How widespread was the Tapanuli orangutan and what led to its decline?

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Abstract

The Tapanuli orangutan (*Pongo tapanuliensis*) is the most threatened great ape species in the world. It is restricted to an area of about 1,000 km^2 of mostly hill forest where fewer than 800

animals survive in three declining subpopulations. Through a historical ecology approach involving analysis of colonial-era and other literature, we demonstrate that historically the Tapanuli orangutan lived in a much larger area, and across a much wider range of habitat types compared to now. Its current range is about 10-20% of the range it had some 150-200 years ago. A combination of historic fragmentation of forest habitats, mostly for small-scale agriculture, and unsustainable hunting likely drove various populations to the south, east and west of the current population to extinction prior to the industrial-scale forest conversion that started in the 1970s. Our findings indicate how sensitive orangutans are to the combined effects of habitat fragmentation and unsustainable mortality or rescue and translocation rates. Saving this species will require prevention of any further fragmentation and any killings or other removal of animals from the remaining population. Without concerted action to achieve this, the remaining populations of Tapanuli orangutan are doomed to become extinct within several orangutan generations.

Introduction

Determining the key drivers of population decline is a primary objective in conservation biology and wildlife management. Many wildlife species are threatened by a range of different and often interacting factors, and developing effective conservation strategies requires unravelling how these threats interact [1]. This is rarely easy, because species operate in complex socio-ecological systems in which different components are affected by a range of anthropomorphic factors such as habitat loss and fragmentation or unsustainable harvest. Evidence-based conservation seeks to address this by quantifying the relationships between conservation actions, change in threat severity and change in conservation status [2, 3]. Collecting evidence is, however, time-consuming, and when conservation problems are “wicked”, i.e., the problems change as solutions are found [4], a stable solution may not be found to a particular

conservation problem [5]. This often means that scientific evidence does not support clear-cut conclusions in value-driven debates that characterize conservation [6]. Nevertheless, conservation advocates often seek simple narratives to convince the public of the urgency of environmental problems and the need to support it. A good example is the polarized debate around oil palm (*Elaeis guineensis*) and orangutans (*Pongo* sp.) where both proponents and opponents of oil palm cherry-pick facts to drive home particular messages, i.e., oil palm is either the greatest evil destroyer of tropical rainforests or a blessing to impoverished rural communities in tropical countries [7]. A similarly polarized debate currently rages between opponents and proponents of a hydropower project in the range of the Tapanuli orangutan (*Pongo tapanuliensis*), an endemic great ape of the Indonesian island of Sumatra [8] (Fig 1).

One way to bring more clarity in muddled or polarized debates is to be more specific about the system in which a particular problem plays out. For example, if the system boundaries are limited to oil palm as an ecological threat to orangutan survival [9], a simple solution would be to ban palm oil use and to stop its production, preventing further deforestation. If the system boundaries are extended to include smallholder farmers who produce palm oil for their own needs as well as international markets, a ban on palm oil would encompass broader ethical connotations as it would affect people's livelihoods [7]. The use of different perspectives in complex conservation contexts may not make it easier to solve them but can provide helpful insights about the boundaries of a particular problem. Are they, for example, mostly ecological, or do they involve human threats, such as hunting, or societal ethics? One such perspective is history. Looking back in time on the development of a particular problem may provide insights about the underlying drivers of that problem. The historical ecology approach builds on this approach by using historical knowledge in the management of ecosystems or species [10]. Referring to historical evidence has, for example, provided valuable understanding about the ecology of orangutans and what likely caused their decline during the Late Pleistocene and

Holocene, which informs their management today [11]. Here we apply an analysis of historical ecology to one particular species of orangutan, the Tapanuli Orangutan, by analysing rarely used colonial-era literature to better understand the historic distribution of the species. Indonesia's colonial literature on natural history was mostly written in Dutch and German, and is not commonly used by conservation scientists working in Indonesia.

The Tapanuli Orangutan was described in 2017 as a third species of orangutan [12], 20 years after this orangutan population was formally reported to modern science [13]. The species is restricted to three areas of mostly upland forest in the Batang Toru area in North Sumatra (Fig 1), totalling approximately 1,023 km^2 [14, 15]. This orangutan population had been largely overlooked by science, despite having been tentatively described in the colonial literature [16]. The estimated total number of wild Tapanuli Orangutans is currently 767 [95%: 213-1,597, 14] making this the great ape species with the lowest number of individuals in the wild and perhaps the most threatened in the world [8].

