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PRIMATES OF SULAWESI: AN UPDATE ON HABITAT DISTRIBUTION, POPULATION AND CONSERVATION

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Abstract
Wallacea holds great significance not only for evolution and biogeography but also for conservation. No less than 98 species of Wallacea's endemic mammals, birds, and amphibians appear on the IUCN Red List of globally threatened species. The primates of Wallacea show high diversity and endemicity within a very narrow range. There are 20 species of primates in Wallacea, of which 18 are found only in Sulawesi and the surrounding islands. Among those, three have been described as new species in only the last 10 years, *Tarsius tumpara, T. wallacei*, and *T. lariang*. Their habitat is located outside of existing protected areas, which means they need special consideration for their conservation. *T. tumpara* is one of the 25 rarest primates in the world while *Macaca nigra* from North Sulawesi has been included as an endangered species on the IUCN Red List. GIS analysis of the habitats of those endemic species shows that the extent of their habitats is shrinking dramatically in North and South Sulawesi and on the small islands of the north and east coast of Sulawesi.

***Keywords*:** Sulawesi, endangered, endemic, mammals, protected areas, *Tarsius*, Wallacea

Introduction

Since Wallacea is composed mainly of small islands, many of which have no connection to other landmasses, it is not surprising that its flora and fauna is not as rich in species as its larger neighboring islands to the west in Sundaland and to the east in New Guinea (Whitten *et al*., 2002). The trend shows gradual impoverishment from west to east within Wallacea, with animals that can fly or swim being present

in greater variety in the west because they can disperse between the islands more efficiently (Whitten *et al*., 2002). Many of the mammals in this region show Asian affinities, but many of the birds, such as the parrots, cockatoos, honeyeaters, and friarbirds, found on most of the islands are derived from Australia (Whitten *et al*., 2002). Wallacea faces severe threats: only 15% of its ~340,000 km^2 of land area retains natural habitat, and only 7.2% of its area has been placed within Indonesia's system of protected areas. No less than 98 of Wallacea's endemic mammals, birds, and amphibians are considered globally threatened according to the IUCN Red List (Mittermeier *et al*., 1998; Brooks *et al*., 2002). Among those mammals, 20 species are primates and 18 are found only in Sulawesi and its surrounding islands. Among those, three species have been described as new species in the last 10 years, *Tarsius tumpara*, *T. wallacei*, and *T. lariang* (Ross *et al*., 2014*).* In fact, *T. tumpara* has been included in the 25 rarest primates in the world (Mittermeier *et al*., 2009).

Research on Sulawesi primates has been extensive. The Macaques, have been studied in a joint Indonesia-United States project called "Sulawesi Primate Project" (Supriatna, 1988; Supriatna *et al*., 1989). This was a collaborative effort between several universities in Indonesia (Universitas Indonesia, Universitas Nasional, Universitas Hasanudin, and Universitas Sam Ratulangi) and several universities in the USA (University of New Mexico, Yale University, Columbia University, University of California, University of Colorado, and University of Georgia). A Japanese team, led by Kyoto University in collaboration with Bogor Agricultural University, was very active in studying the morphogenetic diversity of Sulawesi macaques (Fujita & Watanabe, 1995; Fujita *et al*., 1997; Matsumura, 1998). Research on Sulawesi tarsiers has been conducted by many scientists from the United States (Gursky 1998, Shekele *et al*. 1997) and Germany (Nietsch 1999, Merker and Groves 2006). Most of this work was trying to understand the morphological and genetic diversity of Tarsiers plus the evolutionary explosion of Sulawesi primates into so many unique and endemic species (Shekele *et al*., 1997; Merker, 2010). The seven species of Sulawesi macaques show a very interesting evolutionary process by having hybridization zones in which some species show secondary intergradation stages, where formerly isolated taxa become reintegrated as demonstrated by *M. maura* and *M. tonkeana* (Supriatna *et al*., 1990; Supriatna, 1996; Froehlich & Supriatna, 1996; Bynum *et al*., 1997; Evans *et al*., 2001).

