



Cryptotis nigrescens (Eulipotyphla: Soricidae)

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Abstract: The blackish small-eared shrew, *Cryptotis nigrescens* (Allen, 1895), is a blarinine soricid that occurs in high-elevation premontane wet forest and cloud forest in the Central American countries of Costa Rica and Panama. The species is taxonomically monotypic, although it exhibits size variation that manifests as a gradual increase in size from northwest to southeast. Habitat loss is currently the greatest threat to the species' existence, although populations in the few areas where *C. nigrescens* has been studied appear to be healthy, and the International Union for Conservation of Nature (IUCN) classifies it as a species whose conservation status is "Least Concern" (LC). We include a complete synonymy for the genus *Cryptotis* Pomel, 1848.

Key words: biodiversity, biogeography, blackish small-eared shrew, Central America, cloud forest, Insectivora, montane, natural history, premontane wet forest, Soricomorpha

Resumen: La musaraña negruzca de orejas pequeñas, *Cryptotis nigrescens* (Allen, 1895), es un sorícido blarinino que se encuentra en los bosques húmedos premontanos de gran altura y en los bosques nubosos de los países centroamericanos de Costa Rica y Panamá. La especie es taxonómicamente monotípica, aunque exhibe una variación de tamaño que puede manifestarse como un aumento gradual de tamaño del noroeste al sureste. La pérdida de hábitat es actualmente la mayor amenaza para la existencia de la especie, aunque las poblaciones en las pocas áreas donde se ha estudiado *C. nigrescens* parecen saludables, y la Unión Internacional para la Conservación de la Naturaleza (UICN) la ha clasificado como una especie cuyo estado de conservación es "Least Concern [Preocupación Menor]" (LC). Incluimos una sinonimia completa para el género *Cryptotis* Pomel, 1848.

Palabras clave: biodiversidad, biogeografía, bosque muy húmedo premontano, bosque nuboso, Centroamérica, historia natural, Insectivora, montano, musaraña negruzca de orejas pequeñas, Soricomorpha

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Cryptotis Pomel, 1848

Cryptotis Pomel, 1848:249. Proposed as a subgenus of *Musaraneus* Pomel, 1848. Type Species *Musaraneus* (*Cryptotis*) *cinereus* (Bachman, 1837) = *Sorex cinereus* Bachman, 1837 = *Sorex parvus* Say, 1822 = (*Cryptotis parvus*), by monotypy.

Galemys Pomel, 1848:249. Part; preoccupied by *Galemys* Kaup, 1829, a talpid.

Brachysorex: Pomel, 1848:249. Part; not *Brachysorex* Duvernoy, 1842.

Musaraneus Pomel, 1848:249. Part; not *Musaraneus* Brisson, 1762, which is unavailable (ICZN 1998); *Musaraneus*



Fig. 1.—External view of an adult *Cryptotis nigrescens* from Zarcero Pueblo Nuevo, Alajuela Province, Costa Rica. Photograph by Diego Salas Solano; used with permission.

Pomel, 1848 is a junior synonym of *Crocidura* *Wagler*, 1832 (*Woodman*, 2004).

Blarina: *Baird*, 1857:48. Part; not *Blarina* *Gray*, 1838.

Cryptotus *Milne-Edwards*, 1872:256. Incorrect subsequent spelling of *Cryptotis* *Pomel*, 1848.

Soriciscus *Coues*, 1877:649. Type species “*Sorex parvus* Say or *S. cinereus* Bachm[an]” = *Sorex parvus* *Say*, 1822 (= *Cryptotis parvus*) and *Blarina floridana* *Merriam*, 1895 (= *Cryptotis floridanus*), respectively, by original designation. Proposed as a subgenus of *Blarina* *Gray*, 1838.

Sorieiscus *Elliot*, 1901:382. Incorrect subsequent spelling of *Soriciscus* *Coues*, 1877.

Cryptotis: *Miller*, 1911:221. First use of the name as a genus.

Cryptotys *Saban*, in *Piveteau*, 1958:846. Incorrect subsequent spelling of *Cryptotis* *Pomel*, 1848.

Xenosorex *Schaldach*, 1966:289. Type species *Notiosorex phillipsii* *Schaldach*, 1966 (= *Cryptotis phillipsii*), by original designation. Proposed as a subgenus of *Notiosorex* *Coues*, 1877.

Criptotis *Durant and Péfaur*, 1984:6. Incorrect subsequent spelling of *Cryptotis* *Pomel*, 1848.

CONTEXT AND CONTENT. Order Eulipotyphla, family Soricidae, subfamily Soricinae, tribe Blarinini, genus *Cryptotis* (*Hutterer* 2005; *Woodman* 2018). The genus *Cryptotis*, which included 12 recognized species in 1974 (*Choate and Fleharty* 1974), now includes 56 recognized species (*Woodman* 2018, 2019; *Guevara* 2023; *Woodman* 2023b). Although historically treated as feminine in gender (*Miller* 1912; *Miller and Kellogg* 1955; *Hall and Kelson* 1959; *Hall* 1981), a ruling by ICZN (2006) determined *Cryptotis* should be treated as a masculine noun.

Cryptotis nigrescens (*Allen*, 1895)

Blackish Small-eared Shrew; Musaraña Negruzca de Orejas Pequeñas

Blarina micrura: *Allen*, 1893:238. Not *Sorex micrurus* *Tomes*, 1861:279 = *Blarina tropicalis* *Merriam*, 1895:21 (= *Cryptotis tropicalis*); name preoccupied by *G[alemys]. micrurus* *Pomel*, 1848:249 = *Sorex talpoides* *Gapper*, 1830:202 = *Blarina brevicauda talpoides*.

