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At the Lower Size Limit of Snakes Preying on Bats in the West Indies: The Cuban Boa, *Chilabothrus angulifer* (Boidae)

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Abstract.—Bat predation by snakes has been repeatedly documented in the literature, particularly for boids and colubroids. In the West Indies, species of the genus *Chilabothrus* (Boidae) are the most frequently reported bat predators. However, bats are difficult to capture, and reports of bat-predating snakes smaller than 1 m in total length are very scarce. Herein we report bat predation in very young Cuban Boas (*C. angulifer*), the smallest of which represents the minimum size record for boid snakes preying on bats anywhere in the Neotropics. In contrast to most boids, the large size of neonatal Cuban Boas allows the consumption of endotherms as well as ectotherms soon after birth, including bats captured on the wing while exiting or entering caves.

"For many species of medium-sized to large snakes, bat colonies represent a potential concentration of food to be exploited" (Esbérard and Vrcibradic 2007). This can lead some individuals to "specialize" (in this case more properly "habituate") on bat hunting if large bat populations inhabit their home ranges (Kowalski 1995). Two basic modes of predation on bats are hunting active animals outside or exiting refuges and preying on animals (active or inactive) inside refuges (Esbérard and Vrcibradic 2007). When flying, bats are fast-moving, and capturing them requires skill, strength, and possibly a high expenditure of energy, probably accounting for most records of Neotropical snakes striking at flying bats pertaining to species in the family Boidae (see Esbérard and Vrcibradic 2007 for a review). The prehensile tail and muscular strength of boids (constricting snakes) allow them to wait in ambush for bats while hanging from branches, vines, roots or limestone outcrops at the entrances or ceilings of caves (e.g., Rodríguez-Durán 1996; Puente-Rolón and Bird-Picó 2004; Esbérard and Vrcibradic 2007). Furthermore, this muscular strength must provide an additional advantage when absorbing the impact and stopping the inertia of flying bats. Consistent with this last assumption, despite the fact that colubroids constitute the second most frequently reported Neotropical snake group preying on bats (Esbérard and Vrcibradic 2007), predation on flying bats by colubroids appears to be occasional (e.g., Herreid 1961; Hammer and Arlettaz 1998).

The endemic Cuban Boa, *Chilabothrus angulifer* (Bibron 1840), is the only representative of the family Boidae in Cuba and is the largest snake on the Archipelago (Henderson and Powell 2009). It is widespread across the main island, Isla de la Juventud, and some adjacent keys, ranging in elevation from sea level to 1,214 m (e.g., Henderson and Arias 2001; Rodríguez et al. 2010; Estrada 2012; Rodríguez et al. 2013). This species occurs in a great variety of habitats, but is particularly abundant in karstic situations (e.g., Schwartz and Henderson 1991; Tolson and Henderson 1993; Henderson and Powell 2009).

Suggestions of bat predation by Cuban Boas abound since the beginning of the 20th Century (Miller 1904; Barbour and Ramsden 1919; Barbour 1945; Schwartz and Ogren 1956; Silva and Koopman 1964; Silva 1979; Berovides and Carbonell 1998), but were confirmed on only a few occasions (Hardy 1957; Sheplan and Schwartz 1974; Mancina 2011), despite the fact that it is a relatively common phenomenon in caves throughout Cuba (T.M. Rodríguez-Cabrera, pers. obs.). This behavior also has been reported in at least three other West Indian boid snakes: The Puerto Rican Boa, *C. inornatus* (e.g., Rodríguez and Reagan 1984; Rodríguez-Durán 1996; Wiley 2003; Puente-Rolón and Bird-Picó 2004; Puente-Rolón 2012), the Jamaican Boa, *C. subflavus* (Prior and Gibson 1997; Koenig and Schwartz 2003; Dávalos and Eriksson 2004), and the St. Lucia Boa, *Boa orophias* (Arendt and Anthony 1986). However, only *C.*

inornatus has been widely documented as commonly exploiting bats as a trophic resource in caves. Additionally, bat predation has been suggested for the Grenada Boa, *Corallus grenadensis* (R.W. Henderson in Henderson and Powell 2009) and the Hispaniolan Boa (*Chilabothrus striatus*) has been observed foraging for bats at cave openings (J.A. Ottenwalder in Henderson and Powell 2009), but feeding events have not been confirmed.

