

New records of flying foxes (Chiroptera: *Pteropus* sp.) from Seram, Indonesia, with notes on ecology and conservation status

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ABSTRACT

Bat species in the genus *Pteropus* (flying foxes) occur throughout most of Southeast Asia, but little is known about their distribution and patterns of local diversity across much of Indonesia. To help address this problem, a field survey of *Pteropus* species in Central and West Seram, Maluku Province, Indonesia, was conducted in 2012 and 2013. This study resulted in new records of rare Moluccan bats, including new locality records for four near-endemic species: *P. chrysoproctus*, *P. melanopogon*, *P. ocellaris*, and *P. temminckii*. Together with data from additional specimens, these records provide new information about morphological variation in Moluccan *Pteropus*. High local diversity of large-bodied bats with restricted geographic ranges raises interesting questions about evolution in *Pteropus* and about ecological niche partitioning in Palearctic pteropodid communities. More monitoring efforts in Maluku are needed, as the roosts located during the 2012–2013 survey are some of the only known sites where these species may be found, and none of these sites are located in protected areas. Without updated natural history data and taxonomic revision, proper management decisions cannot be made for any of these threatened species despite mounting anthropogenic pressure on their populations.

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INTRODUCTION

The genus *Pteropus* (Chiroptera: Pteropodidae) includes over 60 species of large fruit bats commonly known as flying foxes. These bats inhabit Paleotropical regions ranging from Madagascar to Australia and the South Pacific, with highest species diversity occurring in Southeast Asia (Mickleburgh et al., 1992; Simmons, 2005). Although some species occupy extensive ranges on continental landmasses, the majority of *Pteropus* species are endemic to islands and coastal areas (Simmons, 2005; Helgen et al., 2009; Almeida et al., 2014). The rarity of and difficulty in locating *Pteropus* in the wild has led to a paucity of data on their occurrence, particularly in island archipelagos that comprise much of Indonesia. This is particularly true in poorly studied areas such as Seram, Maluku Province, Indonesia, where even local forestry rangers may be unfamiliar with these bats. Data on local species diversity, distributions, and roost sites are fragmentary. These data are necessary to any future conservation and research efforts for all *Pteropus* species, many of which are intensely threatened by burgeoning development in Indonesia.

Maluku (= the Moluccas, or Spice Islands) is a large island archipelago between Sulawesi and New Guinea (fig. 1). There is no agreement as to the exact number of islands in Maluku (77,990 km²), which is part of the country of Indonesia, but Maluku is often described as “having 999 islands and being 90% sea” (Monk et al., 1997). As a whole, the region is broken into two administrative provinces: North Maluku (including Bacan, Halmahera, Morotai, Obi, the Sula Islands, Ternate, and Tidore) and Maluku (including Ambon, the Aru Islands, Buru, the Kai Islands [= Kei Islands], and Seram). Seram is the largest (17,429 km²) and highest (3027 m) island in Maluku Province, and it is located centrally in the biogeographically complex region of Wallacea on its own microplate (Linthout and Helmers, 1994). Its geological isolation, size, elevation, and biological diversity have contributed to the recognition of Seram as a hotspot of endemism for vertebrate taxa including birds (Smiet, 1982) and rodents (Helgen, 2003).

Little bat research has been done in Maluku in recent decades despite its recognition as a priority region in the IUCN Old World Fruit Bat Action Plan (Mickleburgh et al., 1992). This has led to a lack of understanding of current levels of chiropteran diversity in the region, which are likely underestimated. Pteropodid species have not been monitored at all for almost two decades in Maluku, a period in which human development has likely changed the landscape significantly. The handful of studies conducted in the 20th century have primarily focused on pteropodids other than *Pteropus* because this genus requires dedicated sampling efforts beyond those usually employed for other bats (e.g., canopy netting and active hunting from roost sites). This has resulted in relatively low representation of Maluku *Pteropus* in museum collections (table 1) (Koopman and Gordon, 1992; Kitchener et al., 1993, 1994, 1995; Kitchener and Maryanto, 1995; Kompanje and Moeliker, 2001). Research on Moluccan pteropodids has primarily focused on smaller species of the genera *Syconycteris* and *Nyctimene* (Kitchener et al., 1993, 1994; Kompanje and Moeliker, 2001). Pteropodid specimens, including *Pteropus*, deposited in the collection of the Zoölogisch Museum of Amsterdam were discussed in detail in Bergmans (2001), though some of these were collected in the earlier part of the 20th century and do not represent more recent survey efforts of the species to determine their population status.

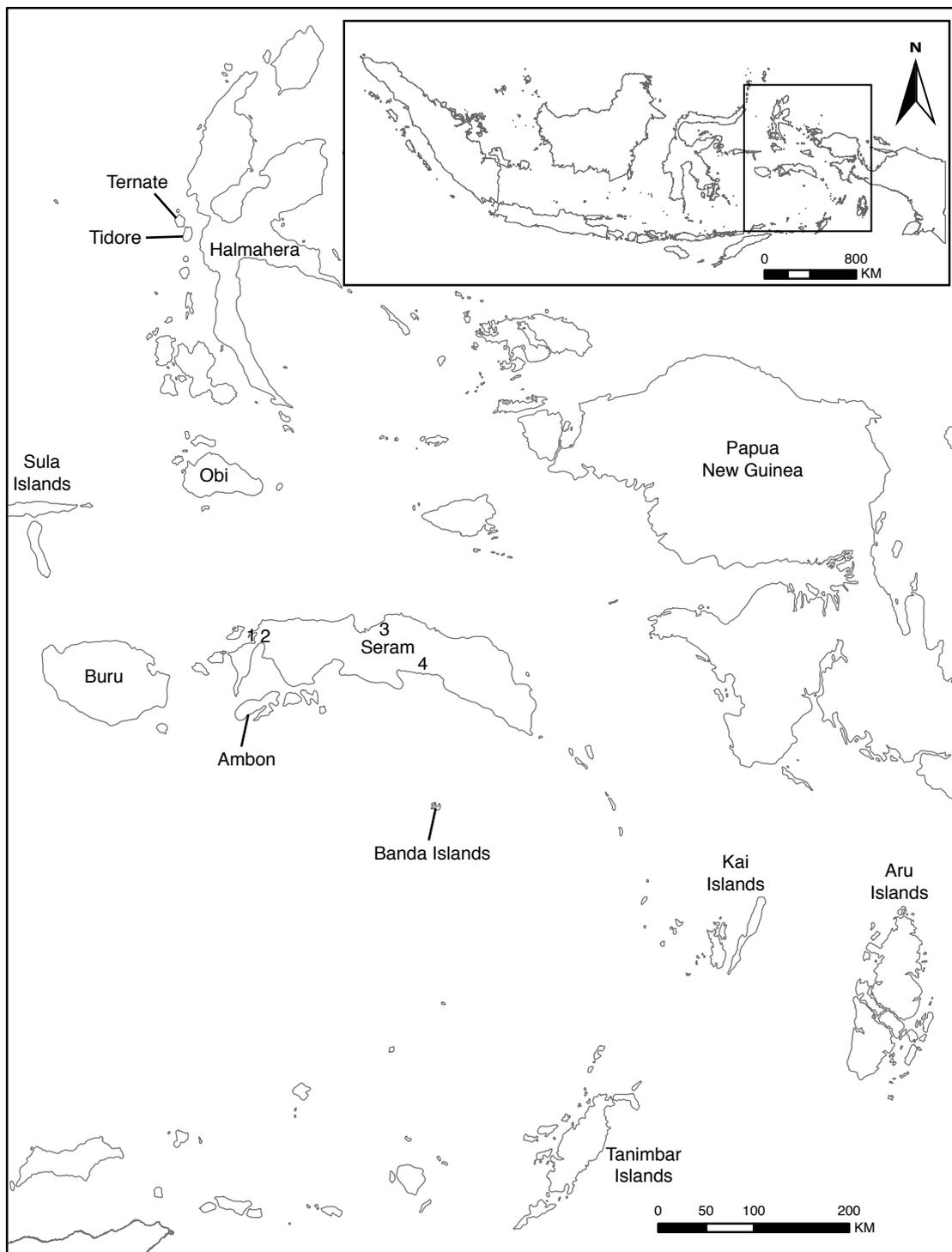


FIG. 1. Map of Maluku Province, Indonesia, showing major islands. Points mark localities visited on Seram in this study: (1) Pulau Marsegu, (2) Sipa, (3) Pulau Raja, and (4) Mosso.

