One hundred and sixty-seven currently recognized species of direct-developing frogs in the genus *Eleutherodactylus* (Eleutherodactylidae) occur in the West Indies and many are single-island endemics (Henderson and Powell 2009; Powell and Henderson 2012). This phenomenal diversity is more than five times the combined number of species inhabiting Belize, Guatemala, Mexico, and the southern United States (AmphibiaWeb 2020). Second only to Hispaniola, the Cuban Archipelago supports the highest diversity, and of the 58 Cuban species only *E. planirostris* is not endemic (Alonso and García 2017). Taxonomic diversity is coupled with ecological diversity and, despite many species having limited distributions, Cuban species of *Eleutherodactylus* collectively occupy most of the available habitat types across the archipelago (e.g., Díaz and Cádiz 2008; Rivalta et al. 2014; Alonso and García 2017). They are the dominant amphibian group in most terrestrial ecosystems of the West Indies and for Cuba, in particular, they represent 86.6% of the total native amphibian fauna (Henderson and Powell 2009; Díaz and Cádiz 2008). However, little is known about the natural history of most species. For instance, basic interspecific interactions, such as predator-prey relationships, have been confirmed for only 29 species (about 17%) (see Henderson and Powell 2009 for a review, and also references in Table 1). In Cuba, about 10 confirmed species and several unidentified species of *Eleutherodactylus* have been reported as prey of various predators in nature. These include arachnids, a freshwater crab, a topminnow, other frogs, lizards, snakes, an owl, and a mammal (Table 1). This relative lack of information results in an incomplete understanding of the roles of these frogs in natural ecosystems. In order to fill some gaps in previously published reports, we herein document several new instances of predation on frogs of the genus *Eleutherodactylus* in western and central Cuba and provide a review of all predators reported for these frogs in Cuba.
Table 1. Known predators of direct-developing frogs in the genus *Eleutherodactylus* (*Eleutherodactylidae*) in Cuba.

| Predator | Prey | Sources |
|----------|------|---------|
| **ARACHNIDA: Araneae** | | |
| *Ohvida vernalis* | *Eleutherodactylus zugi* | Novo et al. (1985) |
| | *Eleutherodactylus cuneatus* | Fong et al. (2012) |
| **ARACHNIDA: Amblypygi** | | |
| *Phrynus* sp. | *Eleutherodactylus* sp. | Schwartz (1958) |
| **ARACHNIDA: Thelyphonida** | | |
| *Sheylayongium pelegrini* | *Eleutherodactylus* sp. | A.R. Estrada *in* Armas (2000) |
| | *Eleutherodactylus* sp. (eggs) | Armas et al. (2009) |
| **ARACHNIDA: Scorpiones** | | |
| *Heteroctenus junceus* | *Eleutherodactylus* sp. | This paper |
| **MALACOSTRACA: Decapoda** | | |
| *Epilobocera cubensis* | *Eleutherodactylus cuneatus* | Fong et al. (2012) |
| **ACTINOPTERYGII: Cyprinodontiformes** | | |
| *Gambusia punctata* | *Eleutherodactylus zugi* | Rodríguez-Cabrera and Rodríguez (2015) |
| **AMPHIBIA: Anura** | | |
| *Eleutherodactylus dimidiatus* | *Eleutherodactylus intermedius* | Fong et al. (2009) |
| | *Eleutherodactylus planirostris* | This paper |
| | *Eleutherodactylus zugi* | This paper |
| *Osteopilus septentrionalis* | *Eleutherodactylus planirostris* | Meshaka (1996) |
| **REPTILIA: Squamata (lizards)** | | |
| *Anolis vermiculatus* | *Eleutherodactylus* sp. | Garrido (1976) |
| *Pholidoscelus auberi* | *Eleutherodactylus planirostris* | Castellón and Rodríguez-Cabrera (2018) |
| **REPTILIA: Squamata (snakes)** | | |
| *Caraiha andreae* | *Eleutherodactylus atkinsi* | Fong (2004); Alfonso et al. (2013) |
| | *Eleutherodactylus cuneatus* | Alfonso et al. (2013) |
| | *Eleutherodactylus dimidiatus* | Fong (2004); Alfonso et al. (2013) |
| | *Eleutherodactylus iberia* | Rodríguez and Alonso (2003a) |
| | *Eleutherodactylus planirostris* | This paper |
| | *Eleutherodactylus sp.* | Vogel (1965); R.W. Henderson *in* Henderson and Crother (1989); Schwartz and Henderson (1991); Fong (2004) |
| *Cubophis cantherigerus* | *Eleutherodactylus planirostris* | Alonso and Rodríguez (2003b) |
| | *Eleutherodactylus sp.* | Crother (1986); Henderson and Sajdak (1996) |
| *Tretanorhinus variabilis* | *Eleutherodactylus riparius* | López Hurtado et al. (2020) |
| *Tropidophis celae* | *Eleutherodactylus blairhedgesi* | Estrada et al. (1997); Hedges et al. (1999) |
| *Tropidophis feicki* | *Eleutherodactylus planirostris* | This paper |
| *Tropidophis galacelidus* | *Eleutherodactylus planirostris* | This paper |
| *Tropidophis hendersoni* | *Eleutherodactylus cf. thomasi* | Diaz et al. (2014) |
| *Tropidophis maculatus* | *Eleutherodactylus goini* | This paper |
| *Tropidophis mekenurus* | *Eleutherodactylus sp.* | This paper |
| *Tropidophis pardalis* | *Eleutherodactylus planirostris* | Armas and Iturriaga (2017); this paper |
| **AVES: Piciformes** | | |
| *Melanerpes superciliaris* | *Eleutherodactylus cf. olbrusi* | This paper |
| | *Eleutherodactylus sp.* | This paper |
| **AVES: Strigiformes** | | |
| *Tyto alba* | *Eleutherodactylus sp.* | Alonso and Rodríguez (2003a, 2003b); Jiménez et al. (2005) |
| **MAMMALIA: Soricomorpha** | | |
| *Solenodon cubanus* | *Eleutherodactylus* sp. | Abréu et al. (1988) |
Methods

