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Status and natural history of *Emballonura semicaudata rotensis* on Aguiguan, Mariana Islands

GARY J. WILES^{1, 5, 8}, THOMAS J. O'SHEA², DAVID J. WORTHINGTON^{3, 6}, JACOB A. ESSELSTYN^{3, 7}, and ERNEST W. VALDEZ⁴

¹Division of Aquatic and Wildlife Resources, 192 Dairy Road, Mangilao, Guam 96913, USA ²United States Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, Colorado, 80526-8118, USA

³Division of Fish and Wildlife, P.O. Box 1397, Rota, Commonwealth of the Northern Mariana Islands 96951, USA

⁴United States Geological Survey, Fort Collins Science Center, Department of Biology, MSC03 2020, 1 University of New Mexico, Albuquerque, New Mexico 87131-0001, USA

⁵Current address: Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501-1091, USA

⁶Current address: Capitol Reef National Park, Torrey, Utah 84775, USA

⁷Current address: Biology Department, Life Sciences Building, Room 428, McMaster University, Hamilton, Ontario L8S4K1, Canada

⁸Corresponding author: E-mail: wilesharkey@yahoo.com

Pacific sheath-tailed bats (*Emballonura semicaudata rotensis*) in the Mariana Islands declined greatly in abundance and distribution during the 20th century. The small island of Aguiguan now supports the only persisting population. We studied abundance and natural history of this population from 1995–2008. There was a likely population increase during the study, with 359–466 (minimum and maximum) bats counted at caves in 2008. Bats roosted only in caves, primarily those of relatively larger size. Bats were detected in only seven of 95 caves; three caves were always occupied when surveyed. One cave consistently had the largest colony ($\bar{x} \pm SD = 333 \pm 33.6$ in 2008). Others held 1–64 bats. Cave environments showed no complexities in temperature or humidity. Preliminary observations indicate a litter size of one and the possibility of birthing timed to coincide with the transitional period leading into the rainy season (June–July). We review potential threats to *E. s. rotensis* on Aguiguan and make suggestions for conservation.

Introduction

The Pacific sheath-tailed bat (*Emballonura semi*caudata) occurs across much of Oceania, including the Mariana and Caroline Islands, Samoa, Tonga, Fiji, and Vanuatu (Flannery, 1995; Koopman, 1997; Helgen and Flannery, 2002). These bats seem common at some locations, especially in the Caroline Islands (e.g., Bruner and Pratt, 1979; Wiles et al., 1997), but populations have inexplicably declined on many other islands (Lemke, 1986; Grant et al., 1994; Flannery, 1995; Hutson et al., 2001; Tarburton, 2002; Palmeirim et al., 2007). In the Mariana Islands, where the endemic E. s. rotensis occurs (there are four putative subspecies — Koopman, 1997), sheath-tailed bats disappeared from Guam, Rota, and Saipan between the late 1940s and 1970s (Lemke, 1986; Wiles et al., 1995). The species occurred in recent prehistoric times on Tinian (Steadman, 1999), but there are no historical records for this island. Lemke (1986) reported possible sightings on Anatahan and Maug in the northern Mariana Islands, but populations there remain unconfirmed. Lemke (1986) found no records of *E. s. rotensis* from Saipan, but we have since found one report (Schnee, 1910) and learned of a sighting of a few small insectivorous bats on Saipan in about 1945 (P. H. Krutzsch, in litt.). Fossil evidence suggests that *E. s. rotensis* was formerly common on Guam and Rota, but possibly less numerous on Tinian (Steadman, 1999; Pregill and Steadman, 2009).

The only known remaining population of this subspecies is on the island of Aguiguan, where it is the sole microchiropteran bat. Biologists first recorded *E. s. rotensis* on Aguiguan in 1984 and 1985, when three or four bats were found in each of two caves, the only bats found in searches of 13 of

the 15 islands or island groups in the Marianas during 1983–1985 (Lemke, 1986; G. Wiles, unpublished data). This prompted Nowak (1994: 92) to state "this subspecies may thus rank as one of the world's most critically endangered mammals." Subsequent observations from 1987 to 1992 documented up to 13 bats at one of the caves, but none was found at any of the few other caves surveyed, also suggesting a very small population (Rice and Taisacan, 1993).

Our objectives were to conduct a new assessment of the status of the Pacific sheath-tailed bat population on Aguiguan by surveying all accessible caves on the island, to characterize cave environments, to summarize previous counts and assess changes in abundance, and to supplement the scant amount of information available on the species' natural history. We also discuss potential threats and suggest measures that could enhance conservation of this population.

MATERIALS AND METHODS

Study Area

Aguiguan (14°51'N, 145°33'E) is in the southern Mariana Islands in western Micronesia and is administered by the U.S.