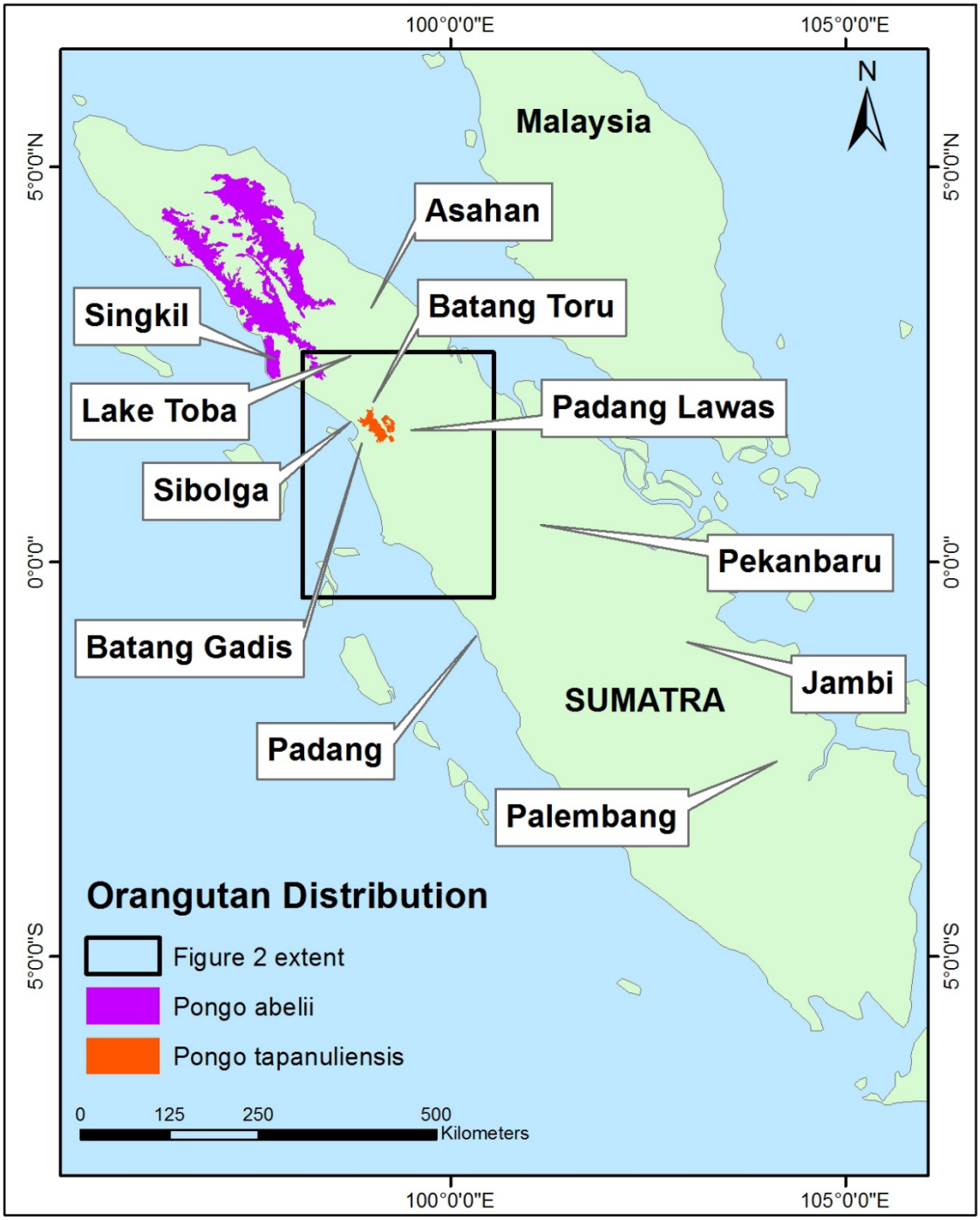

Fig 1. Map of the island of Sumatra, showing the distribution ranges of *P. tapanuliensis* and *P. abelii*, and the main locations (cities, districts and other geographic features) mentioned in the text. The inset shows the area of Fig 2.

The species is currently under threat from habitat loss for agriculture, hunting and conflict killing, and development in the area, for infrastructure, gold mining, and geothermal and hydro-energy, which threaten to further reduce and fragment remaining habitat, reduce dispersal opportunities for the orangutans between subpopulations, and undermine population viability through unsustainable mortality rates [14, 17-20]. Due to its restricted current distribution mostly centred around higher elevations (834.4±219.3m asl) compared to 701.7±454.8 m asl for the Sumatran orangutan (*P. abelii*) and 170.6±187.0 m asl for the Bornean orangutan (*P. pygmaeus*) [21], it has been argued that the individuals of the species have adapted specifically to the uplands that cover most of its current distribution [17]. What is not clear is whether the currently existing altitudinal differences between these orangutan species are the result of ecological specializations to highland ecological conditions, or whether the highland species now occur at higher altitudes because their previous lowland habitats no longer exist or because the species became extinct there. The fossil record for Sumatran orangutans confirms that the genus *Pongo* was once more widespread. Extensive remains from the Late Pleistocene and Holocene have been excavated from a range of caves in the Padang Highlands, some 300 km south of the current range [22] (Fig 1). Why the species disappeared from that part of Sumatra remains unclear but unsustainable hunting is one of the possible explanations, because until recently large areas of suitable forest habitat remained in areas where orangutans are now extinct [23]. Given that, in the past, forest cover was also much more widespread in the range of the Tapanuli Orangutan, it is important to determine whether historically (ca. past 500 years) orangutans did occur in those areas. This would help establish whether the Tapanuli orangutan has indeed evolved to only live in the highlands and estimate what its past distribution could have been.

The aim of this paper is to compile reports of orangutans occurring to the south of the Toba lake (Fig 1) with the focus on determining how reliable these are, and, where feasible, provide a

location for the occurrence of orangutans to assess whether these are predominantly highland sites, and to assess which factors could have led to their disappearance in those areas.