Bat predation has not been reported for West Indian boids smaller than 900 mm SVL. Herein, we report very small Cuban Boas directly preying or foraging for bats inside caves. One of them represents the minimum size record for any boid snake known to prey on bats in the Neotropics. Also, we discuss the possible significance of these findings for the population dynamics and life history of cave-associated Cuban Boas.

Materials and Methods

We conducted nine surveys in two caves (three at Erophylla Cave and six at El Abono Cave) in Sancti-Spíritus Province, central Cuba (Fig. 1) between 2008 and 2013. Erophylla Cave (22°24'16"N, -79°23'25"W; datum WGS 84; 75 m asl) is in Lomas Las Tasajeras, a karstic low ridge northwest of Yaguajay Municipality. The spacious interconnected chambers of this cave harbor a large population (many thousands) of Brown Flower Bats (*Erophylla sezekorni sezekorni*) and a few Jamaican Fruit-eating Bats (*Artibeus jamaicensis*). It also serves as a nocturnal refugium for Cuban Flower Bats (*Phyllonycteris poeyi*) (H. Vela and T.M. Rodríguez-Cabrera, pers. obs.). El Abono Cave (22°03'54"N, -79°40'19"W; datum WGS 84; 200 m asl) is in a submontane limestone-cap at Cariblanca, Fomento Municipality. This cave is a complex web of interconnected narrow galleries alternating with more spacious chambers that harbor a moderate population (hundreds) of *E. s. sezekorni* and a few *A. jamaicensis*. It also is used as a seasonal refuge by Brazilian Free-tailed Bats (*Tadarida brasiliensis*) and as a nocturnal refugium by Waterhouse's Leaf-nosed Bats (*Macrotus waterhousei*) (T.M. Rodríguez-Cabrera, pers. obs.). Although large concentrations of bats occur in both caves, the geomorphology and climatic parameters do not fulfill the criteria for "hot caves" (see Silva 1977, 1979; Cruz 1992). Both caves are surrounded by semideciduous forest interspersed with secondary vegetation.

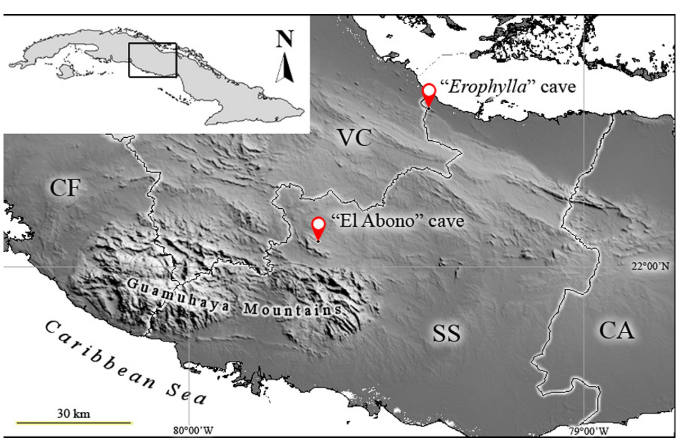

Fig. 1. Location of caves in Sancti Spíritus Province (SS), central Cuba, where juvenile Cuban Boas (*Chilabothrus angulifer*) were observed preying on bats. Abbreviations of other provinces: CF=Cienfuegos, VC=Villa Clara, CA=Ciego de Ávila.

We weighed all captured snakes to the nearest 5 g with a Pesola® spring scale (Medio-Line 600 g), measured snout-vent length (SVL), tail length (TL), and mid-body circumference (MBC) to the nearest 1 mm using a cord and a flexible measuring tape, and head length with a Stainless Steel Vernier Caliper to the nearest 0.05 mm. All means are reported ± one standard deviation (SD). We induced regurgitation in every snake showing evidence of a recent meal by gently pulling the mass toward the mouth. We identified prey items *in situ* to species or subspecies and weighed them to the nearest 0.25 g with a Pesola® spring scale (Micro-Line 30 g). One disadvantage of forced regurgitation is that in cases of advanced digestion or snakes with very small prey items, we might not have noticed the presence of stomach contents. However, more thorough analyses of digestive tract contents by ventral incision require that the snake be killed.