Commonwealth of the Northern Mariana Islands (CNMI). The island is small (7.0 km²) and formed entirely of raised limestone karst, making it geologically similar to the neighboring islands of Tinian, Saipan, Rota, and much of Guam (Butler, 1992; Stafford et al., 2004; Jenson et al., 2006). A large central plateau dominates the terrain, bordered by a series of narrow terraces falling to the ocean (Fig. 1). Coastal escarpments 10-40 m tall surround most of the shoreline. Maximum elevation is 166 m. Morphology of the island's caves is discussed in Stafford (2003) and Stafford et al. (2004). Aguiguan's climate is tropical, with mean daily temperatures ranging from 24°C to 32°C. Annual rainfall averages ≤ 2,000 mm, with almost four times as much rainfall during the wet season as in the dry season (Butler, 1992; Lander, 2004). Rainfall is highest July-October, and lowest December-May (Lander, 2004). Despite ample rainfall, there is no permanent surface freshwater available to bats.

Aguiguan was mostly covered with native limestone forest until 1937, when Japanese colonists began clearing the plateau and larger terraces for sugar cane cultivation (Butler, 1992). About half of the island was cleared by the early 1940s (Engbring et al., 1986). Former crop fields now occupy 23% of the island and are largely revegetated by weedy thickets of introduced plants (Engbring et al., 1986; Butler, 1992; Rice, 1993a; F. Amidon, unpublished data). Native limestone forest remains on 49% of Aguiguan, growing on smaller terraces and steeper slopes, with canopy heights of 7–15 m (Chandran et al., 1992). Goats (Capra hircus) were introduced to the island between about 1820 and 1860 (Butler, 1992). Decades of overbrowsing by feral goats have created an open forest understory dominated by two unpalatable species, Guamia mariannae and

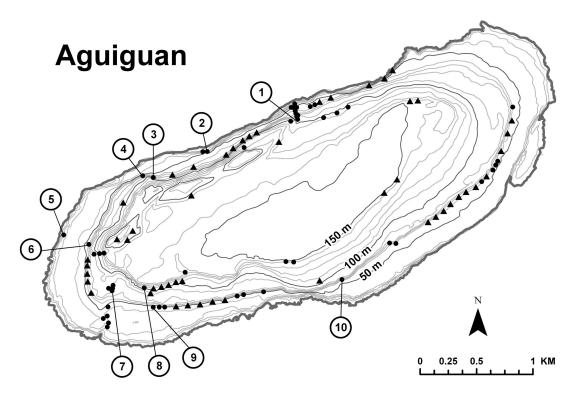


Fig. 1. Map of Aguiguan showing the confirmed (dots) and approximate (triangles) locations of 101 caves on the island. The locations of 13 other caves reported by Stafford (2003) are not known. Labeled caves are as follows: 1 — Fault Line Cave 1; 2 — East Black Noddy Cave; 3 — Cliff Cave; 4 — Pillar Cave; 5 — Landing Cave; 6 — Guano Cave; 7 — New Cave 1; 8 — Dangkolo Cave; 9 — Crevice Cave; and 10 — Krisidu Cave

Cynometra ramiflora, with scant ground cover. Other habitat types include groves of secondary forest comprised primarily of introduced trees at some disturbed sites (about 20% of island cover), grassy and shrubby coastal strand vegetation (4%), and bare ground (5%). Aguiguan has been uninhabited by people since the end of World War II, but is regularly visited by goat and coconut crab (*Birgus latro*) hunters.

Searches of Caves, Counts of Bats, Roost Characterization, and Bat Capture

We surveyed for bat roosts during trips to Aguiguan on 21–27 March 1995, 30 May–7 June 1995, 9–19 September 2003, and 19 June–15 July 2008. Additional observations were made 15–20 March 2002. We visited caves previously known from efforts by others (Lemke, 1986; Rice and Taisacan, 1993) and searched extensively for additional caves, rock crevices, and hollow trees that might serve as roosts. However, searches were incomplete because some caves are inaccessible without technical climbing skills. We did not locate about 13 mostly small caves reported by Butler (1992) and Stafford (2003). K. W. Stafford (in litt.) reported no sightings of bats in these caves in 2003.

We entered all accessible known caves and examined them for evidence of bats, including echolocation calls and bat guano. Direct counts of bats inside caves during the day were made when possible. In 2008, we used an infrared night vision device (model ATN NVM-14-3A, American Technologies Network Corporation, San Francisco, California) and an infrared illuminator at some caves. Interior area of caves was categorized as small, medium, or large. Small caves were generally ≤ 15 m long and 50 m² in floor area, and consisted of low rock overhangs, narrow vertical crevices, or various cavities (often at the bases of cliffs or under large boulders). Medium-sized caves had 50-100 m² of floor space, often with wider rooms than small caves. Large caves were > 100 m² in floor area, with taller ceilings. We also inspected hollow trees during the 1995 surveys for evidence of bats. We sampled temperatures hourly at various locations within caves using Thermocron iButton data loggers (model DS1921, Dallas Semiconductor Corporation) factory calibrated at a level of precision of \pm 1°C. In most cases, we took temperature readings on rock surfaces (these bats roost singly appressed to the rock walls or ceilings). Ambient temperatures were taken at a base camp on the island's central plateau. We measured relative humidity with a sling psychrometer at 1.5 m above the ground.

