Rediscovery, ecology, and identification of rare free-tailed bats (Chiroptera: Molossidae) in Costa Rica

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Five new specimens of the poorly known Sanborn's bonneted bat, *Eumops hansae* (Chiroptera: Molossidae), are reported for Costa Rica's central and northern Pacific lowlands based on a subadult male collected in 1990 and four adult females collected in 2003. We also report the second known specimen of *Eumops underwoodi* from Costa Rica and additional specimens of *Cynomops mexicanus, Eumops glaucinus, Molossus molossus*, and *Molossus pretiosus*. Most of the females captured in August and April were either lactating or pregnant, suggesting that parturition in these molossids occurs in the late dry season and the early to middle rainy season, periods when insects are especially abundant in this dry forest. Characters used previously to distinguish between the similar-sized *E. hansae* and *E. nanus* are evaluated, and external and cranial measurements for the specimens of *E. hansae* are provided. The best single character for distinguishing the two species is size and shape of the upper incisors. In *E. hansae*, the upper incisors are thin and recurved, whereas they are thick, straight, and slightly procumbent in *E. nanus*. The six sympatric species of free-tailed bat found in the gallery forest along the Río Enmedio vary in size, jaw thickness, and wing shape suggesting coexistence through resource partitioning in this molossid bat assemblage.

Key words: Costa Rica, Molossidae, bonneted bats, identification, Eumops hansae

INTRODUCTION

Twelve species of free-tailed bats (Chiroptera: Molossidae) are known from Costa Rica, although little is known about the biology of any of these species in the country (Timm and LaVal, 1998; Rodríguez-H. and Wilson, 1999; Timm et al., 1999; LaVal and Rodríguez-H., 2002). Among the most poorly known New World molossids are the bonneted bats of the genus *Eumops*, a monophyletic lineage of 12-13 species: E. auripendulus, E. bonariensis, E. dabbenei, E. floridanus, E. glaucinus, E. hansae, E. maurus, E. nanus, E. patagonicus, E. perotis, E. trumbulli, E. underwoodi, and undescribed species from western Ecuador (Eger, 1977; Freeman, 1981; Koopman, 1993, 1994; Gregorin and Taddei, 2002; Timm and Genoways, 2004; Gardner, 2008; McDonough et al., In press). One of the most poorly known species in the genus is Eumops hansae. Sanborn (1932) described the species based on a single adult male collected in 1901 at Colonia Hansa, near Joinville, Santa Caterina, Brazil. In subsequent years, few specimens of this small free-tailed bat have been collected from widely scattered localities in Central and South America, including southern Chiapas, México, northern Honduras, southwestern Costa Rica, and eastern Panamá in Central America and in South America from the Guiana region to Argentina (Reid, 1997; Best *et al.*, 2001). Specimens are known from elevations ranging from 45 to 600 m.

Eumops hansae was known previously from Costa Rica on the basis of only a single specimen (LSUMZ 11487) collected on the Osa Peninsula in the southwestern Pacific lowlands in 1966 by A. B. McPherson (Gardner *et al.*, 1970). The adult male was captured in a net set across a stream in an area of tropical moist forest 10 km south of Palmar Sur, Puntarenas Province, at 600 m. Despite extensive netting throughout the country in the intervening years, no additional records of *E. hansae* have been reported. Recent reviews suggest that *E. underwoodi* occurs from the extreme southwestern United States and western México to Honduras (Lee and Bradley, 1992; Kiser, 1995; Reid, 1997). However, Foster and Aguilar (1993) reported a single individual found dead in Costa Rica's lowland tropical dry forest at Cañas. There have been no subsequent reports of *E. underwoodi* occurring either in Costa Rica or neighboring Nicaragua.

Our recent fieldwork in northwestern Costa Rica and study of museum specimens led to the collection and identification of several poorly known molossids. Here, we report these species and provide pertinent ecological information and external and cranial measurements. Additionally, we expand the original description of the species *E. hansae* and make comparisons between *E. hansae* and the similar-sized *E. nanus*.

