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Predation by Giant Centipedes, *Scolopendra gigantea*, on Three Species of Bats in a Venezuelan Cave

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ABSTRACT.—We report the first known cases of predation by centipedes, *Scolopendra gigantea* (Chilopoda, Scolopendromorpha, Scolopendridae), on three species of bats (Mammalia, Chiroptera), *Mormoops megalophylla* and *Pteronotus davyi* (Mormoopidae), and *Leptonycteris curasoae* (Phyllostomidae). Our observations were made in Cueva del Guano, a limestone cave in Paraguaná Peninsula, Venezuela, that harbors important colonies of five bat species. These observations show that, nocturnally and diurnally, centipedes can perform two actions that most other bat predators cannot. First, they climb cave ceilings to catch and eat flying or perching bats. Second, they subdue bats substantially heavier than themselves. Such capabilities may allow large centipedes to prey on bats in what otherwise would be safe roosts.

KEYWORDS.—*Leptonycteris*, *Mormoops*, Paraguaná Peninsula, predation, *Pteronotus*, *Scolopendra*.

Compared to other mammals, bats suffer low predation rates. However, because bats are long-lived and reproduce slowly, the impact of predation on their populations is probably greater than assumed (Tuttle and Stevenson 1982). A large variety of vertebrates prey on bats (Hardy 1957; Barr and Norton 1965; Gillette and Kimbrough 1970; Hopkins and Hopkins 1982; Rodríguez and Reagan 1984; Rodríguez-Durán and Lewis 1985; Rodríguez-Durán 1996; Hutterer and Ray 1997; Souza et al. 1997; Sparks et al. 2000) while the few reports of invertebrate predation involve cockroaches, ants, larval beetles, and araneomorph spiders (Rice 1957; Gillette and Kimbrough 1970; Wilson 1971; McCormick and Polis 1982; Hermanson and Wilkins 1986).

Because of their carnivorous tendency, terrestrial habitat, and either gregarious foraging or large body size, a diversity of arthropods, including praying mantises, wasps, mygalomorph spiders, scorpions, solpugids, decapod crustaceans, and scolopendrid centipedes, are potential bat predators (Hutton 1843; Millot 1943; Grant 1959; Cloudsley-Thompson 1968; Banta and Marer 1972; Gertsch 1979; McCormick and Polis 1982, 1990). Scolopendrid centipedes prey on frogs and toads up to 95 mm long, small lizards, snakes up to 247 mm long, birds up to the size of a sparrow, and both field and house mice (Wells-Cole 1898; Okeden 1903; Shugg 1961; Cloudsley-Thompson 1968; Easterla 1975; Clark 1979; Lewis 1981; McCormick and Polis 1982; Carpenter and Gillingham 1984).

We report predation under natural conditions by the large scolopendrid centipede, *Scolopendra gigantea* (Chilopoda, Scolopendromorpha, Scolopendridae), on three bat species (Mammalia, Chiroptera). Each of these predation cases resulted from an independent fortuitous observation. The study site, Cueva del Guano, is a limestone cave located in a nearly flat thorn-scrub region, in Paraguaná Peninsula, Venezuela, at 69°56′44′′W, 11°53′50′′N, and elevation 120 m. Before entering the cave, one must descend 10 m through a 15 × 6 m sink that leads to the southern edge of a 24 × 20 m antechamber. The cave's entrance is approximately 1 m wide and high, and opens on the western edge of the antechamber. The cave, which consists of a 30 m main gallery followed by two 20 m secondary galleries, harbors 45,000-50,000 bats (SVE 1972; Matson 1974). At daytime, five bat species roost in this refuge: *Mormoops mega-*

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lophylla, *Pteronotus parnellii* and *P. davyi* (Mormoopidae); *Leptonycteris curasoae* (Phyllostomidae); and *Natalus tumidirostris* (Natalidae) (Linares and Ojasti 1974; Matson 1974; Genoud et al. 1990; Bonaccorso et al. 1992; Arends et al. 1995). *Scolopendra gigantea*, the world's largest centipede (maximum length >300 mm; Shelley and Kiser 2000), is common in Paraguaná and easily found in the antechamber.