Studies on Seram have been few and mostly focused solely on areas in or near Manusela National Park in Central Seram Regency (Kitchener and Maryanto, 1995; Kitchener et al., 1995). West Seram Regency is of particular interest to conservationists because of its biodiversity combined with high levels of human activity due to its proximity to Ambon and other urban centers and ports, leading to its popularity as a domestic tourism destination. The regency also faces environmental issues related to blast fishing and overexploitation of live reef fish species, such as grouper (Epinephelinae), coral trout (*Plectropomus* spp.), and wrasse (*Cheillinus undulatus*) for the international fish market (Fanli Marine and Consultancy Sendirian Berhad, 2012). Hunting of wild animals as a preferred protein source, particularly mammals like bats and phalangers, is still prevalent in Central Maluku (Latinis, 1996). The true cumulative effects of hunting on biodiversity are largely unknown, however, because of the lack of taxonomic work conducted in the region. Seram remains a relatively unexplored island, largely because transportation is dependent on unreliable marine means, but plans to further develop roads and bridges on the island will threaten its biota as access increases to allow for further natural resource exploitation.

Four species of *Pteropus* (see below) are known from the islands of Seram (17,100 km²) and Buru (9505 km²). This level of diversity is exceptional, as most similarly sized islands in Southeast Asia usually support only two species of *Pteropus* (Mickleburgh et al., 1992). In comparison, Sulawesi (174,600 km²), more than 10 times larger in area, supports five *Pteropus* species, as does the entire Philippines archipelago (298,170 km²) (Mickleburgh et al., 1992). The evolutionary or ecological drivers behind this species diversity cannot be determined given the paucity of phylogenetic studies or natural history data available currently.

The goal of this study was to review the population and conservation statuses of the near-endemic *Pteropus* species on Seram, Maluku. Four *Pteropus* species are native to Seram: *P. chrysoproctus*, *P. melanopogon*, *P.ocularis*, and *P. temminckii* (Mickleburgh et al., 1992; Simmons, 2005). Little is known about these taxa because they have very restricted ranges. *Pteropus chrysoproctus* is known only from Ambon, Buru, Seram, and small islands east of Seram, and may include more than one species (Simmons, 2005; K. Helgen, personal commun.). Similarly, *Pteropus melanopogon* occurs on Ambon, Buru, Seram, the Banda Islands, Yamdena (in the Tanimbar Islands), and adjacent small islands, and probably also contains more than one species (Simmons, 2005; K. Helgen, personal commun.). *Pteropus temminckii* occurs on Ambon, Buru, Seram, and nearby small islands, perhaps including Timor (Simmons, 2005). *Pteropusocularis* is recorded from just Ambon, Buru, and Seram (Simmons, 2005). Here we present new data on localities, roost sites, and morphology of the Seram *Pteropus* species. Tissue samples collected as part of this project will contribute to ongoing work on diversity, phylogeography, and evolution in this genus.

MATERIALS AND METHODS

All protocols followed the guidelines from the American Society of Mammalogists for collection (Sikes et al., 2011) and were approved by IACUC Committee at City College of New York (protocol no. 896.2). We conducted *Pteropus* surveys from 2012 to 2013 in Central and

TABLE 1. Sites where each pteropodid species was captured from our surveys.

“X” indicates that individuals were captured, “O” indicates that individuals were noted but not captured at each site.

Species	Sites			
	P. Marsegu	Sipa	P. Raja	Mosso
<i>Dobsonia moluccensis</i>		X		X
<i>Dobsonia viridis</i>		X		
<i>Macroglossus minimus</i>		X		X
<i>Nyctimene cephalotes</i>		X		X
<i>Pteropus chrysoproctus</i>			X	O
<i>Pteropus melanopogon</i>	X		O	O
<i>Pteropus ocularis</i>	X			
<i>Pteropus temminckii</i>	X			X
<i>Rousettus amplexicaudatus</i>		X		X
<i>Syconycteris australis</i>		X		X

West Seram regencies, Maluku Province. Bats were captured using a system of two 12 and 6 m canopy mistnets at four sites on Seram as follows: Pulau Marsegu (mangrove near Pulau Osi, West Seram), Sipa (orchard near Pelita Jaya, West Seram), Pulau Raja (mangrove near Sawai, Central Seram), and near Mosso (montane secondary forest, Central Seram). The sites were chosen based on recent sightings of *Pteropus* in the area, and all other pteropodids opportunistically captured were also recorded. Due to permit limitations, only representative individuals were collected as vouchers while others were identified and released.

All pteropodid species captured were identified to species and measurements were taken prior to release or vouchering. Four specimens of *P. chrysoproctus*, one of *P. melanopogon*, one of *P. ocularis*, and three of *P. temminckii* were captured, measured, weighed, and vouchered. Voucher specimens (two males and two females where possible) were skinned, with remaining samples preserved in 8%–10% formalin in the field, and subsequently transferred to 70% ethanol for preservation. A 4 mm² biopsy wing punch was taken along with muscle and liver samples and preserved in 95% ethanol. Associated ectoparasites were collected if present. The specimens are housed at the Museum Zoologicum Bogoriense–LIPI (MZB) in Bogor, Indonesia. Skulls were extracted and measured upon return from the field to MZB. Duplicate tissue samples are housed in the Ambrose Monell Cryo Collection at the American Museum of Natural History in New York.

The following external, cranial, and dental characters were taken using digital calipers: head and body length (HB), ear length (EAR), forearm length (FA), tibia length (TIB), hind foot length (HF), greatest skull length (GSL), zygomatic breadth (ZB), least interorbital width (LIOW), post-orbital width (POW), braincase width (BW), condylobasal length (CBL), condylocanine length (CCL), upper canine to second molar length (CM2), outside upper canine breadth (C1–C1), breadth across the second upper molars (M2–M2), lower canine to third molar length (C–M3). Weight (WT) was measured in grams using Pesola scales. We also measured specimens available

TABLE 2. Skull and dental measurements of Moluccan *Pteropus*.

All measurements in mm, blanks represent unavailable data. Asterisks indicate type specimens.