Evening emergence counts of sheath-tailed bats were made at potentially suitable caves. Observers were positioned near cave openings at the best possible vantage point for counting exiting bats. Counts ended at total darkness or no less than 15 minutes after the last bat emerged. We used ultrasonic detectors (model D-100, Pettersson Elektronik AB, Uppsala, Sweden; AnaBat SD1 CF, Titley Electronics, Ballina, New South Wales, Australia) to assist in detecting emerging bats at some sites. Counts were not made on nights after captures took place. Emergence counts at East Black Noddy and Guano caves included counts made by the same person (GJW) from 1995–2008 that agreed with simultaneous counts made by others, thus observer variation was not a major source of error.

We attempted to capture bats in mist nets and a hand sweep net at caves and as they foraged and dispersed in the forest at night. We measured forearm length (to 0.1 mm) with dial calipers and determined sex of all captured bats. Those captured in 2008 were examined to determine age (adult or volant juvenile) and weighed (to 0.1 g). In 2008, we examined bats with a 20× magnification visor for visible ectoparasites; two individuals that died in handling were examined for ectoparasites under a 14–60× stereo-zoom microscope. Voucher specimens from these two bats were deposited in the Museum of Southwestern Biology, Albuquerque, New Mexico. Bat capture and handling methods were approved by the Institutional Animal Care and Use Committee of the U.S. Geological Survey.

We present data as totals, percentages, arithmetic means with standard deviations, and coefficients of variation (CV). We used Student's *t*-test to evaluate statistical null hypotheses on characteristics of emergence flights in relation to colony size.

RESULTS

Searches of Caves, Counts of Bats, and Roost Characteristics

We inventoried 114 caves (18 large, 9 medium, 74 small, and 13 of undefined size — Fig. 1). Caves were almost always in association with cliffs or fault lines, and most had no evidence of use by sheathtailed bats. In 1995, we counted 98 bats at five of 80 surveyed caves (Table 1). The largest colony (69 bats) was at East Black Noddy Cave, with 2-17 bats at other occupied caves (Table 1). In 2003, we counted 285–364 (minimum and maximum counts) bats at six of 55 caves, with bats present at the same five caves occupied in 1995 and at a newly discovered site with one bat (Table 1). East Black Noddy Cave again held the largest colony (232 and 296 counted on two evenings). Other caves held up to 35 bats. Numbers at Guano and Pillar caves in 2003 were also higher than in 1995.

In 2008, we counted 359-466 bats (sums of minima and maxima) at five of 40 caves, with bats present at four of the six sites used in 1995 or 2003 and at one new site (Table 1). East Black Noddy Cave again had the largest colony with 308-382 bats counted on four nights ($\bar{x} \pm SD = 333 \pm 33.6$, CV = 10.1%). Internal counts at Guano Cave with a night vision device on six dates varied from 43-64 bats $(\bar{x} = 55 \pm 7.0, \text{ CV} = 12.8\%)$. Other occupied caves held 2-12 bats. Compared to 2003, counts in 2008 were higher at East Black Noddy, Guano, and Cliff caves, similar at Crevice Cave, and declined to zero at Pillar Cave and Fault Line Cave 1 (Table 1). All occupied caves were used by bats whenever visited during the 2008 survey except New Cave 1, which had at least five bats on 4 July, but none during three other visits. Ten other caves where surveys were made on multiple (2-8) dates in 2008

TABLE 1. Numbers of Pacific sheath-tailed bats recorded at eight caves on Aguiguan, Mariana Islands, from 1984–2008, as determined by direct counts of day-roosting bats or evening emergence counts. Dashes indicate that no counts were made

					(Cave				
Date					New -	East Blac	ck Noddy		Fault Line	
Date	Landing	Guano	Cliff	Pillar	Cave 1	Upper Entrance	Middle Entrance	Crevice	Cave 1	References ^a
22 Jun 1984	3-4 ^b	_	_	_	_	_	_	_	_	1
Jan 1985	$0^{b,c}$	4 ^b	0^{c}	0^{c}	_	_	_	_	_	1, 2
18 Jul 1985	_	2^{b}	_	_	_	_	_	_	_	3
28 Feb-1 Mar 1987	0^{c}	3 ^b	_	0^{c}	_	_	_	_	_	3, 4, 5
6–9 Jun 1988	0^{c}	5 ^b	_	0^{c}	0^{c}	_	_	_	_	3, 4, 5
21 Sep 1989	-	13 ^b	_	_	_	_	_	-	_	3, 5
Mar 1992	$0_{\rm p}$	9^{b}	0^{c}	0^{c}	_	_	_	_	_	3, 4
23 May 1992	2^{c}	_	_	_	_	_	_	_	_	6
23, 26 Mar 1995	$0_{\rm p}$	15 ^b , 16 ^b	0^{c}	0^{c}	_	64 ^c	5°	_	_	7
31 May-6 Jun 1995	$0^{b,c}$	17 ^{b, c} , 16 ^b	7 ^c	2^{c}	_	_	_	$3^{b,c}$	_	7
15-20 Mar 2002	$0_{\rm p}$	15 ^c	_	5°	_	_	_	_	_	7
13, 28 May 2003	_	_	_	_	_	_d	_d	2^{b}	_	8
9–19 Sep 2003	$0_{\rm p}$	25–35°	4 ^e	$5-10^{c}$	$0_{\rm p}$	248c, f	16 ^c	2^{c}	1 ^b	7
19 Jun-15 Jul 2008	$0_{\rm p}$	55 ^{b, g}	$6-12^{c}$	0^{c}	0, 5 ^{b, c}	277 ^{c, f}	56 ^{c, f}	2, 3 ^{b, c}	0_{p}	7

