis spp. also infest distantly related avian species on the same island (Dodge and Aitken 1968), lending some credibility to the P. pici hypothesis. For example, on Santa Cruz island in the Galápagos, the introduced P. downsi infests species representing at least two different orders and three families (Passeriformes: Thraupidae and Parulidae, and Cuculiformes: Cuculidae; Fessl et al. 2001). However, M.A. Quiroga (pers. comm.) recently identified P. porteri also parasitizing Ridgway's Hawk, and other yet to be documented or even described species might also be present on Hispaniola. More clearly delineating Philornis species boundaries and these species' geographic ranges will be important for future conservation work since larvae can negatively impact threatened and endangered species.

The documentation of *Philornis* parasitizing an adult ANPS highlights the need for a more in-depth study on the breeding biology and natural history of this poorly known swift species.

Of special importance will be confirming Philornis parasitism of ANPS nestlings. Philornis typically targets nestlings, where the static environment would conceivably be more conducive for locating and infecting hosts. Although records of Philornis larva infesting adult birds are increasingly recognized and reported (Quiroga et al. 2020, LaPergola 2021), evidence thus far supports the hypothesis that adult infestation is incidental. For example, in the comparatively less aerial Hispaniolan Woodpecker, Philornis parasites were only slightly more likely to occur on nestlings than on adult birds, but the parasite loads of nestlings were ~3.5 times greater on average than those of adult woodpeckers (LaPergola 2021). On Puerto Rico, Pearly-eyed Thrasher (Margarops fuscatus) nestlings were far more likely than adults to be infested with P. deceptivus larvae (Arendt 1985b). These patterns suggest that *Philornis* almost certainly also infests nestling ANPS. We suggest that monitoring ANPS nests for Philornis would therefore be fruitful and important for understanding the impact of such parasitism on ANPS breeding success (see references in Dudaniec and Kleindorfer 2006 for examples of relevant studies). Other important details of ANPS natural history, such as duration of incubation and nestling periods and factors affecting breeding success, remain poorly documented or wholly unknown (Chantler 1999).

That the parasitized bird we documented was an adult raises additional questions about Philornis and its relationship with ANPS. Specifically, how does Philornis infest adult birds and how does that infestation impact adult survival? The aerial foraging habits of swifts might make Philornis targeting adults less feasible and less successful as a strategy. The most likely route to infestation would be when an adult remains in contact with an infested nest for a prolonged period of time, such as during incubation or brooding (Quiroga et al. 2020, LaPergola 2021). The incubation behavior of ANPS is unknown, but in at least some swift species, both parents incubate and brood young (Steeves et al. 2020, Gunn et al. 2021), so the specimen here might have been infested while brooding or roosting with young. Of great importance, too, is the coincidence of Philornis parasitism and mortality that we observed. The ANPS specimen had \geq 4 *Philornis* wounds, including two still containing larvae. Extrapolating from the mean mass for third instar *P. pici* larvae (mean \pm SD = 0.130 \pm 0.083 g, N = 189; M.A. Quiroga, pers. comm.) suggests that this bird carried a combined mass of ~0.52 g of ectoparasites, corresponding to ~6.5% of the swift's total mass (8 g). For such a small bird completely dependent on flying to acquire nutrition, these relatively large Philornis larvae (Fig. 2B) might have dramatically impacted survival by increasing metabolic demands directly or indirectly. Future work should consider the prevalence of Philornis infestation among adult ANPS and the degree to which such parasitism reduces adult survival more generally in this species.

