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Population Status and Natural History of *Pteropus mariannus* on Ulithi Atoll, Caroline Islands[1]

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ABSTRACT: A census of fruit bats (*Pteropus mariannus ulthiensis*) was conducted on Ulithi Atoll, Caroline Islands, in March 1986. We observed 715 bats in 3.2 km^2 of habitat on 14 of 43 islets, yielding a minimum average density of 210 bats/km^2. The population of the entire atoll was estimated to be about 1200 bats at an overall density of 280 bats/km^2. During the day, most (89%) bats roosted in colonies of ≥ 5 animals. Colonies, which were typically composed of harem groups and bachelor males, occurred most commonly in two species of trees, *Pisonia grandis* and *Artocarpus altilis*. We recorded nine species of plants eaten by bats, with the fruit of *Pandanus tectorius* and the fruit and leaf stems of *Guettarda speciosa* and *A. altilis* fed on most frequently.

MOUNTING PRESSURE TO HARVEST fruit bats[5] (*Pteropus* spp.) for commercial purposes in the Pacific has caused an immediate need to learn more about the abundance and biology of these bats (Wiles and Payne 1986). Information that can be used for management purposes is lacking for most species of fruit bats in the region. Bat populations on atolls are particularly vulnerable to overhunting because atolls have small land areas and lack inaccessible sites in which bats can seek refuge. In addition, *Pteropus* populations residing on atolls are of ecological interest because they inhabit forests characterized by low floral diversity (Wiens 1962, Manner 1987).

Pteropus mariannus ulthiensis is endemic to Ulithi Atoll in the western Caroline Islands and is one of six subspecies of *P. mariannus* recognized in Micronesia (Yamashina 1932, Kuroda 1940). The objectives of this study were to conduct a census of the bat population on Ulithi Atoll and to gather information on the natural history of *P. m. ulthiensis*, which has been previously unstudied.

Ulithi Atoll (9° 57′ N, 139° 42′ E) encloses a 20-by-30-km central lagoon (Figure 1). There are 37 low (maximum elevation, 7 m) coral islets surrounding the lagoon and six outlier islets located 9 km east of the atoll (Bryan 1971). Total land area is 4.4 km^2. About 22 of the islands are sufficiently large to be forested and used by fruit bats. Native strand forest and agricultural forest (agroforest) occur on these islands, with the most common trees being *Cocos nucifera*, *Pandanus tectorius*, *Artocarpus altilis*, *A. mariannensis*, *Guettarda speciosa*, *Neisosperma oppositifolia*, *Ficus prolixa*, *Pisonia grandis*, and *Musa* spp. Canopy height ranges from 10 to 18 m. Ulithi's climate is warm and humid year-round. Rainfall averages about 290 cm/yr, most of which occurs during a rainy season from May to November (Craib 1980). The atoll has a population of about 800 residents

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[5] The term "fruit bat" is used here instead of "flying fox" for the following reasons: (1) the argument has been made that the name fruit bat should be used only for neotropical pysllostomatids and the name flying fox given to all paleotropical pteropodids; however, phyllostomatids are all partially insectivorous while all pteropodids feed entirely on fruits and flowers; (2) The U.S. Fish and Wildlife Service refers to these bats as fruit bats on their endangered species lists; and (3) currently everyone working on bats in Micronesia refers to them as fruit bats and this is the English term by which all Micronesian islanders know these bats.