Methods

We compiled records of orangutans from historic sources by searching natural history books, scientific papers, and historic newspapers from before 1940. We searched databases with location specific keywords such as Sumatra, Batang Toeroe, and Tapanoeli, using Dutch spelling. We combined this with searches for terms specifically referring to orangutans: Orang oetan, orang-oetan, orangutan, and also mawas, mias and maias (local names for orangutan commonly used in historic literature), using a variety of spellings. For the period since 1940, we used the sources from the review in Rijksen and Meijaard [23] as well as scientific papers and personal communications. To determine the locations of the historic sightings or captures we consulted the online Leiden University Library colonial map repository (http://maps.library.leiden.edu/apps/s7). In some cases, rivers or villages were indicated which made it feasible to estimate the location of the sightings quite accurately. In other cases, the area of the sighting or captures was indicated in a broader area which reduced accuracy (tens of kilometers).

We assessed the likely vegetation types that Tapanuli Orangutans would have occurred in, and determined the altitude at which they were reported from the global SRTM layer (30m accuracy). For this, we digitized the first official forest cover map of Indonesia [24], which is likely based on maps produced by the Netherlands-Indies cartographic service from the 1930s and 1940s. We carried out the digitization of the 1950 Indonesia forest cover map using ArcScan extension in ArcGIS. ArcScan is an extension in ArcGIS that converts scanned raster images into vector-based GIS layers [25]. Prior to digitization, the Indonesia forest cover map

was georeferenced. This is because scanned raster maps mostly do not contain spatial reference information. Georeferencing helps to assign the coordinate systems of the map and output of ArcScan. Digitization of raster map via ArcScan resulted in polylines. These polylines were useful in constructing vegetation polygons of the area of interest. Therefore, it is important to clear any unrelated polylines generated in the ArcScan output to ensure polygons could be properly identified and constructed. We completed the construction of polygons using advance editing tool in ArcGIS. This tool closed and converted polylines into polygons. Polygons constructed represent different vegetation types in the area. We then classified the polygons in accordance to their vegetation type with reference to the Indonesia forest cover map. Before vegetation types assignment, we ensured that different vegetation types were represented with separate polygons.

The exact location of the historic orangutan sightings cannot be determined with certainty but the descriptions often provide sufficient detail through names of rivers and villages to estimate the location on a map. Due to this uncertainty the altitude was extracted as a range for some locations. Altitude was determined from the altitude layer in Google Earth Pro. We used the vegetation map for Sumatra [26] in combination with knowledge gained by co-author SW during surveys in the region to assign one of the forest categories to an estimated historic location.

Results

Historic accounts

We report the various historic accounts of orangutan sightings or specimens from outside the currently known range in chronological order, starting with Schlegel and Mueller [27] who reported on two orangutan crania that were obtained by a military doctor in the surroundings of

Jambi, some 650 km south-east of the current closest orangutan population. It is unclear whether these animals were obtained in Jambi from the wild or whether they were in captivity and possibly originated from northern Sumatra. Schlegel and Mueller reported that the two skulls were housed in the “Rijks-Museum”, which presumably refers to the Leiden Museum of Natural History. Furthermore, they wrote that on the west coast of Sumatra, especially north of the equator, the orangutan was known by the name *mawej*, although in areas further south such as Indrapura and Bengkulu, the names *orang-panda* or *orang-pandak* were used. The authors acknowledged that the orangutan was especially common in the north-east of Sumatra, but that occasionally they were encountered further south and along the western shores of Sumatra. Also, the species had been reported from Indrapura (in present-day Riau Province) and near Padang (in West Sumatra, Fig 1), although the descriptions by Schlegel and Mueller are insufficient to confirm that these reports referred to orangutans. Co-author Onrizal, remembers growing up east of Padang (Sungai Dareh) listening to stories about *orang-pendek*, human-like creatures living in the forest, which reportedly ceased to exist in the area in the 1970s. Stories of such *orang-pendek* abound in other parts of southern Sumatra and there has been speculation for over a century that these could be remnant orangutan populations [28, 29], although firm evidence remains lacking. For the purpose of the current paper we do not focus on the *orang-pendek* narratives.

In a description of their travels across Sumatra, Müller and Horner [30] wrote that orangutans were not unknown in the Tapanuli area and especially common in “Taroemon”, i.e., present-day Trumon in the Singkil area (Fig 1), which is part of the *Pongo abelii* range. They report that people distinguished between two types of orangutans, the *maweh baroet* (baroet meaning monkey in the local language) and *maweh orang* (the ‘human’ orangutan). Von Rosenberg [31] did not provide much detail but similarly mentioned that orangutans were present north of “Tapanoeli” (what is now Sibolga) to Singkil, indicating presence of the species in the coastal

lowlands west of Lake Toba (no. 1 in Fig 2). He saw two orangutans but did not clarify where he saw them.

