



New Dietary Records for Three Cuban Snakes in the Genus *Tropidophis* (Tropidophiidae), with Comments on Possible Niche Partitioning by Cuban Tropes

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The diets of West Indian snakes in the genus *Tropidophis* (Tropidophiidae) are poorly known (see Henderson and Powell 2009 for a review). Dietary information exists only for 15 of the 27 West Indian species and most of it consists of isolated records (Henderson and Powell 2009; Table 1). The available data suggest that they feed mostly on ectotherms such as anurans and lizards, although the largest species such as the Hispaniolan Trope (*T. haetianus*) (to >550 mm SVL) and the Giant Trope (*T. melanurus*) (to > 1,000 mm SVL) may consume endotherms (e.g., small rodents and birds) (e.g., Henderson and Powell 2009; Rodríguez-Cabrera et al. 2017) (Table 1). Cuba is the center of diversification in the genus, with 16 currently recognized endemic species (e.g., Hedges et al. 2002; Domínguez et al. 2006; Uetz et al. 2020). However, the feeding habits of most Cuban species are virtually unknown. Herein we provide the first dietary records for the Gracile Banded Trope (*T. wrighti*) and the Yellow Banded Trope (*T. semicinctus*), and the second dietary record for the Broad-banded Trope (*T. feicki*). We also provide a

review of the prey of West Indian species and comment on possible niche partitioning in Cuban species.

At 1030 h on 10 December 1997, we found an adult female *T. wrighti* (274 mm SVL) with a stomach bulge at Piedra La Vela, Yateras Municipality, Guantánamo Province (20°24'05.0"N, 74°56'23.0"W; 680 m asl). The snake was under the bark of a pine tree 0.6 m above the ground in a reforested pinewood. After being placed in a container, the snake regurgitated a female Cuban Dark Bark Anole (*Anolis argillaceus*) (33 mm SVL). The lizard apparently had been captured the night before since signs of digestion were not evident. The snake was deposited in the herpetological collection of the Centro Oriental de Ecosistemas y Biodiversidad (BIOECO; voucher: BSC.H-1460). This is the first confirmed dietary record for the Gracile Banded Trope.

At 1115 h on 30 October 2014, we found a juvenile male *T. semicinctus* (165 mm SVL) with a stomach bulge (Fig. 1) at El Nicho, Cumanayagua Municipality, Cienfuegos Province (22°01'50.0"N, 80°07'16.0"W; 430 m asl). The snake was



Fig. 1. A juvenile male Yellow-banded Trope (*Tropidophis semicinctus*) from El Nicho in Cienfuegos Province, freshly captured with a stomach bulge (left) and regurgitating a Cuban Brown Anole (*Anolis sagrei*) (right) after palpation of the abdomen. Photographs © T.M. Rodríguez-Cabrera.

Table 1. Prey reported for West Indian snakes of the genus *Tropidophis* (Tropidophiidae) in nature. An asterisk (*) indicates an unsuccessful predation event. Two asterisks (**) indicate probable incidental ingestion.