The Cuban Boa is known to be aggressive, and this is particularly evident in younger animals (e.g., Huff 1976; Murphy et al. 1978; Morell 2009). To avoid injuries to both the boas and the researchers, the snakes' heads were covered with small cloth bags fastened just behind the jaws (Fig. 2). This procedure also effectively calms the snakes and consequently facilitates accurate measurements. We marked all captured snakes using Brown and Parker's (1976) ventral scale clipping system before releasing them at the site of capture.

Results

We captured 57 boas (27 at Erophylla Cave and 30 at El Abono Cave). During three of the nine surveys, we found a total of four boas with evidence of a recent meal (two boas during one survey at Erophylla Cave and one boa during each of two surveys at "El Abono" cave), and on two occasions observed boas handling freshly captured prey (one at each cave). Two of the snakes (one with stomach contents and one handling freshly captured prey) had SVLs above 1,000 mm and are not considered further in this work. The maximum number of boas observed in a single night was 14 at Erophylla Cave (23 January 2012) and seven at El Abono Cave (30 March and 8 June 2008 and 6 August 2010). The fewest boas observed in a single survey was five at Erophylla Cave (5 July 2012) and one at El Abono Cave (10 April 2013). The proportion of snakes observed foraging and/or with stomach contents varied between 25–64% at Erophylla Cave and 25–100% at El Abono Cave. Additionally, on 5 July 2012, we recaptured four boas at Erophylla Cave, 164 days after the initial capture on 23 January 2012.

Fig. 2. Young female Cuban Boa (*Chilabothrus angulifer*; Snake No. 7, 950 mm SVL) immediately after capture with the head covered by a cloth bag. Notice the bulge at midbody (arrow) containing an adult male Cuban Flower Bat (*Phyllonycteris poeyi*).

El Abono Cave.—On 30 March 2008, we found a juvenile boa (780 mm SVL; Snake No. 1, Table 1) in foraging position inside the cave, but did not observe predation. On 8 June 2008, another juvenile boa (980 mm SVL; Snake No. 2, Table 1) regurgitated three juvenile Brown Flower Bats (*Erophylla sezekorni sezekorni*) (stage I, following Silva 1979), constituting the first confirmed case of Cuban Boas preying on this bat species. At 2100 h on 31 January 2013, we found a juvenile with an umbilical scar (665 mm SVL; Snake No. 3, Table 1) in foraging position on a limestone outcrop inside the cave, but did not observe predation.

Erophylla Cave.—At 1510 h on 20 May 2013, we found a young *C. angulifer* with an umbilical scar (660 mm SVL; Snake No. 4, Table 1) resting in a wall crevice at the main entrance (Fig. 3A). Forced regurgitation revealed an adult male Cuban Flower Bat (*Phyllonycteris poeyi*) with no visible signs of advanced digestion, suggesting that it was ingested at most the previous night (Fig. 3B–C). After a heavy rain on the same day at 2130 h, we found a second juvenile with an umbilical scar (635 mm SVL; Snake No. 5, Table 1) outside the entrance in foraging position on a branch of a shrub 150 cm above the ground (Fig. 3D). At 2200 h, we observed a third juvenile with an umbilical scar (505 mm SVL; Snake No. 6, Table 1) hanging from a limestone outcrop (50 cm above the ground) in the wall of a secondary opening and swallowing a freshly captured adult female *P. poeyi* (Fig. 4). We collected a fourth young boa (950 mm SVL; Snake No. 7, Table 1) at 2230 h crawling on the ground inside the cave; it regurgitated a recently ingested adult male *P. poeyi*. All three bats were ingested headfirst (Fig. 3C).

Table 1. Data on juvenile Cuban Boas (*Chilabothrus angulifer*) observed at El Abono and Erophylla caves and their prey. SVL = snout-vent length, TL = tail length, HL = head length, MBC = mid-body circumference, NPI = number of prey items, APM = absolute prey mass, RPM = relative prey mass. Situation (Sit.) when first observed: F = foraging, SC = with stomach content, or SW = swallowing prey. Body measurements are in millimeters (mm) and grams (g).