In instances involving snakes as predators we applied forced regurgitation by palpation of the stomach in order to obtain the prey items, although in some cases the snake regurgitated spontaneously. This method has proven to be safe for the snakes, especially when compared to the traditional ventral incision method that necessarily involves sacrificing the animals (Luiselli and Amori 2016). In the case of frogs eating frogs, we flushed stomachs in order to obtain the ingested prey items (e.g., Solé et al. 2005) or analyzed photographs taken in situ and identified the prey items to the lowest taxonomic resolution possible. We measured the snakes and the frogs for snout-vent length (SVL) to the nearest 0.5 mm. We took direct measurements with a measuring tape or a caliper, or from photographs using the program ImageJ (v. 1.43; available at: https://imagej.nih.gov/ij/). Additionally, in those instances involving woodpeckers as predators, we analyzed a series of high-resolution photographs of parents taking food to their chicks. Those photographs were taken with a digital Nikon D300 coupled with a 70–300 mm lens. In some instances, we measured climatic variables with a Kestrel 3500 Pocket Weather Meter. Voucher specimens (usually stomach contents) were preserved in ethanol (75%) and deposited in the zoological collection of the Museo de Historia Natural “Tranquilino Sandalio de Noda” (MHN.TSN), Pinar del Río. Datum for all geographic coordinates is WGS 84.

Results

In 1980 (by day), we found an adult female Cuban Lesser Racer, *Caraiba andreae* (ca. 550 mm SVL), by a stream in the “Virginia” neighborhood of Santa Clara, Villa Clara Province (22°24'20.2", -79°59'15.4"; 110 m asl). Forced regurgitation revealed nine adult Cuban Flat-headed Frogs (*E. planirostris*). This is a highly urbanized area with scattered secondary vegetation in the suburbs of Santa Clara.