| Species | Prey | Source |
|--|---|---|
| Navassa Trope (<i>T. bucculentus</i>) | Navassa Galliwasp (<i>Celestus badius</i>) | Thomas 1966 |
| Inagua Trope (<i>T. canus</i>) | Southern Bahamas Anole (<i>Anolis scriptus</i>) Inagua Groundlizard (<i>Pholidoscelis maynardii</i>) | Noble and Klingel 1932 |
| Grand Cayman Trope (<i>T. caymanensis</i>) | Cuban Treefrog (<i>Osteopilus septentrionalis</i>) Unidentified frog (<i>Eleutherodactylus</i> sp.) Unidentified anole (<i>Anolis</i> sp.) | Schwartz and Henderson 1991 |
| Canasi Trope (<i>T. celiae</i>) | Canasi Frog (<i>E. blairhedgesi</i>) | Estrada et al. 1997; Hedges et al. 1999 |
| Northern Bahamas Trope (<i>T. curtus</i>) | Cuban Treefrog (<i>O. septentrionalis</i>) Unidentified geckolet (<i>Sphaerodactylus</i> sp.) Unidentified anole (<i>Anolis</i> sp.) Cuban Groundlizard (<i>P. auberi</i>) | Schwartz and Henderson 1991 |
| Broad-banded Trope (<i>T. feicki</i>) | Cuban Flat-headed Frog (<i>E. planirostris</i>) Cuban White-fanned Anole (<i>A. homolechis</i>) | Rodríguez-Cabrera et al. 2020c this paper |
| Escambray White-necked Trope (<i>T. galacelidus</i>) | Cuban Flat-headed Frog (<i>E. planirostris</i>) | Rodríguez-Cabrera et al. 2020c |
| Caicos Trope (<i>T. greenwayi</i>) | Southern Bahamas Anole (<i>A. scriptus</i>) Caicos Geckolet (<i>S. caicosensis</i>) | Iverson 1986 |
| Hispaniolan Trope (<i>T. haetianus</i>) | Unidentified frog (<i>Eleutherodactylus</i> sp.) Unidentified anole (<i>Anolis</i> sp.) Baoruco Giant Anole (<i>A. barabonae</i>) Unidentified groundlizard (<i>Pholidoscelis</i> sp.) Unidentified geckolet (<i>Sphaerodactylus</i> sp.) Unidentified rodents Hispaniolan Yellow Treefrog (<i>O. pulchrrilineatus</i>) | Schwartz and Henderson 1991 Schmidt 1921 |
| Cuban Khaki Trope (<i>T. hendersoni</i>) | Cuban Cave Frog (<i>E. cf. thomasi</i>) | Díaz et al. 2014 |
| Jamaican Brown Trope (<i>T. jamaicensis</i>) | Stripe-footed Anole (<i>A. lineatopus</i>) | Wilson and Vogel 2000; B.S. Wilson <i>in</i> Henderson and Powell 2009 |
| Spotted Red Trope (<i>T. maculatus</i>) | Guaniguanico Yellow-mottled Frog (<i>E. goini</i>) Cuban Twig Anole (<i>A. angusticeps</i>) Blue-eyed Twig Anole (<i>A. alutaceus</i>) Cuban White-fanned Anole (<i>A. homolechis</i>) Unidentified anole (<i>Anolis</i> sp., possibly <i>A. sagrei</i>) Beetle (Curculionidae)** Heteropteran (Cydnidae)** Unidentified spider** Little Fire Ant (<i>Wasmannia auropunctata</i>)** | Rodríguez-Cabrera et al. 2020c Collette 1961 Rodríguez-Cabrera et al. 2020a |
| Giant Trope (<i>T. melanurus</i>) | Cuban Treefrog (<i>O. septentrionalis</i>) | G. Bibron <i>in</i> Cocteau and Bibron 1843 (as “Batracienos anouros de la familia Hylaeiformes [...] Traquicéfalo marmoreo”) |

(continued)

| Species | Prey | Source |
|---|---|---|
| | Cuban Treefrog (tadpoles) (<i>O. septentrionalis</i>) | Estrada 1994 |
| | Cuban Treefrog (<i>O. septentrionalis</i>) | Schwartz and Henderson 1991 |
| | Unidentified anole (<i>Anolis</i> sp.) | |
| | House Mouse (<i>Mus musculus</i>) | |
| | Unidentified frog (<i>Eleutherodactylus</i> sp.) | Rodríguez-Cabrera et al. 2020c |
| | Eastern Cuba Giant Toad (<i>Peltophryne peltoccephala</i>)* | Fong et al. 2013 |
| | Western Cuba Giant Toad (<i>Peltophryne fustiger</i>)* | L.M. Díaz, in litt. 1.vii.2020 |
| | Slender Cliff Anole (<i>Anolis lucius</i>) | |
| | Pinar del Rio Cliff Anole (<i>A. bartschi</i>) | Holanova and Hribal 2004 |
| | Cuban Green Anole (<i>A. porcatius</i>) | V. Holanova, in litt. 10.vi.2020 |
| | Unidentified frog (<i>Eleutherodactylus</i> sp.) | |
| | Oriente Bearded Anole (<i>A. porcus</i>)* | Torres et al. 2014 |
| | Lizard | T. Barbour <i>in</i> Stull 1928 |
| | Frogs, lizards, birds, rodents | Greene 1983; A. Fong <i>in</i> Fong et al. 2013 |
| | Yellow-faced Grassquit (<i>Tiaris olivaceus</i>) (caged?) | Stull 1928; Rodríguez-Cabrera et al. 2017 |
| | Dove (caged) | Barbour and Ramsden 1919 |
| Spotted Brown Trope (<i>T. pardalis</i>) | Cuban Flat-headed Frog (<i>E. planirostris</i>) | Armas and Iturriaga 2017; |
| | Tropical House Gecko (<i>Hemidactylus mabouia</i>) | Rodríguez-Cabrera et al. 2020c |
| Little Cayman Trope (<i>T. parkeri</i>) | Cuban Treefrog (<i>O. septentrionalis</i>) | Thomas 1963; Grant 1940 |
| Yellow-banded Trope (<i>T. semicinctus</i>) | Cuban Brown Anole (<i>A. sagrei</i>) | This paper |
| Gracile Banded Trope (<i>T. wrighti</i>) | Cuban Dark Bark Anole (<i>A. argillaceus</i>) | This paper |