Coll.ID	Age/Sex	GSL	ZB	LIOW	POW	BW	CBL	CCL	CM2	C-C	M2-M2	CM3
<i>Pteropus chrysoproctus</i>												
MZB 1077	A ♂	71.5	38.7	10.2	6.5	23.4	66.8	62.5	27.2	12.3	18.1	31.1
MZB 13568	A ♂	73.4	41.0	9.3	7.9	23.1	71.8	66.3	28.9	13.5	17.3	32.0
ZMA 16.369 ^a	A ♂	73.6										
MZB 1076	SA ♂	59.1	29.4	7.6	9.8	23.3	56.5	52.5	23.9	10.5	14.3	26.0
MZB 36911	SA ♂	68.4	34.5	10.4	10.7	23.7	67.6	61.6	26.4	11.6	16.2	28.7
MZB 36909	A ♀	76.6	41.4	10.0	7.9	24.4	76.2	69.4	29.1	13.6	19.5	32.5
MZB 1078	A ♀	67.6	38.3	9.3	7.5	22.8	66.8	61.8	26.1	12.5	16.5	
ZMA 16.370 ^a	A ♀	76.5										
MZB 36908	SA ♀	60.7	30.7	8.7	11.3	23.5	58.0	52.9	24.6	11.9	16.0	27.6
MZB 36910	SA ♀	67.0	33.4	9.1	9.6	24.8	65.8	59.5	26.2	11.9	16.3	28.4
MZB 0219	A	63.3	31.3	8.4	8.8	21.8	61.1	55.7	25.2	9.8	15.2	27.5
<i>Pteropus melanopogon</i>												
MZB 13566	A ♂	79.3	40.4	10.7	8.2	24.3	80.0	73.6	30.9	14.1	18.6	35.0
MZB 13569	A ♂	81.3	45.0	11.4	7.4	24.1	81.0	75.0	31.9	15.3	19.4	36.3
MZB 13570	A ♂	80.6	45.0	11.7	11.7	23.6	78.4	71.4	30.4	16.1	19.5	34.7
MZB 1075	A ♂	85.5	46.9	11.4	7.9	28.1	83.0	76.3	32.5	16.0		36.3
MZB 36927	Juv ♂	48.8	26.0	7.6	11.1	22.0	45.0					
MZB 1074	A ♀	79.5	45.4	11.0	7.9	25.0			30.6	14.7	20.0	34.7
ZMA 16.368 ^a	A ♀	78.8										
FMNH 8228	SA	71.7	38.2	9.7	9.9	23.4	71.7	65.8	26.1	13.7	4.2	32.7
MZB 1059	A	84.4	45.4	11.4	7.5	24.9	82.7	76.5	31.8	14.9	19.7	36.2
var. <i>keyensis</i>												
*ZMB 4752	A ♂		46.3	11.0	7.6	26.3				14.6		
*ZMB 4701	A ♀	74.9	41.1	9.3	7.4	26.2	73.3	67.6	29.4	14.5	19.4	33.3
var. <i>aruensis</i>												
*ZMB 4703	A ♂	76.4	40.3	10.7	10.2	26.3	74.4	68.6	30.3	15.2	18.0	34.8
*ZMB 4962	A ♂			11.4	9.1				31.4	15.7	21.1	34.9
<i>Pteropusocularis</i>												
*ZMB 2958	A ♂		35.0	7.0	7.5	22.3			24.5	11.9	15.8	27.4
MZB 36928	SA ♂	62.3	33.4	6.9	7.5	22.1	61.6	56.5	23.3	11.7	16.2	26.7
MZB 13361	A ♀	59.9	32.1	7.7		21.9	57.9	53.7	23.0	11.3	14.7	25.3
<i>Pteropus temminckii</i>												
*ZMB 4964	A ♂		28.8	7.5	9.1	20.2			18.7	10.2	13.2	21.3
*ZMB 3473	A ♂								18.6	9.5	12.6	20.8
MZB 36925	A ♂	51.4	28.1	6.6	9.8	20.3	49.1	44.8	18.8	9.3	12.9	20.5
MZB 2155	A ♀	50.8	26.8	6.7	7.9	19.7	49.7	44.5	17.0	9.1	11.8	20.0
MZB 15597	A ♀	53.8	29.8	7.0	7.5	19.9	51.6	47.4	20.0	10.0	13.7	21.9

Coll.ID	Age/Sex	GSL	ZB	LIOW	POW	BW	CBL	CCL	CM2	C-C	M2-M2	CM3
MZB 36924	A ♀	51.7	29.1	7.8	9.2	20.3	50.1	45.6	19.2	9.4	13.9	21.8
MZB 36926	A ♀	51.2	28.1	6.8	9.1	20.2	48.5	43.6	18.3	9.4	13.1	20.1
MZB 8341	A ♀		29.3	6.9	9.9	28.3	48.0	43.9	19.0	9.8	13.1	20.9
ZMA 3080 ^a	SA ♀	44.9										
ZMA 3084 ^a	A ♀	50.4										

^a From Bergmans 2001.

in the collections at MZB, AMNH, and FMNH (see below), and extracted available measurements from the literature for comparative purposes. Comparative photos of skulls and jaws of representatives of each of the four *Pteropus* species from Seram are provided in figures 2–6.

Museum collections are abbreviated as follows: **AMNH**, American Museum of Natural History, New York; **AM**, Australian Museum, Sydney; **BMNH**, British Museum of Natural History, London; **FMNH**, Field Museum of Natural History, Chicago; **MZB**, Museum Zoologicum Bogoriense, Indonesian Institute of Sciences, Bogor; **NMNL**, National Museum of Natural History Naturalis Leiden; **ZMB**, Universität Humboldt Museum für Naturkunde, Berlin.

RESULTS AND DISCUSSION

All 10 species of pteropodids known to be native to Seram (Mickleburgh et al., 1992; Simmons, 1995) were captured and identified during our surveys: *Dobsonia moluccensis*, *D. viridis*, *Macroglossus minimus*, *Nyctimene cephalotes*, *Pteropus chrysoproctus*, *P. melanopogon*, *P. ocularis*, *P. temminckii*, *Rousettus amplexicaudatus*, and *Syconycteris australis* (table 1). Since the primary targets of the study were *Pteropus* species, we describe here only vouchered *Pteropus* individuals. No *Pteropus* were found at the Sipa site despite earlier reports by forestry officials and local people that the flying foxes foraged there. We did, however, find bite marks on overripe *jambu* fruit (*Syzygium* sp.) at the Sipa site that suggest that flying foxes had been there recently.

Craniodental measurements (table 2) and external measurements (table 3) of Moluccan *Pteropus* specimens from the MZB, FMNH, and AMNH were compared with those captured during our survey. The newly captured adult specimens fall well within the expected range of forearm and cranial measurements for each species, as suggested by data from Flannery (1995), Bergmans (2001), and historical specimens.

Pteropus chrysoproctus (Temminck, 1837)

Moluccan flying fox

TYPE LOCALITY: Ambon, Central Maluku, Indonesia.

NEW MATERIAL: Pulau Raja, offshore from Sawai, Maluku Tengah Regency, Maluku Province, Indonesia. Collected by Sigit Wiantoro and Susan M. Tsang, 3 females: MZB 36908, MZB 36909, MZB 36910, 1 male MZB 36911.

OTHER SPECIMENS EXAMINED: MZB 0219, MZB 1076, MZB 1077, MZB 1078, MZB 13568, and ZMB 2626.

OCCURRENCE AND IDENTIFICATION: *Pteropus chrysoproctus* is rare in collections, but likely not uncommon despite anecdotal evidence of historical decline according to the IUCN red list assessment (Huston and Helgen, 2013). The individuals encountered at Pulau Raja in Seram resemble specimens from older collections purportedly from Ambon and Seram, including the poorly preserved syntype in Berlin (ZMB 2626). Unlike the other three sympatric species, the ears (>30 mm) are distinctly longer than the CM2 length. The pelage is dark reddish brown over most of the body, appearing a bit brighter on the ruff and darker red on the belly—another unique characteristic among Moluccan species. Compared to the sympatric *P. melanopogon*, *P. chrysoproctus* is smaller in size and has a much narrower skull: FA 170–180 mm, GSL 63–77 mm, ZB 31–42 mm, LIOW 8–10.5 mm (compared to FA >185 mm, GSL >75 mm, ZB >40 mm, LIOW >10 mm in *P. melanopogon*) (tables 2 and 3). Similarity between individuals from Ambon and Seram is important to note, as populations of *P. chrysoproctus* from different Moluccan islands may represent distinct subspecies or species (K. Helgen, personal commun.).

HUMAN DISTURBANCE: Hunting of *P. chrysoproctus*, along with habitat loss, threatens the species. Thought to occur only in small groups, our survey found a roost of approximately 300 individuals in a patch of mangrove trees (primarily *Rhizophora* sp.) near Manusela National Park. According to the local villagers in Sawai and forestry rangers, the roost is present year-round and will likely not be lost to development in the near future since it is protected as an ecotourism attraction by local resorts. However, according to forestry rangers, this is the only roost site for this species currently known on Seram. There were no indications of presence of *P. chrysoproctus* colonies at any of the other sites we surveyed.