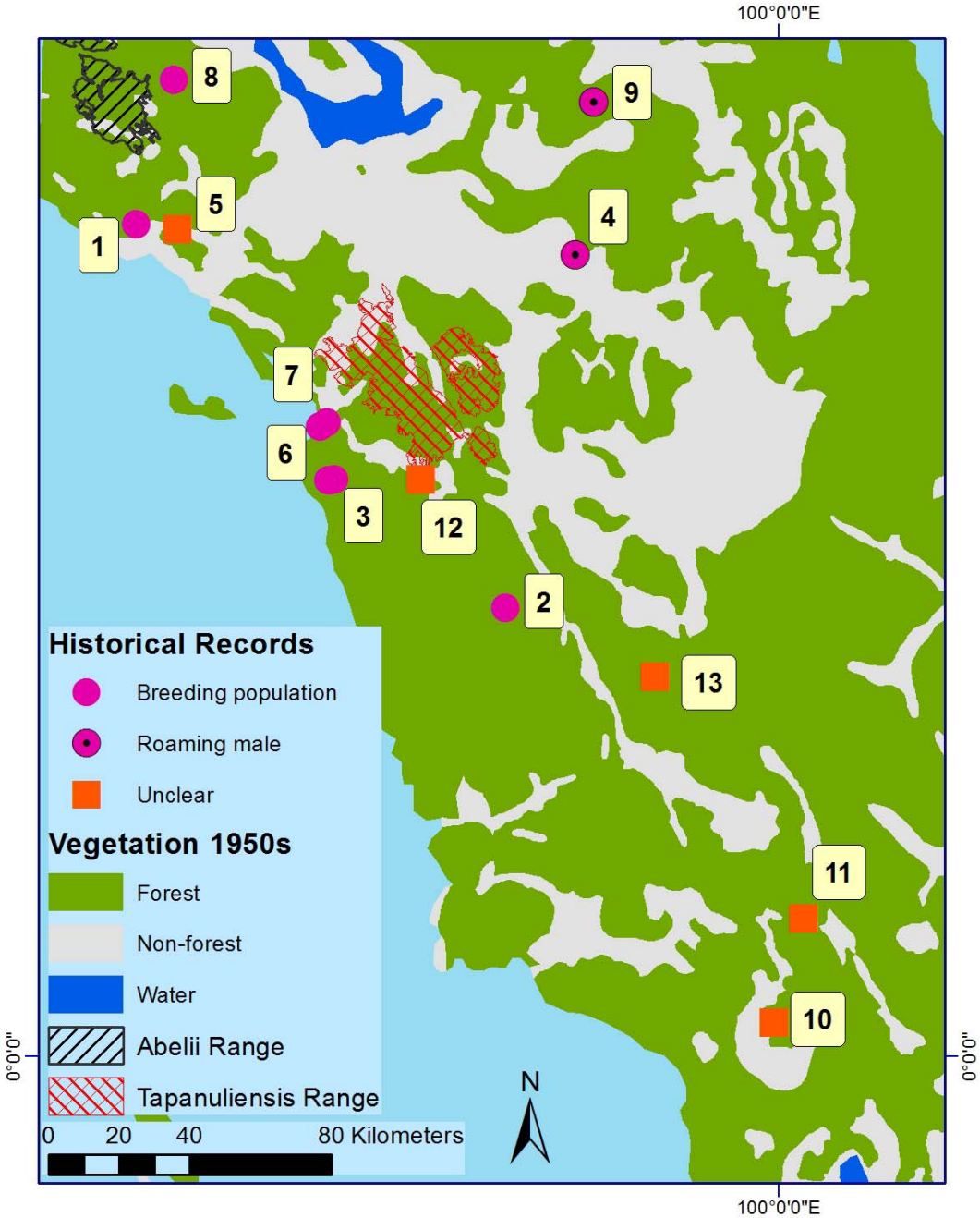

Fig 2. Map showing points where orangutans where historically reported and the forest cover in 1950 before large-scale commercial forest exploitation began.

Kramm [32] reported on a hunting expedition near "Soeroe Mantinggi", where he found several orangutans and observed them for several hours. The location likely referred to Sayur Matinggi (no. 2 in Fig 2), which is currently located in the Batang Gadis area, some 50 km south of the current range of *P. tapanuliensis*. Kramm mentioned that Soeroe Mantinggi is located at a distance of 22 “*palen*” from Padang Sidempoean. A “paal” was a measurement used in the Netherlands-Indies, equalling 1852 m on Sumatra, indicating a distance of about 40 km for 22 “*palen*”. Sayur Matinggi is currently located some 26 km from Padangsidempuan as the crow flies which indicates that indeed this is likely to be the location where Kramm observed orangutans. Kramm was familiar with orangutans which he reported to have also encountered in "Loemoet" and "Batang-Taro". We believe that the former refers to Lumut (no. 3 in Fig 2), just south of Sibolga, and that Batang-Taro is an older name for the Batang Toru area, where *P. tapanuliensis* occurs until today.