under a rock in a secondary grassland by a road in a rural area. We forced regurgitation by palpation of the abdomen in order to obtain the prey item for identification and measurements. The prey item was a juvenile Cuban Brown Anole (*A. sagrei*) (32 mm SVL), with indications of digestion on the head (Fig. 1). The snake was released at the site of its capture and the prey item was preserved in 75% ethanol and depos-

ited in the personal collection of the senior author. This is the first dietary record for the Yellow Banded Trope.

At 1913 h on 21 December 2016, we found an adult female *T. feicki* (355 mm SVL) swallowing an adult female Cuban White-fanned Anole (*A. homolechis*) (45 mm SVL), near the Santa Cruz River in the Sierra del Rosario Mountain Range, San Cristóbal Municipality, Artemisa Province (22°44'58.2"N,



Fig. 2. A female Broad-banded Trope (*Tropidophis feicki*) from the Santa Cruz River in Artemisa Province, swallowing an adult female Cuban White-fanned Anole (*Anolis homolechis*) when first seen (left) and with ingestion nearly complete five minutes later (right). Photographs © Raimundo López-Silvero (left) and Rosario Domínguez (right).

83°08'59.3"W; 160 m asl). When first seen, the snake had swallowed the head and neck of the anole (Fig. 2). Complete ingestion ended five minutes later at 1918 h (Fig. 2). The predation event took place on a fallen dead palm frond about 0.2 m above a limestone substrate at the edge of a semi-deciduous forest. We forced regurgitation to obtain the prey item for measurements. The snake was released at the site of its capture and the prey item was preserved in 75% ethanol and deposited in the personal collection of the senior author. This is the second dietary record for the Broad-banded Trope (Table 1).

Anoles are diurnal and the prey species reported above are mostly arboreal (e.g., Rodríguez 1999; Henderson and Powell 2009; Losos 2009). This suggests that these three snakes accessed their sleeping prey by employing an active-foraging mode at night. All three of these snakes have slender bodies and have been reported foraging in vegetation at night (Schwartz and Henderson 1991; Hedges 2002; Henderson and Powell 2009; Díaz et al. 2014). *Tropidophis feicki* also has been observed foraging in caves and on rocky cliffs and in associated vegetation at night (Schwartz 1957; Schwartz and Henderson 1991; García-Padrón et al. 2020; Rodríguez-Cabrera et al. 2020b; Fig. 3). Díaz et al. (2014) found as many as 20 Gracile Banded Tropes foraging on thin branches from 0.5–5.0 m above the ground in a single night (see also Henderson and Powell 2009 for a review). Díaz et al. (2014) also mentioned sleeping anoles as prey of *T. wrighti*, but they did not provide any details. Rodríguez-Cabrera et al. (2020a) described a similar foraging strategy in Spotted Red Tropes (*T. maculatus*), another gracile species from western and central Cuba that also feeds on anoles (Fig. 4; Table 1). We have repeatedly observed *T. wrighti* and *T. semicinctus* foraging in the vegetation at night at several localities in eastern and central Cuba, respectively (Fig. 4). We also have seen captive snakes of all of these species actively forage at night.