Blarina (*Soriciscus*) *nigrescens* *Allen*, 1895:339. Type locality “San Isidro (San José), Costa Rica.” Holotype: skin and skull of an individual of unknown sex, AMNH (American Museum of Natural History) number 9591/7952.

C[ryptotis]. nigrescens: *Miller*, 1911:222. First use of current name combination.

Cryptotis zeteki *Setzer*, 1950:299. Type locality “Cerro Punta (lat. 8°42′ N, long. 82°48′ W), 6,500 feet, Chiriquí Province, Republic of Panama.” Holotype: skin and skull of an adult female, USNM (U.S. National Museum of Natural History) number 290466.

Cryptotis tersus *Goodwin*, 1954:1. Type locality “Santa Clara, 4200 feet elevation, on the Pan American Highway, 15 miles from the border of Costa Rica, Chiriquí Province, Republic of Panama.” Holotype: skin and skull of an adult male, AMNH number 164695.

C[ryptotis]. nigricans: *Goodwin*, 1954:2. Incorrect subsequent spelling of *Blarina nigrescens* *Allen*, 1895 (= *Cryptotis nigrescens*).

Cryptotis nigrescens zeteki: *Handley*, 1966:756. Name combination.

Cryptotis parva orophila: *Choate*, 1970:262. Part, not *Blarina* (*Soriciscus*) *orophila* *Allen*, 1895 (= *Cryptotis orophilus*).

Cryptotis nigrescens nigrescens: *Choate*, 1970:279. Name combination.

CONTEXT AND CONTENT. *Cryptotis nigrescens* is monotypic; subspecies previously recognized as comprising *C. nigrescens* (e.g., *C. n. mayensis*, *C. n. merriami*—see *Choate*, 1970) are now recognized as separate species (*Woodman and Timm* 1993; *Burgin* 2018; *Woodman* 2018). *Cryptotis nigrescens* is a member of the *C. nigrescens* group, an informal morphological grouping (*Choate* 1970; *Woodman* 2018) and genetic clade (*He et al.* 2015; *Baird et al.* 2017; *Mejía-Fontecha et al.* 2021) that includes the Eastern Cordillera small-eared shrew, *C. brachyonyx* *Woodman*, 2003; Colombian small-eared shrew, *C. colombianus* *Woodman and Timm*, 1993; Honduran small-eared shrew, *C. hondurensis* *Woodman and Timm*, 1992; Lacandona small-eared shrew, *C. lacandonensis* *Guevara et al.*, 2014; Yucatan small-eared shrew, *C. mayensis* (*Merriam*, 1901); Merriam’s small-eared shrew, *C. merriami* *Choate*, 1970; and Darién small-eared shrew, *C. merus* *Goldman*, 1912. The synonymies are adapted and updated from *Woodman and Timm* (1993) and *Woodman* (2018).

DIAGNOSIS

Cryptotis nigrescens is a small- to medium-sized member of the genus as measured by head–body length, condylobasal length of the skull (CBL), and mass (*Table 1*). It has dark blackish-brown dorsal pelage, which exhibits little contrast with its ventral pelage, and a moderately long tail that typically averages about 42% of head–body length (*Fig. 1*; *Table 1*). Five other species of small-eared shrews are known to occur in Costa Rica and western Panama (*Table 2*). *Cryptotis nigrescens* is much smaller in head–body length and condylobasal length, has a much shorter tail, and a shorter, less robust humerus than either Ender’s small-eared shrew, *C. endersi* *Setzer*, 1950, or the Monteverde small-eared shrew, *C. monteverdensis* *Woodman and Timm*, 2017. From the Talamanca small-eared shrew, *C. gracilis* *Miller*, 1911, *C. nigrescens* can be distinguished by its much shorter relative tail length, broader zygomatic plate, shorter and broader rostrum, higher coronoid process of the dentary, and less robust humerus with smaller processes; from the Central American least shrew, *C. orophilus* (*Allen*, 1895), by its much darker dorsal and ventral

Table 1.—Comparison of selected measurements of *Cryptotis nigrescens* from Monteverde, Costa Rica; central and southeastern Costa Rica; and Panama. Statistics include mean \pm standard deviation followed by range and sample size and are based on measurements taken by the authors.

Variable	Monteverde, Costa Rica	Central & southeastern Costa Rica	Western Panama	All <i>Cryptotis nigrescens</i>
Head–body length	67 \pm 5 53–79 (<i>n</i> = 99)	70 \pm 9 55–81 (<i>n</i> = 18)	70 \pm 8 49–83 (<i>n</i> = 41)	68 \pm 7 49–83 (<i>n</i> = 158)
Tail length	29 \pm 3 20–35 (<i>n</i> = 99)	24 \pm 3 20–31 (<i>n</i> = 18)	29 \pm 5 19–38 (<i>n</i> = 41)	28 \pm 4 19–38 (<i>n</i> = 158)
Relative tail length	43 \pm 5% 32–57 (<i>n</i> = 99)	34 \pm 5% 28–43 (<i>n</i> = 18)	42 \pm 6% 28–57 (<i>n</i> = 41)	42 \pm 6% 28–57 (<i>n</i> = 158)
Hind foot length	12 \pm 1 10–14 (<i>n</i> = 99)	11 \pm 1 10–13 (<i>n</i> = 13)	13 \pm 1 9–14 (<i>n</i> = 32)	12 \pm 1 9–14 (<i>n</i> = 144)
Mass	5.7 \pm 1.0 2.5–9.0 (<i>n</i> = 92)	7.3 \pm 1.6 4.0–9.0 (<i>n</i> = 10)	4.5 \pm 1.7 2.5–6.0 (<i>n</i> = 5)	5.8 \pm 1.2 2.5–9.0 (<i>n</i> = 107)
Condylobasal length	18.1 \pm 0.5 16.9–19.4 (<i>n</i> = 71)	18.5 \pm 0.8 17.1–19.4 (<i>n</i> = 10)	19.0 \pm 0.6 17.8–20.2 (<i>n</i> = 34)	18.4 \pm 0.7 16.9–20.2 (<i>n</i> = 115)
Palatal breadth across M2s	5.3 \pm 0.2 4.9–5.6 (<i>n</i> = 71)	5.7 \pm 0.2 5.3–5.9 (<i>n</i> = 10)	5.7 \pm 0.2 5.2–6.0 (<i>n</i> = 33)	5.4 \pm 0.2 4.9–6.0 (<i>n</i> = 114)