Nocturnal predation on Mormoops megalophylla.—On 21 December 2000, at 21:45 h, we found a *S. gigantea* perching from the ceiling of the northeastern antechamber's edge, 5 m north and 22 m east of the cave's entrance, while feeding on a dead *M. megalophylla* (Fig. 1). The centipede was 0.3 m from the nearest vertical wall and 2 m from the ground. Since the centipede and bat were easily visible, we are confident that we did not overlook them during a careful examination of this area concluded at 19:30 h. Therefore, the centipede had been manipulating the bat where we found it (no guano, sand, or clay on the pelage) for not longer than 2 h and 15 min. Before collecting both specimens, we observed them using flashlights for 30 min from less than 1 m away. During this period, the centipede remained attached to the ceiling with only the last five pairs of legs, held the bat using its first eight pairs of legs (excluding the forcipules, or poison claws), and fed while it moved its head from side to side. The bat, a non-reproducing adult female, had blood in the wounds, lax wings and legs, patagia fully retained their natural elasticity, and fecal pellets protruded from the anus and adhered to the uropatagium. Its forearm was 55.9 mm long, which equals the mean for adult females of *M. megalophylla* from Cueva del Guano. Mean body mass for these females is 16.5 g. An ectoparasitic bat fly, *Nycterophilia mormoopsis* (Diptera, Streblidae) was attached to the bat's abdominal hair. The heel, toes, and claws of the feet had tangled agglomerations of hair from the upper abdomen and lower chest of the bat (Fig. 1). Embedded in these agglomerations, was another *N. mormoopsis* (the alimentary tract of the centipede also contained flies of this species; Table 1). Fecal pellets found inside the bat's intestine contained the remains of a noctuid moth (Lepidoptera).

FIG. 1. A centipede, *Scolopendra gigantea*, holding and eating a freshly-killed bat, *Mormoops megalophylla*, while hanging from the ceiling in the antechamber of Cueva del Guano, Paraguaná Peninsula, Venezuela.

The centipede was a 15.2 g (probably 9.0-9.5 g before eating) and 145 mm female that had mature reproductive organs. We divided its 6.3 g (including bat remains) and 124 mm alimentary tract into nine sections, which we dissected separately (Table 1). To determine the bat's body region from which hair in the alimentary tract came from, we compared it with hair still on the bat and with that of complete specimens of *M. megalophylla* from the same locality and date.

The centipede started eating around the bat's neck, continued into the chest, and then into the abdominal region (Table 1). When we collected the two specimens, the centipede had devoured about 35% of the bat's body mass. Necropsy of the bat showed that it was in the following conditions: left temporal region of cranium with-

TABLE 1. Sequence of consumption of body parts of a preyed bat individual, *Mormoops megalophylla*, as reflected by the contents of nine dissected sections, ordered from anus to mouth, of the alimentary tract of a centipede predator, *Scolopendra gigantea*.

	Part of alimentary tract								
Anatomic region	Hindgut		Mid-gut					Esophagus	
Dissected section	9^{th}	8^{th}	7^{th}	6^{th}	5^{th}	4^{th}	3^{rd}	2^{nd}	1^{st}
Length of section (mm)	130	130	136	136	136	136	136	150	150
	Contents of alimentary tract								
Hair tufts without skin	●	●							
Hair tufts joined by skin			●	●	○	○	○	○	○
Hair (neck)	+	+							
Hair (chest)	+	+	+	+	+[2]				
Hair (lower chest)				+	+	+	+		
Hair (upper abdomen)				+	+	+	+		
Hair (abdomen)							+	+	+
Ectoparasitic bat flies[1]			○						
Propatagium				○					
Muscle			●	●	●	●	●	○	○
Heart					○				
Lung					●	●			
Gut							●	●	●
Liver								○	
Kidney								○	

● = Predominant tissue fragments; ○ = minor tissue fragments, or other lesser components; + = present.
[1]Two flies (*Nycterophilia mormoopsis*) adhered to hair tufts; [2]chest hair prevails over hair from other body regions of the bat.

out muscle; left mandible disarticulated, without muscle covering the masseteric fossa and the angular and coronoid processes; left ectotympanic bone displaced from its natural position; cervical vertebrae ventrally and sinistrally without muscle and vascular tissues, no vestiges of trachea; left half of neck devoid of a circular patch (6 mm diameter), carved from inside, of dorsal skin; left propatagium partially missing along its external edge; left half of thorax almost completely devoid of skin; right half of thorax devoid of skin near sternum; left upper abdomen without skin; left pectoral muscles almost completely missing; right pectoral muscles retaining about one-fourth of their mass; left ribs exposed, detached from sternum, and displaced to form a large opening to the middle of the pectoral cavity; right ribs exposed, in their natural position; pectoral cavity empty; left scapula ventrally without muscle; hypodermis of skin between scapulae exposed, skin intact; most of digestive tube missing; liver and left kidney in their natural position, retaining most of their mass, right kidney intact; no bones missing.