In this paper, we review the status of, extent of available habitat for, and conservation efforts on behalf of, the primates of the Wallacea region. Although primates are found on islands other than Sulawesi, for example, Lombok, West Nusa Tenggara, the species there originally came from Bali (*Presbytis cristatus* and *Macaca fascicularis*). Only *M. fascicularis* has migrated from Lombok to other islands of West and East Nusa Tenggara (Dennell *et al*., 2013). Therefore, since the primates of Sulawesi are all endemic, we will focus only on Sulawesi primates. Sulawesi Island harbours a suite of endemic species whose intraspecific differentiation or interspecific divergence may have been catalyzed by habitat fragmentation. Results from many studies support the role of habitat fragmentation on the population structure of Sulawesi macaques and tarsiers (Gursky-Doyen & Supriatna, 2010). Habitat fragmentation, therefore, may also have affected other taxa on this island such as, for example, toads (Evans *et al*., 2008).

Materials and methods

We updated the status of tarsiers and macaques by reviewing research and studies conducted in Sulawesi. Current

conservation status was based on the IUCN red list (IUCN, 2015). We then mapped remaining habitat suitable for tarsiers and macaques with GIS landsat analysis.

To calculate habitat loss between 1990 and 2010, we used methods for the calculation of deforestation following Supriatna and Mariati (2014). We calculated average deforestation rates from Landsat images using the formula of Puyravaud (2003). Percentage calculations of deforestation of concession areas and National Parks were made using the Ministry of Forestry formula (Departemen Kehutanan, 2008). Satellite images were validated using Google map and ESRI online base map. Deforestation was calculated based on intact forest cover in 1990 and 2010, Landsat images had to be free of cloud, and all forms of land use, particularly parks, forest concession and protected forest were analyzed for available primate habitat.

Results and Discussions

Several authors have updated the status and population sizes of Sulawesi tarsiers and macaques (Riley, 2010; Ross *et al*., 2014). In this paper, we used conservation status based on the IUCN red list (Table 1; IUCN, 2015). Our GIS analysis shows that between 1990 and 2010, the habitat remaining available to primates in Sulawesi varied between 23 and 39% of the original. *M. tonkeana* and *M. togeanus/balantakensis* suffered the greatest habitat loss among all the macaque species at approximately 34% while *M.hecki* suffered the least at 23%. Although M. tonkeana lost the greatest percentage of its habitat it has the largest estimated population and the greatest area of available habitat among all macaques (Table 2). For tarsiers, *T. dianae* lost approximately 39% of its habitat while *T. pumillus* lost the least at 30%. *T. fuscus* had the largest area of remaining habitat. It is difficult to obtain information for many of the tarsier species as they are island endemics with no detail information on available potential habitat, for example, *T. sangirensis* and *T. pelengensis* (Table 2). To date, what protection there is for the tarsiers and macaques of Sulawesi is found in 16 protected areas including national parks (Table 3).

Research and Research Stations in Sulawesi: Primate research in Sulawesi has been facilitated by the establishment of many field research stations within Sulawesi since the early 1980s (Fig. 1: pl. 10). An early research station was established by John and Kathy MacKinnon who studied primates in Tangkoko Batuangus. This station was later used by Timothy and Margaret Kinnard of the Wildlife Conservation Society and Sharon Gursky from New York State University as well as staff and students from Sam Ratulangi University in collaboration with the University of Washington Primate Centre. Currently, this work is being continued by the German Primate Centre. While in Gorontalo, Oxford University scientist, Lynn Clayton, established a research station that has been visited by many students over the years, to study Sulawesi endemic mammals such as *Babyrousa babyrousa*, as well as some primates.