METHODS AND MATERIALS

On 18 August 2003, one of us (WP) set two mist nets (2 × 10 m) across the Río Enmedio in a V-shaped pattern at Refugio Nacional de Vida Silvestre Bosque Nacional Diría (10°10'24"N, 85°35'39"W, 128 m a.s.l.), 11 km southwest of Santa Cruz, Guanacaste Province, Costa Rica. The nets were open from 18:00 h to 19:35 h. One net extended from the dry riverbed over rocks and sand to the middle of the river and the other from this point over shallow water (60 cm deep) to the other riverbank. WP returned to this site on 18 April 2004 and set two mist nets in the same positions from 18:00 h to 21:00 h. The river is ca. 40 m wide here and surrounded by gallery forest with trees 30 m tall, including Anacardium excelsum, Ceiba pentandra, Ochroma pyramidale, and low shrubs. Costa Rica's northwestern Pacific lowlands are characterized by tropical dry forest, with a pronounced dry season from November to May, and a rainy season from June to October (1,000-2,000 mm). Most of the Central American dry forest has been cleared; lowland areas are especially subjected to intense agriculture and extensive livestock use (Mata and Echeverría, 2004). The gallery forest along the Río Enmedio is one of the few such tracts of intact forest remaining.

Forearms (FA) and crania of specimens collected in these field trips were measured by RMT with dial calipers to the nearest 0.1 mm. External measurements, other than forearm length, are those recorded on specimen labels by collectors, as are testis measurements. The following cranial measures were taken: greatest length of skull, condylobasal length, zygomatic breadth, postorbital constriction, mastoid breadth, length of maxillary toothrow, greatest alveolar breadth of upper canines (C–C), and breadth across crowns of upper molars $(M^3–M^3)$. Greatest length of skull includes incisors; measurements of the maxillary toothrow are of the greatest alveolar length and forearms were measured from the proximal extension of the radius-ulna (elbow) to the distalmost extension of the carpals (flexed wrist). We provide for comparison between E. hansae and E. nanus, external and cranial measurements for 4 adult females, and the previously reported adult male E. hansae from Costa Rica, an adult male E. nanus from Nicaragua and an adult female from Panama (Table 1). We follow Peters *et al.* (2002) in recognizing *Cynomops mexicanus* as the correct name for the dog-faced bats of the lower Central American dry forest.

RESULTS

In August 2003, 23 individuals of five species of molossids were captured in nets set across the Río Enmedio. They include: Cynomops mexicanus (3 adult $\mathcal{Q}\mathcal{Q}$; all lactating), *E. hansae* (4 adult $\mathcal{Q}\mathcal{Q}$; all lactating), E. underwoodi (1 adult ♀; lactating), Molossus molossus (1 adult \mathcal{Q} ; lactating), and M. pre*tiosus* (4 adult $\bigcirc \bigcirc \bigcirc$ and 10 adult $\bigcirc \bigcirc$; 7 lactating, 2 others pregnant). All individuals but one were caught in the net set over shallow water and the majority (83%) captured on the upstream side of the nets. These are the first records of E. hansae from the Central American tropical dry forest and extend the geographic distribution 300 km northwest from the only previously known locality in Costa Rica. This is the second record of E. underwoodi from Costa Rica; both are from the dry forest. The single E. underwoodi from Bosque Diría was an adult lactating female (FA = 72 mm), and provides documentation that the species breeds in Costa Rica. While this bat was being handled in the mist net, it emitted loud vocalizations that were audible to the human ear. In apparent response, another large bat flew over the net in two or three fast passes, suggesting that it was responding to the calls.

In April 2004, two nets set at the same site were used to capture 10 individuals of three species of molossids: *C. mexicanus* (6 adult QQ; all lactating), *Eumops glaucinus* (1 adult d), and *M. pretiosus* (3 adult QQ; 2 lactating, 1 pregnant); all individuals were caught in the net set over shallow water. This is the first record of *E. glaucinus* from the tropical dry forest in Costa Rica. Other species captured were: 1 *Rhynchonycteris naso*, 1 *Noctilio leporinus*, 1 *Pteronotus gymnonotus*, 1 *Chrotopterus auritus*, 2 *Micronycteris hirsuta*, 2 *Carollia perspicillata*, 1 *C. subrufa*, 2 *Glossophaga soricina*, 1 *Artibeus phaeotis*, 1 *Platyrrhinus helleri*, 8 *Sturnira lilium*, and 2 *Uroderma bilobatum*.

nanus and E. hansae from Central America. Acronyms used are: LSUMZ: Museum of Zoology, Louisiana

External and cranial measurements (in mm) and body mass (in g) of E.