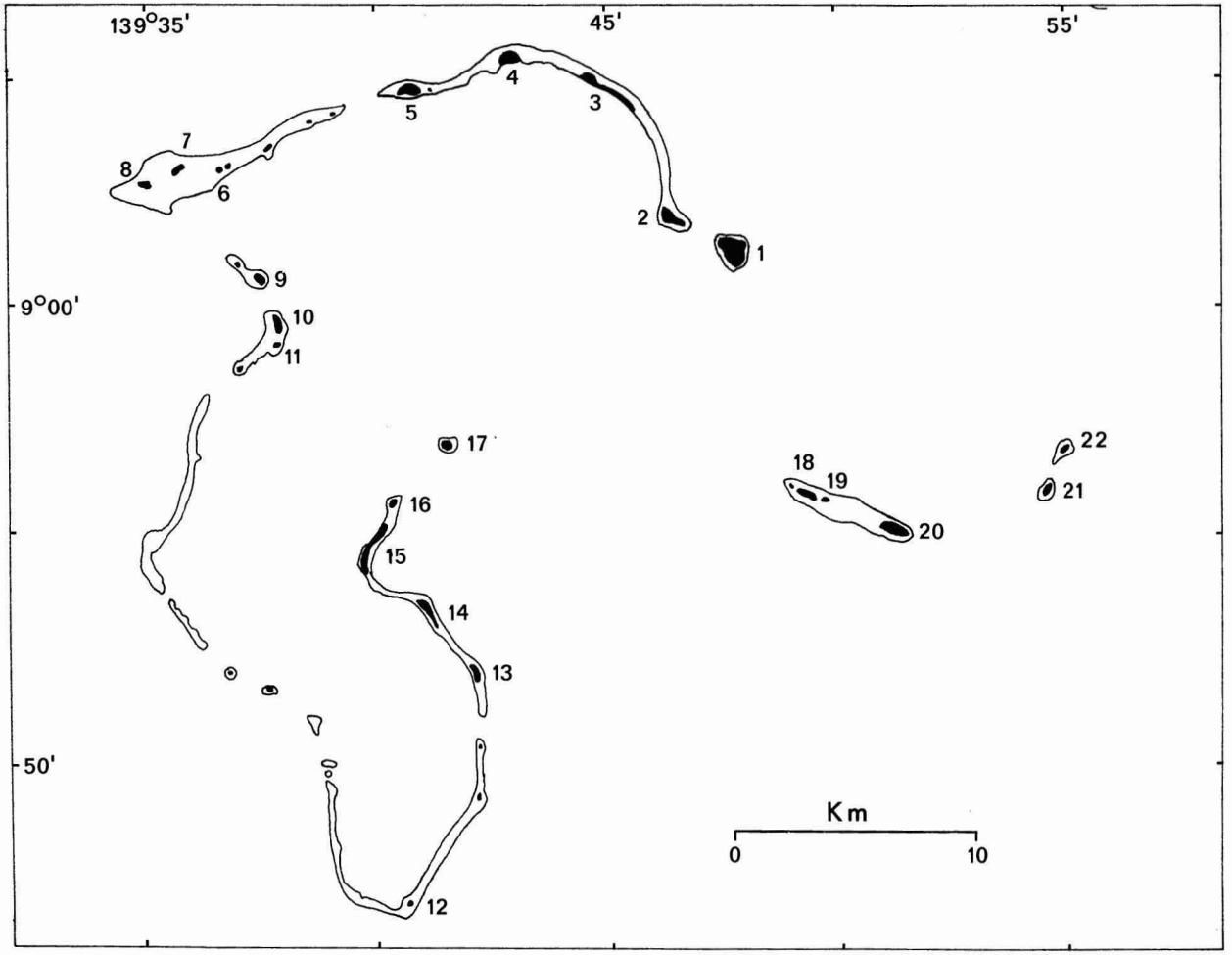

FIGURE 1. Map of Ulithi Atoll, Caroline Islands. Islands are represented by darkened areas and are surrounded by reef flats. Island names are as follows: 1, Falalop; 2, Asor; 3, Sorlen; 4, Mogmog; 5, Potangeras; 6, Piras; 7, Lam; 8, Sorenleng; 9, Song; 10, Pigelelel; 11, Elipig; 12, Pig; 13, Feitabul; 14, Lossau; 15, Fossarai; 16, Lolang; 17, Mangejang; 18, Pau; 19, Bulubul; 20, Losiep; 21, Iar; and 22, Gielap.

on the islets of Falalop, Asor, Mogmog, and Fossarai. Ulithi Atoll is administered as part of Yap State in the Federated States of Micronesia.