Table 1: List of Sulawesi primates, their status and distribution; NE, near threatened; VU, vulnerable EN, endangered; CE, critically endangered; DD, data deficient

Species (Latin, English, local name)	Distribution
Tarsius fuscus[NE] Makasar tarsier Tarsius Makasar	SW peninsula of Sulawesi, presumably S of the Lake Tempe Depression.
Tarsius dentatus[VU] Dian's tarsier	E portion of the central core of Sulawesi to the tip of the E peninsula, the N boundary is the Isthmus of Palu (between

Tangkasi Diana	Marantale, Ampibabo and Tomini Bay), the S boundary from Lore Lindu National Park to the E coast is unknown, but the W boundary appears to extend at least to the Palu River and S as far as Gimpu.
Tarsius pelengensis[EN] Peleng tarsier Tangkasi peleng	Peleng Island, off the coast of the E peninsula of Sulawesi; it may also occur on other islands of the Banggai Archipelago.
Tarsius spectrum (*T. Tarsier*)[VU] Spectral tarsier Tangkasi	Sulawesi, Buton, Muna, Kabaena, Selayar, and the Togian Islands, except those portions of Sulawesi that lie within the ranges of *T. dentatus* and *T. lariang.* Four acoustic forms are acknowledged, Tinombo form, Togian form, Selayar form and the Kabaena form
Tarsius sangirensis[EN] Great Sangihe tarsier Tangkasi Sangihe	Great Sangihe Island, c. 200 km N of Sulawesi; it may also occur on other islands in the Sangihe chain
Tarsius wallacei[DD] Wallace tarsier Tangkasi Wallace	NW Sulawesi (discontinuous range in Central Sulawesi Province); the N form occurs on the Isthmus of Palu from just W of the village of Tomini to the NE (c. E120°30'), the coastlines of the Isthmus of Palu to the E and to the W, to the villages of Ampibabo and Marantale in the S (c. S0°30'); the S form occurs in a very fragmented area W to SW of Palu, around the type locality Uwemanje
Tarsius tumpara[CE] Siau Island tarsier Tangkasi Siau	Siau Island, in the Sangihe Archipelago, c. 100 km N of Sulawesi; it may occur also on some small islands close to Siau
Tarsius lariang[DD] Lariang tarsier Tangkasi lariang	WC Sulawesi in the Lariang River Basin near the confluence with its tributary, the Meweh River, and extending N as far as Gimpu; the precise limits of its distribution may be much wider than those confirmed to date.
Tarsius pumilus[DD] Pygmy tarsier Tangkasi kerdil	S and C Sulawesi (known only from Rano Rano and the Latimojong Mts); distribution fragmented on isolated mountain tops.
Macaca nigra[CE] Crested macaque Yaki	North Sulawesi
Macaca nigrescens[VU] Gorontalo macaque Dihe	N Sulawesi, E of Gorontalo to Onggak Dumoga River in the N peninsula
Macaca hecki[VU] Heck's macaque Dige	NW Sulawesi from the base of the N peninsula (Isthmus of Palu) NE to just E of Gorontalo.
Macaca tonkeana[VU] Tonkean macaque Boti	C Sulawesi (S to Latimojong, SW to the base of the Toraja highlands at the Tempe Depression, SE toward, but not at, the lakes region of the SE peninsula, and NW to the isthmus between Palu and Parigi) and Togian Islands
Macaca Maura[EN] Moor macaque Dare	SW Sulawesi up to Tempe Depression
Macaca ochreata[VU] Booted macaque Hada	SE Sulawesi, through the entire SE peninsula, extending to the N of the lakes region; with La River is border with tonkeana, while in the W it extends along the coast, across the Karaena River in its lower course, but not reaching into uplands further inland

Macaca brunescens Buton macaque Endoke	Muna and Buton islands, Southeast Sulawesi. M. brunnescens is still listed under M. ochreata according to IUCN (2015). No IUCN status is available