			Snakes						Prey	
No.	SVL	TL	HL	MBC	Mass	Sex	Sit.	NPI	APM	RPM
1	780	105	35	74	215	M	F	—	—	—
2	980	105	40	105	500	F	SC	3	22.5	0.045
3	665	70	30	45	145	F	F	—	—	—
4	660	70	31	63	160	M	SC	1	26.0	0.165
5	635	72	29	65	100	F	F	—	—	—
6	505	58	29	55	80	F	SW	1	21.5	0.269
7	950	115	41	100	550	F	SC	1	23.0	0.042

Fig. 3. The smallest juvenile Cuban Boa (*Chilabothrus angulifer*; Snake No. 6, 505 mm SVL) found preying on bats at Erophylla Cave: (A) Immediately after swallowing a freshly captured bat; (B) on the ground after capture, note the bulge in the esophageal area; (C) regurgitating an adult female Cuban Flower Bat (*Phyllonycteris poeyi*); and (D) after regurgitation.

Discussion

The abundance of snakes and recaptures of five individuals in the same cave after nearly six months suggest that Cuban Boas frequently forage in these caves.

Few studies record small Neotropical snakes (<1,000 mm total length) preying on bats. The smallest boid known to prey on bats was a juvenile female Amazon Treeboa (*Corallus hortulanus*; 676 mm SVL, 155 mm TL) from Ecuador (L.J. Vitt and J.P. Caldwell in Martins and Oliveira 1999). Esbérard and Vrcibradic (2007) observed a juvenile Boa Constrictor (*Boa constrictor*; estimated total length ca. 1,000 mm) capturing and swallowing a Lesser Bulldog Bat (*Noctilio albiventris*).

Koenig and Schwartz (2003) recorded the smallest West Indian boid snake preying on bats, a juvenile female *Chilabothrus subflavus* (940 mm SVL, 345 g) that captured and ate a Jamaican Fruit-eating Bat (*Artibeus jamaicensis*) at the entrance of Windsor Great Cave, Jamaica. Two other juvenile boas (850 mm SVL, 195 g and 920 mm SVL, 395 g) apparently were foraging for bats in the same cave. Prior and Gibson (1997) described a juvenile *C. subflavus* (950 mm SVL, 320 g) repeatedly striking at flying bats while hanging from vegetation growing on the cliff above the entrance of this same cave, but they did not confirm any captures. Puente-Rolón and Bird-Picó (2004) mentioned a small radio-tracked male *C. inornatus* (450 mm SVL, 120 mm TL) in Cueva de los Culebrones in Puerto Rico, but they did not confirm predation on bats. Arendt and Anthony (1986) reported a juvenile St. Lucian Boa (*Boa orophias*; 1,100 mm total length) preying on Antillean Fruit-eating Bats (*Brachyphylla cavernarum*). Individuals of the extensively studied *C. inornatus* reported preying on bats were 1,200–2,000 mm in total length (Rodríguez and Reagan 1984; Rodríguez-Durán 1996; Puente-Rolón 2012).

Cuban Boas smaller than 1,000 mm SVL have not been reported preying on bats or associated with bat caves. The boas studied by Hardy (1957) in a cave at Guanayara, near Trinidad, were 1,220–2,440 mm in total length (N = 41). Berovides and Carbonell (1998) recorded a mean SVL of

Fig. 4. Juvenile Cuban Boas (*Chilabothrus angulifer*) at Erophylla Cave: (A) Snake No. 4 just after capture (arrow indicates the umbilical scar); also notice the bulge at midbody; (B) same individual regurgitating an adult male Cuban Flower Bat (*Phyllonycteris poeyi*); (C) freshly regurgitated bat; and (D) snake No. 5 in foraging position outside the cave entrance.

1,560 ± 19.6 mm (1,000–1,990 mm; N = 19) in a cave-associated group of Cuban Boas near Sierra del Rosario, Artemisa Province.