Note: Results from Cliff and Pillar caves in 1985–1992 were obtained during evening arrival counts of Mariana swiftlets (Rice, 1993b; Rice and Taisacan, 1993). Bats were not detected during bat emergence counts at Dangkolo, Krisidu, West Black Noddy, New Cave 3, and No. 18 caves in 1995; at Dangkolo, Krisidu, and E caves in 2003; or at Dangkolo, New Caves 2 and 3, No. 26, 28, 64, 65, 66, 67, 95, and 102 caves in 2008.

^a References: 1 — Lemke (1986), 2 — Reichel and Glass (1988), 3 — Rice and Taisacan (1993), 4 — Rice (1993b), 5 — unpublished CNMI Division of Fish and Wildlife trip reports, 6 — Craig and Chandran (1992), 7 — this study, and 8 — K. W. Stafford (personal communication); ^b Direct roost count; ^c Emergence count; ^d Bats were not detected and were likely missed; ^e Partial emergence count; ^f Number represents the mean of multiple emergence counts; ^g Number represents the mean of six direct roost counts made with a night vision device

showed no daytime use by bats, including Fault Line Cave 1.

Three caves had bats on each visit from 1995 to 2008: Guano Cave, East Black Noddy Cave, and Crevice Cave (Table 1). Guano and East Black Noddy caves had the largest colonies, whereas Crevice Cave had only 2–3 adult bats at each count. Caves with variability in presence/absence among visits only had small numbers of bats. Landing Cave was visited 11 times between 1984 and 2008, with bats seen only twice and always ≤ 4 (Table 1). Fault Line Cave 1 had one bat during the day in 2003, but none was present during the day on eight dates in 2008; five bats were observed at New Cave 1 on 4 July 2008, but none on 25 June, 5 July, or 10 July in 2008; Cliff Cave had no bats in March 1995, but seven in June; and Pillar Cave had none in March 1995, but two in June. Seasonality in attendance was not indicated by counts (Table 1).

Sheath-tailed bats on Aguiguan seem to prefer larger caves. We found day-roosting bats in six large caves, one medium-sized cave, and one of unrecorded size. Interior dimensions of occupied caves varied from 15–58 m long, 0.7–12 m wide, and 2–25 m high. Primary entrance dimensions of these caves ranged from about 0.6–1 m in diameter to 8.5 m wide by 16 m tall. Mariana swiftlets (*Aerodramus bartschi*) occurred in seven of eight caves inhabited

by bats. We found no evidence that these bats roost in narrow rock crevices on Aguiguan. We examined trunk cavities of 22 hollow trees (21 *Pisonia grandis*, 1 *Psychotria mariana*), but found no evidence of bats. *Pisonia* hollows were typically 1–4 m tall and 20–45 cm in diameter, with openings usually near the base of the trunk.

Hourly ambient temperatures at base camp averaged 27.0 ± 2.4 °C at 2 m height (n = 408 readings on 18 dates in 2008), fluctuating from 22°C to 32.8°C. Temperatures at 28 stations in seven caves were much less variable than ambient, ranging from no variation to at most a 3°C range; mean temperatures at each location were either 26°C or 27°C regardless of position within caves (n = 6,672 temperature readings at 28 locations). Hourly temperatures within most caves at depths of 20 m or more and heights of 1–3 m were essentially constant. Maximum temperatures in caves also spanned a narrow range, from 26°C to 28°C. There were no obvious differences in thermal regimes among caves sampled regardless of history of occupancy by bats. We recorded relative humidity in five caves at locations ≥ 10 m from entrances. Three were identical at 92%, whereas New Cave 1 and Dangkolo Cave were slightly more humid at 96%. The latter cave has no history of bat occupancy and was the only cave we entered that had occasional dripping

water. Daytime relative humidity outside of caves was generally lower, ranging from 74% to 92%.