Anecdotal evidence suggests that these bats have been hunted intensely and have either moved permanently or are locally extirpated at other sites. According to the local people, *P. chrysoproctus*, along with *P. temminckii*, were once the most commonly encountered species by hunting parties seeking *Pteropus*, particularly at their foraging sites. Patchy forests near villages such as Mosso in Central Seram were known to be foraging areas for many pteropodids, including *Pteropus*, *Nyctimene*, and *Syconycteris*. Through interviews with local residents, we learned that Muslim villagers do not enter the forest to forage because of their belief that it is a sacred area, but Christian villagers from the other side of the forest enter often to hunt bats. The Christian villagers stated that there were more bats in the area in the past decades than there are now, and described three distinct types: the “red one” (likely *P. chrysoproctus*), the “white one” (likely *P. temminckii*), and the “black one” (likely *P. melanopogon*). We concluded that the “black one” was *P. melanopogon* and not *P. ocularis* based on size descriptions (“very big”) and distinct markings (“white belly”), and we were able to confirm this visually when we were shown a small group of *P. melanopogon* by villagers in the nearby forest.

Villagers near Manusela National Park customarily go into stands of *kapok* trees (*Ceiba pentandra*) where *Pteropus* were known to forage in order to shoot bats for food. It is customary for the men to hunt *Pteropus* as an appetizer for drinking parties. Even if roosting sites are within the limits of a national park, there is no guarantee of protection for *Pteropus* species because the bats may be vulnerable to hunters when foraging outside park boundaries. Forestry rangers indicated that after severe storms battered the mangroves in 2010, the colony of *P.*



FIG. 2. Dorsal views of skulls of **A**, *Pteropus chrysoproctus* (MZB 36909 ♀); **B**, *Pteropus melanopogon* (MZB 1075 ♂); **C**, *Pteropusocularis* (MZB 36928 ♂); **D**, *Pteropus temminckii* (MZB 36925 ♂).

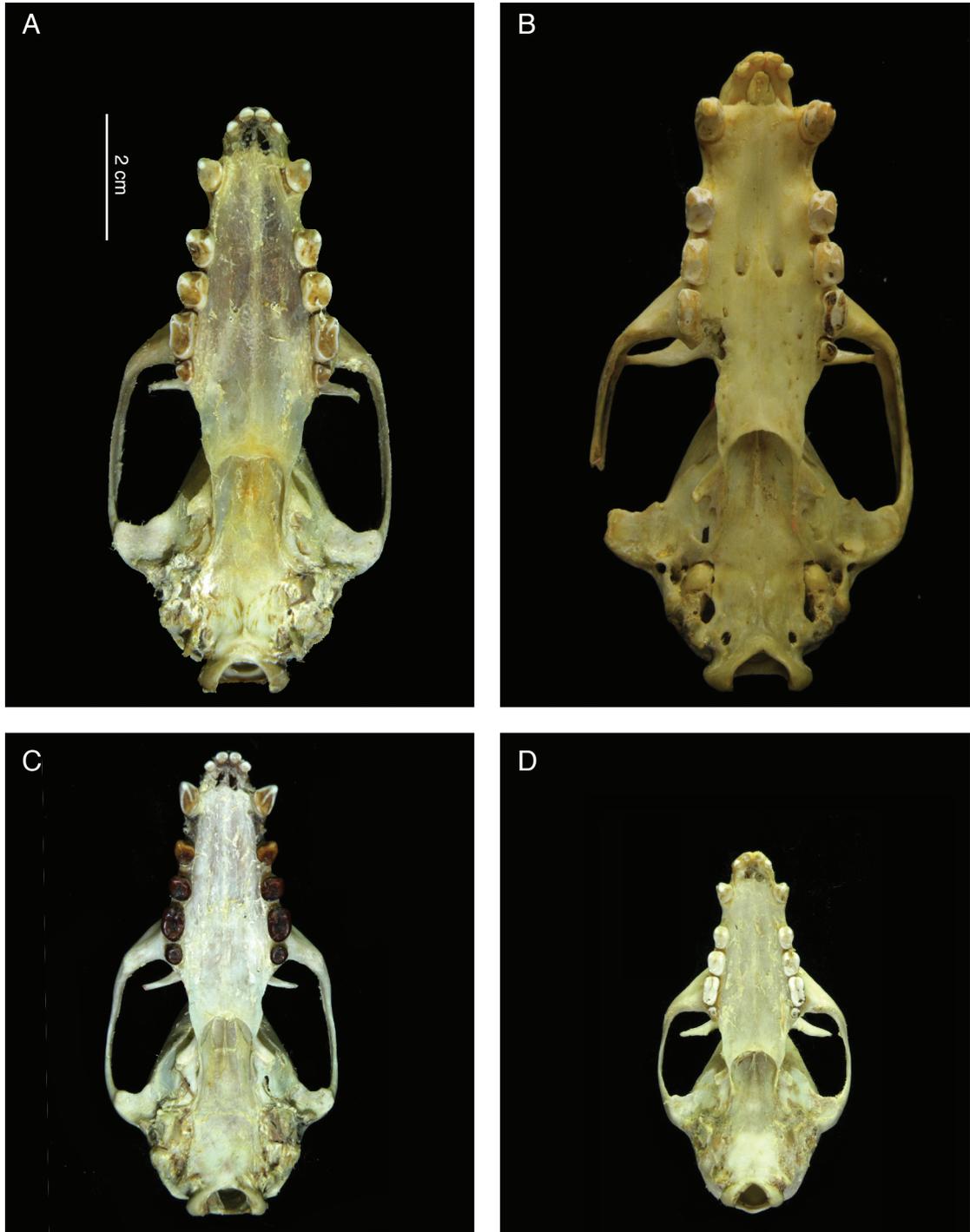


FIG. 3. Ventral views of skulls of **A**, *Pteropus chrysoproctus* (MZB 36909 ♀); **B**, *Pteropus melanopogon* (MZB 1075 ♂); **C**, *Pteropus ocularis* (MZB 36928 ♂); **D**, *Pteropus temminckii* (MZB 36925 ♂).

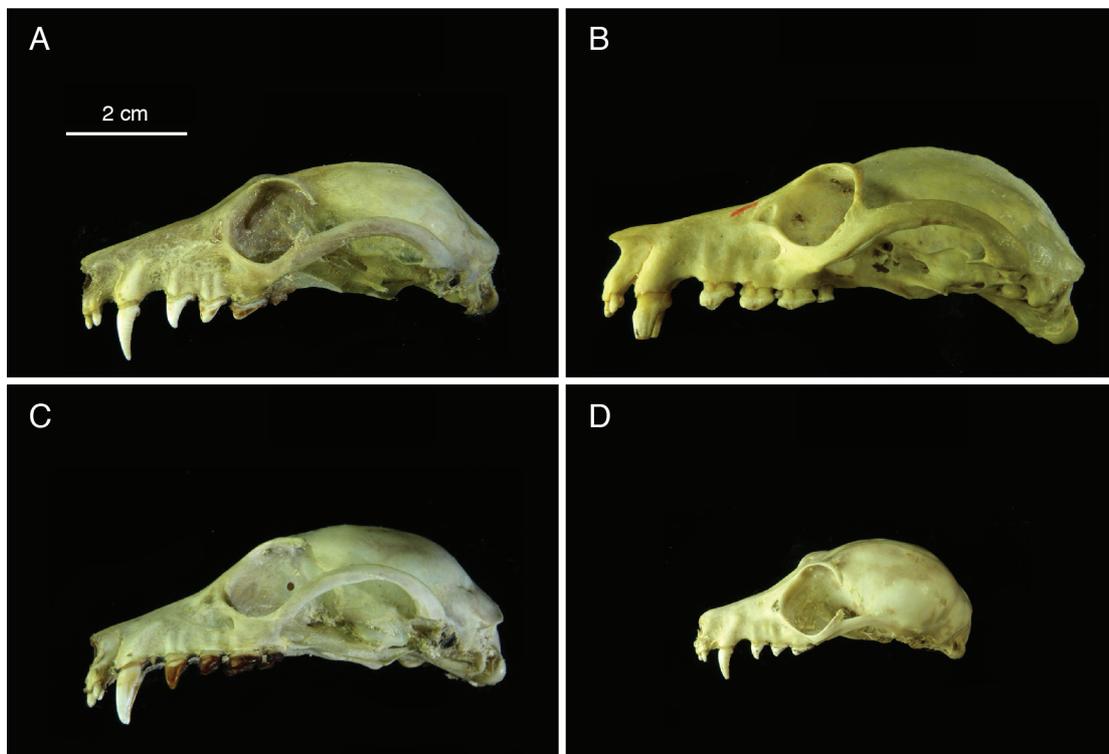


FIG. 4. Lateral views of skulls of **A**, *Pteropus chrysoproctus* (MZB 36909 ♀); **B**, *Pteropus melanopogon* (MZB 1075 ♂); **C**, *Pteropus ocularis* (MZB 36928 ♂); **D**, *Pteropus temminckii* (MZB 36925 ♂).

chrysoproctus temporarily moved to areas surrounding the national park, including villages where bat consumption is common. The *P. chrysoproctus* population was purportedly much larger prior to this storm.