Orangutans also seem to have occurred northeast of the current range of the Tapanuli Orangutan. Neumann [33] described the species from “Hadjoran”, which was located in the watershed of the “Batang Si Ombal” and “Aek Hiloeng”, and for which the following coordinates were given: N 2°1’25” and E 99°29’, in the current district of Padang Lawas (Fig 1, no. 4 in Fig 2). This is about 50 km northeast of the most eastern current range of Tapanuli Orangutan. The detailed description, however, suggests that the species was very rare there, and the people of “Hadjoran” had not seen the orangutan there before. The animal was shot, with descriptions of the local people suggesting it was at least 1 m tall, possibly indicating an adult male, which are known to roam far from breeding populations. Neumann writes that he travelled extensively through forest areas in the Padang Lawas area searching for orangutans but never managed to encounter one.

Hagen [34, p. 66] stated that orangutans were known from the west coast between Tapanuli and Singkil (no. 5 in Fig 2), although Singkil is in the range of *Pongo abelii* and it is not clear

whether the coastal Tapanuli reference referred to the area of the current range of *P. tapanuliensis*, or whether it referred to what is now the Central Tapanuli District which extends to the southern part of Singkil, west of Lake Toba. Interestingly, he referred to an orangutan from the interior of Padang (in reference to an article by S. Jentink, Aardrijkskundig Weekblad, 1881, No. 44, p. 287 – not seen by the authors), in west Sumatra that ended up in the Rotterdam Zoo where it died of a bone deformation disease (the skull is kept in the Natural History museum in Leiden, the Netherlands: RMNH.MAM.544).

Miller [35, p. 483] in his account about the mammals collected by W.L. Abbott on the west coast of Sumatra in 1901 and 1902 mentioned the following about orangutans: “The orang utan exists, but not abundantly, about Tapanuli Bay. Two miles up the Jaga Jaga River (no. 7 in Fig 2) some nibong palms were seen that had been broken off by orangs, and also an old sarong (shelter), but the traces were old. There were said to be more a few miles farther inland, particularly up the Berdiri River (no. 6 in Fig 2). The natives say they always go about in pairs.” Miller described the Jaga Jaga River as “a stream near the south end of the Tapanuli or Sibolga Bay”. We located the Berdiri River on an old map under the name “Bardari River”, and we located “Djaga Djaga” as well. It seems clear from this that orangutans occurred in the area inland from the southern part of Sibolga Bay (Fig 1) where there are currently no longer any orangutans.

Beccari [36] reported orangutans around Rambung, in the Tapanuli region, and in the hinterland of Sibolga, where he collected a specimen. We were unable to determine the location of Rambung but there is a Rambong north of the Singkil area, and thus well in *P. abelli* range. The hinterland of Sibolga could either refer to the current *P. tapanuliensis* population or the historic range. He further stated that “In the Zoological Museum at Florence is the skeleton of a young orang-utan, described as coming from Palembang (Fig 1), on the east coast of Sumatra”, some 800 km southeast of the nearest current orangutan population. We contacted the curator of the Florence museum, who wrote in response that the specimen was indeed present under

specimen number MZUF-12: “The specimen was purchased in 1889 in London (G.A. Frank, 9 Haverstock Hill, London). It is a subadult male. The place of origin is Palembang, but may have been captured elsewhere. There are no manifest connections with O. Beccari.” Gustav Adolf Frank was a well-known natural history trader based in Amsterdam and London, and he probably had a good network of local suppliers. Description of the skeleton is provided by Agnelli, Becchi [37] is inconclusive as to what species it belongs to. We can therefore not know for sure whether the animal was caught near Palembang and transported to Europe from there, or whether it originated from northern Sumatra (either of the two known species).

Volz [38] wrote about the distribution of orangutans on Sumatra, although it is not clear to what extend the information is informed by Volz’ own surveys or interpretation of secondary information. Volz suggested that there were no orangutans east of the Langkat River, which he thought was likely the remnant of a large bay or sea connection that once separated north and south Sumatra approximately in a line from Sibolga to north of Medan. He expanded on this in his work a few years later [39], in which he also described additional orangutan sightings. This included a sighting in the upland area west of Lake Toba at an elevation of 1,400 m asl. Referring to the same area, Kohler [40] described a visit to Sibolga where the guest had a young orangutan which had also been caught in the forest on the west of the Toba lake, indicating a breeding population there. Volz [38] also described a sighting of an orangutan east of Lake Toba in the upper Kualu River area (ca. N 2°26’ E 99°32’, no. 8 in Fig 2). Again, however, the description of a large ape that moved ‘slowly and ponderously’ may suggest an adult male, and because people there are not familiar with the species, possibly a wandering male outside the range of a breeding population.

Delmont [41] described a hunting expedition on the upper Musi River, near “Sekajoe” in the foothills of the Barisan mountain range in what is now South Sumatra Province. His informant, Mr Ghoba Ramah, told him that orangutans were particularly common in the area and were

raiding the crops of local farmers. After four weeks, they managed to catch seven orangutans. They then moved to a location four hours rowing upstream, where they quickly observed a female orangutan with young. They set out cages with fruit bait for capturing orangutans, but the first morning after arrival they had only managed to catch some monkeys and a pig. After that they were more successful and claimed to have caught one male orangutan and a female with young, and over the next few days they caught several more orangutans. Delmont's stories are intriguing but strike us as somewhat fantastical, as it is unlikely that anyone could catch significant numbers of orangutans with baited cages. More likely these could be Pig-tailed Macaques, *Macaca nemestrina*, who indeed move about in groups, raid crops and can be trapped in cages. We therefore do not consider this source to be reliable.