Although ANPS is currently considered a species of Least Concern, it belongs to the aerial insectivore guild, a group of birds facing an uncertain future. Aerial insectivores, including the flycatchers, swifts, swallows, potoos, and nightjars, specialize on airborne insects (aerial plankton) for food, and over the last three decades, their populations have shown noticeable declines throughout much of North America (Nebel *et al.* 2010, Spiller and Dettmers 2019). Unfortunately, population trends of aerial insectivores in the Caribbean are mostly unknown. Improving knowledge of Caribbean aerial insectivores for conservation and monitoring will require identifying nesting localities, which for ANPS remain poorly documented. In this case, the exact origin for our focal individual remains uncertain despite common sightings of the species in the Rabo de Gato area. Many tall royal palms (*Roystonea* sp.) and Hispaniolan palmetto (*Sabal domingensis*) occur in nearby open fields (I. Mota pers. comm.). Because ANPS nest in *S. domingensis* at other localities in the Dominican Republic (e.g., La Vega province; JBL pers. obs.), we suspect that the collected individual came from from an unidentified local breeding colony.

Regarding aerial insectivore declines in North America, many researchers hypothesize that the underlying problems are large-scale decreases in food abundance and changes in food availability (Nebel *et al.* 2010, Nocera *et al.* 2012, Pomfret *et al.* 2012, Robillard *et al.* 2013, Spiller and Dettmers 2019). Others have shown that considerable changes have been made to the guild's various nesting and foraging habitats in the past decade (Evans *et al.* 2007, Grüebler *et al.* 2010, McCracken 2013, Spiller and Dettmers 2019). To our knowledge, no studies have looked at the holistic impact of parasitism across the guild. Our findings of *Philornis* larvae parasitizing an adult ANPS introduce parasitism by *Philornis* and other flies (e.g., *Protocalliphora*) as yet another potentially important variable that should be considered within the current amalgam of causes contributing to aerial insectivore decline.

The full scale of Philornis parasitism and its impacts on wild bird populations remains unclear, and we need a greater understanding of the ecological importance of this genus, including a more complete picture of its taxonomic and geographic spread. We urge other researchers to document and report cases of Philornis parasitism in their work, and just as important, to report when Philornis is not observed. Noting the absence of Philornis in previously documented host species, habitats, and localities will be especially important. Even old wounds from subcutaneous fly larvae can be externally visible for some time after infection (e.g., see LaPergola 2021), thus we suggest that it would be valuable to review museum collections for any evidence of Philornis in other adult specimens of Neotropical bird species. To avoid specimen damage, such data could be gleaned from less invasive methods, such as through x-ray micro-computed tomography, which has successfully visualized internal parasites as small as 40 µm (Martín-Vega et al. 2018). Because infections of adult birds tend to be less common (but see LaPergola 2021), conducting inspections for Philornis pupae on nestlings or by examining collected nests would be most useful. Indeed, as the need to know more about Philornis biology increases, inspecting museum collections more broadly could be very informative.

Acknowledgments

We gratefully acknowledge the assistance of the Museo Nacional de Historia Natural, Santo Domingo. We also thank Eladio M. Fernández (International League of Conservation Photographers) for his photographic contributions and Dr. Martin Quiroga (Universidad Nacional del Litoral) for helping with *Philornis* identification. Comments and suggestions from Seth E. Inman, Dr. Daniel Ardia (Franklin and Marshall College), Dr. Mariana Bulgarella, an anonymous reviewer, and Dr. Jason Townsend greatly improved the quality of this manuscript. We also thank Dr. Terry Whitworth for providing his exceptionally timely and detailed insights on Protocalliphora and Trypocalliphora biology, which proved invaluable for supporting the identification of our larva without genetic analysis. We also thank Dr. Matt Bertone for lending his insight into dipteran larval morphology. Research activity related to Hispaniolan Woodpeckers was approved by the Dominican Republic's Ministerio de Medio Ambiente y Recursos Naturales and conducted in accordance with IACUC protocol 2008-0185 at Cornell University. JBL was supported by a Kramer Graduate Fellowship and a Charles Walcott Graduate Fellowship from the Cornell Lab of Ornithology at the time of the specimen work and relevant Hispaniolan Woodpecker field work. Author contributions: KJW made the field observations and collected the specimen; JBL inspected the ANPS specimen and parasite larva; HA collected morphometric measurements and additional data on the ANPS specimen; JBL and CJP wrote and substantially edited the manuscript; all authors contributed to editing various drafts.