Table 2.—Comparison of selected measurements of five species of soricids that occur in Costa Rica and western Panama. Species are ordered by mean head–body length. Statistics include mean \pm standard deviation followed by range and sample size and are based on measurements taken by the authors.

Variable	<i>C. orophilus</i> (<i>n</i> = 22)	<i>C. gracilis</i> (<i>n</i> = 36)	<i>C. merriami</i> (<i>n</i> = 2)	<i>C. monteverdensis</i> (<i>n</i> = 1)	<i>C. endersi</i> (<i>n</i> = 2)
Head–body length	63 \pm 7 48–77	68 \pm 7 57–78	69 (<i>n</i> = 1)	80	73, 89
Tail length	21 \pm 2 17–24	36 \pm 3 29–42	27 (<i>n</i> = 1)	46	36, 49
Relative tail length	34 \pm 4% 29–42	54 \pm 7% 42–68	39%	58%	49, 55%
Hind foot length	11 \pm 1 10–12 (<i>n</i> = 10)	14 \pm 1 11–15	11 (<i>n</i> = 1)	—	—
Mass	5.7 \pm 1.9 3.0–10.0 (<i>n</i> = 15)	7.0 \pm 1.8 4.5–10.5 (<i>n</i> = 21)	7.8 (<i>n</i> = 1)	—	—
Condylobasal length	16.9 \pm 0.4 16.1–17.7 (<i>n</i> = 11)	19.3 \pm 0.6 17.9–20.4	19.2, 20.3	20.3	20.4, 21.3
Palatal breadth across M2s	5.2 \pm 0.2 4.9–5.5 (<i>n</i> = 18)	5.2 \pm 0.2 4.9–5.6	6.0, 6.3	5.8	5.8, 5.8

pelage, much longer relative tail length, and relatively broader zygomatic plate; and from *C. merriami* by its darker pelage, lack of bulbous dentition, and relatively shorter and narrower palate (Woodman and Timm 1993, 2017; Woodman 2000; Pine et al. 2002; Woodman and Gaffney 2014).

GENERAL CHARACTERS

Terminology for dentition and dental characteristics follows Choate (1970); for cranial anatomy and measurements,

Woodman and Timm (1993, 1999); for postcranial anatomy, Reed (1951). A mensural character is considered “very small” if its mean is ≥ 1 *SD* below the mean for the genus *Cryptotis*, “small” if its mean is 0.5–1.0 *SD* below the mean for the genus, “moderate” if within ± 0.5 *SD* of the genus mean, “large” if 0.5–1.0 *SD* above the genus mean, and “very large” if ≥ 1 *SD* above the genus mean. The mean for the genus was calculated from mean measurements from up to 62 species, subspecies, and distinctive populations of *Cryptotis*. Most measurements reported herein are from the authors.

Like other Blarinini shrews, *Cryptotis nigrescens* is small with a fusiform body shape, elongate and pointed rostrum, minute eyes, and pinnae reduced to slit-like openings that are hidden by its fur (Fig. 1). Among the small-eared shrews of the genus *Cryptotis*, it is small to medium in body size, with head–body length averaging 68 mm and tail averaging 28 mm in length or 42% of head–body length (Table 1). Dorsal hairs are approximately 4.5 mm long (range: 4–5 mm) and appear two-banded. Pelage is dark; dorsal and lateral pelage Mummy Brown or Clove Brown; ventral pelage slightly paler—Buffy Brown, Saccardo’s UMBER, Olive Brown, or Mouse Gray (colors after Ridgway 1912). Video by James Wolfe taken 2.3 km NNW of St. Elena, Costa Rica, and illustrating the external characteristics and foraging behavior of *C. nigrescens* can be found at <https://mammalsofcostarica.com/order-eulipotyphia-shrews/>. Two videos of a live *C. nigrescens* taken at 0830 h on 24 April 2020 by Wilson Salas along the Nuboso Trail in the Monteverde Cloud Forest Reserve, Costa Rica, are referenced in Supplementary Data SD1 and SD2.