METHODS

From 10 to 17 March 1986, we counted fruit bats on 14 of Ulithi's larger islets, which comprised 77% of the atoll's total land area. Counts, made during the day when bats were roosting, involved four observers traversing each island and searching 50–90% of the forest on all islands visited. The observers began at one end of an island and walked steadily for 1–3 hr through the forest along separate and roughly parallel routes, counting all bats seen. We believe that nearly all fruit bat colonies (defined as roosting aggregations of ≥ 5 bats) were located during censuses because the bats usually occurred in conspicuous trees and were relatively noisy. Care was taken not to disturb roosting animals to avoid counting them a second time. The rounder islands of Falalop, Asor, and Mogmog were divided in half and two observers searched each half for bats. After an island was surveyed, the observers compared notes and the total number of bats counted was tallied. An estimate of the bat population on the island was made based on: (1) the percentage of the island covered by the observers, (2) the quality and amount of forest on the island, and (3) the amount of feeding evidence found. Each estimate was given an arbitrary measure of variability (i.e., 5 bats for populations of <40 animals, 10 bats for populations of 40–100 animals, and 25 bats for populations of >100 animals. Disturbances during counts on Falalop and Fossarai may have resulted in some flying bats being counted more than once. Estimates for both islands were slightly reduced because of this problem.

On Falalop, Asor, Mogmog, Sorenleng, and Fossarai, observers stationed themselves on beaches at dawn and dusk to look for fruit bats flying over the forest canopy or between islands. With these counts, it was possible to locate some colonies by the numbers of bats seen and their directions of flight. Estimated densities of fruit bats on inhabited islands were compared with those of uninhabited islands using a Mann-Whitney *U*-test (Sokal and Rohlf 1981).

Information on foods of fruit bats was based mainly on feeding sign (discarded fruit and leaves, chewed pellets of fruit or leaf stem pulp) found on the ground, although some sightings of bats actually feeding or carrying fruit in their mouths also were made. Behavioral observations were made with $7\times$ binoculars. Interviews with several atoll residents knowledgeable of the habits of fruit bats yielded additional information.

RESULTS AND DISCUSSION

Pteropus m. ulthiensis was recorded on each of the 14 islands visited, with 715 bats observed during censuses (Table 1). The total population for these islands was estimated at 895–1060 bats, an overall density of 263–312 bats/km^2 (Table 1). Fruit bats were most numerous on Sorlen, Fossarai (including Lolang), and Asor, with each island having an estimated population of ≥ 120 animals. The largest number and highest density of bats occurred on Sorlen, where a colony of 146 bats resided. Some fruit bats from Sorlen likely dispersed at night to feed on the neighboring islands of Mogmog, Asor, and Falalop. A combined estimate of 150–175 bats was made for Fossarai and Lolang, which lie only 750 m apart, because large numbers of bats flew between the two islands after disturbances during censuses. Most other islands had estimated populations of 40–70 bats each (Table 1). The low count on Lossau probably resulted from much of the census being conducted in rain.

Eight other islands in the atoll contain suitable habitat for fruit bats but were not visited during the survey. These islands total 89 ha, or 20% of the land area of Ulithi. If fruit bats occur at similar densities on these islands, then another 233–278 bats would be present in the population. Thus, we estimated a total population of 1128–1333 bats for the entire atoll. These unsurveyed islands and their estimated population sizes were as follows:

TABLE 1

RESULTS OF CENSUSES, ESTIMATED POPULATION SIZES AND DENSITIES, AND SIZES OF COLONIES OF *Pteropus mariannus ulthiensis* ON 14 ISLANDS IN ULITHI ATOLL, MARCH 1986

ISLAND	SIZE (ha)	PROPORTION OF ISLAND SURVEYED (%)	ESTIMATED AREA OF POTENTIAL HABITAT (ha)	INDEX OF HABITAT QUALITY	INDEX OF FEEDING EVIDENCE	NO. OF BATS OBSERVED IN COLONIES	MAXIMUM NO. OF BATS RECORDED IN ONE CENSUS	MINIMUM POPULATION DENSITY (bats/km^2)	ESTIMATED POPULATION SIZE	ESTIMATED POPULATION DENSITY (bats/km^2)
Falalop	93	80	74	moderate	high	26	50	54	50–60	54–65
Asor	34	90	32	moderate	high	46, 31, 5	95	279	120–145	353–426
Sorlen	33	80	33	high	high	146, 21, 14, 7	195	591	200–225	606–682
Mogmog	26	90	24	moderate	high	41	49	188	60–70	231–269
Potangeras	19	80	19	high	high	19, 7	49	258	70–80	368–421
Lam	12	80	12	high	high	15, 6	22	183	40–50	333–417
Sorenleng	11	90	11	high	none	30, 8	46	418	60–70	545–636
Pigelelel	18	70	18	high	low		17	94	20–25	111–139
Elipig	5	90	5	high	none		3	60	5–10	100–200
Feitabul	16	70	16	high	high	6	24	150	40–50	250–313
Lossau	19	50	19	high	moderate		8	42	40–50	211–263
Fossarai and Lolang[a]	34	80	32	high	high	125, 14, 12	125	298	150–175	357–417
Mangejang	8	90	8	high	low					
Total	12	80	12	high	high	9	32	267	40–50	333–417
	340						715	210	895–1,060	263–312