[ABLE 1.]

Food items found in August in the stomachs of these free-tailed bats include the following: *E. hansae* — Coleoptera and Diptera (Tipulidae); *E. underwoodi* — Hymenoptera (Formicidae) and possibly Neuroptera; *C. mexicanus* — Coleoptera, Hemiptera, and Hymenoptera (Formicidae); and *M. pretiosus* — Coleoptera, Hemiptera, and Hymenoptera (Formicidae). Winged ants (Hymenoptera, Formicidae) were the most abundant food items in *C. mexicanus, E. underwoodi*, and *M. pretiosus*, suggesting that these bats feed opportunistically on winged ants when they are abundant.

DISCUSSION

The published descriptions of E. hansae can be expanded upon based on our comparisons of the Costa Rican specimens from the Pacific lowlands with other populations. Sanborn (1932: 356), in his description of E. hansae, made direct comparisons of the single adult male available to him to specimens of the similar-sized E. nanus, noting that the upper incisors of E. hansae have the tips widely separated and the lower incisors "are not bunched, but are almost in a straight line, the outer about half the size of the inner." [Upon direct comparison, all specimens of E. hansae are larger than the species we now recognize as E. nanus] Gardner et al. (1970: 726) provided the following comparisons to distinguish E. hansae from E. nanus: "color darker; upper incisors with widely separated tips; lower incisors less crowded and almost in a straight line; ... palate extending behind the last molars; basisphenoid pits conspicuously large, deep, and well defined." Reid (1997: 168) described the pelage of all Central American molossids, noting characteristics of each. She characterized *E. hansae* as "Upperparts dark brown or blackish, hair dark to base ... underparts dark gray-brown, slightly paler than upperparts" and E. nanus as, "Upperparts gray-brown or brown, base of hair pale; underparts gray-brown, tips of hairs frosted."

In comparing *E. hansae* from Costa Rica to an adult male and female *E. nanus* from Nicaragua and Panama, respectively, we noted that the upper incisors are widely separated at the tips in *E. hansae*, whereas they converge in *E. nanus*. Additionally, the incisors are thin and slightly curved in *E. hansae*, almost hooklike, whereas they are thick and somewhat procumbent in *E. nanus*. The size and shape differences in the upper incisors of these two species have not been noted previously. The basisphenoid pits are ovoid and deep in *E. hansae*, and proportionally deeper and longer than in *E. nanus*.

State University Institution	, MNC	CR: Museo	Nacional	de Costa Ric	a, KU: Mu	iseum of Nat	State University, MNCR: Museo Nacional de Costa Rica, KU: Museum of Natural History, Kansas University, USNM: United States National Museum of Natural History, Smithsonian Institution	nsas Univ	versity, U	SNM: Unit	ed States Nat	tional Museu	m of Natur	al History, S	mithsonian
Specimens Sex	Sex	Total length	Tail length	Length of hind foot	Length of ear	Length of tragus	Length Length Body Greatest of tragus of forearm mass skull	dy Gr	eatest igth of kull	Condylo- basal length	Zygomatic breadth	Post- orbital constriction	Mastoid breadth	Length of upper toothrow	Breadth across M ³ –M ³
							E. hansae (Costa Rica)	sta Rica)							
LSUMZ 11487*	۶0 *	Ι	Ι	I	Ι	Ι	40.2 -	- 2	20.7	19.4	11.7	4.2	10.6	7.5	8.2
MNCR 1488	0+	102	35	6	17	7	36.8 –	- -	18.5	17.8	10.6	3.8	10.0	6.6	7.6
MNCR 1489	0+	98	38	8	18	2	35.8 -	-	8.3	17.4	10.7	4.0	9.7	6.8	7.8
MNCR 1494	0+	100	35	6	16	2	36.4 –	-	8.8	17.5	10.6	3.8	9.9	6.7	7.4
KU 114142	60	92	31	10	15	I	E. nanus (Nicaragua) 38.8 –	aragua) - 1	17.1	15.7	10.3	4.1	9.7	6.2	9.6
USNM 331971	0+	86	28	٢	12	I	<i>E. nanus</i> (Panama) 39.4 8		16.7	15.1	9.6	3.5	I	5.9	7.2
* — data from Gardner <i>et al.</i> (1970)	ardner e	t al. (1970)													