Literature Cited

- Abràmoff, M.D., P.J. Magelhães, and S.J. Ram. 2004. Image processing with ImageJ. Biophotonics International 11:36–42.
- Arendt, W.J. 1985a. *Philornis* ectoparasitism of Pearly-eyed Thrashers. I. Impact on growth and development of nestlings. Auk 102:270–280.
- Arendt, W.J. 1985b. *Philornis* ectoparasitism of Pearly-eyed Thrashers. II. Effects on adults and reproduction. Auk 102:281–292.
- Barbour, T. 1943. Cuban Ornithology. Nuttall Ornithological Club, Cambridge, MA.
- BirdLife International. 2016. *Tachornis phoenicobia*. The IUCN Red List of Threatened Species 2016:e.T22686742A93124942.
- Bond, J. 1928. The distribution and habits of the birds of the Republic of Haiti. Proceedings of the Academy of Natural Sciences of Philadelphia 80:483–521.
- Brown, C.R., and M.B. Brown. 1996. Coloniality in the Cliff Swallow: the effect of group size on social behavior. The University of Chicago Press, Chicago, IL.
- Bulgarella, M., M.A. Quiroga, G.A.B. Vera, J.S. Dregni, F. Cunninghame, D.A.M. Muñoz, L.D. Monje, C.E. Causton, and G.E. Heimpel. 2015. *Philornis downsi* (Diptera: Muscidae), an avian nest parasite invasive to the Galápagos Islands, in Mainland Ecuador. Annals of the Entomological Society of America 108:242–250.
- Carvalho, C.J.B., M.S. Couri, A.C. Pont, D. Pamplona, and S.M. Lopes. 2005. A catalogue of the Muscidae (Diptera) of the Neotropical region. Zootaxa 860:1–282.
- Chantler, P. 1999. Family Apodidae (Swifts). Pp. 388–466 in Handbook of the Birds of the World, Vol. 5 (J. del Hoyo, A. Elliot, and J. Sargatal, eds.). Lynx Edicions, Barcelona, Spain.
- Chantler, P., and G. Driessens. 2000. Swifts: a guide to the swifts and treeswifts of the world. 2nd edn. Yale University Press, New Haven, CT.
- Common, L.K., R.Y. Dudaniec, D. Colombelli-Négrel, and S. Kleindorfer. 2019. Taxonomic shifts in *Philornis* larval behaviour and rapid changes in *Philornis downsi* Dodge & Aitken

(Diptera: Muscidae): an invasive avian parasite on the Galápagos Islands. Pp. 1–22 *in* Life cycle and development of Diptera (M. Sarwar, ed.). IntechOpen, London, UK.