The species has a short skull, condylobasal length (CBL) averaging 18.4 ± 0.7 mm (Fig. 2); relatively short rostrum (palatal length [PL] averages $42.7 \pm 0.7\%$ of CBL, $n = 107$); moderately broad interorbital breadth ($23.6 \pm 0.9\%$ of CBL, $n = 107$) and braincase ($49.9 \pm 1.2\%$ of CBL, $n = 100$); often two dorsal foramina (68%, $n = 59$), small to large in size and positioned close to suture between frontals; typically no foramen posterior to the dorsal articular facet (88%, $n = 57$); generally a well-developed foramen dorsal to external capitular facet on one (2%, $n = 57$) or both sides of the skull (93%); however, this foramen may be minute (3%); lacks a large, obvious foramen on the posterior edge of the tympanic process of the petromastoids; zygomatic plate broad in proportion to CBL ($10.6 \pm 0.8\%$, $n = 108$), very broad in proportion to PL ($24.8 \pm 2.1\%$, $n = 119$); anterior border of zygomatic plate aligned with mesostyle to mesostyle–metastyle valley of M1, posterior border with the posterior one-half of mesostyle–metastyle valley of M2 to middle of M3, and usually near the middle of the base of the maxillary process, but can be positioned from the anterior one-half of this process to posterior to the process; palate relatively broad (breadth across upper second molars averages $69.2 \pm 2.1\%$ of PL, $n = 120$).

Dentition not bulbous; upper toothrow generally uncrowded (Fig. 3); unicuspid toothrow moderately long (averaging $12.9 \pm 0.6\%$ of CBL, $n = 108$); upper fourth unicuspid (U4) typically in line with the rest of the unicuspid toothrow and preventing contact between the upper third unicuspid (U3) and the upper fourth premolar (P4); U4 usually obscured by P4 in lateral view of the skull, but sometimes partly visible; posterior borders of P4, M1, and M2 unrecessed or only slightly recessed; M3 typically possesses a well-developed paracrista, and paracone, reduced precentrocrista and mesostyle, poorly developed, but often pigmented postcentrocrista and metacone (but postcentrocrista short with mesostyle and metacone closely associated), protocone present and often pigmented, and poorly developed hypocone often present.

Dentary short (length = $6.2 \pm 0.3\%$, $n = 119$); coronoid process low relative to dentary length ($71.2 \pm 2.6\%$, $n = 117$) and joins the horizontal ramus of the dentary at a steep angle;



Fig. 2.—Dorsal, ventral, and lateral views of the cranium and lateral view of the right dentary of an adult female *Cryptotis nigrescens* from Monteverde Cloud Forest Reserve, Puntarenas Province, Costa Rica (KU [University of Kansas Biodiversity Institute] 143379; condylobasal length of skull = 18.5 mm).

very short posterior dentary ($72.6 \pm 2.8\%$ of dentary length, $n = 119$); articular condyle relatively short and narrow; lower sigmoid notch very shallow; posterior border of lower incisor reaches almost to posterior border of cingulum of p4; vestigial entoconid occasionally present in talonid of m3 (38%, $n = 50$). The humerus (Fig. 4) appears relatively long and narrow with weakly developed processes (Woodman and Timm 1993, 2017; Woodman 2000; Woodman and Gaffney 2014).

DISTRIBUTION

Cryptotis nigrescens occurs in highlands above 800 m in the Tilarán, Central, and Talamanca cordilleras of Costa Rica and



Fig. 3.—Right maxillary (A) and mandibular (B) toothrows of an adult female *Cryptotis nigrescens* from Monteverde Cloud Forest Reserve, Puntarenas Province, Costa Rica (KU 143379).

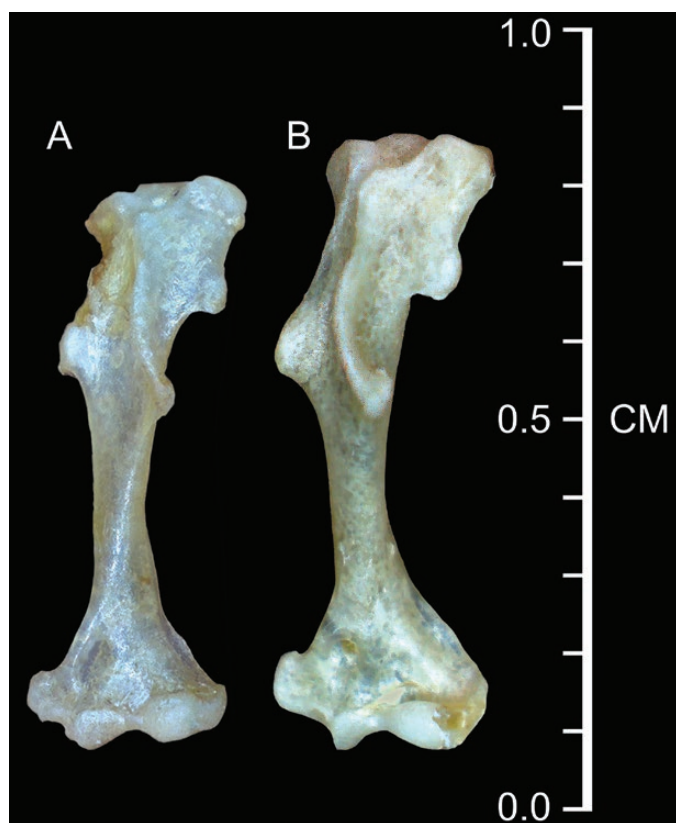


Fig. 4.—Anterior aspect of the left humeri of two *Cryptotis nigrescens* from Costa Rica illustrating the geographic difference in size between individuals from Monteverde, the northernmost locality for the species (A: KU 143377; length = 7.20 mm), and 5.1 km SW of San Vito, near the Panamanian border (B: KU 158568; 7.93 mm).

the Chiriquí Cordillera of western Panama (Fig. 5). The recorded elevational distribution is 870–2,865 m in Costa Rica and 820–2,400 m in Panama (Woodman and Timm 1993; McCain 2004;

Timm and LaVal 2016). There is as yet no fossil record for *C. nigrescens*.