Observations on Captured Bats

We captured 18 adult bats, six in September 2003 and 12 from late June to mid-July 2008. All but two were released after capture. No examined bats had visible ectoparasites. Fourteen adult females were caught in mist nets at caves (six at Guano Cave in 2003, five at Guano Cave, and three at East Black Noddy Cave in 2008). Four adult males were captured at dusk in hand-held sweep nets as they dispersed up a rocky hill from an unknown roost on three nights in 2008. Forearm length averaged 45.2 ± 1.2 mm (range 43.5-46.0) in males and 45.8 \pm 1.0 mm (43.8–47.3) in females. Body mass averaged 5.5 ± 0.5 g (range 5.1-5.8) in three males and 6.9 ± 0.9 g (5.8–8.0) in eight females in 2008. Bats were very difficult to capture while foraging and were sensitive to handling. We set sub-canopy mist nets in native limestone forest on nine nights in 2008 (273 m total length of nets). At times, bats flew directly to within 1 m or less of nets but easily avoided them and none was captured. We captured four males in hand-held sweep nets. Three bats captured on three separate dates in 2008 responded poorly while measured and inspected. One died during handling, and two appeared stunned and would not fly on release until 20–30 min after being placed on a rock face to recuperate. Subsequently, we placed bats in individual cloth bags at capture and left them in quiet areas 10-30 min prior to handling. These bats responded well and flew immediately upon release.

Most (7 of 8) adult females captured at two caves from late June to mid-July 2008 were pregnant (5) or lactating (2). None of six females captured at Guano Cave in September 2003 was palpably pregnant. Four males examined in June-July 2008 had no external evidence of distended testes or epididymides, and one prepared as a museum specimen had no swelling of the epididymides and small $(1 \times 3 \text{ mm})$ abdominal testes. A litter size of one was indicated by several observations. The female that died on 30 June 2008 had one embryo (crown-rump length 23 mm). One young was attached to a female captured at Guano Cave on 12 July 2008. Observations at Crevice Cave on 23 and 27 June 2008 with the night-vision device documented one juvenile with two adults on both dates. Observations at Guano Cave on 25 June 2008 showed 10 smaller bats each roosting next to single larger bats assumed to be their mothers.

Behavioral Observations

At Guano Cave, all bats roosted in one small dome-like area of the ceiling about 12 m high at the rear of the cave's main room. This was the highest point and was completely dark. Observations made on six dates with the night-vision scope showed that the bats roosted singly (or as lone adults next to lone young), spaced about 5–30 cm apart on the ceiling and upper walls of the dome, ventral surfaces appressed to the rock surface with heads facing downwards, with spacing intermediate between regular and random patterns. The cave was also used by \geq 250 swiftlets that did not roost in the dome, but in the large adjoining section of the main room nearer the cave entrance. At Crevice Cave in 1995, three bats roosted about 30 cm apart against the vertical wall of a side chamber, the darkest portion of the cave (dim twilight). This same place was occupied in 2003 and 2008. Few if any uncounted bats were hidden in cracks or crevices in the two caves because emergence counts were similar to internal counts. Bats always seemed wary, readily flew within the roost if we approached, did not cluster, and did not enter torpor when resting in cloth bags.

Sheath-tailed bats emerged early in relation to sunset. Exits began before sunset on most nights (12 of 18 emergences at five caves), with the first bat departing 5.3 ± 10.0 min before sunset and the last bat 12.3 ± 10.0 min after sunset. Emergence of most bats occurred earlier than when most swiftlets began returning for the night, and typically ended well before swiftlets had completely gone to roost. Total duration of sheath-tailed bat emergences from roosting caves averaged $18.3 \pm 11.7 \text{ min } (n = 18).$ Emergence at larger colonies took longer and began earlier than at smaller colonies, but ended at about the same time relative to sunset (Table 2). Bats sometimes emitted audible calls prior to emerging. Most exited caves by flying straight from the entrance, but some circled briefly in the vicinity. Bats at smaller colonies exited singly, but at East Black Noddy Cave some left in groups of two to four. On 17 September 2003, a light rain shower several minutes after all bats had departed East Black Noddy Cave caused 50-75 bats to return immediately, suggesting that these bats lingered in the area after emerging. No bats remained inside Guano Cave immediately after emergences in 2003 and 2008.

In 2008, we detected early nighttime use of caves not occupied in the day. We saw 13 bats enter Pillar Cave at 18:47–19:02 (sunset = 18:50) on 21 June and heard chattering vocalizations inside afterwards.

TABLE 2. Temporal characteristics of Pacific sheath-tailed bat emergences at large (≥ 232 bats) and small (≤ 69 bats) colonies on Aguiguan, Mariana Islands, 1995–2008. Values are presented as means ± SD (in minutes) with sample sizes in parentheses. Emergence data for large colonies came from one cave (East Black Noddy Cave), whereas those for small colonies came from five caves (Cliff Cave, Crevice Cave, East Black Noddy Cave, Guano Cave, and Pillar Cave)

Parameter	Large colonies	Small colonies	<i>t</i> -statistic (<i>P</i> -value)		
Duration	27.5 ± 8.3 (6)	13.7 ± 10.7 (12)	2.8 (0.013)		
Start relative to sunset	$14.0 \pm 4.0 \text{ before } (6)$	1.4 ± 9.4 before (12)	3.1 (0.007)		
End relative to sunset	13.5 ± 6.0 after (6)	12.6 ± 7.7 after (11)	0.2 (0.864)		

These bats were gone when we inspected the cave with night vision equipment at 20:00–20:15. Similarly, 21 bats entered this cave at 18:41–18:56 (sunset = 18:52) on 7 July. On 24 June, we observed a single bat circling repeatedly inside the main entryway of a different cave at 19:37. On 11 July at 18:47, we observed similar behavior by a bat that flew into Fault Line Cave 1 and made audible vocalizations (short 'chirps') as it remained inside for a few minutes before exiting.