- Couri, M.S. 1999. Myiasis caused by obligatory parasites. Ia. *Philornis* Meinert (Muscidae). Pp. 51–70 *in* Myiasis in man and animals in the Neotropical region (J.H. Guimarães and N. Papavero, eds.). Editora Pleiade, Sao Paulo, Brazil.
- Couri, M.S., L.R. Antoniazzi, P.M. Beldomenico, and M.A. Quiroga. 2009. Argentine *Philornis* Meinert species (Diptera: Muscidae) with synonymic notes. Zootaxa 2261:52–62.
- Damaj, O. 2020. Antillean Palm Swift (*Tachornis phoenicobia*), version 1.0. *In* Birds of the World (T.S. Schulenberg, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- Di Iorio, O., and P. Turienzo. 2009. Insects found in birds' nests from the Neotropical Region (except Argentina) and immigrant species of Neotropical origin in the Nearctic Region. Zootaxa 2187:1–144.
- Dodge, H.R. 1955. New muscid flies from Florida and the West Indies (Diptera: Muscidae). Florida Entomologist 38:147–151.
- Dodge, H.R., and T.H.G. Aitken. 1968. *Philornis* flies from Trinidad (Diptera: Muscidae). Journal of the Kansas Entomological Society 41:134–154.
- Dudaniec, R.Y., and S. Kleindorfer. 2006. Effects of the parasitic flies of the genus *Philornis* (Diptera: Muscidae) on birds. Emu Austral Ornithology 106:13–20.
- Dudaniec, R.Y., B. Fessl, and S. Kleindorfer. 2007. Interannual and interspecific variation in intensity of the parasitic fly, *Philornis downsi*, in Darwin's finches. Biological Conservation 139:325–332.
- eBird. 2015. eBird: an Online Database of Bird Distribution and Abundance. eBird, Ithaca, NY. ebird.org.
- Evans, K.L., J.D. Wilson, and R.B. Bradbury. 2007. Effects of crop type and aerial invertebrate abundance on foraging Barn Swallows *Hirundo rustica*. Agriculture, Ecosystems and Environment 122:267–273.
- Fessl, B., M.S. Couri, and S. Tebbich. 2001. *Philornis downsi* Dodge and Aitken, new to the Galapagos Islands (Diptera, Muscidae). Studia Dipterologica 8:317–322.
- Gosse, P.H. 1847. The birds of Jamaica. John Van Voorst, London, UK.
- Grüebler, M.U., F. Korner-Nievergelt, and J. Von Hirschheydt. 2010. The reproductive benefits of livestock farming in Barn Swallows *Hirundo rustica*: quality of nest site or foraging habitat? Journal of Applied Ecology 47:1340–1347.
- Gunn, C., P.E. Lowther, C.T. Collins, J.P. Beason, K. Potter, and M. Webb. 2021. Black Swift (*Cypseloides niger*), version 2.0. *In* Birds of the World (S.M. Billerman and B.K. Keeney, eds.). Cornell Lab of Ornithology, Ithaca, NY.
- Hayes, C.D., T.I. Hayes, C.J.W. McClure, M. Quiroga, R.K. Thorstrom, and D.L. Anderson 2019. Native parasitic nest fly impacts reproductive success of an island-endemic host. Animal Conservation 22:157–164.
- Hoogland, J.L., and P.W. Sherman. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecological Monographs 46:33–58.
- Iwasa, M., and K. Hori. 1990. The calliphorid larvae parasitic on birds in Japan (Diptera: Calliphoridae). Medical and Veterinary Entomology 4:141–146.