Caves harboring large bat populations are abundant in Cuba (e.g., Silva 1979), and in those ones with *C. angulifer*, the boas appear capable of exploiting these concentrations of food beginning very early in their lives. Parturition in Cuban Boas occurs mostly from September to December, with a peak in October and November (e.g., Tolson and Teubner 1987; Tolson 1992; Morell et al. 1998). Based on very small sizes and presence of umbilical scars, four of the snakes observed in January and May probably were no more than a few months old. The smaller three boas observed at Erophylla Cave apparently belonged to the same cohort. We observed copulating Cuban Boas inside Erophylla Cave, suggesting that reproductive activity of cave-associated populations occurs in these highly productive habitats that provide an abundance of food for both adult and very young individuals. Also, the stable climatic conditions of "hot caves," with temperatures of 28–40°C and a relative humidity near saturation (90–99%) inside the hottest galleries (e.g., Silva 1977, 1979; Cruz 1992) could provide females with effective thermoregulatory gradients during pregnancy. Puente-Rolón and Bird-Picó (2004) found a similar situation in Puerto Rican Boas, and noted that individuals from cave-associated populations tend to remain near bat caves (see also Puente-Rolón 2012). Our recaptures of some individuals in the same cave after nearly six months suggest that a similar situation could occur in Cuban Boas.

Similar to what apparently occurs in *C. inornatus* (Puente-Rolón 2012), *C. angulifer* seems to experience an ontogenetic shift in niche, with bat caves sustaining a particular cohort. All of the approximately 100 boas measured by the senior author over several years and associated with these kinds of caves in central and western Cuba ranged in size from 563 to 2,035 mm in total length (see also Hardy 1957; Berovides and Carbonell 1998). Koenig and Schwartz (2003) mentioned that "hunting for bats appears restricted to juveniles" and listed two possible factors that might be responsible: (1) Physical constraints of the hunting perch, the imposition of gravity on blood circulation when larger snakes hang vertically (see also Chandler and Tolson 1990; Lillywhite and Henderson 1993); (2) bats represent low- or marginal-energy prey items for adult snakes (see also Cundall and Greene 2002). Limitations for bat hunting in *C. angulifer* apparently commence as boas approach 2,000 mm in total length, which corresponds to small adult snakes (T.M. Rodríguez-Cabrera et al., in prep.). Larger individuals appear to abandon bat predation and search instead for more energetically rewarding prey such as rats, birds, hutias, and domestic animals.

Cuban Boas are among the largest and stoutest West Indian snakes, with individuals exceeding 4,000 mm SVL (e.g., Schwartz and Henderson 1991; Tolson and Henderson 1993; Henderson and Powell 2009). Gundlach (1880) reported snakes 6.4 m in total length. Unlike any other *Chilabothrus* and most boids, neonatal Cuban Boas are very large, with body masses frequently exceeding 180 g and SVLs usually >600 mm (e.g., Tolson 1992; Polo and Moreno 2007; Morell 2009). The sharp ontogenetic shift in diet from ectothermic to endothermic prey observed in other species of *Chilabothrus* (Reagan 1984; Henderson et al. 1987; Wiley 2003; Tolson et al. 2007), *Corallus* (Henderson 1993, 2002), *Candoia* (Harlow and Shine 1992), erycine boas (e.g., Rodríguez-Robles et al. 1999), and some pythons (e.g., Slip and Shine 1988; Shine and Slip 1990) is less evident in Cuban Boas. The smaller neonatal sizes of most boids in the genera listed (i.e., 320–470 mm SVL and 7–22 g for West Indian boids; see Tolson and Henderson 1993; Henderson and Powell 2009) impose initial diets comprised largely of smaller ectotherms (e.g., lizards), with most able to consume some rodents only after reaching about 600 mm SVL and finally shifting to a diet composed mostly of endotherms as they approach 1,000 mm SVL (see references above). Neonatal sizes of *C. angulifer* correspond with those of other constricting snakes when ontogenetic shifts in diet commence. Consequently, *C. angulifer* can prey on ectotherms as well as on endotherms almost immediately after birth and at least during the first two years of life, after which they feed predominantly on birds and mammals (T.M. Rodríguez-Cabrera et al., in prep.). The Cuban Boa is the only *Chilabothrus* with heat-sensing labial pits (e.g., Tolson 1987; Reynolds et al. 2013), which detect the heat produced by endotherms, and these structures are present and presumably functional at birth (Fig. 5).