Another series of notable observations in 2008 was the early evening (18:41–19:20) passage of 43–47 sheath-tailed bats flying singly up the same steep rocky slope on several nights. All followed a similar route through the understory, moving uphill from an undetermined point (none came from known caves in the immediate area). These bats sometimes foraged (occasional prey pursuit phases heard on echolocation detectors) in elliptical circuits about 20 m long for periods of 2–4 minutes as they passed up the hill. Based on bat detector recordings, few if any of the bats remained in the area from 19:20–22:00. All four bats captured at this site (see above) were adult males. In addition to calls heard at caves, communication calls were heard as bats dispersed and foraged in the forest. Audible calls were high-pitched chirps emitted in one to five syllable sequences. In one area on two nights, we observed bats flying about 2–4 m above the forest floor vocalizing, once saw three bats flying in a group, and observed one bat chasing another below the canopy.

DISCUSSION

Status and Natural History of Pacific Sheath-Tailed Bats on Aguiguan

Our surveys are the first relatively comprehensive assessments of the status of sheath-tailed bats on Aguiguan. Counts increased during the study, with 98 bats in 1995, 285–364 bats (minimum and maximum counts) in 2003, and 359–466 bats in 2008. Bats occurred in only seven of 95 caves surveyed, even though many unoccupied sites appeared

suitable. Despite good coverage of the island's inland cave system during the study, we suspect that a few undocumented caves also may be used by bats. Most coastal cliffs ringing the island could not be surveyed due to inaccessibility. Some caves are visible from the sea in these escarpments, and because E. semicaudata inhabits sea caves elsewhere (Grant et al., 1994), assessment of their use as roosts is needed. With one exception, acoustic surveys conducted across the island in 2003 and 2008 did not detect high echolocation activity far from known colonies (Esselstyn et al., 2004; Gorresen et al., 2009). Substantial early evening echolocation activity was noted in 2008 on northeastern Aguiguan not near any known roost (Gorresen et al., 2009), but near our sightings and captures of male bats dispersing uphill at dusk, suggesting an undocumented colony in that vicinity. However, Pacific sheathtailed bats can commute distances exceeding 5 km to reach foraging sites in Palau (Wiles et al., 1997), and it is feasible that the bats detected or observed in northeastern Aguiguan originated from East Black Noddy Cave (0.8–1.6 km west of the survey and sighting areas). If there are undiscovered colonies, the sheath-tailed bat population on Aguiguan may number more than our maximum count of 466 in 2008.

Increases in counts at caves on Aguiguan likely indicate population growth. Colony size grew at three of five caves from 1995 to 2003, expanding four-fold at East Black Noddy Cave, with more modest growth there continuing to 2008. Numbers at Guano Cave increased from four in 1985 (Lemke, 1986) to a mean of 55 in 2008. Variability in replicated counts in 2008 (CV of 10–13%) may indicate daily movement of small numbers of bats among roosts, but such movements seem unlikely to explain the larger increases noted over the years at some colonies. An increasing trend in the sheathtailed bat population on Aguiguan since 1995 is noteworthy given the many declines in the species elsewhere (Lemke, 1986; Grant et al., 1994; Flannery, 1995; Hutson et al., 2001; Tarburton, 2002; Palmeirim et al., 2007). Is such an increase

biologically plausible? Application of a basic model for assessing population growth rate (λ) from trends in count data (e.g., Eberhardt, 2002) to survey results between 1995 and 2008 (Table 1) yields an estimated $\lambda = 1.13$ at East Black Noddy Cave and $\lambda = 1.10$ at Guano Cave. Given that the species is extinct elsewhere in the Mariana Islands, any increase must be attributable to intrinsic processes of reproduction and survival rather than immigration. The few empirical estimates of λ based on such vital rates for increasing populations of other species of insectivorous bats with seasonal breeding and annual litter sizes of one range from $\lambda = 1.03$ to $\lambda = 1.22$ (O'Shea et al., 2011 and references therein). Thus it is biologically feasible that the increases in counts may reflect true population growth during the 13 years of our study. However, we caution that these are very crude calculations without extensive data, made only to demonstrate plausibility of an increasing trend, and should not be considered accurate or precise estimates of population growth rates.

The colony of up to 382 bats at East Black Noddy Cave is the largest ever recorded for *E. s. rotensis*. Counts at other caves on Aguiguan ranged from 1–64 individuals. The capture of 11 females and no males at Guano Cave in 2003 and 2008 suggests this was mostly a colony of females. Aggregations of fewer than 25 bats and segregation of the sexes are common in *Emballonura* (Jackson, 1962; Medway, 1978; Flannery, 1995; Bonaccorso, 1998). Nevertheless, large colonies may once have been common in the Mariana Islands, as has been found in Palau (Wiles and Conry, 1990; Wiles *et al.*, 1997), Chuuk (Bruner and Pratt, 1979), and American Samoa (Amerson *et al.*, 1982).