- Kepler, C.B. 1971. First Puerto Rican record of the Antillean Palm Swift. Wilson Bulletin 83:309–310.
- Kirwan, G.M., A. Levesque, M. Oberle, and C.J. Sharpe. 2019. Birds of the West Indies. Lynx and Birdlife International Field Guides. Lynx Edicions, Barcelona, Spain.
- Kirwan, G.M., R.S.R. Williams, and C.G. Bradshaw. 2002. Antillean Palm Swift *Tachornis phoenicobia* nesting in sea caves in the Dominican Republic. El Pitirre 15:65–66.
- LaPergola, J.B. 2021. Life-stage and sex influence *Philornis* ectoparasitism in a Neotropical woodpecker (*Melanerpes striatus*) with essential male parental care. bioRxiv 2021.12.22.473830.
- LaPergola, J.B., and C. Riehl. 2022. Opportunity is not everything: genetic monogamy and limited brood parasitism in a colonial woodpecker. Behavioral Ecology and Sociobiology 76:72.
- Latta, S.C. 2012. Avian research in the Caribbean: past contributions and current priorities. Journal of Field Ornithology 83:107–121.
- Latta, S.C., and R.E. Ricklefs. 2010. Prevalence patterns of avian haemosporida on Hispaniola. Journal of Avian Biology 41:25–33.
- Little, S.E. 2009. Myiasis in wild birds. Pp. 546–556 *in* Parasitic Diseases of Wild Birds (C.T. Atkinson, N.J. Thomas, and D.B. Hunter, eds.). Wiley-Blackwell, Oxford, UK.
- Lowther, P.E., and C.T. Collins. 2002. Black Swift (*Cypseloides ni-ger*), version 2.0. *In* The Birds of North America (A.F. Poole and F.B. Gill, eds.). Cornell Lab of Ornithology, Ithaca, NY.
- Löwenberg-Neto, P. 2008. The structure of the parasite-host interactions between *Philornis* (Diptera: Muscidae) and Neo-tropical birds. Journal of Tropical Ecology 24:575–580.
- Macquart, P.M. 1853. Notice sur une nouvelle espèce d'aricie, diptère de la tribu des anthomyzides. Annales de la Société Entomologique de France Series 3:657–660.
- Marín, M. 1999. Growth rates in the Black Swift: temperate versus tropical comparisons. Ornitología Neotropical 10:179–192.
- Martín-Vega, D., A. Garbout, F. Ahmed, M. Wicklein, C.P. Goater, D.D. Colwell, and M.J.R. Hall. 2018. 3D virtual histology at the host/parasite interface: visualisation of the master manipulator, *Dicrocoelium dendriticum*, in the brain of its ant host. Scientific Reports 8:1–10.
- McCracken, J.D. 2013. The mysterious decline of aerial insectivores. Pp. 6–9 *in* Connecticut State of the Birds 2013: the Seventh Habitat & Decline of Our Aerial Insectivores (M.G. Bull, ed.). Connecticut Audubon Society, Fairfield, CT.
- Nebel, S., A. Mills, J.D. McCracken, and P.D. Taylor. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology 5:1–14.
- Nocera, J.J., J.M. Blais, D.V. Beresford, L.K. Finity, C. Grooms, L.E. Kimpe, K. Kyser, N. Michelutti, M.W. Reudink, and J.P. Smol. 2012. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous Chimney Swifts. Proceedings of the Royal Society of London B: Biological Sciences 279:3114–3120.
- Pomfret, J.K., J.J. Nocera, T.K. Kyser, and M.W. Reudink. 2012. Linking population declines with diet quality in Vaux's Swifts. Northwest Science 88:305–313.
- Pont, A.C. 2012. Muscoidea (Fanniidae, Anthomyiidae, Muscidae) described by P.J.M. Macquart (Insecta, Diptera). Zoosystema 34:39–111.

Proctor, C.J. 2016. Discovering gold in the Greater Antilles: the

natural history, breeding biology, and conservation of the Hispaniolan Golden Swallow, followed by, the status of the critically endangered Jamaican Golden Swallow. M.S. Thesis. Cornell University, Ithaca, NY.