In 1980 (by day), we found a juvenile Giant Trope, *Tropidophis melanurus* (ca. 300 mm SVL), under a rock between the “Virginia” and “José Martí” neighborhoods, Santa Clara, Villa Clara Province (22°24'19.7", -79°59'52.7"; 110 m asl). Forced regurgitation revealed a partially digested individual of an unidentified frog of the genus *Eleutherodactylus*. The predominant vegetation in the area is *Eucalyptus* plantations and secondary shrubwoods on serpentine soil.

Between 2010 and 2013, we recorded three different instances of predation by West Indian Woodpeckers (*Melanerpes superciliaris*) on frogs of the genus *Eleutherodactylus* near the Santa Cruz River, San Cristóbal, Artemisa Province. In all instances the parent woodpeckers were carrying food to their chicks in cavity nests in palm tree trunks (*Roystonea regia*). At 1730 h on 21 April 2010, we observed a male woodpecker carrying an individual of an unidentified species of *Eleutherodactylus* to its nest (Fig. 1) in a palm tree about 140 m from the river (22°45'25.0", -83°08'56.0"; 220 m asl). At 1100 h on 3 June 2010, we observed a second case involving a male woodpecker carrying a frog of the genus *Eleutherodactylus*, probably a Pinar del Río Bromeliad Frog (*E. olibrus*; Fig. 2), to its nest in a different palm tree very close to the first one and adjacent to a patch of secondary forest. At 1110 h on 27 May 2013, we observed a female woodpecker carrying an individual of an unidentified species of *Eleutherodactylus* to its nest (Fig. 3) in a third palm tree about 350 m southeast of the other two observations and about 225 m from the river (22°45'14.1", -83°08'50.8"; 270 m asl). The vegetation in the area is composed mostly of secondary grasslands, secondary groves, and semideciduous forest, although the three nests were in isolated palm trees in secondary grassland with scattered bushes.

Fig. 2. Sequence of photographs showing a male West Indian Woodpecker (*Melanerpes superciliaris*) with a frog of the genus *Eleutherodactylus*, probably a Pinar del Río Bromeliad Frog (*E. olibrus*) (left), carried to its nest (right) near the Santa Cruz River, Artemisa Province, in June 2010. Photographs © Raimundo López-Silvero.
At 2110 h on 7 October 2011, we found an adult (unsexed) Broad-banded Trope, *Tropidophis feicki* (412 mm SVL, 41 mm tail length) in the “Orquideario de Soroa” Botanical Garden, Candelaria, Artemisa Province (22°47’32.8”, -83°00’34.5”; 230 m asl). Forced regurgitation revealed a partially digested Cuban Flat-headed Frog and fragments of an unidentified spider (MHN.TSN-35-CL). This is a suburban area with abundant secondary vegetation, gardens, and tourist facilities surrounded by semideciduous forest.

At about 1200 h on 4 November 2014, we found a juvenile Spotted Brown Trope, *T. pardalis* (133 mm SVL, 14 tail length; Fig. 4) under a rock in the backyard of the Facultad de Biología, Universidad de La Habana, Vedado neighborhood, Plaza de la Revolución, La Habana Province (23°08’09.8”, -82°23’06.6”; 30 m asl). Forced regurgitation revealed a partially digested Cuban Flat-headed Frog (ca. 20 mm SVL) that had been ingested head first. This is a highly urbanized area in the middle of Havana, with only secondary vegetation associated with gardens and backyards.

At 0900 h on 24 November 2014, we found a juvenile Spotted Red Trope, *T. maculatus* (130 mm SVL, 15 mm tail length; Fig. 5) under a rock near the biological field station of the “Sierra del Rosario” Biosphere Reserve at Las Terrazas, Candelaria, Artemisa Province (22°50’57.6”, -82°55’55.1”; 170 m asl). Forced regurgitation revealed a partially digested Guaniguanico Yellow-mottled Frog (*E. goini*) that had been ingested head first. The vegetation in the area is composed mostly of secondary forests, secondary pinewoods, and semideciduous forest.