CONSERVATION: *Pteropus chrysoproctus* is currently listed as Near Threatened by the IUCN, but our data suggests that the species should be listed as Vulnerable under criteria B1a, b (iii, iv). This categorization means that the extent of the species occurrence is less than 20,000 km², with fewer than 10 known localities, and continuing decline in both habitat and number of subpopulations. It is extremely unlikely *P. chrysoproctus* is still on Ambon since its colonial behavior would attract the attention of the local forestry rangers. While the colony of *P. chrysoproctus* in Sawai is an ecotourism attraction and will likely remain undisturbed, it is not under the protection of Manusela National Park nor local forestry services. The site merits some official level of recognition for its uniqueness and high conservation value.

Pteropus melanopogon (Peters, 1867)

Black-bearded flying fox

TYPE LOCALITY: Amboina (= Ambon), Central Maluku, Indonesia.

NEW MATERIAL: Pulau Marsegu, Seram Bagian Barat Regency, Maluku Province, Indonesia. Collected by Sigit Wiantoro and Susan M. Tsang, 1 female MZB 36927.

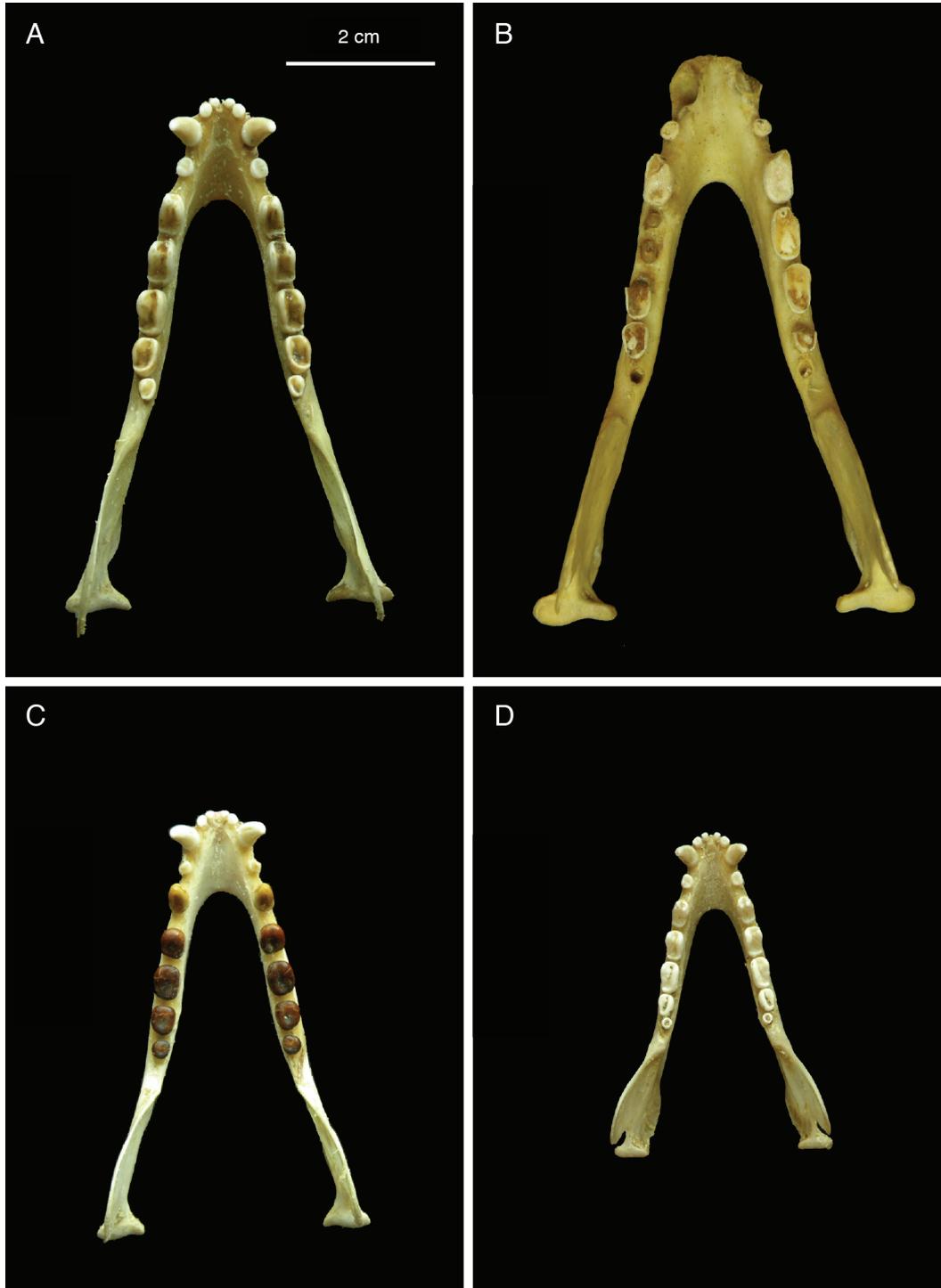


FIG. 5. Dorsal views of lower jaws of **A**, *Pteropus chrysoproctus* (MZB 36909 ♀); **B**, *Pteropus melanopogon* (MZB 1075 ♂); **C**, *Pteropus ocularis* (MZB 36928 ♂); **D**, *Pteropus temminckii* (MZB 36925 ♂).