The various historic accounts above where summarized in a map drawn by van Heurn [42] which shows that clearly the conservation community was aware of the existence of orangutans south, west and east of Lake Toba. Interestingly, though this map depicts the current Batang Toru population to be part of the range where the species had become extinct, while the only extant population is a narrow band to the east of Lake Toba in the Asahan District (Fig 1), where the species is not currently known. It suggests that information about orangutan distribution was still rudimentary in the 1930s, which may have the reason for a request to Carpenter [43] who conducted a survey on behalf of the Nederlandsch-Indische Vereeniging tot Natuurbescherming. He worked mostly in the northern parts of Sumatra but sent questionnaires to Dutch soldiers stationed in areas where orangutans could potentially occur. Carpenter assumed that orangutan did not occur south of a line drawn from Singkil to Sumatran east coast, thus overlooking much of the historic evidence of orangutans south of Lake Toba. Carpenter's questionnaires included two reports of orangutans outside the known range. The first is from Captain H.J. Kloprogge who had been based in Siak, Indrapura and Pekanbaru (Fig 1) and claimed to have seen orangutans several times during forest patrols. Second, Captain M.

Kooistredie reported seeing 12 orangutans near Jambi (Muara Tembesi) (Fig 1) of which he shot two and later another one. Again, we treat these reports as unreliable also because Carpenter did not actually refer to them in his report and presumably did not assume the reports to be accurate.

There seems to be a gap in records between the 1930s and 1970s, but in the early 1970s, the Indonesian forester K. S. Depari reported orangutan sightings along the Batang Toru River and in the Rimbu Panti Wildlife Reserve (no. 9 in Fig 2) [16]. Borner [44] also noted that in Rimbu Panti one orangutan had been shot, while Wilson and Wilson [45] confirmed the presence of orangutans in South Tapanuli, while also reporting them around Pekanbaru, in Riau Province. Finally, the presence of orangutans was indicated by a botanist and a wildlife researcher on Gunung Talamau (no. 10 in Fig 2; Laumonier, pers. comm.). Presence in this region was confirmed by a survey in 1996 by Rijksen, Meijaard and van Schaik [13], when several nests were found on the edge of this Reserve, but follow up surveys by SW could not confirm this report and suggested that the nests may have been eagle nests. More recently, Wich et al. [46] found several orangutan nests in the peat swamp forests near Lumut (no. 1 in Fig 2) and heard a male long call in the same area. Local community members mentioned that they had also seen orangutans in the area [46]. Approximately 2 km south of the Batang Toru River (southeast of the village of Batang Toru), a geologist (Martin Jones) spotted a solitary orangutan in the forest in 2004 (no. 12 in Fig 2). Finally, Bradshaw, Isagi [47] reported on orangutans in the Barumun Wildlife Reserve in the Padang Lawas District (no. 13 in Fig 2). Nests were reportedly encountered and one staff of the local conservation department reported a direct encounter with an orangutan in 2009.

While there is significant spatial inaccuracy in the historic records of *P. tapanuliensis* outside the current range, we can still make an educated guess of the different habitats and altitudes in which these populations occurred (Table 1). Habitats in which the species once occurred

included tall peat swamp forest, freshwater swamp forest mosaic and secondary forest, forest on limestone, hill forest between 300 and 1,000 a.s.l., and submontane forest between 1,000 and 1,800 m a.s.l., indicating the full range of habitats that is also used by *P. abelii* [16].

Table 1. Orangutan records, most likely *P. tapanuliensis*, but outside the current range, that we consider to be reliable.

Number	**Location**	**Source**	**Vegetation**	**Likely status**
1[a]	Tapanoeli	Von Rosenberg 1878	Forest 300-1000m (logged)	Breeding population
2	Sayur Matinggi	Kramm 1879	Limestone/Secondary Forest 300 - 1000m	Breeding populaton
3	Loemoet	Kramm 1879	Tall Peat Swamp Forest	Breeding population
4	Hadjoran	Neumann 1885	Forest 300-1000m (Sibolangit)	Roaming male
5	West Coast	Hagen 1890	Forest 300-1000m (logged)	Unclear
6	Berdiri	Miller 1903	Secondary Mosaic <300m	Breeding population
7	Jaga Jaga	Miller 1903	Tall Swamp Forest (Shallow Peat)	Breeding population
8	Upland areas west of Lake Toba	Volz 1912	1400 m	Breeding population
9	Kualu River	Volz 1912	Forest <300m	Roaming male
10	Talamau Mountain	Laumonier 1983	Submontane Forest	Unclear

			1000 - 1800m	
11	Rimbu Panti	Meijaard 1997	Forest 300 - 1000m (Singkel)	Unclear
3	Lumut	Nests observed by Serge Wich and Tine Geurts in June 2001	Tall Peat Swamp Forest	Breeding population
3	Nests near Lumut	Nests observed by Serge Wich and Tine Geurts in June 2001	Tall Peat Swamp Forest	Breeding population
12	South of Batang Toru	Orangutan observed by Martin Jones (geologist) in 2004	Secondary Mosaic <300m	Unclear
13	Barumun	Bradshaw et al. 2007		Unclear

[a] Point numbers in the table correspond to the numbers in Fig 1. Vegetation information was derived from Laumonier [26].