[a] Data from Fossarai and Lolang were combined into a single census.

Piras, 6 ha, 16–19 bats; Song, 11 ha, 29–34 bats; Pig, 5 ha, 13–16 bats; Pau, 15 ha, 39–47 bats; Bulubul, 5 ha, 13–16 bats; Losiep, 21 ha, 55–65 bats; Iar, 16 ha, 42–50 bats; and Gielap, 10 ha, 26–31 bats.

Estimated densities of fruit bats on the four inhabited islands, covered predominantly by agroforest, were not significantly different from those on uninhabited islands (Mann-Whitney U-test, $n_1 = 9$, $n_2 = 4$, $U = 21$, $P = .68$). This suggests that bats did not specifically avoid islands with people. However, bats avoided villages by day, entering them only at dusk and at night to feed. The lowest density of fruit bats occurred on Falalop, which is the most developed and populated island in the atoll. During the day, bats were restricted to the least disturbed portion of the island on the southeast corner in an area with some remaining native trees. Similarly, bats roosted on the north end of Fossarai, about 1.2 km away from that island's village, or on the small uninhabited and neighboring islet of Lolang. In contrast, bat colonies on Mogmog and Asor occurred 100–200 m beyond the edges of villages. Ulithians sometimes deliberately disturb roosting bats. We witnessed three men throwing rocks at a small roost on Falalop. Also, small numbers of fruit bats are occasionally shot by hunters.

Our estimated numbers are the highest densities reported for the genus *Pteropus* and may result from limited hunting. Population densities of 0.4–150 bats/km^2 were reported from the Mariana Islands, where heavy hunting on some islands has almost eliminated bats (Wiles et al. 1989). In the Ngerukewid Islands Wildlife Preserve in Palau, a small set of raised limestone islands, fruit bats occurred at an estimated density of 125–175 animals/km^2 under conditions of little human exploitation (Wiles and Conry 1990). Dolbeer et al. (1988) reported densities of 60–210 bats/km^2 in the Maldive Islands.

We did not note, and residents did not report, large nightly movements of fruit bats between Ulithi's islands during the study. However, such movements could occur after darkness and go largely unnoticed. Our survey was made during the windy part of the year before the peak of the breadfruit fruiting season, when, according to residents, bats fly infrequently between islands. A single notable exception to this occurred when most of the large colony on Fossarai flushed during a census and flew to Lolang. *Pteropus* are strong fliers (Nowak and Paradiso 1983) and probably have little trouble reaching any island in the atoll.

Day roosting in *P. m. ulthiensis* primarily was colonial. Of 473 bats observed by G.J.W. and J.E. during the survey, 68% roosted in colonies of >20 bats, 21% occurred in small colonies with 5 to 20 animals, 6% roosted in small groups of two to four animals, and 5% were solitary. These data may be slightly biased toward larger groups, which were probably more easily detected by observers. Solitary individuals and small groups were more likely to be hidden in foliage and overlooked during surveys. A total of 20 colonies was recorded, with all but two of these having <50 animals (Table 1). The largest colonies occurred on Sorlen (146 bats) and Fossarai (125 bats). Colonies were present on most islands and, with the possible exception of the colony on Sorlen, there was no indication that bats sought refuge by congregating at centralized roosting sites on a few remote islands. This further supports the premise that inter-island movements may be limited at this time of the year.