- Pyle, P. 1997. Identification guide to North American birds: Part I, Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.
- Quiroga, M.A., T.I. Hayes, C.D. Hayes, H. Garrod, L. Soares, S.A. Knutie, S.C. Latta, and D.L. Anderson. 2020. More than just nestlings: incidence of subcutaneous *Philornis* (Diptera: Muscidae) nest flies in adult birds. Parasitology Research 119:2337–2342.
- Rabuffetti, F.L., and J.C. Reboreda. 2007. Early infestation by bot flies (*Philornis seguyi*) decreases chick survival and nesting success in Chalk-browed Mockingbirds (*Mimus saturninus*). Auk 124:898–906.
- Raffaele, H.A., J.W. Wiley, O.H. Garrido, A. Keith, and J.I. Raffaele. 1998. A guide to the birds of the West Indies. Princeton University Press, Princeton, NJ.
- Ralph, C.J., G.R. Geupel, P. Pyle, T.E. Martin, and D.F. DeSante. 1993. Handbook of Field Methods for Monitoring Landbirds. USDA Forest Service Gen. Tech. Rep. PSW-GTR-144. Albany, CA.
- Robillard, A., D. Garant, and M. Bélisle. 2013. The swallow and the sparrow: how agricultural intensification affects abundance, nest site selection and competitive interactions. Landscape Ecology 28:201–215.
- Rognes, K. 1984. Revision of the bird-parasitic blowfly genus *Trypocalliphora* Peus, 1960 (Diptera: Calliphoridae). Entomologica Scandinavica 15:371–382.
- Sabrosky, C.W., G.F. Bennett, and T.L. Whitworth. 1989. Bird Blow Flies (*Protocalliphora*) in North America (Diptera: Calliphoridae), with Notes on the Palearctic Species. Smithsonian Institution Press, Washington, D.C.
- Segura, L.N., and J.C. Reboreda. 2011. Botfly parasitism effects on nestling growth and mortality of Red-crested Cardinals. Wilson Journal of Ornithology 123:107–115.
- Sick, H. 1958. Distribution and nests of *Panyptila cayennensis* in Brazil. Auk 75:217–220.
- Skidmore, P. 1985. The Biology of the Muscidae of the World. Dr. W. Junk Publishers, Dordrecht, Netherlands.
- Snyder, N.F.R., J.W. Wiley, and C.B. Kepler. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, CA.
- Spiller, K.J., and R. Dettmers. 2019. Evidence for multiple drivers of aerial insectivore declines in North America. Condor 121:1–13.
- Stager, M., E. Lopresti, F. Angulo Pratolongo, D.R. Ardia, D. Caceres, C.B. Cooper, E.E. Iñigo-Elias, J. Molina, N. Taylor, and D.W. Winkler. 2012. Reproductive biology of a narrowly endemic *Tachycineta* swallow in dry, seasonal forest in coastal Peru. Ornitología Neotropical 23:95–112.
- Steeves, T.K., S.B. Kearney-McGee, M.A. Rubega, C.L. Cink, and C.T. Collins. 2020. Chimney Swift (*Chaetura pelagica*), version 1.0. *In* Birds of the World (A.F. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- Teixeira, D.M. 1999. Myiasis caused by obligatory parasites. Ib. General observations on the biology of the species of the ge-

nus *Philornis* Meinert, 1890 (Diptera, Muscidae). Pp. 71–96 *in* Myiasis in Man and Animals in the Neotropical Region: Bibliographic Database (J.H. Guimarães and N. Papavero, eds.). Editora Pleiade, Sao Paulo, Brazil.

- Verrill, A.E., and A.H. Verrill. 1909. Notes on the birds of San Domingo, with a list of the species, including a new hawk. Proceedings of the Academy of Natural Science of Philadelphia 61:352–366.
- Wetmore, A., and F.C. Lincoln. 1933. Additional notes on the birds of Haiti and the Dominican Republic. Proceedings of the United States National Museum 82:1–68.
- Wetmore, A., and B.H. Swales. 1931. The Birds of Haiti and the Dominican Republic. Bulletin of the United States National Museum i-iv:1–483.
- Whitworth, T.L. 2003. A key to the puparia of 27 species of North American *Protocalliphora* Hough (Diptera: Calliphoridae) from

bird nests and two new puparial descriptions. Proceedings of the Entomological Society of Washington 105:995–1033.

- Wiggins, D.A. 2004. Black Swift (*Cypseloides niger*): a technical conservation assessment. Project report for the USDA Forest Service, Rocky Mountain Region, Species Conservation Project, Lakewood, CO.
- Wiley, J.W. 2006. The ecology, behavior, and conservation of a West Indian corvid, the White-necked Crow (*Corvus leucognaphalus*). Ornitología Neotropical 17:105–146.
- Woolaver, L.G., R.K. Nichols, E.S. Morton, and B.J.M. Stutchbury. 2015. Breeding ecology and predictors of nest success in the Critically Endangered Ridgway's Hawk *Buteo ridgwayi*. Bird Conservation International 25:385–398.
- Young, B.E. 1993. Effects of the parasitic botfly *Philornis carinatus* on nestling House Wrens, *Troglodytes aedon*, in Costa Rica. Oecologia 93:256–262.