Tabel 2: Estimates of remained habitat of Primates in Sulawesi

Species	Habitat in hectare		Population estimated	Sources for population estimate
	1990	2010		
Tarsius dianae	1,204,201	733,939	180,000	Tremble *et al*., 1993
Tarsius pumillus	3,275,657	2,282,405	NA	
Tarsius fuscus	9,951,683	6,723,824	NA	
Tarsius sangiriensis	?	2,077	1,505–52,734	Shekelle & Salim, 2009
Tarsius pelengensis	?	5,000	NA	
Tarsius lariang	NA		NA	
Tarsius wallacei	NA		NA	
Tarsius tumpara	NA		1,358–12,470	Shekelle & Salim, 2009
Macaca balantakensis	163,983	108,823	NA	
Macaca brunnescens	325,455	222,442	3,752	Riley, 2010 (compilation from several sources)
Macaca nigra	348,821	236,715	4000–6000	
Macaca maura	296,902	201,733	<5000	
Macaca nigrescens	609,218	428,919	30,000–45,000	
Macaca ochreata	2,067,194	1,346,931	71,000	
Macaca hecki	1,761,848	1,355,829	100,000	
Macaca tonkeana	6,578,616	4,343,239	150,000	

Table 3: Summary of Sulawesi Primates Species Representation in Protected areas

Sulawesi Primates	Protected areas and national parks															
	Buton Utara PA (82,000 ha)	**Babul NP (43,750)**	**Kalaena PA (110,000)**	**Rawa Aopa (105.114)**	**Mekongga (258,529 ha)**	**Faruhumpenai PA (90,000)**	**Lore Lindu NP (229,0000**	**Morowali PA (225,000)**	**Buol PA (Duko, Pamona & Tinombala (19,500; 25,700; 37,106)**	**Gunung Sojol (64,448)**	**Nantu PA (48,000)**	**Panua PA (45,000)**	**Teluk Apar PA (33,638)**	**Dumoga Bone NP(287,115)**	**Batuambang PA (8,638)**	**Tangkoko –Duasaudara PA (8000)**
Tarsius fuscus		X														
T. dentatus							X									
T. pelengensis																
T. tarsier																X
T. sangirensis																
T. wallacei																
T. tumpara																
T. lariang							X									
T. pumilus							X									
Macaca nigra											X				X	X
M. nigrescens														X		
M. hecki									X			X	X			
M. tonkeana							X	X								
M. maura		X	X													
M. ochreata				X	X	X										
M. brunescens	X															

A consortium of US universities established the Sulawesi Primate Project in collaboration with the University of Indonesia. One research station was built in

Dumoga Bone National Park, close to Kotamobagu City, led by Jeffrey W. Froehlich (University of New Mexico) and Charles Southwick (University of Colorado), and another was set up in the isthmus of Central Sulawesi at Puncak Beringin, led by Nora Bynum (Yale University). In Central Sulawesi, the oldest research station was established at Lore Lindu National Park by many primatologists who studied the macaques and tarsiers (Michael Tremble from the University of New Mexico, visited by many students from Indonesia and other countries). Currently, in Lore Lindu, there is also a research station established by Erin Riley close to the Lindu Lake. Other research stations in central Sulawesi were established by the Indonesia Biodiversity Foundation in the Togian Islands, called Malenge Research Station, and by the Alto Foundation at Tombopati.

In South Sulawesi, the University of New Mexico, in collaboration with the University of Indonesia, set up a research station in Karaenta Nature Reserve, which operated between 1986 and 1990. This station has been used by students from Hasanuddin University in Makasar and also several students from Jakarta. In Southeast Sulawesi, there are field sites managed by World Wide Fund for Nature (WWF) and The Nature Conservancy (TNC) . In the Buton Islands, there is also a research station run by Operation Wallacea.

Indonesia and Wallacea Primates: The high endemicity of Indonesia's primates is mirrored by their diversity in morphology, ecology, and behaviour. Indonesia harbours one of the most diverse collections of primates on earth. The country boasts more than 58 out of the world's approximately 195 species. Indonesia's primates are from five families and nine genera with 21 species being Indonesian endemics (Ross *et al*., 2014). The species are distributed across the archipelago from north Kalimantan to the south coast of Java, and from western-most Sumatra east to Bacan and East Timor. Indonesia contains primates of every evolutionary type, from primitive 'living fossils' such as tarsiers through to the very advanced apes, such as lesser apes (gibbons) and great apes (orangutan), which are closely related to humans (Mittermeier *et al*., 2014).