FORM AND FUNCTION

Like most other species of small-eared shrews that have been examined for sexual dimorphism, female and male *Cryptotis nigrescens* do not differ substantially in body size (Table 3) and are difficult to distinguish externally. Woodman and Timm (1993) discovered no significant sexual dimorphism in external measurements within populations of *C. nigrescens* from Monteverde, Costa Rica ($n = 16$ females, 16 males), or from San Félix, Panama ($n = 8$ females, 9 males). Similarly, there were no significant differences between the sexes in multivariate size or shape of the cranium within either the Monteverde ($n = 12$ females, 14 males) or San Félix ($n = 10$ females, 13 males) populations (Table 3).

Woodman and Timm (1993) demonstrated that the population of *C. nigrescens* from Monteverde in northwestern Costa Rica averaged distinctly smaller than populations from near San Félix, western Panama, and speculated that *C. nigrescens* might be a complex of species. Woodman (2000) subsequently documented possible clinal variation in size throughout the distribution of *C. nigrescens*, with western Panamanian populations averaging about 7% larger in head-and-body length and 5% larger in condylobasal length than populations in northern Costa Rica (Table 1). See also the comparison of humeri in Fig. 4.

Subtle geographic variation in pelage coloration has been reported, with shrews in the Monteverde population typically possessing slightly darker pelage than those in the San Félix population in the Chiriquí highlands of western Panama. The darkest pelage, however, is found among individuals from Fish Camp, Bocas del Toro Province, Panama (Woodman and Timm 1993).

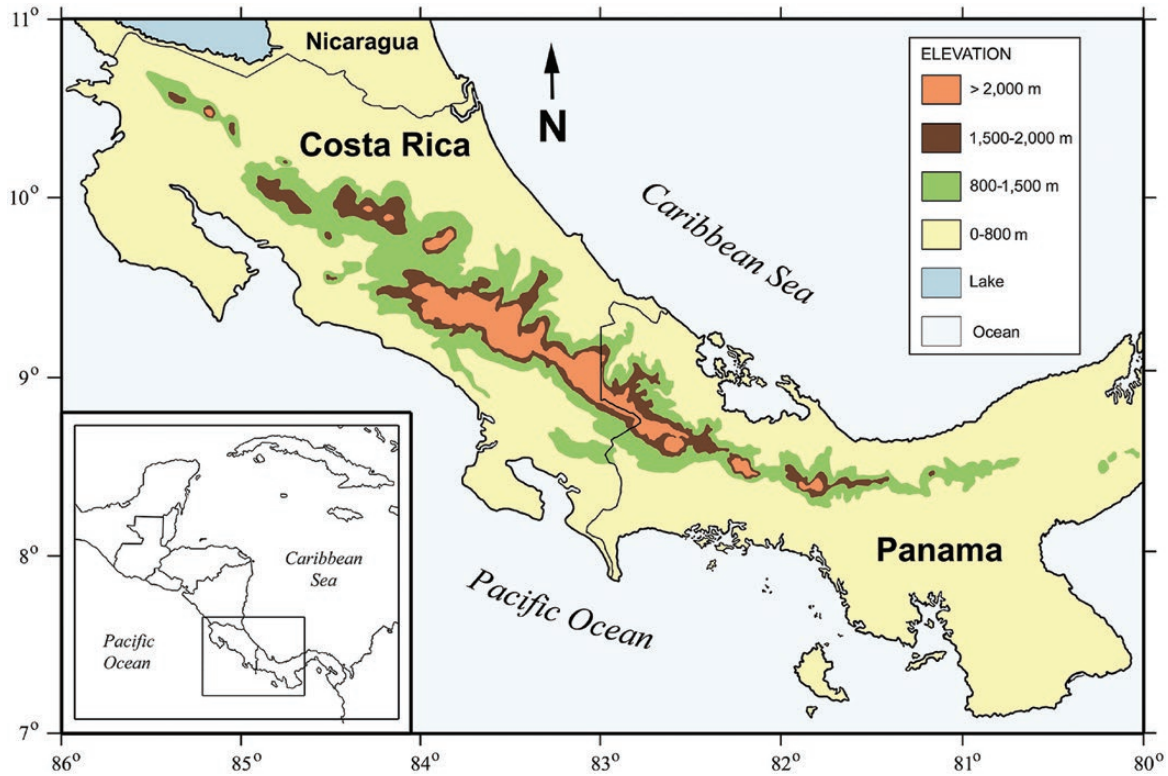


Fig. 5.—Map of Costa Rica and western Panama showing the approximate distribution of *Cryptotis nigrescens* as indicated by areas above the 800 m contour.

Table 3.—Comparison of selected measurements of up to 45 female and 37 male *Cryptotis nigrescens* from Monteverde, Costa Rica. Statistics include mean \pm standard deviation followed by range and sample size and are based on measurements taken by the authors.