In addition to similarities in body shapes and foraging strategies, many of these gracile tropes occupy similar habitats. *Tropidophis wrighti*, *T. maculatus*, and *T. semicinctus* have relatively wide distributions and occupy a wide range of

habitats from sea level to over 900 m (Rodríguez et al. 2010, 2013; Blanco and Fong 2011; Henderson and Powell 2009). During the day they shelter under rocks and tree bark, apparently emerging to forage in vegetation at night (Henderson and Powell 2009; Blanco and Fong 2011). These three species even occur in altered suburban and urban areas, and at least *T. semicinctus* has been found to be relatively common under rocks in pastures with isolated shrubs (authors, pers. obs.). On the contrary, *T. feicki* seems to have more specific habitat requirements, occurring almost exclusively in mesic limestone areas covered by primary forest in western and central Cuba (Schwartz and Henderson 1991; Rodríguez-Cabrera et al. 2020b).

The three snakes described herein in most cases co-occur with other species of *Tropidophis*. Giant Tropes and Cuban Dusky Tropes (*T. fuscus*) potentially coexist with *T. wrighti* in the Sagua-Baracoa Massif where Piedra La Vela is located (e.g., Rodríguez et al. 2013). Other species observed coexisting sympatrically with *T. semicinctus* at El Nicho were *T. melanurus* and the Escambray White-necked Trope (*T. galacelidus*) (Torres and Rodríguez-Cabrera 2020; T.M. Rodríguez-Cabrera, pers. obs.). In the area around the Santa Cruz River, other species observed coexisting sympatrically or parapatrically with *T. feicki* were *T. melanurus*, *T. maculatus*, and the Spotted Brown Trope (*T. pardalis*). This coexistence of species with different body shapes is suggestive of structural habitat niche partitioning.

Apparently, well-defined species assemblages of *Tropidophis* are repeated across the Cuban Archipelago (Fig. 5). These vary in species composition according to the region but not in body shapes of the species that constitute them (see Rodríguez et al. 2013 for a review on species distributions). Such assemblages seem to be composed of three to four species at the most, each belonging to one of three basic ecotypes: (1) generalist, (2) terrestrial, and (3) semi-arboreal (see also Díaz et al. 2014; Rodríguez-Cabrera et al. 2016; Torres and Rodríguez-Cabrera 2020) (Fig. 5). The generalist ecotype is always represented by the Giant Trope, the largest species,



Fig. 3. *Tropidophis feicki* is a gracile snake that is frequently observed foraging on limestone (left) and in the associated vegetation (right) at night. Photographs © Raimundo López-Silvero.



Fig. 4. Gracile species of Cuban tropes (*Tropidophis*) are frequently observed foraging in vegetation at night and most seem to prey on sleeping anoles, which suggests that they are active foragers. Spotted Red Trope (*T. maculatus*) (upper left), Yellow-banded Trope (*T. semicinctus*) (upper right), Gracile Banded Trope (*T. wrighti*) (lower left), and Sancti Spiritus Trope (*T. spiritus*) (lower right). Photographs © Rolando Teruel, T.M. Rodríguez-Cabrera, Ruben Marrero, and Aslam I. Castellón.