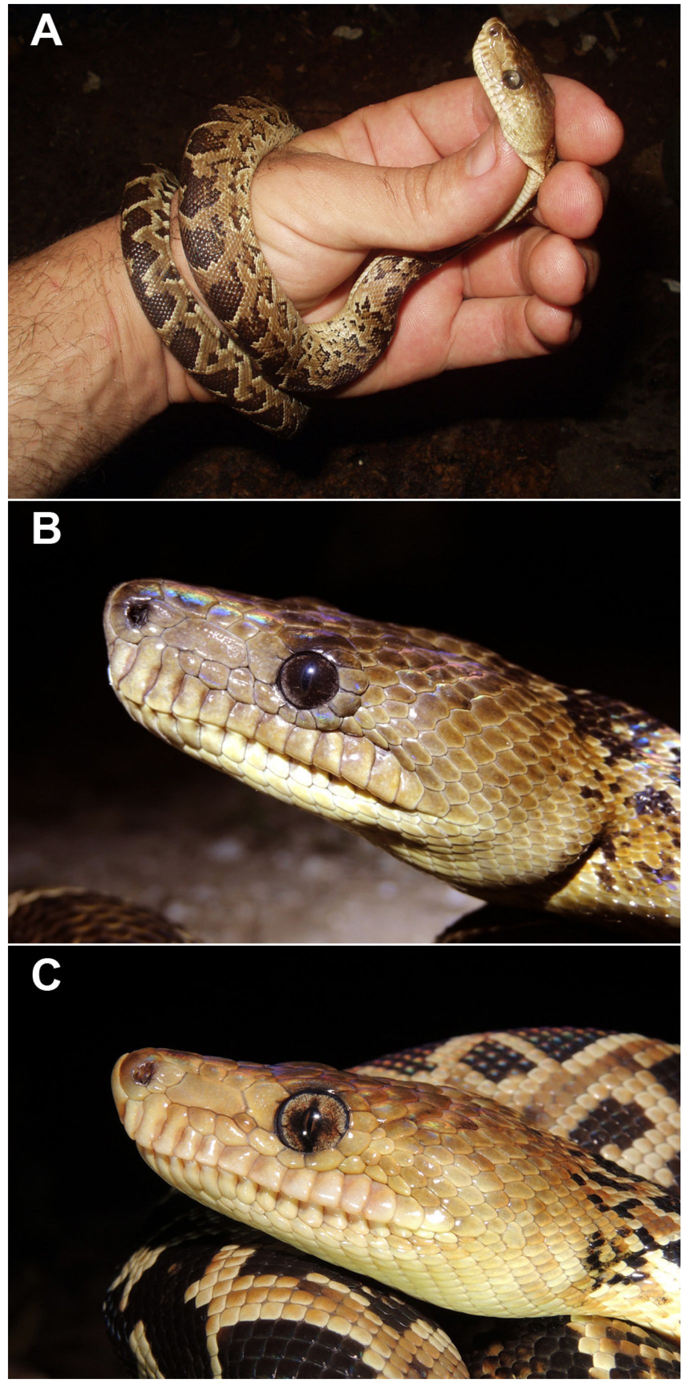

Fig. 5. Heat-sensing labial pits in the smallest juvenile Cuban Boa (*Chilabothrus angulifer*; Snake No. 6) observed at Erophylla Cave (A), in an adult male (1,370 mm SVL, 1,920 g) from El Indio Cave, Jaruco, Mayabeque Province (B), and in a juvenile with an umbilical scar (652 mm SVL, 157 g) from Ambrosio Cave, Varadero, Matanzas Province (C).

Some boas and pythons are known to consume prey approaching or even exceeding their own body masses, especially when young (e.g., Rivas 1999; Rodríguez-Robles et al. 1999; Fearn et al. 2001). The proportionately larger head of small individuals allows them to consume relatively larger prey than adult snakes (e.g., Pizzatto et al. 2009). The average maximum mass of all living species of Cuban bats (21.6 ± 18.8 g, 3–87 g; Silva 1979; García and Mancina 2011; Mancina and García 2011) is far below the average mass reported for neonatal Cuban Boas (146.6 ± 26.2 g, 88–203.6 g; Huff 1976; Murphy et al. 1978; Tolson 1983, 1992; Polo and Moreno 2007). Despite the exceptionally small size of one of the boas reported here (i.e., 505 mm SVL, 80 g), its prey represented only 26.9% of body mass.

Our data suggest that even the smallest Cuban Boas are capable of preying on medium-sized bats (21–26 g) as they exit or enter caves. However, cave-associated young boas probably are opportunistic predators that also take easily accessible bats roosting in caves and juvenile bats that frequently fall to the ground and are incapable of strong flight.

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