Discussion

Possible drivers of historical declines

Our historical ecology analysis of *P. tapanuliensis* has revealed that the species occurred beyond its current range until quite recently. Breeding populations occurred in the Batang Gadis area (Fig 1), probably through much of today's South Tapanuli and Mandailing Natal Regencies. The historic records to the north of the current *P. tapanuliensis* range make it difficult to judge whether these are part of *P. abelii* or *P. tapanuliensis*. For example, the records of orangutans west of Lake Toba, could also refer to populations that still occur in the Pakpak Bharat Regency [48] and the Batu Ardan and Siranggas forest blocks in the Dairi Regency [49], which genetically are closer to *P. abelii* than *P. tapanuliensis* [50]. It is not clear whether the records in the Padang Highlands, Rimbu Panti and Padang Lawas referred to itinerant males or breeding

populations but the scarcity of records could indicate that breeding populations became extinct there earlier.

Because of the uncertainties in population status (breeding or not) and taxonomy, it is not currently possible on the basis of the historic data to determine how large the former range of *P. tapanuliensis* was. We know from evidence of Late Pleistocene orangutan fossils in the Padang area (Lida Ajer, Ngalau Sampit, Ngalau Gupin) [51], that orangutans lived in this part of Sumatra at least until some 50,000 years ago. What we don't know is whether this was *P. abelii*, *P. tapanuliensis,* or a species different from both, as suggested by Drawhorn [52]. No specimens of Tapanuli Orangutan were collected by any of the historic sources, except those reported by Hagen [34] and Beccari [36], but these have not been genetically analysed yet. There is therefore no robust evidence as to whether the orangutans reported from outside the current Tapanuli Orangutan range were *P. tapanuliensis* or *P. abelii*. Further genetic study of the specimens reportedly originating from Padang (RMNH.MAM.544) and Palembang (MZUF-12), and also of fossil teeth from the Padang Caves area could shed light on the taxonomic status of the orangutans in Central Sumatra, and their relationship to *P. tapanuliensis*. Based on distribution range patterns, with *P. abelii* clearly restricted to the northern parts of Sumatra [12, 46], we consider it most likely that all historic orangutan populations south and south-east of the current range of *P. tapanuliensis* were indeed *P. tapanuliensis*. This would indicate that the species currently retains some 10-20% of the range it occupied some 150 to 200 years ago. This raises the question why the species declined.

It is unclear when the populations outside the current range became extinct. Some populations such as those in Lumut, seen by Neumann in 1885 and by SW in 2001, but not seen since, may have become extinct quite recently because of forest loss. Other populations likely disappeared sometime in the 20th century. There have been no recent records from areas west or southwest of Lake Toba, nor from the Batang Gadis region, south of the current populations. Also, while

there are a number of alleged records from the area east of Padang City (nos 12 and 13 in Fig 1), there are no confirmed recent records. It thus appears that a lot of these populations disappeared around a time when forests were still extensive and the commercial exploitation of forest for timber (starting in the 1970s) or their conversion to plantations (starting in the 1990s) had not yet decimated available habitats. Nevertheless, there had been significant historic deforestation prior to 1950 as shown in Fig 1, mostly for small-holder agriculture and livestock, firewood and timber, and as result of wars and fires [53, 54]. For example, the colonial-era district of *Tapanoeli* (now North, South and Central Tapanuli) had an estimated forest cover of 19000 km^2 in a total area of 39,481 km^2 (48% forested) in the 1930s [53]. Some populations therefore appear to have become isolated in historic times, when early agricultural development created large grassland areas. So, why did these populations become extinct? This appears to have been a combination of habitat loss and population fragmentation, and mortality rates that exceeded reproductive replacement rates.

Several authors have suggested that orangutan density and range on both Borneo and Sumatra were primarily determined by the ability of people to access areas and hunt orangutans [55, 56]. For example, Jentink (1889) writes that orangutans in Sumatra are only common in swamp areas like those in Singkil which are so inaccessible that there are rarely “stepped on by human feet”, apparently quoting von Rosenberg [31], who had made a similar statement a decade earlier. Wallace (1869) similarly argued that orangutans were common in swamp forest, not because these were particularly suitable ecologically but rather because human hunters rarely went there. Such hunting was certainly common in the orangutan’s range in Sumatra. Schneider [57], for example, writes that Batak people hunt orangutans with blow pipe, spears or shotguns, while young animals are often caught and sold to plantation owners.