Colonies typically resided in the upper halves of emergent trees with crowns extending several meters above the surrounding forest canopy. Selection of this type of site probably allowed bats to become airborne and land more easily, and escape more quickly during disturbances. Of 32 roost trees observed with five or more bats, *Pisonia grandis* (41%) and *Artocarpus altilis* (31%) were the species selected most frequently. Other trees used included *Calophyllum inophyllum* (13%), *Casuarina litorea* (6%), *Ficus prolixa* (6%), and an unidentified species (3%). Colonies avoided *Cocos nucifera*, a major component of the canopy but rarely an emergent. On Guam, *P. mariannus* colonies roost mainly in large *Ficus* (Wiles 1987), but in Ulithi, these trees were not used commonly despite their wide availability. All roosts were located in the interiors of islands rather than along

TABLE 2

FOODS OF *Pteropus mariannus ulthiensis* ON ULITHI ATOLL, MARCH 1986, BASED ON FEEDING EVIDENCE AND DIRECT OBSERVATIONS

SPECIES	PLANT PARTS EATEN			
	FRUIT	LEAF STEMS	FLOWERS	SAP
Pandanus tectorius	12			
Guettarda speciosa	8	8		
Artocarpus altilis	4	2		
Neisosperma oppositifolia	4			
Eugenia javanicum	4			
Calophyllum inophyllum	1			
Ficus prolixa	1			
Musa sp.	+		+	
Cocos nucifera				+

NOTE: Numbers listed represent the number of islands on which a food was recorded eaten. Pluses (+) designate foods that residents report are also consumed.

shorelines, possibly because interior sites are better shielded from wind.

Colonies were composed primarily of one or more harem groups, each of which contained a single male and several females roosting within 0.3–3.0 m of each other. Of five harems observed in detail, one contained seven females, three held six, and one had four. Harem males aggressively challenged intruding bats trying to enter their harems, especially other males. Colonies usually contained some solitary individuals, most of which were males. These animals roosted in the same trees with harems or in adjacent trees. Similar social behavior has been observed among *P. mariannus* on Guam (Wiles 1987).

Courtship behavior and copulations were noted commonly at and away from colonies. Females with small, medium-sized, and large young were recorded regularly during the survey. Systematic but brief observations at colonies revealed that of 19 females identified, 3 possessed small young and 1 had a medium-sized young. Falanruw (1988*a*) examined three adult female *P. m. ulthiensis* killed in April 1981 and found one pregnant animal, one lactating, and the third not in breeding condition. Other subspecies of *P. mariannus* on Yap and Guam appear to breed year-round (Wiles 1987, Falanruw 1988*a*).

Feeding data were obtained on 12 of the 14 islands visited. We recorded nine species of plants eaten by fruit bats. These included the fruit of eight species, the leaf stems of two species, the flowers of *Musa* sp., and the sap of *Cocos nucifera* (Table 2). The fruit of *Pandanus tectorius* and the fruit and leaf stems of *Guettarda speciosa* and breadfruit were the most commonly recorded foods (Table 2). Numerous *Pandanus* seeds were found eaten and scattered over most of the islands visited. The occurrence of breadfruit in the diet probably was underrepresented, because this tree species was just entering its fruiting season at the time of our survey. Residents reported that bats feed heavily on breadfruit from April to September.

Fresh leaves of *G. speciosa* and *A. altilis* with chewed stems were found on the ground singly or in small groups with pellets of stem pulp sometimes present. The blades of the leaves were never eaten. Additionally, islanders reported that bats occasionally drink from containers of sweet coconut sap gathered for the production of toddy. The containers are placed in the crowns of coconut trees and collect sap from cuts made daily in the stalks of coconut flowers. *Pteropus* feeds on the flowers of *C. nucifera* on other Pacific islands (Sanborn and Nicholson 1950, Wodzicki and Felten 1980, Wiles 1987), but we did not record this abundant flower being used on Ulithi. On several occasions, we noted bats licking water from the surface of leaves after

rain showers. This is a common behavior on Guam (Wiles, pers. observ.) and may be a way for fruit bats to supplement their moisture requirements.

We observed bats to feed for 1 hr on a ripe breadfruit at dusk in the village on Fossarai. Between 1830 and 1900 hr, several bats fed individually on the fruit for 15 sec to several minutes. One ate for 3 min, then flew with a mouthful of fruit to a large *Calophyllum* tree 50 m away. After consuming the fruit, it returned to the breadfruit three more times, each time taking a mouthful of fruit and flying back to the *Calophyllum*. During that time, other bats flew over the breadfruit tree, occasionally landing elsewhere in its crown to feed on several other available fruit.