The palate in both E. hansae and E. nanus extends posteriorly to just beyond the last molar, contrary to what has appeared in the literature. The cranium, when viewed laterally, is more bulbous in E. hansae than in E. nanus. In E. nanus, the profile of the skull is nearly flat. The pelage characters suggested by Reid (1997: 168) for distinguishing E. hansae from other molossids include upper parts dark brown, hair dark to base, and underparts paler than upperparts. The most definitive characters to distinguish E. hansae from E. nanus other than size are the upper incisors, with those of E. hansae being thin, widely separated at the tips, and slightly recurved inward, whereas those of E. nanus converge distally, are considerably more massive, and are somewhat procumbent. Use of the combination of pelage characters provided by Reid (1997) and cranial characters provided herein should facilitate identification of the two species in the field as well as in museum collections.

Eumops nanus has been reported previously from Costa Rica on the basis of three specimens, two from the Caribbean lowlands and one from the Pacific lowlands (Rodríguez F. and Chinchilla, 1996). We have searched extensively for these specimens in the collection of the Universidad de Costa Rica (as well as in other collections) and have not been able to locate them to reconfirm the identifications. They are cataloged in the Universidad de Costa Rica collection with the following localities: Limón Province, Parque Nacional Cahuita (UCR-175, UCR-515) and Puntarenas Province, Parrita, Isla Palo Seco (UCR-785). We concur with Eger (2008) in recognizing E. nanus as representing a species level taxon different from E. bonariensis, E. delticus, and E. patagonicus. Eger (1977) treated both *delticus* and *nanus* as subspecies of *E. bona*riensis, and recognized that there were morphological differences between these taxa. Eumops nanus is now known to occur in southern Mexico, throughout Central America, and in northwestern South America (Eger, 2008).

Eumops underwoodi is a rare species throughout its range (Reid, 1997), and it is considered (in addition to *M. pretiosus*, another species captured) endemic to the dry forest (LaVal, 2004), one of the most endangered ecosystems in the Neotropics. Foster and Aguilar (1993) reported this species in Costa Rica based on a single young male (LACM 47106) found dead in the lowland Guanacaste dry forest in 1974.

Of the 18 female molossids captured in northwestern Costa Rica in August, 17 were either lactating or obviously pregnant, and in April, all females were lactating or pregnant. Parturition occurs in both the late dry season and in the early and middle rainy season when insects are especially abundant (Janzen, 2004). From the reproductive data taken in the rainy and dry seasons, at least two species, C. mexicanus and M. pretiosus, give birth in both seasons, an unusual reproductive pattern in molossids. LaVal and Finch (1977) found pregnant female M. pretiosus primarily in May and June, with a lesser number in October. Our data suggest that most of these molossids reproduce in both seasons, but there are almost certainly some species which reproduce only once a year. The beginning of the rainy season in Costa Rica's dry forest corresponds to a striking increase in insect diversity and abundance resulting from a combination of the emergence of adults that had been hidden in moist microhabitats, maturation of adults from pupae in cocoons or the soil, and migrating of adults from cloud forest and rain forest (Janzen, 2004). Winged ants (e.g., Atta cephalotes) can be found in great numbers and fly high during their mating flights in the rainy season in the tropical dry forest (Stevens, 1983).