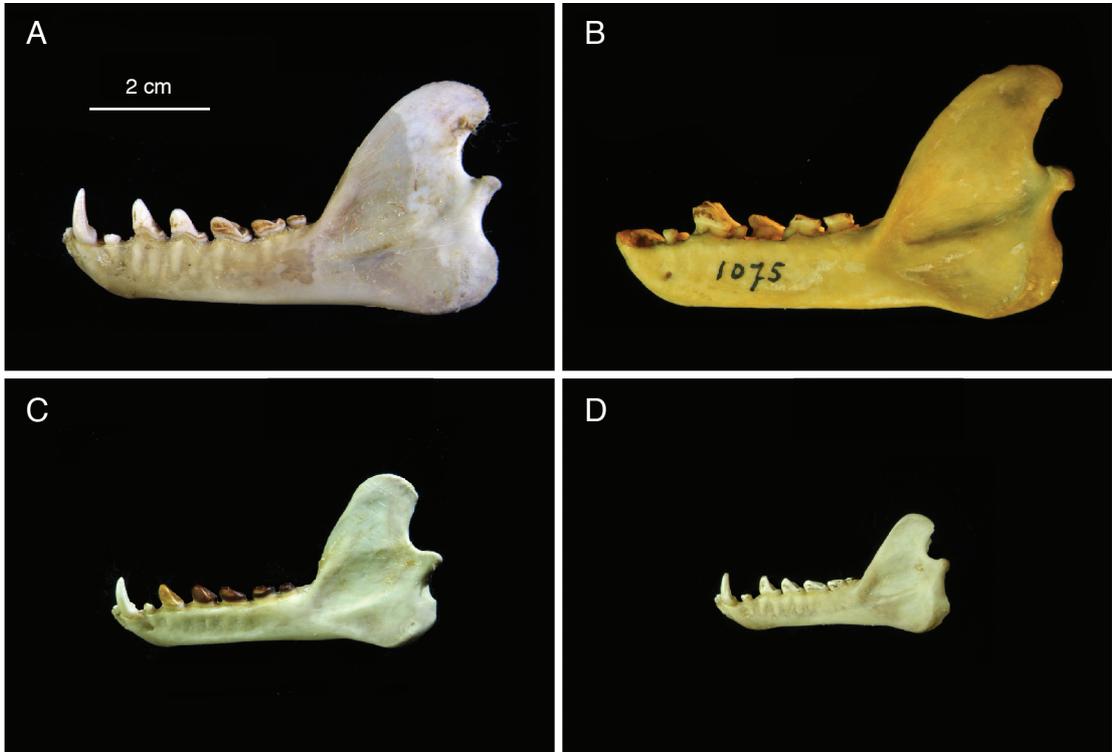


FIG. 6. Lateral views of lower jaws of **A**, *Pteropus chrysoproctus* (MZB 36909♀); **B**, *Pteropus melanopogon* (MZB 1075♂); **C**, *Pteropus ocularis* (MZB 36928♂); **D**, *Pteropus temminckii* (MZB 36925♂).

OTHER SPECIMENS EXAMINED: MZB 1059, MZB 1074, MZB 1075, MZB 13566, MZB 13569, MZB 13570, FMNH 8228, ZMB 4752, ZMB 4701, ZMB 4703, and ZMB 4962.

OCCURRENCE AND IDENTIFICATION: *Pteropus melanopogon* were found roosting in a colony of approximately 200 individuals in two patches of mangrove trees (*Rhizophora* sp.) on Pulau Marsegu, an island named for the presence of the bat colony (*marsegu* is the local word for “flying fox”). Only a single injured juvenile was captured, meaning we could not corroborate species identity by using available adult craniodental or external measurements. Photographic and video documentation of the roosting groups were collected to corroborate species identity by SMT since no adults were captured at this site. The adult *P. melanopogon* we observed in the colony in Seram fit the description of the nominotypical form of this species provided by Andersen (1912): “blackish back, chestnut head and collar, golden-buffy underside of body.” These individuals all appear to be part of a single colony of bats that moves between trees on the island of Pulau Marsegu throughout the course of the day; at dusk, there is only one large group that was observed exiting from the roost. We are confident that the juvenile we collected is *P. melanopogon* because we opportunistically collected this individual from under the roosting tree after the main colony of adult *P. melanopogon* had departed.

Occasionally, *P. melanopogon* were spotted roosting with the main *P. chrysoproctus* colony, though they remained on separate trees. When we visited the Sawai site in June 2012, a small

TABLE 3. External measurements of Moluccan *Pteropus*.

Most external character data are not available for the specimen, as skins are difficult to manipulate. Weight is in grams, all other measurements are in mm, blanks represent unavailable data. Asterisks indicate type specimens.

Coll.ID	Age/Sex	WT	FA	HB	EAR	TIB	HF
<i>Pteropus chrysoproctus</i>							
*ZMB 2626	A ♂		145				52
MZB 13568	A ♂		174			82.00	
ZMA 16.369 ^a	A ♂		166				
MZB 36911	SA ♂	420	144	220	30.91	65.72	52.66
MZB 36909	A ♀	780	180	265	30.81	79.91	52.00
MZB 1078	A ♀	670					
ZMA 16.370 ^a	A ♀		170				
MZB 36908	SA ♀	290	138	190	27.08	62.39	48.73
MZB 36910	SA ♀	380	150	210	32.09	66.14	49.26
MZB 0219	A		140				
<i>Pteropus melanopogon</i>							
MZB 13566	A ♂	510	188				
MZB 13569	A ♂	882	205				
MZB 13570	A ♂	900	204				
MZB 1075	A ♂		192				
MZB 36927	Juv ♂	150	91	146	23.71	38.31	45.33
MZB 1074	A ♀		192				
FMNH 8228	SA		169				
MZB 1059	A		198				
var. <i>keyensis</i>							
*ZMB 4752	A ♂		172				55
*ZMB 4701	A ♀		174		31	80	53
var. <i>aruensis</i>							
*ZMB 4703	A ♂		181		38	87	66
*ZMB 4962	A ♂		183				
<i>Pteropus ocularis</i>							
*ZMB 2958	A ♂		138				
AMNH 234939	A ♂		118				
MZB 36928	SA ♂	400	144	195	26.29	60.89	44.38
MZB 13361	A ♀	220	142		24		37
MZB 0112	A ♀		132		18.41		
<i>Pteropus temminckii</i>							
*ZMB 2633	A ♂		96				30
*ZMB 4964	A ♂		101				30
*ZMB 3473	A ♂		97				

MZB 36925	A ♂	150	97	160	23.92	45.59	30.09
MZB 14839	A ♂	150	100	155	22		22
MZB 36924	A ♀	200	106	155	22.71	47.10	32.38
MZB 36926	A ♀	160	102	140	22.88	44.86	31.51
MZB 8341	A ♀	175	100				
MZB 15597	A ♀		105			46	
MZB 2155	A ♀		104				
ZMA 3084 ^a	A ♀		101				

^aFrom Bergmans, 2001.

group of *P. melanopogon* was seen roosting a short distance away from the main *P. chrysoproctus* colony. The *P. melanopogon* colony we located on Pulau Marsegu has previously been seen feeding on flowers of durian trees (*Durio* sp.), which are very abundant in this part of Seram. No colonies of *P. melanopogon* are currently known from Ambon, but more surveys are needed to verify this claim. As indicated in the earlier discussion of *P. chrysoproctus*, a small group of *P. melanopogon* was found roosting in disturbed forest near Mosso, but none were captured nor seen emerging at dusk.

Pteropus melanopogon and *P. chrysoproctus* are sympatric but are easily distinguished from one another. While *P. melanopogon* has highly variable pelage coloration across its geographic range, its massive size (FA >185 mm) and robust skull (GSL >75 mm, ZB >40 mm, LIOW >10 mm) make it unmistakable (tables 2 and 3, fig. 2). Like the colony sighted in our survey, the specimens at MZB are similar to the nominotypical form according to Andersen (1912) in both coloration and size with a brownish-yellow head, darker brown mantle, pale yellowish-buff abdomen, massive overall body size, ears shorter than CM2 length, an interfemoral membrane that is short in the center, and a practically naked forearm and tibia. Given its size, it is likely that *P. melanopogon* is one of the heavier pteropodid species; one of our specimens weighed 900 g (table 3).

Despite being abundant in the 19th century, previous modern survey efforts had failed to locate a single colony of *P. melanopogon* on either Buru or Seram (Flannery, 1995). Morphological similarities of previously collected specimens suggest an affinity between the populations of *P. melanopogon* on Buru and Seram, but comparisons with specimens from other Moluccan islands, especially Aru and Kai, are needed for a thorough review. A comprehensive analysis of the *P. melanopogon* complex (inclusive of *P. keyensis* and *P. aruensis*) is a high priority since *P. aruensis* is severely threatened by conversion of the Aru Islands into corporate plantations (Amianti, 2015). Like *P. chrysoproctus*, *P. melanopogon* is also likely no longer extant on Ambon, as there have been no recent reports of colonies, but more surveys are needed.

HUMAN DISTURBANCE: The roosting colony of *P. melanopogon* in West Seram is extremely vulnerable to hunting. While the local fishermen do not hunt bats, the site is easily accessible to bushmeat hunters from other provinces. Disturbance from hunting affects both the numbers and distribution of the bats. We were unsuccessful in capturing any individuals during our 2012 visit because a hunter from a different province had apparently killed many bats with a gun at

the roost a few days prior to our arrival, and this proved enough of a disturbance to disperse the colony. We were informed by the local villagers that disturbed bat colonies moved from their original isolated roosts to suboptimal sites (e.g. shorter trees in the forest closer to villages), which were often actually easier for hunters to reach. Clearly such events can threaten the stability of the colony.