At 1900 hr, a male bat arrived at the partially eaten breadfruit and began to defend the roughly 4-by-3-by-3-m area around it from other bats. During the next 20 min, intruding bats landed on nearby branches 18 times and all were immediately approached by the male and chased off. Once, it flew to a coconut frond 5 m away to chase away a newly arrived bat. During these encounters, the male's approach was enough to frighten some intruders away, but for other bats, it performed rapid flaps of its partially spread wings to scare them away. The male also successfully defended several times against bats flying close overhead by spreading its wings almost fully and pivoting to face the approaching bats fully. Agonistic growling was commonly heard at night at other feeding sites in Ulithi, but this male remained silent during its defense, perhaps because no physical contact was made with any intruder. On three occasions, the bat rubbed its neck scent glands on leaves near the breadfruit. It returned to feed on the breadfruit between encounters, but spent about half of the 20-min period watching vigilantly for other bats and chasing off any that landed. Despite the intensity of this activity, the male departed abruptly at 1920 hr. A female arrived several minutes later and fed undisturbed on the breadfruit. By the next morning, the fruit was completely consumed except for its hard inner core.

These brief observations suggest that under certain circumstances, dominant *P. m. ulthiensis*, perhaps mostly adult males, establish temporary feeding territories around concentrated food sources. Large fruit (e.g., breadfruit, which typically weigh 0.5–2.0 kg) or perhaps dense clumps of smaller fruit or flowers may be defended, particularly where high densities of bats occur, such as in Ulithi. Gould (1978) described similar behavior in *P. vampyrus*, which defended the flowers of *Durio zibethinus* from conspecifics. *Pteropus m. pelewensis* was observed to repulse intruding bats from clumps of small but abundant flowers of *Intsia bijuga* in Palau (Wiles and Conry 1990). These observations support Marshall's (1985) contention that *Pteropus* and some other pteropodids defend food resources more commonly than previously believed (Fleming 1982, Marshall 1983).

In Ulithi, fruit bats undoubtedly play a major role in dispersing fruits of trees that have seeds >1 cm in diameter, such as *Pandanus*, *Guettarda*, *Neisosperma*, *Eugenia*, and *Calophyllum*. Micronesian starlings (*Aplonis opaca*) are the only other frugivorous vertebrates on the atoll, but they feed primarily on smaller fruit and fruit with smaller seeds (Baker 1951, Jenkins 1983). Coconut crabs (*Birgus latro*) feed on fallen fruit (Reyne 1939, Holthuis 1963) and may rival *Pteropus* as seed dispersal agents for some island tree species, but this aspect of crab biology is poorly understood.

Fruit bats have been protected from hunting since 1981 throughout Yap State (Falanruw 1988*a*,*b*). Although most residents of Ulithi do not like to eat bats, a few people continue to harvest small numbers of bats for subsistence use. The amount of hunting probably had little effect on the atoll's overall bat population, but may have slightly reduced densities. Most bats are killed with air guns.

In November 1988, the government of Yap opened a month-long hunting season for fruit bats on Ulithi. Methods of harvest other than air guns and traditional methods were prohibited. The number of animals killed during the season is unknown, but two shipments totaling 37 bats were exported to Guam.

Ulithi was struck by two severe typhoons with winds of 130 kmph in December 1986 and 185 kmph in January 1987. Many buildings

and at least half of the atoll's breadfruit trees were damaged or destroyed by the storms. It is unknown what effects the storms had on the fruit bat population; however, typhoons have caused considerable mortality to *Pteropus* on islands in the Indian Ocean (Cheke and Dahl 1981).

Inquiries to islanders resulted in reports of fruit bats occurring on several other atolls and islands in western Micronesia where bats previously were unreported. Fruit bats reportedly occur on Fais and Satawal, single islands located 80 km east and 800 km southeast of Ulithi, respectively, and Woleai, an atoll 500 km southeast of Ulithi. The exact identities of these bats are unknown, but presumably they are *P. mariannus*, possibly *P. m. ulthiensis*, or perhaps *P. insularis*, a smaller species known from Truk in the central Carolines.

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