Variable	Females	Males
Head–body length	68 \pm 6	67 \pm 4
	53–79 (n = 45)	59–76 (n = 37)
Tail length	30 \pm 2	29 \pm 3
	25–35 (n = 45)	20–34 (n = 37)
Hind foot length	12 \pm 1	12 \pm 1
	10–14 (n = 45)	10–13 (n = 37)
Mass	5.8 \pm 1.1	5.7 \pm 1.0
	2.5–7.5 (n = 42)	3.5–9.0 (n = 36)
Condylbasal length	18.3 \pm 0.5	18.1 \pm 0.4
	17.5–19.4 (n = 30)	16.9–19.0 (n = 26)
Humerus length	7.2 \pm 0.2	7.2 \pm 0.3
	6.8–7.6 (n = 17)	6.6–7.7 (n = 17)
Distal width of humerus	2.5 \pm 0.1	2.5 \pm 0.1
	2.4–2.8 (n = 17)	2.4–2.8 (n = 17)

Lateral flank glands are often present in male and female soricids, and they are believed to play a role in reproductive behavior (Hamilton 1929; Dryden and Conaway 1967; Hawes

1976). The glands are typically small and hidden by the pelage in females, whereas in mature males, the glands may be visible externally as oval patches of thickened skin covered by very short, pale bristles (Johnsen 1914; Eadie 1938; Carraway 2009). Inspection of 26 male *C. nigrescens* from throughout the species' geographic range showed well-developed lateral glands on 20 individuals collected in May through the beginning of July. Six males lacking well-developed lateral glands were obtained in February (n = 1), March (n = 2), April (n = 1), and July (n = 2—Woodman and Timm 1993).

The forelimb of *C. nigrescens* exhibits few of the structural modifications associated with semi-fossoriality that are seen in some other members of the genus, such as in the *C. mexicanus* group and the *C. goldmani* group (see Woodman and Gaffney 2014). The foreclaws are relatively short and narrow; the bones of the manus are long and narrow with the exception of the distal phalanges, which are short and narrow and support only about half the length of the foreclaws; the humerus is relatively long and narrow with relatively small processes for muscle attachments (Fig. 4). Based on its limb morphology, locomotor behavior of *C. nigrescens* is classified as one of the most ambulatory species in the genus (Woodman and Morgan 2005; Woodman and Gaffney 2014; Woodman 2023a). Individuals we observed running on the ground at Monteverde moved very quickly.

The axial skeleton of *C. nigrescens* exhibits some variation in number and position of vertebrae. Typically, there are

seven cervical vertebrae ($n = 16$ Panama, 36 Costa Rica), although one Costa Rican specimen (KU [University of Kansas Biodiversity Institute] 143377) has a rib attached to the left side only of its seventh cervical vertebra. The modal number of thoracic vertebrae is 13, with ranges of 13–14 in Costa Rica ($n = 36$) and 12–14 in Panama ($n = 14$). The modal number of lumbar vertebrae is 6, with ranges of 5–6 in Costa Rica ($n = 36$) and 5–7 in Panama ($n = 11$). The mode of sacral vertebrae fused to each other at the centrum and sacral crest is four, with a range of 3–4 (Costa Rica, $n = 29$; Panama, $n = 15$). Occasionally, the last lumbar vertebra is fused to one (USNM [National Museum of Natural History] 541028) or both (USNM 541034) innominates, but not to the sacrum. Caudal vertebrae exhibit notable variation in numbers between populations. In Costa Rica, the mode is 14 with a range of 14–16 ($n = 19$), whereas in Panama, the mode is 16 with a range of 14–16 ($n = 8$). Total numbers of vertebrae vary similarly. The mode in Costa Rica is 44 with a range of 44–46 ($n = 16$), and the mode in Panama is 46 with a range of 44–46 ($n = 8$). Numbers of ribs also vary, with a mode in both countries of 13 pairs. The range in Costa Rica is 13–14 pairs ($n = 36$; this total does not include one individual with 13 right and 14 left ribs: KU 143377), and the range in Panama is 14–15 pairs ($n = 14$).

A young adult female (KU 143393) captured at Monteverde on 15 May 1989 lacked digits on its right forefoot. The vestigial first digit was the only one bearing a claw, and this was poorly formed. The shape of the foot suggests that the digits were never fully developed during ontogeny rather than lost later due to an accident or to intraspecific aggression as reported for other species of soricids (Stephens et al. 2018).

ONTOGENY AND REPRODUCTION

Few reproductive data are available for *Cryptotis nigrescens*. Gravid females have been recorded in February, May, and July (Fig. 6), and a female taken on 13 October had an enlarged uterus, suggesting recent parturition. Lactating females have been recorded in March, May, October, and December. Taken together, these data suggest that reproduction occurs throughout the year rather than being synchronized with the onset of the wet season (May through December). If so, *C. nigrescens* is similar in this respect to other Neotropical soricids (Woodman and Díaz de Pascual 2004; Woodman et al. 2012). Females have a total of four (two pairs) inguinal nipples. Average recorded litter size is 2, with a range of 1–3 ($n = 4$). This compares well with ranges of 1–2 offspring for species of *Sorex* and 2–3 offspring for species of *Cryptotis* in Guatemala and Honduras (Woodman et al. 2012).

Average testis size of males appears to increase from March through late June or early July (Fig. 6), but the significance of such an increase is difficult to determine. Most likely, it is related to the maturing of young males born earlier in the year. Woodman and Timm (1993) reported two individuals on 9 May and 18 May from Monteverde that had melanistic sheaths

surrounding the testes. Both shrews had well-developed lateral glands and enlarged testes, measuring 3.5 by 2.5 mm and 4 by 2.5 mm. The significance of the melanism is unknown, particularly as the testes of soricids are inguinal throughout their lives.