On Aguiguan, E. s. rotensis appears to roost exclusively in caves and not under overhanging rocks, in tree hollows, or in human-built structures, unlike E. s. sulcata colonies on Pohnpei (Jackson, 1962; D. W. Buden, personal communication). Most other species of Emballonura roost in caves (e.g., Bonaccorso, 1998; Goodman et al., 2006), especially in or near the twilight zones of smaller caves, but some will roost in foliage, hollow logs, and anthropogenic structures (Medway, 1978; Flannery, 1995). Sheathtailed bats may occupy certain caves on Aguiguan for many years. Guano Cave was occupied on every visit since 1985, and three other caves (Crevice, East Black Noddy, and Cliff caves) were occupied during our visits in 1995, 2003, and 2008. Other sites seem to be used temporarily. Caves are also used by E. semicaudata at night, as first documented in this study. Caves are abundant on Aguiguan but very few

are occupied, suggesting that roosts are not currently a limiting resource. We did not observe major differences in temperature or humidity among caves, and these factors seem unlikely to preclude the use of unoccupied caves as roosts. None of the caves we entered had internal complexities that could create strong heterogeneity in internal microclimates, and we did not observe notable air movements within them. Cave temperatures reflect the mean annual surface air temperatures of a region (Dwyer, 1971). Mean annual temperatures at the three closest longterm weather stations are 26.2-27.7°C (Guam -National Oceanic and Atmospheric Administration, 2008), consistent with the temperatures in caves on Aguiguan. Mean annual maxima and minima at weather stations on Guam vary from 22.6-30.7°C, suggesting that the ranges of air temperatures that might occur in trapped internal air masses would be small even if caves were complex. Thermal environments of caves used by species of bats that do not regularly enter torpor are less important than those of caves used by more heterothermic bats at higher latitudes (Dwyer, 1971). We saw no evidence that Pacific sheath-tailed bats enter torpor readily; homeothermy under normal environmental conditions is typical of tropical emballonurids (Bonaccorso, 1998; Genoud and Bonaccorso, 1986; Genoud et al., 1990). Temperatures of roosts used by three other species of tropical emballonurids have been measured and are very similar to those of caves on Aguiguan (Genoud and Bonaccorso, 1986; Genoud et al., 1990; Avila-Flores and Medellín, 2004), also suggesting that thermal characteristics of caves on Aguiguan do not limit their use by E. s. rotensis. Because there is no surface freshwater for drinking by bats on Aguiguan, roost environments that minimize evaporative water loss may be important. However, given the high humidity in the caves that we measured, it seems unlikely that variation in humidity among caves is a limiting factor. Humidities we observed were within the ranges found in caves used as roosts by many other tropical bats elsewhere (McNab, 1969).

Pacific sheath-tailed bats are difficult to capture, perhaps contributing to a lack of basic information on body size and reproduction. Published morphometric data for this subspecies are apparently limited to measurements of two bats from Rota (Yamashina, 1943) and two from Aguiguan (Lemke, 1986). Forearm lengths and body masses of bats we measured improve estimates of the range of body sizes known for *E. s. rotensis*. Our measurements of forearm lengths show that the Aguiguan population

overlaps in body size with all other subspecies (see measurements in Yamashina, 1932; Tate, 1934; Tate and Archbold, 1939; Sanborn, 1949; Johnson, 1962; Bruner and Pratt, 1979; Flannery, 1995). Subspecies designations for *E. semicaudata* follow their island distributions and qualitative features of skull morphology, but also reference body size, which was thought to form a linear series from *E. s. semicaudata - E. s. palauensis - E. s. rotensis - E. s. sulcata* (Koopman, 1997; Helgen and Flannery, 2002). However, subspecies taxonomy in *E. semicaudata* is in need of further study.

Births in sheath-tailed bats on Aguiguan may be seasonal and timed to coincide with the transitional period leading into the rainy season. In the seasonal tropics, many insectivorous bat species time reproduction to coincide with rainy season productivity and are non-reproductive during dry seasons (Racey and Entwistle, 2000). This is due to increased insect abundance during predictable rainy seasons and is known for other emballonurids (Bradbury and Vehrencamp, 1976; McWilliam, 1987). Eight of ten adult females captured in June by us and Lemke (1986) were pregnant or lactating, and we observed 11 single pups in roosts in June and July; six bats caught in September 2003 were not pregnant (lactation status not determined). All 12 bats caught at three locations in June and July 2008 were adults; the absence of readily discernible volant young in our samples suggests that reproduction was limited over the preceding few months of the late dry season. However, the seasonal birthing pattern in sheath-tailed bats on Aguiguan could be more complex and also requires additional study. Two records of single embryos and observations of single pups indicate a litter size of one, consistent with limited data on litter size in other Emballonura (Medway, 1978; Bonaccorso, 1998; Goodman et al., 2006), and suggesting that sheath-tailed bats on Aguiguan may be at the low range of reproductive potential for bats if they give birth once annually to single young.