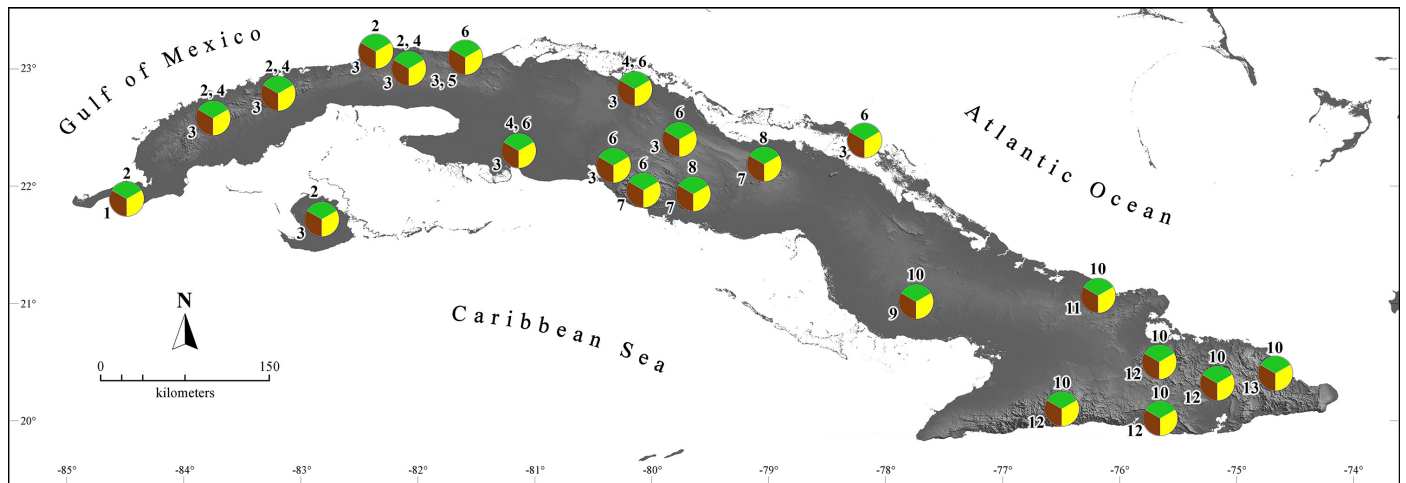


Fig. 5. Composition of species assemblages of *Tropidophis* in Cuba. Yellow represents the generalist ecotype (always *T. melanurus*), brown the terrestrial ecotype, and green the semi-arboreal ecotype. Species are: (1) *T. xanthogaster*, (2) *T. maculatus*, (3) *T. pardalis*, (4) *T. feicki*, (5) *T. celiae*, (6) *T. semicinatus*, (7) *T. galacelidus*, (8) *T. spiritus*, (9) *T. nigriventris*, (10) *T. wrighti*, (11) *T. hendersoni*, (12) *T. pilsbryi*, and (13) *T. fuscus*. *Tropidophis hardyi* and *T. morenoi* are not included because their taxonomic status is in need of revision since they might be conspecific with some of the species listed above.

which is widely distributed in Cuba and has the most varied diet (Rodríguez et al. 2013; Table 1). The terrestrial ecotype is represented by stout, small to medium-sized species (to ca. 400 mm SVL) (i.e., Canasí Trope, *T. celiae*; Cuban Dusky Trope; Escambray White-necked Trope; Escambray Small-headed Trope, *T. hardyi*; Cuban Khaki Trope, *T. hendersoni*; Dark-bellied Trope, *T. nigriventris*; Spotted Brown Trope; Oriente White-necked Trope, *T. pilsbryi*, and Guanahacabibes Trope, *T. xanthogaster*), all of whose diets are little known, but at least some of them have been reported to feed on frogs of the genus *Eleutherodactylus* and lizards (Table 1). The semi-arboreal ecotype is represented by gracile medium-sized species (to ca. 500 mm SVL) (i.e., Broad-banded Trope; Spotted Red Trope; Zebra Trope, *T. morenoi*; Yellow-banded Trope; Sancti Spiritus Trope, *T. spiritus*, and Gracile Banded Trope), all of which apparently feed on anoles and seem to use an active-foraging mode (see above). Díaz et al. (2014) also suggested that microhabitat segregation existed between the gracile and semi-arboreal *T. wrighti* and the stouter and largely ground-dwelling species, *T. hendersoni* and *T. melanurus*, north of Holguín Province in eastern Cuba. A fourth variant of the semi-arboreal ecotype, always represented by *T. feicki*, occurs in some localities in western and central Cuba (e.g., Rodríguez-Cabrera et al. 2020b). It can co-occur with either *T. maculatus* or *T. semicinatus* (Fig. 5). Assuming that those two species might compete with *T. feicki* is reasonable, since they all have similar body shapes (e.g., Hedges 2002) and use similar foraging strategies. However, according to our observations, they seem to be parapatric. *Tropidophis feicki* occupies densely forested areas on limestone substrates, whereas *T. maculatus* and *T. semicinatus* occupy areas with more open vegetation, such as grasslands, scrublands, ecotonal, and/or secondary vegetation. This parapatric co-occurrence between *T. feicki*