ECOLOGY

At Monteverde, *Cryptotis nigrescens* occurs in cloud forest, forest fragments, and pastures at elevations from 870 to 1,660 m (Fig. 7). Woodman and Timm (1993) and Timm and LaVal (2016) reported finding the species in a variety of habitats, including Tropical Premontane Rain Forest, Tropical Premontane Moist Forest, Tropical Premontane Wet Forest, and Tropical Lower Montane Wet Forest (as defined by Holdridge 1947). Other nonvolant small mammals commonly taken in these habitats include the Talamancan deer mouse, *Peromyscus nudipes*; cloud-dwelling spiny mouse, *Heteromys nubicolens*; Boquete rice rat, *Nephelomys devius*; short-tailed singing mouse, *Scotinomys teguina*; and Talamancan harvest mouse, *Reithrodontomys creper*.

In western Panama, *C. nigrescens* has been taken in cloud forest, disturbed cloud forest, elfin woodland, and foggy, but relatively drier Pacific slope forest at elevations of 1,275–1,856 m. In May–July 1980, on Cerro Bollo, R. H. Pine, R. J. Izor, and J. A. Wagner captured 14 *C. nigrescens* with one *C. endersi* in cloud forest and disturbed cloud forest at 1,800–1,856 m elevation, along with the sprightly pygmy rice rat, *Oligoryzomys vegetus*; *Nephelomys devius*; *Reithrodontomys creper*; Chiriquí harvest mouse, *Reithrodontomys garichensis*; and long-tailed singing mouse, *Scotinomys xerampelinus*.

Pino (2016) found *C. nigrescens* to be common and easy to capture in Sherman live traps (H. B. Sherman Traps, Inc.; Tallahassee, Florida) in cloud forest at 2,270 m elevation at Las Nubes, Parque Nacional La Amistad, Panama. He estimated an average of 5.3 individuals per hectare, with a possible range of 2.4–19 individuals per hectare.

Like most shrews, *C. nigrescens* is probably periodically active through the 24-h cycle, including during the day. Trapping on a 60 by 70 m grid in western Panama with two 5 by 6 by 16 cm Sherman traps baited with a peanut butter, vanilla, and oats mixture at each corner of each 10 by 10 m grid cell (112 traps total), Pino (2016) captured an average of 2.2 individuals per day during May–August 2004, even though his traps were open only during daylight hours, from 0600 through 1300 h.

Cryptotis is the only genus of soricid present in Costa Rica and Panama (Reid 2009; Woodman et al. 2012). Five other species of small-eared shrews also occur in this region, but syntopy among species appears to be minimal, possibly in part because of different elevational distributions, foraging behaviors, and habitat requirements. At Monteverde, Costa Rica, where *C. nigrescens* is relatively common at elevations from 870 to 1,840 m (McCain 2004; Timm and LaVal 2016), *C. merriami* (known elevational distribution 565–1,650 m) and *C. monteverdensis* (1,560 m) appear to be rare members of the small mammal

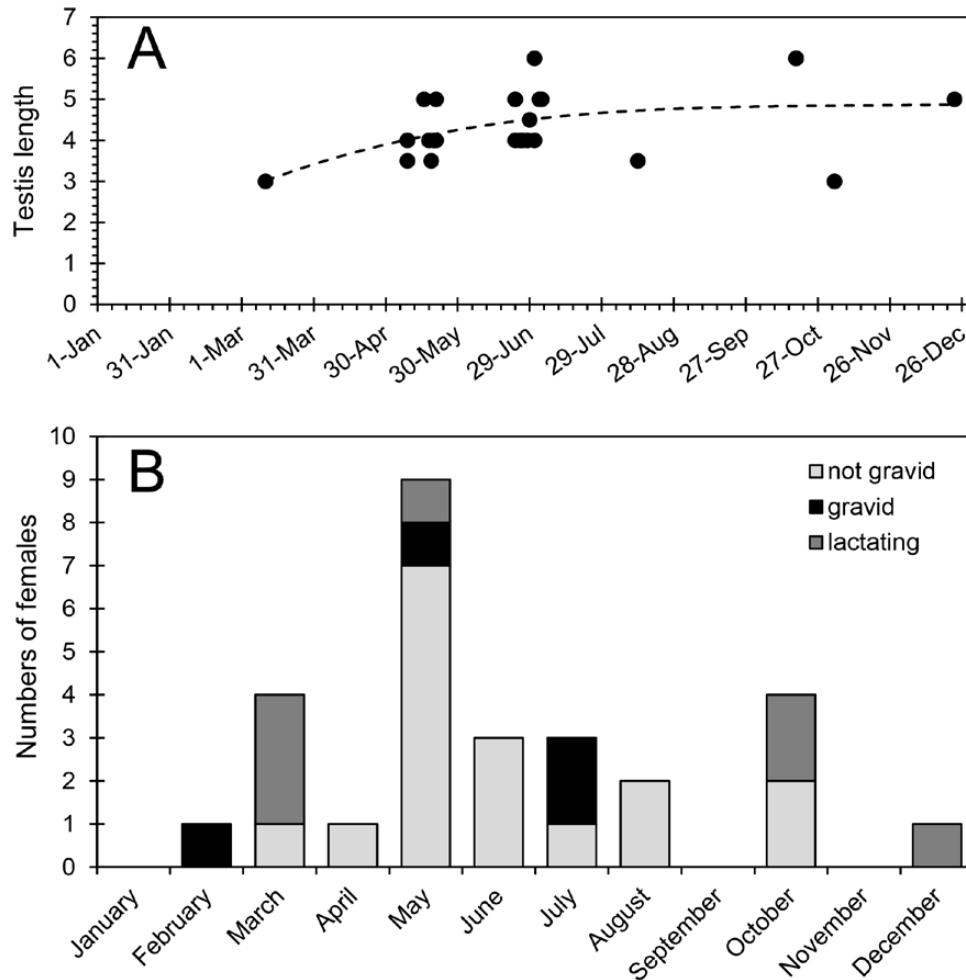


Fig. 6.—Reproductive characteristics of *Cryptotis nigrescens* in Costa Rica and Panama. (A) Graph of testis size through the year for males ($n = 22$). The equation for the trend line is $y = -1E - 06x^3 + 0.1128x^2 - 4137x + 5E + 07$; $R^2 = 0.3268$. (B) Graph of female reproductive status ($n = 25$). The category “not gravid” refers to females that are neither gravid nor lactating.