Diurnal predation on Leptonycteris curasoae.—On 7 December 2001, at 12:00 h, we found a ~210 mm *S. gigantea* feeding on a dead *L. curasoae* on the floor of the antechamber's tunnel connecting to the cave, nearly directly below the cave's entrance. Mean forearm length for adult *L. curasoae* from Cueva del Guano is 54.3 mm, and mean body mass is 26.5 g. The centipede used its first eight pairs of legs (excluding forcipules) to hold the bat. We touched the centipede several times with a stick, attempting to scare it away and release the bat, but contrary to what we expected, the centipede responded by partly coiling around the bat and holding it more tenaciously. During 30 min of observations, the centipede fed without interruption, carving a wound in the bat's lower abdomen. The bat also had a second and smaller wound on the upper back, which probably represented the initial bite of the centipede. The wings were lax, the exposed flesh was bloodstained, and the pelage was clean.

Diurnal predation on Pteronotus davyi.—On 13 March 2003, at about 11:30 h, we found a ~160 mm *S. gigantea* feeding on a dead *P. davyi* while perching from the ceiling of the antechamber's tunnel connecting to the cave, 1 m away from the cave's entrance, 0.2 m from the nearest vertical wall, and 1.5 m above the cave's floor. Mean forearm length for adult *P. davyi* from Cueva del Guano is 47.7 mm, and mean body mass is 9.7 g. The centipede handled the bat in a posture similar to that shown in Fig. 1. However, the centipede remained attached to the ceiling with the last eight pairs of legs, and held the bat using its first seven pairs of legs (excluding forcipules). During 30 min of observations, the centipede fed on the bat's chest and abdomen. The bat also had a large wound on the back resulting from previous eating by the centipede. As in the other two cases, the dead bat was lax, bleeding, and had no dirt on pelage.

Discussion.—We are convinced that the centipedes killed the three bats *in situ* shortly before we found them. Absence of rigor mortis, presence of fresh blood in wounds, and cleanliness of pelage indicate that the bats died shortly before and were not transported from other places. Since ectoparasitic flies stay on a dead bat only while it remains warm, the *N. mormoopsis* on the *M. megalophylla* and in the alimentary tract of the associated centipede show that the bat died just before being rapidly eaten. Fecal pellets found on this bat suggest that it had foraged and fully digested prey the same night. Further evidence of predation on this bat is the tangled pectoral hair found in its toes (Fig. 1), which indicates an energetic attempt to dislodge the centipede. Carrion-eating insects in Cueva del Guano are superabundant and quickly feed on fallen bats, thus their absence on the *L. curasoae* indicates a recent death and fall to the floor. Resistance of the centipede to release this bat suggests that it confused human interference with struggling by prey. This behavior would not be expected if the centipede had not killed the bat.

The centipedes most likely seized the bats in the ceiling of the antechamber of Cueva del Guano by one of three methods. Firstly, the centipedes may have crawled along the ceiling, with their venters facing upwards, actively searching for perching bats. However, scolopendrids do not usually pounce upon prey from a distance (Manton 1965). Secondly, the centipedes may have waited statically on the ceiling for a bat to perch within striking distance (we have seen centipedes "resting" for hours on the walls and ceiling of the antechamber). This could be the case because scolopendrids learn to climb high substrates where airborne insects alight, and even hang from such substrates using their rear legs (Remmington 1950). Thirdly, the centipeds may have employed a strategy used by snakes to seize bats in caves and trees (e.g., Hardy 1957; Barr and Norton 1965; Hopkins and Hopkins 1982; Rodríguez and Reagan, 1984), i.e., hang from the ceiling and wait for a bat to fly close enough to catch it in mid-air (as suggested by the posture in which we observed the centipede eating the *M. megalophylla* and the *P. davyi*, Fig. 1). In spite of the vigor expected from a flying bat, this could also be the case because scolopendrids (1) can use multiple pairs of legs to get firmly anchored to substrates, (2) can quickly immobilize prey with their legs and with their venom, (3) seize flying prey in mid-air by raising the anterior part of the body, (4) hold struggling prey tenaciously (Cloudsley-Thompson 1968; Lewis 1981), and (5) the tunnel in which *L. curasoae* and the *P. davyi* were being eaten is a high traffic flyway in which bats seldom perch. Whichever was the case, our observations on predation on *M. megalophylla* and *P. davyi* show that, unlike most predators, large scolopendrids can crawl, with their ventral region facing upwards, along cave ceilings in search of flying or perching bats in what otherwise would be safe roosts. In this context, the *L. curasoe* eaten on the ground was likely a result of the centipede's fall while struggling with the bat.