Factors Influencing Population Status on Aguiguan and Recommendations for Conservation

The persistence of *E. s. rotensis* on Aguiguan contrasts with their loss from the other southern Mariana Islands, where causes for their extirpation remain undetermined. Human occupation and warfare during World War II heavily impacted many caves in the Marianas (Steadman, 2006). However, there was no combat or destructive use of munitions

in caves on Aguiguan (Butler, 1992), possibly contributing to the persistence of its bats. Other factors that may have contributed to declines and loss of Pacific sheath-tailed bats elsewhere in the Mariana Islands include liberal use of pesticides such as DDT and malathion from the 1940s through 1970s (Baker, 1946; Townes, 1946; Jenkins, 1983). Applications were most intense on Guam, Saipan, and Tinian (Townes, 1946). It is unknown if Japanese plantation operators used pesticides on Aguiguan prior to World War II, but DDT was not manufactured until the early 1940s (Metcalf, 1973). Aguiguan was neither populated by humans nor used agriculturally after the war, thus it is unlikely that significant amounts of insecticides were later applied to the island. We found no evidence of predation on sheath-tailed bats on Aguiguan, and diseases of this species are undocumented. Exotic monitor lizards (Varanus indicus) are an abundant potential predator. They are adept climbers and could reach day-roosting bats in hollow tree trunks or smaller caves. Although such predation may currently be insignificant, it could have influenced the selection of the roost sites in larger caves now used by bats. Exotic rats (Rattus exulans) and large geckos (Gehyra oceanica) are common in some caves and are potential predators on young bats at roosts. Avian predation is probably limited. Owls occur only as rare migrants; the resident diurnal collared kingfisher (Todiramphus chloris) could take bats during early emergence. Introduced brown tree snakes (Boiga irregularis) do not occur on Aguiguan, but have the potential to prey on sheath-tailed bats if they were to reach the island. On Guam, tree snakes are a significant predator of Mariana swiftlets roosting in caves (Wiles et al., 2003). Predation by tree snakes possibly caused losses of sheathtailed bats in southern Guam in the 1950s and 1960s, but snakes invaded northernmost Guam too late (i.e., in the late 1970s — Wiles et al., 2003) to have played a role in the bat's extirpation there.

A succession of severe typhoons may have contributed to declines of *E. s. semicaudata* in Samoa (Grant *et al.*, 1994). Aguiguan has a small land area and small bat population restricted to a few caves. An unusually intense storm or series of storms could severely impact these bats by precluding foraging during storms, damaging limited foraging habitat, flooding colonies in seaside caves, or causing direct mortality from high winds blowing into exposed caves. Two major typhoons struck Aguiguan in 1997 and 2004, but increases in counts suggest that neither typhoon severely impacted the population.

Emballonura s. rotensis forages almost exclusively in forests, especially native limestone forest, on Aguiguan (Esselstyn et al., 2004; Gorresen et al., 2009). Few of the fields cleared for agriculture before World War II have returned to native forest. With only 3.4 km² of the island remaining in native forest, past deforestation may be a principal factor limiting the current population.

When viewed in conjunction with the extirpation of Pacific sheath-tailed bats on other Mariana Islands, this study suggests that *E. s. rotensis* is highly vulnerable to extinction, with probably no more than a few hundred individuals restricted to one small island. The continued existence of this bat hinges on the maintenance of forested habitat and safe roosting sites. Eradication of feral goats could greatly improve regeneration of native tree species and insure the long-term stability of forests on Aguiguan. A reforestation program to replant sizable areas of weedy fields with native trees could also benefit the population.

Although not frequent, human visitation to Aguiguan occurs, primarily by hunters from Tinian. If visitation increases from hunting or ecotourism, bat colonies at accessible and well known caves (e.g., Guano Cave) will be at risk. Additionally, ongoing efforts to prevent the establishment of brown tree snakes in the CNMI are an obvious priority for protecting this bat. Further study of sheath-tailed bats on Aguiguan would provide additional data on population size, vital parameters, basic ecology and natural history, genetics, and limiting factors. Priorities for future status surveys should include assessment of coastal caves in areas that can only be reached with technical climbing expertise, and resurvey of caves visited in the past. Zooarchaeological excavations of cave sediments would provide data on past use of caves by bats on Aguiguan. A systematic review and new morphometric and molecular genetic analyses would improve understanding of the differentiation among the putative subspecies throughout the range of the species (Koopman, 1997; Helgen and Flannery, 2002).

Despite its rarity, neither the Pacific sheath-tailed bat nor its habitat is afforded protection in the U.S. possessions where it occurs. The bat is on the CNMI list of threatened or endangered species, but this provides no actual protection to the bat or its habitat. Under U.S. law, the bat is categorized as a candidate species, meaning that sufficient information is available to consider listing it as endangered or threatened. However, lack of funding, subspecific status, and other constraints have precluded

proceeding with listing (U.S. Fish and Wildlife Service, 2010). This study supports the listing of *E. s. rotensis* as endangered under the U.S. Endangered Species Act. Greater legal protection might increase resources needed to help enhance its habitat and conservation.

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