The number of recognised Indonesian primates has increased from 40 species in 2001 (Supriatna & Hendras, 2001) to 45 species just a few years later (Grooves, 2004) and now sits at 58 or 59 species depending on the authority consulted (Ross *et al*. 2014). The number of recognized Sulawesi macaque species ranges from 6–8 while the number of Sulawesi tarsiers ranges from 8-9 species (Riley, 2010; Ross *et al*., 2014; IUCN, 2015).

In Sulawesi primates, hybrids and backcrosses of macaque species are fertile for multiple generations and hybrids have been observed at the contact zones between *parapatric* species on Sulawesi (Ciani *et al*., 1989; Supriatna, 1991; Watanabe & Matsumura, 1991; Bynum *et al*., 1997; Evans *et al*., 2001). While the differentiation of tarsiers was originally made using various genetic markers, pelage colour, tail tuft and vocalizations, genetic analyses prove that Y-chromosomal and mitochondrial DNA sequences and also microsatellite allele frequencies are absolutely diagnostic (Merker *et al*., 2010).

The island of Sulawesi is of similar importance for primate diversity, though not at the same scale, as the importance of Madagascar. Sulawesi and its adjacent islands are home to seven macaque species and nine species of tarsier. These species comprise more than 5% of all primate diversity and astonishingly 100% are endemic to Sulawesi. Of the seven macaque species, six are classified as threatened; *Macaca nigra* is listed as Critically Endangered (CR), *M. hecki, M.*

ochreata, *M. nigrescens*, and *M. tonkeana* are listed as Vulnerable (VU), and *M. maura* as Endangered (EN) (IUCN, 2015). The tarsiers have a different story to tell. Field research suggests that there may be many undescribed species. The vertical differentiation in distribution of tarsiers over a short distance was shown in Lore Lindu National Park, where populations of *T. spectrum* and *T. pumillus* probably overlap (Supriatna and Hendras 2000).

Tarsiers: the smallest monkey in Indonesia: Tarsiers are one of the smallest monkeys in the world with adult male body weight being only 71–120 grams. In general, tarsiers in Sulawesi and the adjacent islands live in small territorial family groups. There are 11 species of tarsiers currently recognized, nine of which occur in Sulawesi and surrounding islands (Ross et al. 2014); *Tarsius tarsier*, *T. fuscus*, *T. dentatus*, *T. pelengensis*, *T. sangirensis*, *T. tumpara*, *T. pumilus*, *T. lariang*, *T. wallacei* (Ross, 2014; Fig. 2: pl. 10). Tarsier families have stable monogamy, with family size ranges from 3–7 individuals. *T. pumillus*, which is the smallest and darkest species lives in the moist forest more than 2000 m above sea level.

The tarsiers have sometimes been called "living fossils" (Supriatna & Hendras, 2000; Wright, 2003). The name Tarsier comes from tarsus, Latin for the area between foot and leg. The proportions of the limbs, which indicate their tree-hoping gait, are very similar to those of earlier primates of the Eocene period. The hind limb is long compare to body size and this is very much related to the way they move and jump (Wright *et al*., 2003). They have a long scratching claws on their third toe as well as a less pronounced one on their second toe. Enormous eyes and large ears indicate their nocturnal habits. The tail is long with a fine hair at the tip and is used as a support. The tarsiers can turn their heads through 180 degrees and look directly backward, and they also have the ability to turn their bodies through 180 degrees in mid-air when leaping (Wright *et al*. 2003).