Venomous arthropods capture larger prey than non-venomous ones (McCormick and Polis 1982). Therefore, the more venomous the arthropod the larger the prey it should be able to catch. Two of our cases (*M. megalophylla*, *L. curasoe*), in which prey may have nearly doubled the body masses of their victimizers, show the extraordinary predatory capabilities of an arthropod with a potent venom. These cases are more remarkable because of the difficulties involved in capturing energetic and volant prey while hanging from cave ceilings. Centipedes are known to use up to eight pairs of their anterior legs to manipulate prey, with the number of pairs involved varying proportionally with prey size (Lewis 1961, 1981; Elzinga 1994). Therefore, in both cases, use of the first eight pairs of legs to hold the bats suggests that such prey may have been around the maximum permissible size for the centipedes.

Scolopendrids often inflict an initial puncture with their forcipules on the neck of vertebrate prey (Shugg 1961; Cloudsley-Thompson 1968). This should quickly immobilize the prey because the neurotoxic venom (Bücherl 1946; Stankiewicz et al. 1999) is injected near the brain. The consumption of the *M. megalophylla* began behind the bat's head. This may also have happened to the *L. curasoae* and the *P. davyi*, as suggested by the wounds on their backs. Therefore, injection of venom near the brain may have occurred and facilitated subduing the three bats. Although the toxicity of centipede venom to bats is unknown, intravenous injection of the venom gland extract of *Scolopendra viridicornis* kills mice in 20-32 sec, and direct puncture of the forcipules of this centipede in the tail of mice is always lethal, causing death in a mean time of 3 min (Bücherl 1946).

Even though arthropods comprise the bulk of the diet of all centipedes (Lewis 1981; Cloudsley-Thompson 1968), large scolopendrids do not miss the opportunity to feed on vertebrates (Wells-Cole 1898; Okeden 1903; Shugg 1961; Easterla 1975; Clark 1979; Lewis 1981; McCormick and Polis 1982; Carpenter and Gillingham 1984). Mice were used as the main food for captive *S. gigantaea*, which "devoured them with alacrity" (Cloudsley-Thompson 1968). A 120 mm centipede consumed a large chunk of flesh from a human corpse (Harada et al. 1999). Our observations took place in an environment providing extraordinary abundance of arthropod prey, especially large (45 mm) cockroaches, *Blaberus discoidalis* (Blattaria, Blaberidae) which we have seen caught and eaten by *S. gigantea*. This suggests that vertebrates may be particularly rewarding prey for centipedes because of their nutritional composition, or because the quantity of nutrients per individual prey exceeds that provided by invertebrates.

Scolopendrids belong to a major and ancient arthropod lineage, are morphologically disctinctive, some are among the largest terrestrial arthropods, are common in the tropics, and are of medical and pharmacological interest (Manton 1965; Cloudsley-Thompson 1968; Lewis 1981; McCormick and Polis 1982; Knysak et al. 1998; Stankiewicz et al. 1999). Despite their importance, little information exists on their behavior under natural conditions. On the other hand, most observations of predation on bats involve easily observed raptorial birds around North American caves (Gillette and Kimbrough 1970; Sparks et al. 2000). There is little information on other predators, particularly in the tropics where bats and their enemies are most diverse. Research is needed both to learn more about the foraging ecology of scolopendrids, especially of large ones, and to evaluate the impact of diverse predators on tropical bat populations.

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