On 12 July 2014, we found an adult female Cuban Scorpion, *Heteroctenus junceus* (Scorpiones: Buthidae), devouring an individual of an unidentified species of *Eleutherodactylus* near the Minerva Dam, Santa Clara, Villa Clara Province (22°26’00.2”, -79°47’35.2”; 70 m asl). The scorpion was detected at night using ultraviolet light. The frog was in a very advanced state of digestion probably due to the action of the scorpion’s enzymes and cheliceral maceration. The vegetation in the area is composed mostly of secondary grassland with scattered shrubs and trees on serpentine soil.

On 18 March 2019, we found a juvenile Escambray White-necked Trope, *T. galacelidus* (147 mm SVL, 23
mm tail length; Fig. 6) at La Sabina Field Station, “Lomas de Banao” Ecological Reserve, Guamuhaya Massif, Sancti Spíritus Province (21°52'59.3", -79°35'55.3"; 620 m asl). It was placed in a container for a further session of photographs and the next day it had regurgitated a partially digested Cuban Flat-headed Frog (ca. 18 mm SVL) that had been ingested head first. The predominant vegetation around the field station is largely secondary pinewoods and evergreen mesophyllous forest.

At 2155 h on 13 July 2019, we observed an adult Cuban Long-legged Frog, *Eleutherodactylus dimidiatus* (37.5 mm SVL) preying upon a Cuban Flat-headed Frog (18.5 mm SVL) about 480 m northeast of the biological field station, “La Sabina,” “Lomas de Banao” Ecological Reserve, Guamuhaya Massif, Sancti Spíritus Province (21°53'09.5", -79°35'42.6"; 620 m asl). When first seen, the prey was alive and was being swallowed with the hindlimbs first (Fig. 7). The Cuban Flat-headed Frog struggled continuously in an attempt to escape but the predator swallowed a bit more with every movement of its prey, using its forelimbs to help push the prey farther into its mouth. Complete ingestion took about 20 min after the initial observation. The air temperature was 27 °C and the relative humidity was 83%. The predominant vegetation in the area is evergreen mesophyllous forest.

At 2145 h on 22 March 2020, we found an adult male Cuban Long-legged Frog (22.7 mm SVL) near the biological field station of the “Sierra del Rosario” Biosphere Reserve at Las Terrazas, Candelaria, Artemisa Province (22°51'02.3", -82°55'54.7"; 170 m asl). Its stomach contained a Rosario Red-legged Frog, *E. zugi* (ca. 15 mm SVL), in a very advanced state of digestion. The air temperature was 24.8 °C and the relative humidity was 83.5%. The vegetation in the area is composed mostly of secondary forests, secondary pinewoods, and semideciduous forest.

Discussion

More than 80 different species have been confirmed as predators of frogs of the genus *Eleutherodactylus* in the West Indies (see Henderson and Powell 2009 for a review; this paper). About 34% of all predator species are snakes, followed by arachnids (15%), lizards (13%), and birds (12%). In Cuba, snakes (41%) and arachnids (18%) also are the most frequently recorded predators (Table 1). The Cuban Lesser Racer (*Caraiba andreae*) and several species of dwarf boas (*Tropidophis* spp.) have the highest incidence of predation on these frogs. Predation by the Escambray White-necked Trope is the first dietary information for that critically endangered species (Rodríguez Schettino 2012).

The diets of most Cuban species of *Eleutherodactylus* are unknown. Most of the available information suggests that they feed mostly on small invertebrates such as insects and their larvae, arachnids, isopods, and snails (see Henderson and Powell 2009 for a review; this paper). About 34% of all predator species are snakes, followed by arachnids (15%), lizards (13%), and birds (12%). In Cuba, snakes (41%) and arachnids (18%) also are the most frequently recorded predators (Table 1). The Cuban Lesser Racer (*Caraiba andreae*) and several species of dwarf boas (*Tropidophis* spp.) have the highest incidence of predation on these frogs. Predation by the Escambray White-necked Trope is the first dietary information for that critically endangered species (Rodríguez Schettino 2012).