CONSERVATION: Currently, IUCN lists *P. melanopogon* as Endangered under criteria A3c, d since it has not been recorded within the entirety of its range on any Moluccan islands in the past 20 years (Helgen and Salas, 2013a). This threat categorization means that there is a projected decline of $\geq 50\%$ of the population in the next three generations due to deforestation and hunting. Our results indicate that the Pulau Marsegu roost is the only known colony found on Seram within the past several decades. But the Pulau Marsegu roost is not in a protected area and merits protection for its high conservation value.

Pteropus ocularis (Peters, 1867)

Seram flying fox

TYPE LOCALITY: Seram, Central Maluku, Indonesia.

NEW MATERIAL: Pulau Marsegu, Seram Bagian Barat Regency, Maluku Province, Indonesia. Collected by Sigit Wiantoro and Susan M. Tsang, 1 male MZB 36928.

OTHER SPECIMENS EXAMINED: MZB 0112, MZB 13361, AMNH 234939, ZMB 2958. Additional specimens that we did not examine for this study are housed at the AM and BMNH.

OCCURRENCE AND IDENTIFICATION: *Pteropus ocularis* is a species that is very rare in collections. We suspect *P. ocularis* is unlikely to be found in colonies based on our inability to locate any colonies, the lack of historical or current colony information from local forestry rangers, and having captured an individual under similar circumstances as the other noncolonial *Pteropus* species, *P. temminckii*. The IUCN red list assessment of *P. ocularis* states that it has been collected only four times (Helgen and Salas, 2013b) although we are aware of six previous records: the holotype collected by Alfred Russel Wallace (at ZMB), two females (one collected in 1915 and another from 1982) housed at MZB, a series at BMNH, a series from Ambon at NMNL, a female at AM in Sydney (Flannery, 1995), and a male at AMNH with vague locality data (“Moluccas”). The MZB and BMNH specimens are from Buru, whereas the AM specimen is from an area near Manusela National Park, Seram. Unfortunately, the tag on the holotype and the original description by Peters (1867) only states that it is from Wallace’s “Ceram” collection. We are doubtful of the species identity of the AMNH specimen because the forearm length (FA = 118 mm) is significantly smaller than expected, and we also ruled out the possibility that it was not a mature adult. Additionally, the ventral fur has a distinct, large, light blond patch that is not characteristic of *P. ocularis*. We could not further investigate because the skin is in such poor condition with the skull still inside.

Our collection of *P. ocularis* is likely the first record from West Seram. Our identification of this specimen is based on pelage pattern and morphological measurements. Dobson (1878) noted that that *P. ocularis* has distinctive light reddish-brown rings around the eyes similar to

P. conspicillatus, however, *P. ocularis* is much smaller in size and the body shape of *P. ocularis* is “*Pteropus griseus*-like” with an interfemoral membrane that is narrow in the middle. Our specimen conforms to this description. Our specimen also falls within the expected range of measurements for this species: FA 130 to 145 mm, GSL 59 to 63 mm, ZB 32 to 34 mm, LIOW 6 to 7 mm (tables 2 and 3, fig. 2).

Our specimen was captured in a mangrove forest. The IUCN red list assessment states that *P. ocularis* “probably occurs only in old growth forest,” but the habitat of this specimen indicates that more extensive surveying is necessary to understand the habitat preferences of this species.

HUMAN DISTURBANCE: It remains unclear whether *P. ocularis* faces persistent, targeted hunting pressure like *P. chrysoproctus* and *P. melanopogon* since it is a solitary species and relatively rarely encountered. There were no indications that the local villagers knew this species very well from any particular location, but they may consume it as a result of incidental capture.

CONSERVATION: *P. ocularis* is currently listed by the IUCN as Vulnerable B1 a, b (iii, v). This categorization means that the extent of the species occurrence is less than 20,000 km², with fewer than 10 known localities, and continuing decline in both habitat and number of subpopulations. Deforestation in and around Manusela National Park probably affects this species. It is unclear whether the apparent rarity of *P. ocularis* is due to low relative abundance or cryptic behavior or whether populations are declining. Further monitoring is necessary to determine whether an IUCN Endangered status may be more appropriate for *P. ocularis* than its current one of Vulnerable.

Pteropus temminckii (Peters, 1867)

Temminck's flying fox

TYPE LOCALITY: Amboina (= Ambon), Central Maluku, Indonesia.

NEW MATERIAL: Pulau Marsegu, Seram Bagian Barat Regency, Maluku Province, Indonesia. Collected by Sigit Wiantoro and Susan M. Tsang, 1 female MZB 36926, 1 male MZB 36925. Mosso Village, Maluku Tengah Regency, Maluku Province, Indonesia. Collected by Sigit Wiantoro and Susan M. Tsang, 1 female MZB 36924.

OTHER SPECIMENS EXAMINED: MZB 15597, MZB 8341, MZB 2155, MZB 14839, ZMB 2633, ZMB 4964, and ZMB 3473.

OCCURRENCE AND IDENTIFICATION: *Pteropus temminckii* was captured in both West and Central Seram, in both mangrove (Pulau Marsegu) and secondary forest (Mosso) habitats. A foliage rooster that is unlikely to occur in large colonies (Helgen and Bonaccorso, 2013), *P. temminckii* is not easily detected. Of the four Moluccan *Pteropus* species, *P. temminckii* is best represented by previous collection efforts throughout its range. Combined records from our expeditions and previous collection efforts suggest that *P. temminckii* is relatively common compared to *P. ocularis*. Flannery (1995) states that *P. temminckii* likely prefers primary forest based on a report that researchers from AM captured large numbers in primary forests at ~800 m elevation in Ambon. However, in Seram *P. temminckii* is apparently most commonly encountered today in secondary forest. Local villagers describe encountering these

bats relatively often in the small patches of secondary forest that frequently occur between villages, and we were able to capture a female in this habitat. These fragmented forests are used as orchards or hunting areas by Christian villagers. The mangrove habitat where one male and one female *P. temminckii* were captured was also unexpected, as this species has not been previously reported in mangrove forest and our mistnets were set with the goal of capturing the *P. melanopogon*.

Pteropus temminckii is significantly smaller than other *Pteropus* species on Seram, and comparatively easy to identify. Adults have a forearm length <110 mm and GSL <55mm, which is significantly smaller than the next largest species found on Seram, *P. ocularis* (tables 2 and 3, fig. 2). Our specimens all exhibit uniquely dense pale yellowish-buff silky fur described by Dobson (1878) as diagnostic for the species. The coloration and fur thickness are similar to *P. personatus*, a North Moluccan species, but *P. temminckii* does not have a black facial mask.

HUMAN DISTURBANCE: *P. temminckii* is threatened by habitat loss and by bushmeat hunting (Helgen and Bonaccorso, 2013). As a species commonly encountered by hunters, more data is needed to determine how intensely hunting has affected population trends.

CONSERVATION: Currently, the IUCN lists *P. temminckii* as Vulnerable under criteria A2c, meaning a projected decline of $\geq 30\%$ of the population in the next three generations due to a decline in habitat. *Pteropus temminckii* was the only species that we found at multiple survey sites and habitats (including disturbed areas), and it was the most commonly encountered of the four *Pteropus* found in Seram during our survey. Our observations indicate that this species has broader habitat preferences than previously reported. We did not directly observe or capture the species in Manusela National Park, though it has previously been recorded there according to park staff. We found foraging sites with telltale bite marks on fruits for *P. temminckii* within Manusela National Park, but did not find any foliage roosts. *Pteropus temminckii* will likely face increased extinction pressure as habitat continues to be degraded, but our observations suggest it is likely the least threatened of the four *Pteropus* species in Seram.