community (Woodman 2000; Woodman and Timm 2016). Trapping and museum records indicate that *C. nigrescens*, *Cryptotis orophilus* (1,150–1,985 m), and *C. gracilis* (1,828–3,536 m) have all been taken at various times and localities on Volcán Irazú in Costa Rica, and *C. nigrescens* and *C. gracilis* have been captured at El Volcán, Cerro Punta, and Las Nubes in Panama. In addition, *C. nigrescens* and the rare *C. endersi* were taken on the same trapline in cloud forest at Cerro Bollo, Panama (Pine et al. 2002).

No studies of foraging strategy or analyses of stomach contents have been performed for any species of shrews in Costa Rica or Panama. Based on its size and its cranial and postcranial morphology, however, *C. nigrescens*, like other small-bodied shrews, presumably focuses on foraging for small epigeal invertebrates in the ground vegetation, leaf litter, and soil surface (Whitaker 1974; Churchfield 1990; Woodman and Gaffney 2014).

Species of the genus *Cryptotis* are hosts for a variety of internal and external parasites, including various families of

mites and ticks (Arachnida: Parasitiformes and Acariformes), fleas (Siphonaptera), round worms (Nematoda), tape worms (Cestoda), and parasitic alveolates (Apicomplexa). External parasites recorded for *C. nigrescens* in Panama include three species of mites: the chigger *Sasacarus panamense* Goff, 1987 (Arachnida: Trombidiformes; Trombiculidae); *Psorergates cryptotis* Giesen and Lukoschus, 1983 (Arachnida: Trombidiformes; Psorergatidae), which is found on the hind legs at the border of the soft hair-bearing skin; and *Protomyobia panamensis* Lukoschus et al., 1988 (Acarina: Prostigmata; Myobiidae—Giesen and Lukoschus 1983; Goff 1987; Lukoschus et al. 1988). The host of *P. panamensis* originally was identified as *Cryptotis orophilus*, a species that does not occur in Panama. Based on the locality and museum records, the host shrew was almost certainly *C. nigrescens*. Fairchild et al. (1966) reported larval ticks (Arachnida: Ixodida; Ixodidae) of an unknown species of *Dermacentor* and of a second unknown species, possibly of the genus *Ixodes*, from *C. nigrescens* in Panama.



Fig. 7.—Typical habitat for 1,550 m at Monteverde, Puntarenas Province, Costa Rica, where *Cryptotis nigrescens* is an abundant component of the small mammal community. Photograph by RMT.

GENETICS

A variety of analyses using sequences from the mitochondrial cytochrome *b* gene (*cyt b*) alone and combined with sequences from 16S rRNA, Apolipoprotein B [APOB], and breast cancer type 1 susceptibility protein (BRCA1) indicate that *Cryptotis nigrescens* is sister to a group of species that includes *C. lacondonensis*, *C. mayensis*, and *C. merriami* (He et al. 2015, 2021; Baird et al. 2017; Mejía-Fontecha et al. 2021). These studies appear to confirm the *C. nigrescens* group as a clade. Genes from other members of the group—*C. brachyonyx*, *C. colombianus*, and *C. merus*—however, remain to be sequenced.

Analysis of *cyt b* and concatenated alignment of mitochondrial and nuclear genes indicated the *C. nigrescens* group is most closely related to a clade that includes Central American *C. gracilis* and South American Evaristo's small-eared shrew, *C. evaristoi*; wandering small-eared shrew, *C. montivagus*; Tama small-eared shrew, *C. tamensis*; and Thomas's small-eared shrew, *C. thomasi* (He et al. 2021; Mejía-Fontecha et al. 2021).

CONSERVATION

Cryptotis nigrescens is classified as a species of “Least Concern” (LC) by the International Union for Conservation of Nature (IUCN; Naylor and Roach 2016), notwithstanding threats to its habitat imposed by forest clearance for agriculture (Pino 2016) and by climate change. The species also faces threats from domestic and feral cats (Loss et al. 2013; Orduña-Villaseñor et al. 2023) and discarded bottles (Brannon and Bargelt 2013; Ferri et al. 2023). A number of specimens obtained by the authors from Monteverde were shrews killed by roaming domestic cats and saved for us by local residents.

SUPPLEMENTARY DATA

Supplementary data are available at *Mammalian Species* online.

Supplementary Data SD1.—A video (ca. 17 s) of a live *Cryptotis nigrescens* taken at 0830 h on 24 April 2020 by Wilson Salas at about 1,550 m along the Nuboso Trail in the Monteverde Cloud Forest Reserve, Costa Rica.

Supplementary Data SD2.—A video (ca. 15 s) of a live *Cryptotis nigrescens* taken at 0830 h on 24 April 2020 by Wilson Salas at about 1,550 m along the Nuboso Trail in the Monteverde Cloud Forest Reserve, Costa Rica.

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