Batang Gadis was populated by Loeboe people [58, p. 327] who were nomadic tribes that also occurred in Padang Lawas and “Groot-Mandailing” [59-61]. Another nomadic tribe, the Oeloes

occurred around Muara Si Pongi and Pahantan (now Pakantan) [59, 62]. Similar to other nomadic people such as the Kubu further south in Sumatra [63] or the Punan of Borneo [64], nomadic people often prefer primate meat over other meat sources. Kreemer [61] mentioned that the Loeboe people consider primate meat a delicacy. They hunted primates, including Siamang *Symphalangus syndactylus* with blowpipes, and used snares for pigs and deer. Still, there are to our knowledge no specific accounts of people from the historic range of *P. tapanuliensis* hunting and eating orangutans. Nevertheless, we consider it likely that, similar to Borneo, orangutans would have been hunted for food. Van den Burg [65], in a general account about orangutans, describes how generally orangutans were shot with poison darts, after which they fell out of the trees and were killed with spears. Alternatively, they were caught alive and killed later. The whitish meat was generally grilled over a fire, and was described as soft and sweet [65]. This is also suggested by the use in local language of *juhut bontar*, or white meat, to describe orangutan or pig-tailed macaque *Macaca nemestrina*, while such descriptions of sweet meat were similarly recorded by EM on Borneo [23]. Orangutan fat, especially from adult males, was often saved for later use in the preparation of other dishes [65].

Marshall et al. [66] examined population viability models with 1%, 2%, and 3% additional mortality in all age classes, running 500 iterations with populations of 250 orangutans. In the best quality orangutan habitats, i.e., mosaic landscapes of swamp, riparian and hill forests [23], annual hunting rates of 1% did not cause population extinction, but did decrease population size. In less than optimal habitats, e.g., forests at higher elevation, a 1% level of hunting caused declines to extinction irrespective of initial population size. Higher rates of hunting were unsustainable even in the highest quality habitats [66]. These models were conducted for Bornean orangutan *P. pygmaeus*, but the authors thought that hunting effects would be similar for Sumatran orangutans. The best orangutan habitats would like be those with the highest soil fertility, which at levels of intermediate rainfall would also be the best areas for agriculture [67]. It

is thus likely that historically most Tapanuli orangutans would occur in suboptimal habitats, where the removal of one animal from a population of 100 per year, would drive such a population to extinction. Given the available information, we consider it most likely that the Tapanuli orangutan was hunted to extinction in the increasingly fragmented parts of its former range and only survived in the remote and rugged Batang Toru mountains which may have provided orangutans with a refuge from hunting.

Implications for species conservation

What do our findings mean for conservation? The Tapanuli orangutan's remaining three subpopulations are in apparent decline, threatened by conflict killing and hunting, and loss of lowland habitat [14, 19, 20, 68]. Our insights from past population declines, driven by habitat loss and fragmentation and probably unsustainable mortality rates, indicate that without preventing further losses to the population, even if in the single numbers per year, the last remaining populations of the species are doomed to rapidly decline within several orangutan generation lengths [estimated at 25 years, 21]. Current killing rates of *P. tapanuliensis* already meet or exceed this threshold. Two wild-captured infant Tapanuli orangutan were reported thus far in 2020, with one confiscated from the owner and the other illegally released to avoid legal repercussions [69, 70]. Obtaining wild orangutan infants necessitates killing the mother in nearly all cases [23, 71], hence these infants are assumed to represent two adult females killed in the first six months of 2020 alone. Such records are indicative of a lowest minimum number of killings, as they represent only criminal acts that have been detected and acted upon, which is a fraction of the total orangutan-related wildlife crime [72, 73]. Records of an adult male killed in 2013 (OIC pers. comm. 2020), a male severely injured by humans in 2019 [74], and another male captured and translocated twice in the past 12 months due to complaints about crop raiding from local community members [75] suggest that killings have been ongoing in recent

years, although prior to 2017 most detected incidents would have been recorded as *P. abelii*. While translocation has been used as a response to Tapanuli orangutans in conflict with humans, translocated animals are not monitored beyond a few days following release, and their long-term survival is not known. Behavioural traits of female site fidelity and male territoriality, and adaption issues of Bornean orangutans released in unfamiliar habitats indicate that translocation risks are high and survival rates may be low [72, 76].

Long-term protection of the Tapanuli Orangutan requires that mortality rates of <1% per year are maintained over long (decadal) time frames across the species' range. This also means that that all subpopulations have to remain connected, because once connections between populations are lost this should result in higher extinction risks for the remaining subpopulations, as was modeled for Bornean orangutan *P. pygmaeus* [77]. Within the subpopulations, the prevention of killing is urgently needed, which requires innovative management of crop conflicts [78, 79], and effective law enforcement and awareness campaigns. Such campaigns have so far had insufficient impact on reducing orangutan losses and new approaches may be required [80]. This could include, for example, direct conditional payments to rural communities for maintaining habitats and preventing any deaths or harm, i.e., orangutan guardians [81] or support for "buffer gardens" to concentrate crop losses from orangutan foraging into areas acceptable to communities [82].

Given the high extinction risks, it is important that a comprehensive plan of action is developed for the species that accurately determines how many animals remain, the level of gene flow between subpopulations, current loss rates (including removal of animals in rescues and translocations), and works towards full and permanent protection of all remaining habitat. Such a conservation management plan would need clarity about long-term funding, organizational responsibilities, and clear, science-based plan to allow the Tapanuli orangutan population to stop declining, or better, increase to safer population numbers. Without such concerted and

coordinated action, the remaining populations of the Tapanuli orangutan are doomed to follow their historic predecessors on their path to rapid extinction.

Acknowledgements

We thank XXX reviewers for their constructive comments on an earlier version of this manuscript.

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