DIRECTIONS FOR FUTURE RESEARCH

Our surveys confirmed the occurrence of four native *Pteropus* species on Seram, and resulted in documentation of several roosting colonies of high conservation value. Voucher specimens we collected were compared to available specimens from other islands available from historic collection to confirm characteristics of each species, but we did not attempt a complete revision of these taxa, which in most cases have ranges extending far beyond Seram. Future systematic studies should include a comprehensive revision of *P. melanopogon*, which likely represents a complex of more than one species. The original variants recorded in Dobson (1878) are now recognized as separate species (*P. neohibernicus*, *P. aruensis*, and *P. keyensis*), but the species status of populations occurring on other remote Indonesian islands is unknown (Simmons, 2005). Poor understanding of variation within Moluccan *Pteropus* species may result in an underestimated level of phylogenetic diversity, a measure often used by biodiversity management and conservation biologists to evaluate areas of

endemism, which in turn influences priorities for establishing new protected areas. Oceanic islands such as those in Maluku have a mammal fauna composed primarily of bats and rodents, and updated data on all species is needed to inform management decisions. Many Moluccan *Pteropus* species likely have unrecognized endemic subspecies, but incomplete collections have resulted in hypotheses of geographically widespread species complexes with vague species limits. Additional research likely will result in many distinct, new threatened taxa with small, circumscribed geographic ranges.

The current study represents the first effort in decades to comprehensively review all known *Pteropus* from Seram. We provide comparisons of their occurrences, particularly in light of recent anthropogenic disturbance. More detailed studies of the effect of anthropogenic change on six other pteropodid species, as well as the four *Pteropus* species, are needed. At the two disturbed sites that we sampled (Sipa and Mosso), we were able to capture all pteropodid species other than *Pteropus* known to be present on the island (table 1). Comparisons to previously collected specimens of these taxa from throughout their ranges should be made to evaluate variation and species/subspecies limits. For example, a comparison to other *P. chrysoproctus* specimens deposited at the Australian Museum from Buru (AM 29985) and Bisa in the Obi Group (AM 28901 and AM 28902)—something unfortunately beyond the scope of this study—would help in understanding variation throughout Maluku (Flannery, 1995). Unfortunately, no tissue samples are available from these specimens.

Determining the level of molecular diversity within each population and connectivity between island populations is recommended to further assess the status of these bats. This has already started through genetic analyses of the tissue samples collected during the surveys reported here. Using next-generation sequencing methods, historical specimens may be able to provide genetic information previously unavailable to determine whether human encroachment has had any effect on genetic diversity and population connectivity. More information about the foraging and roosting ecology of these bats are needed to understand potential localized migration patterns as it pertains to their demographic histories. If observation conditions do not permit adequate sampling of feeding behavior, a metagenomic study of food remains from feces is recommended to provide a preliminary understanding of their diets.

Our data suggest that *Pteropus temminckii* may adapt to light disturbance, as these bats are found in gardens, orchards, and disturbed secondary broadleaf forests. Determining which species occur in mangrove forests in addition to primary forests is also important, as we found large roosting colonies of *P. chrysoproctus* and *P. melanopogon* along with a single *P. ocularis* in mangroves. The degree of prevalence of *Pteropus* in disturbed areas or mangroves is unknown, especially for poorly known Moluccan species. It remains unclear whether these two habitats are highly seasonal and timed to the flowering of a few tree species or they are alternate roosts following previous human disturbance in primary forests. More concerted survey efforts will be needed in the future to corroborate population trends and habitat preferences of all pteropodid species since our data are not fully representative of occurrence patterns and could be misleading. Due to the small sample size, we could not determine whether habitat preference was statistically correlated with other traits (e.g. body size or feeding ecology). Estimating these

characteristics may be possible when more data are available from future surveys on Seram and other Moluccan islands. Information from such surveys could thus assist planners in assessing where protected areas should be situated to encompass both the foraging and the roosting sites for bats.

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APPENDIX
SPECIMENS EXAMINED

Coll.ID	Year	Site Name	Island	Collector(s)	Latitude	Longitude
<i>Pteropus chrysoproctus</i>						
MZB 1077	1921	Leksula	Buru	L.J. Toxopeus	3°46'S	126°35'E
MZB 13568	1982	Wamlana	Buru	Asep & J. Hardjono	3°7'41"S	126°33'46"E
ZMA 16.369	1922		Buru			
MZB 1076	1921	Leksula	Buru	L.J. Toxopeus	3°46'S	126°35'E
MZB 36911	2014	Pulau Raja	Seram	S. Wiantoro & S.M. Tsang	2°55'7"S	129°9'46"E
MZB 36909	2014	Pulau Raja	Seram	S. Wiantoro & S.M. Tsang	2°55'7"S	129°9'46"E
MZB 1078	1921	Leksula	Buru	L.J. Toxopeus	3°46'S	126°35'E
ZMA 16.370	1922		Buru			
MZB 36908	2014	Pulau Raja	Seram	S. Wiantoro & S.M. Tsang	2°55'7"S	129°9'46"E
MZB 36910	2014	Pulau Raja	Seram	S. Wiantoro & S.M. Tsang	2°55'7"S	129°9'46"E
MZB 0219	1913		Buru			
*ZMB 2626	1828		Ambon	S. Müller		
<i>Pteropus melanopogon</i>						
MZB 13566	1983	Wamlana	Buru	Asep & J. Hardjono	3°7'41"S	126°33'46"E
MZB 13569	1983	Wamlana	Buru	Asep & J. Hardjono	3°7'41"S	126°33'46"E
MZB 13570	1983	Wamlana	Buru	Asep & J. Hardjono	3°7'41"S	126°33'46"E
MZB 1075	1921	Nal-Besi	Buru	L.J. Toxopeus	3°26'S	126°32'E
MZB 36927	2014	Pulau Marsegu	Seram	S. Wiantoro & S.M. Tsang	3°0'45"S	128°2'60"E
MZB 1074	1921	Rana-Meer	Buru	L.J. Toxopeus	3°25'60"S	126°34'1"E
ZMA 16.368	1921	Leksula	Buru	L.J. Toxopeus	3°46'S	126°35'E
FMNH 8228	1898	Kajeli	Buru	A. Everett	3°22'60"S	127°5'60"E
MZB 1059	1918	Kali Toam	Seram			
var. <i>keyensis</i>						
*ZMB 4752	1865		Kai	von Rosenberg		
*ZMB 4701	1865		Kai	O. Beccari		
var. <i>aruensis</i>						
*ZMB 4703	1865- 1867		Aru	O. Beccari		
*ZMB 4962			Aru	Bernstein		
<i>Pteropus ocularis</i>						
*ZMB 2958	1860		Seram	A.R. Wallace		
AMNH 234939	1973		"Moluccas"	A.S. Bickmore		
MZB 36928	2014	Pulau Marsegu	Seram	S. Wiantoro & S.M. Tsang	3°0'45"S	128°2'60"E
MZB 13361	1982	Wamlana	Buru	Asep & J. Hardjono	3°7'41"S	126°33'46"E
MZB 0112	1915		Buru	Denin		

Coll.ID	Year	Site Name	Island	Collector(s)	Latitude	Longitude
<i>Pteropus temminckii</i>						
*ZMB 2633			Ambon	S. Müller		
*ZMB 4964			Ambon	Bernstein		
*ZMB 3473			Ambon	von Rosenberg		
MZB 36925	2014	Pulau Marsegu	Seram	S. Wiantoro & S.M. Tsang	3°0'45"S	128°2'60"E
MZB 2155	1921		Buru	L.J. Toxopeus		
MZB 15597	1984		Seram	Djafar		
MZB 14839	1987	Solea	Seram	B.J. Christiansen		
MZB 36924	2014	Mosso	Seram	S. Wiantoro & S.M. Tsang	3°18'30"S	129°35'60"E
MZB 36926	2014	Pulau Marsegu	Seram	S. Wiantoro & S.M. Tsang	3°0'45"S	128°2'60"E
MZB 8341	1969	Waii	Ambon	Saan		
ZMA 3080 ^a	1922		Buru	L.J. Toxopeus	3°27'S	126°40'E
ZMA 3084 ^a	1913		Ambon	Willemsz Geeroms	3°41'S	128°01'E

^a From Bergmans 2001.

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