and *T. maculatus* or *T. semicinatus* can be observed in several localities across the Guaniguanico Mountain Range in western Cuba and at the “Mogotes de Jumagua” Ecological Reserve in central Cuba, respectively (e.g., Rivalta-G. et al. 2013; Rodríguez-Cabrera et al. 2020b; T.M. Rodríguez-Cabrera, pers. obs.) (Fig. 5). *Tropidophis maculatus* and *T. semicinatus* seem to be mutually exclusive, with only a small overlap, if any, in their distributions (e.g., Rodríguez et al. 2013). A similar exclusion seems to occur between the gracile species inhabiting the Guamuhaya Massif in south-central Cuba. This mountain range is divided by the Agabama River Basin and forms two main topographical units: the Trinidad Range in the west and the Sancti Spiritus Range in the east (e.g., Mateo-Rodríguez and Acevedo-González 1989). The gracile species occurring in the Trinidad Range is *T. semicinatus*, which coexists with *T. melanurus* and *T. galacelidus* (e.g., Rodríguez et al. 2013; Torres and Rodríguez-Cabrera 2020; T.M. Rodríguez-Cabrera, pers. obs.). In the Sancti Spiritus Range, the assemblage is essentially the same, except that the gracile species is replaced by *T. spiritus* (e.g., Rodríguez et al. 2013; Torres and Rodríguez-Cabrera 2020; Figs. 4 and 5). Two terrestrial species, *T. pardalis* and *T. celiae*, are known to co-occur at least at Canasí, on the northern coast of Mayabeque Province. The only two specimens of *T. celiae* collected at this locality were found on bare limestone along the shoreline (Hedges et al. 1999; Torres et al. 2016), whereas the single specimen of *T. pardalis* was found farther inland in a stand of Sea Grapes (J. Torres, unpubl. data). However, given the wide size range of terrestrial species, additional observations are needed to determine if niche partitioning exists within that ecotype.

Morphological divergence in body shapes probably plays an important role in niche partitioning by species of *Tropidophis*, allowing coexistence of different species.

Niche partitioning associated with body shapes has been found in other West Indian taxa such as frogs of the genus *Eleutherodactylus*, lizards of the genus *Anolis*, and snakes of the genus *Chilabothrus* (e.g., Henderson et al. 1987; Losos 2009; Reynolds et al. 2016; Rodríguez-Cabrera et al. 2016; Dugo-Cota et al. 2019). Additionally, species with similar body plans might have evolved physiological and behavioral traits allowing macrohabitat segregation (e.g., Williams 1983). Similar ecotypes of *Tropidophis* apparently do not coexist, which probably is attributable to competitive exclusion (e.g., Gause 1934, 1935; Connell 1961). Nonetheless, in some recent compilations on the distributions of *Tropidophis* in Cuba (e.g., Rodríguez et al. 2013), this principle seems to be contradicted, as more than one species with the same body plan have been reported from the same localities. However, some of those records might represent misidentifications, since some of these species are phenotypically similar (e.g., Tolson and Henderson 1993; Hedges 2002, 2020). This apparent habitat segregation and morphological and behavioral divergence of species in the genus *Tropidophis* has not been observed elsewhere in the West Indies, where multiple species do not co-occur (e.g., Schwartz and Henderson 1991; Tolson and Henderson 1993; Powell and Henderson 2012; Díaz et al. 2014; Rodríguez-Cabrera et al. 2016). The only island with multiple species other than Cuba is Jamaica, with three species, but the distributions of those species do not overlap (e.g., Schwartz and Henderson 1991; Tolson and Henderson 1993; Hedges 2020). Additional studies are needed to test hypotheses related to niche partitioning, niche overlap, and the evolution of body shapes in the Cuban assemblages of *Tropidophis*.

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