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The only case of anurophagy reported in nature refers to an adult Cuban Long-legged Frog (26.1 mm SVL) preying on an adult Oriente Dark-bellied Frog (*E. intermedius*; 18.6 mm SVL; Fong et al. 2009). Valdés and Ruíz (1980) also reported a case of cannibalism in Cuban Stream Frogs (*E. riparius*) in captivity. The two cases reported herein involving Cuban Long-legged Frogs as predators represent the second and third records of anurophagy by wild frogs of the genus *Eleutherodactylus* in this country. Outside Cuba, the Puerto Rican Melodius Frog (*E. wightmanae*) is known to prey on the Puerto Rican Frog (*E. coqui*; Stewart and Woolbright 1996), and the latter is known to prey on other frogs of the genus *Eleutherodactylus*, including conspecifics (see Henderson and Powell 2009 for a review). The Puerto Rican Cave Frog (*E. cookei*) and the Puerto Rican White-eyed Frog (*E. portoricensis*) also are known to be cannibalistic, which includes the consumption of conspecific ova, in nature (see Henderson and Powell 2009 for a review). The behavior during ingestion of a smaller frog by one of the Cuban Long-legged Frogs that we observed largely coincides with that described by Valdés and Ruíz (1980) and Fong et al. (2009). Repeated observations suggest that frogs may represent important prey in the diets of Cuban Long-legged Frogs, and we do not discount the possibility of cannibalism in this species as well.

Cuban birds, including herons, cuckoos, diving birds, rails, terns, curlews, owls, diurnal raptors, and woodpeckers, are frequent predators of frogs (Garrido and Kirkconnell 2011). However, actual incidents of birds as predators of Cuban frogs in the genus *Eleutherodactylus* are rarely reported. Bones of relatively large frogs of the genus *Eleutherodactylus* (presumably *E. pinarensis*) have been found in pellets of Barn Owls (*Tyto alba*) in caves of western Cuba (Alonso and Rodríguez 2003a). Jiménez et al. (2005) found more than 200 Cuban Treefrogs and one *Eleutherodactylus* sp. in pellets of Barn Owls in a cave south of Havana. These authors also found remains of frogs of the genus *Eleutherodactylus* in a fossil Barn Owl dietary deposit dating from the Pleistocene-Holocene in the same region. With a few exceptions (i.e., *E. cuneatus*, *E. greyi*, *E. pezopetrous*, *E. pinarensis*, *E. symingtoni*, *E. turquinensis*, and *E. zeus*), most Cuban species of *Eleutherodactylus* are relatively small (<50 mm SVL; Díaz and Cádiz 2008; Henderson and Powell 2009). Therefore, most of these frogs undoubtedly are prey items with little energetic reward for a Barn Owl (a relatively large bird at >400 g; Sibley 2017), which might explain the rarity of *Eleutherodactylus* frogs in the diet of these owls.

Our reports of frogs in the genus *Eleutherodactylus*, particularly arboreal species, as prey of the West Indian Woodpecker is not surprising. We have repeatedly observed this woodpecker searching for prey inside bromeliads (Fig. 8). West Indian Woodpeckers also have been reported carrying Cuban Treefrogs and lizards to their nestlings in Cuba and on other West Indian islands (Johnston 1975; Estrada 1993; del Hoyo et al. 2002; Rivalta and Díaz 2003; Rodríguez
and Alonso 2003b; Garrido and Kirkconnell 2011). Frogs and lizards have been reported also in the diet of the Cuban Green Woodpecker, Xiphius peregrinus (Garrido and Kirkconnell 2011). Many species of woodpeckers, including those that are mostly frugivorous, increase the rate of predation on invertebrates and even on small vertebrates during the breeding season, apparently in order to provide the growing nestlings with protein-rich food (see del Hoyo et al. 2002 for a review; also Ojeda and Chazarreta 2006; Koenig et al. 2008; Vukovich and Kilgo 2019). Kirkconnell (2011) observed that many West Indian species of Eleutherodactylus are threatened (e.g., Hedges and Díaz 2010; Alonso and García 2017; AmphibiaWeb 2020; IUCN 2020). A better understanding of the threats, both natural and anthropogenic, facing these species is of paramount importance for developing and implementing appropriate management plans to conserve them and their predators.

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