Freeman (1981) predicted that the coexistence of several species of molossids was possible based on three attributes: differences in size (as assessed by greatest skull length), food preferences (as assessed by jaw thickness), and shape of wings (broad or narrow). She combined these attributes in a morphological niche matrix of exclusive cells occupied by different species of the molossid assemblage allowing resource partitioning in order to avoid competition. Interestingly, the molossid bat assemblage at Bosque Diría corresponds to Freeman's (1981) predictions about mechanisms of coexistence of sympatric molossid bats. At Bosque Diría, we found two large, narrow-winged species with a moderately thick jaw (E. glaucinus and E. underwoodi), two medium-sized, narrow-winged species with moderately thick jaws (C. mexicanus and E. hansae), and two medium-sized, narrow-winged species with thick jaws (M. molossus and M. pretiosus). Thus, these six sympatric species of molossids correspond to three different cells in this morphological matrix and differ in jaw thickness and size, suggesting that this free-tailed bat assemblage shows relative resource partitioning in these two aspects.

Bats of the genus *Eumops* are generally considered to be rare or uncommon in Central America; however, they are probably much more common than collection records indicate because they fly relatively high and hence are rarely netted. Richard K. LaVal (personal communication) detected various species of Eumops at 32 of the 43 localities sampled throughout Costa Rica during recent acoustical surveys using the Anabat bat-detecting system (Titley Electronics, Ballina, New South Wales, Australia). Some of these localities are as high as 1,500 m a.s.l. Unfortunately, identification of Eumops to species with Anabat data files is not possible at this time. Because it is likely that E. hansae and E. nanus are found sympatrically, especially in the Pacific lowlands of Central America, it is imperative that researchers undertaking ecological studies correctly identify these similar sized species. Given the difficulty in identification of these species and the possibility of as yet unrecognized species in the genus *Eumops*, voucher specimens need to be taken and deposited in an approved museum.

In a key to the Brazilian bats, Gregorin and Taddei (2002) recently provided characters to distinguish between E. bonariensis, E. hansae, and E. patagonicus, and Eger (2008) published a key to all of the currently recognized Central and South American species. Whether the populations assigned to E. hansae in Central America are truly conspecific with those of Brazil near the type locality remains an open question and we suspect that they will in fact be recognized as separate species upon future study. Additional work on distributions, abundance, and natural history of Central American molossids is critically needed. Many species are difficult to distinguish both morphologically and acoustically and a deeper knowledge on taxonomy also is needed in this group.

