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 davisi* (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; Oskeden 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 6°56′44″W, 11°53′30″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 megalophylla*...
lophylla, Pteronotus parnaellii and P. davii (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).

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-
out muscle; left mandible disarticulated, without muscle covering the massteric fossa and the angular and coronoid pro-
cesses; 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 dor-
sal skin; left propatagium partially missing along its external edge; left half of thorax devoid of 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; hypo-
dermis of skin between scapulae exposed, skin intact; most of digestive tube missing; liver and left kidney in their natural posi-
tion, 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 ante-
chamber’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 tena-
ciously. During 30 min of observations, the centipede fed without interruption, carving a wound in the bat’s lower abdo-
men. The bat also had a second and smaller wound on the upper back, which probably represented the initial bite of the cen-
tipede. The wings were lax, the exposed

<table>
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<tr>
<th>Part of alimentary tract</th>
<th>Hindgut</th>
<th>Mid-gut</th>
<th>Esophagus</th>
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<tr>
<td>Dissected section</td>
<td>9th</td>
<td>8th</td>
<td>7th</td>
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<td>Length of section (mm)</td>
<td>130</td>
<td>130</td>
<td>136</td>
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<table>
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<tr>
<th>Contents of alimentary tract</th>
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<tr>
<td>Hair tufts without skin</td>
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<td>Hair tufts joined by skin</td>
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<td>Hair (neck)</td>
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<td>Hair (chest)</td>
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<td>Hair (lower chest)</td>
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<td>Hair (upper abdomen)</td>
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<tr>
<td>Hair (abdomen)</td>
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<td>Ectoparasitic bat flies¹</td>
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<td>Propatagium</td>
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<td>Kidney</td>
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●● = Predominant tissue fragments; ○ = minor tissue fragments, or other lesser components; + = present.

¹Two flies (*Nycterophilia mormoopsis*) adhered to hair tufts; ²chest hair prevails over hair from other body regions of the bat.
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 tangle of 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. curasoe 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 centipedes 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; Rodriguez 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. curasoe and the P. davyi were being eaten is a high traffic flyway in which bats seldom perch. Whatever 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

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should be able to catch. Two of our cases 
(*M. megalophylla*, *L. curasoae*), 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 re-
markable because of the difficulties in-
volved 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 im-
mobilize the prey because the neurotoxic 
venom (Bücherl 1946; Stankiewicz et al. 
1999) is injected near the brain. The con-
sumption 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 tox-
icity of centipede venom to bats is un-
known, 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; 
Okened 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. gigantea*, which “devoured them 
with alacrity” (Cloudsley-Thompson 1968). 
A 120 mm centipede consumed a large 
chunk of flesh from a human corpse (Ha-
rada et al. 1999). Our observations took 
place in an environment providing extraor-
dinary abundance of arthropod prey, espe-
cially large (45 mm) cockroaches, *Blaberus 
discoidalis* (Blattaria, Blaberidae) which we 
have seen caught and eaten by *S. gigantea*. 
This suggests that vertebrates may be par-
cularly rewarding prey for centipedes be-
cause of their nutritional composition, or 
because the quantity of nutrients per indi-
vidual prey exceeds that provided by in-
vertebrates.

Scolopendrids belong to a major and an-
cient arthropod lineage, are morphologi-
cally distinctive, some are among the larg-
est terrestrial arthropods, are common in 
the tropics, and are of medical and phar-
macological interest (Manton 1965; Cloud-
sley-Thompson 1968; Lewis 1981; McCor-
mick and Polis 1982; Knysak et al. 1998; 
Stankiewicz et al. 1999). Despite their im-
portance, 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 (Gil-
lette 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 scolopen-
drids, especially of large ones, and to evalu-
ate the impact of diverse predators on 
tropical bat populations.

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