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LITERATURE CITED

- BEST, T. L., J. L. HUNT, L. A. MCWILLIAMS, and K. G. SMITH. 2001. Eumops hansae. Mammalian Species, 687: 1–3.
- EGER, J. L. 1977. Systematics of the genus *Eumops* (Chiroptera: Molossidae). Life Sciences Contributions, Royal Ontario Museum, 110: 1–69.
- EGER, J. L. 2008 [for 2007]. Genus *Eumops* Miller, 1906. Pp. 407–416, *in* Mammals of South America. Volume 1: Marsupials, xenarthrans, shrews, and bats (A. L. GARDNER, ed.). The University of Chicago Press, Chicago, 669 pp.
- FOSTER, M. S., and R. AGUILAR. 1993. Primer registro de *Eumops underwoodi* (Chiroptera: Molossidae) en Costa Rica. Brenesia, 39–40: 179–180.
- FREEMAN, P. W. 1981. A multivariate study of the family Molossidae (Mammalia, Chiroptera): morphology, ecology, evolution. Fieldiana: Zoology (N.S.), 7: vii + 1–173.
- GARDNER, A. L. (ed.). 2008 [for 2007]. Mammals of South America. Volume 1: Marsupials, xenarthrans, shrews, and bats. The University of Chicago Press, Chicago, 669 pp.
- GARDNER, A. L., R. K. LAVAL, and D. E. WILSON. 1970. The distributional status of some Costa Rican bats. Journal of Mammalogy, 51: 712–729.
- GREGORIN, R., and V. A. TADDEI. 2002. Chave artificial para a identificação de molossídeos brasileiros (Mammalia, Chiroptera). Mastozoología Neotropical, 9: 13–32.
- JANZEN, D. H. 2004. Ecology of dry-forest wildland insects in the Area de Conservación Guanacaste. Pp. 80–96, *in* Biodiversity conservation in Costa Rica: learning the lessons in a seasonal dry forest (G. W. FRANKIE, A. MATA, and S. B. VINSON, eds.). University of California Press, Berkeley, 341 pp.
- KISER, W. M. 1995. Eumops underwoodi. Mammalian Species, 516: 1–4.
- KOOPMAN, K. F. 1993. Order Chiroptera. Pp. 137–241, *in* Mammal species of the World: a taxonomic and geographic reference (D. E. WILSON and D. M. REEDER, eds.). Smithsonian Institution Press, Washington D.C., xviii + 1206 pp.
- KOOPMAN, K. F. 1994. Chiroptera: systematics. Handbook of Zoology. Vol. 8, Part 60: Mammalia. Walter de Gruyter, Berlin, 217 pp.
- LAVAL, R. K. 2004. An ultrasonically silent night: the tropical dry forest without bats. Pp. 160–173, *in* Biodiversity conservation in Costa Rica: learning the lessons in a seasonal dry forest (G. W. FRANKIE, A. MATA, and S. B. VINSON, eds.). University of California Press, Berkeley, 341 pp.
- LAVAL, R. K., and H. S. FINCH. 1977. Structure, movements and reproduction of three Costa Rican bat communities. Occasional Papers, Museum of Natural History of the University of Kansas, 69: 1–28.
- LAVAL, R. K., and B. RODRÍGUEZ-H. 2002. Murciélagos de Costa Rica: bats. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica, 320 pp.
- LEE, T. E., JR., and R. D. BRADLEY. 1992. New distributional records of some mammals from Honduras. Texas Journal of Science, 44: 109–111.
- McDonough, M. M., L. K. AMMERMAN, R. M. TIMM, H. H. GENOWAYS, P. A. LARSEN, and R. J. BAKER. In press. Speciation within the *Eumops glaucinus* complex: the value of multiple datasets (morphological, mitochondrial, and nuclear) in systematics. Journal of Mammalogy.
- MATA, A., and J. ECHEVERRÍA. 2004. Introduction. Pp. 1–12, *in* Biodiversity conservation in Costa Rica: learning the

lessons in a seasonal dry forest (G. W. FRANKIE, A. MATA, and S. B. VINSON, eds.). University of California Press, Berkeley, 341 pp.

- PETERS, S. L., B. K. LIM, and M. D. ENGSTROM. 2002. Systematics of dog-faced bats (*Cynomops*) based on molecular and morphometric data. Journal of Mammalogy, 83: 1097–1110.
- REID, F. A. 1997. A field guide to the mammals of Central America & southeast Mexico. Oxford University Press, New York, 334 pp.
- RODRÍGUEZ F. J., and F. A. CHINCHILLA. 1996. Lista de mamíferos de Costa Rica. Revista de Biología Tropical, 44: 877–890.
- RODRÍGUEZ-H., B., and D. E. WILSON. 1999. Lista y distribución de las especies de murciélagos de Costa Rica. Occasional Papers in Conservation Biology, Conservation International, 5: 1–34.

- SANBORN, C. C. 1932. The bats of the genus *Eumops*. Journal of Mammalogy, 13: 347–357.
- STEVENS, G. C. 1983. Atta cephalotes (zompopas, leaf-cutting ants). Pp. 688–690, in Costa Rican natural history (D. H. JANZEN, ed.). The University of Chicago Press, Chicago, 816 pp.
- TIMM, R. M., and H. H. GENOWAYS. 2004. The Florida bonneted bat, *Eumops floridanus* (Chiroptera: Molossidae): distribution, morphometrics, systematics, and ecology. Journal of Mammalogy, 85: 852–865.
- TIMM, R. M., and R. K. LAVAL. 1998. A field key to the bats of Costa Rica. Occasional Publications Series, Center of Latin American Studies, University of Kansas, 22: 1–30.
- TIMM, R. M., R. K. LAVAL, and B. RODRÍGUEZ-H. 1999. Clave de campo para los murciélagos de Costa Rica. Brenesia, 52: 1–32.

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