There have been many revisions of tarsier species in Sulawesi and new species have been recognised. For example, *Tarsius tarsier* was formerly known as *T. spectrum*. Brandon-Jones *et al.* (2004) argued that *T. spectrum* is a junior synonym of *T. tarsier* and this has since been confirmed by Groves (2005), although the IUCN red list acknowledged *T.spectrum* as *T.tarsier*. There are four acoustic forms of *T. tarsier* which are the Tinombo form, the Togian form, the Selayar form and the Kabaena form (Gursky *et al*., 2008). Another population of *T. tarsier* was also confirmed by Groves and Shekelle (2010) restricted to Selayar island (see also Ross *et al*., 2014). However, in this paper we still use *T. spectrum* to avoid confusion as many scientists still use that name.

Sulawesi tarsier distributions are unique being endemic both latitudinally and altitudinally (Table 1). Distributions are based on the shape of Sulawesi and associated islands. The K-shape of the island reflects the complexity of its geology and tectonics, which is mirrored in the distribution patterns of tarsiers. Each species is restricted to particular part of the island (Fig. 2: pl. 10). Four species are found in the small islands, T. *pelengensis* in Peleng Island, *T. sangirensis* in Sangihe Island and small islands close by, *T. tumpara* at Siau Island and *T. tarsier* at Selayar Island. Four more species, *T. dentatus*, *T. fuscus*, *T. wallacei* and *T. lariang* are found in the lowland forests, while only one species is found in the high mountains, *T. pumilus* (Ross *et al*., 2014). In Togean, there may be one new species *Tarsius togeanus* (Supriatna & Hendras, 2000) although it has not been accepted in the IUCN redlist. Merker & Groves (2006) studied *T. wallacei* in the south-eastern Sulawesi and proposed a new species called *Tarsius*

lariang. Recently, Myron Shekelle and his colleagues studied many sites in Sulawesi and proposed at least 17 different taxa. They also proposed a new species, *Tarsius tumpara,* from a small tiny island, Siau, in North Sulawesi (Shekelle *et al*., 2004).

Potential predators of tarsiers include civets, arboreal snakes, monitor lizards, and raptors including owls (Gursky, 1997; Jachowski & Pizzaras, 2005; Gursky, 2002c) as well as feral cats (MacKinnon & MacKinnon, 1980; Jachowski & Pizzaras, 2005). Among wild spectral tarsiers (*T. tarsier*), if a snake threat is identified, mobbing behaviour of all members of the group will be displayed through lunging, vocalizing and even biting (Gursky, 2002b, c). Interestingly, when spectral tarsier groups do not contain more than one adult male, the presence of other males from other groups has been noted during mobbing of a predator (Gursky, 2002c, 2005b, 2006).

The sleeping sites of tarsiers vary with habitat type. In primary forest, they often sleep in tree cavities, mainly of strangler figs, *Ficus* sp. (Moraceae) (Gursky, 1998, 2010). In secondary habitats they may sleep in tree cavities, but also bamboo stands or shrubs (MacKinnon & MacKinnon, 1980; Tremble *et al*., 1993; Leksono *et al*., 1997). Gursky (1998) found that *Ficus caulocarpa* was most often used as sleeping site for the tarsiers in Tangkoko-Batuangus Nature Reserve. When the small nocturnal tarsiers retire to their sleeping trees in the morning, they usually perform duet calls at or close to the trees containing their sleeping sites. Sleeping site trees are only occupied by one group usually consisting of one adult male, one adult female, and their offspring (MacKinnon & MacKinnon, 1980; Gursky 1998). The morning duets are territorial as well as providing a social bonding component among members of the groups (Nietsch & Kopp, 1998; Nietsch, 1999).

Tarsier population densities are variable. Fogden (1974) and Niemitz (1984) stated that *T. bancanus* is common in secondary forest. Merker & Muehlenberg (2000) found that the highest density of *T. dentatus* was in forest with interspersed small plantations, which contained even slightly more tarsier groups than the same area of primary habitat. Even in plantations, *T. dentatus* prefers areas with dense shrubs (Merker, 2010). MacKinnon & MacKinnon (1980) also found that the population density of *T. spectrum* in shrubby habitat at sea level (10 individual/ha) was greater than in primary forest at 1000m above sea level (5 individual/ha). However, Gursky (1998) reported that *T. spectrum* were more abundant inside the conservation area of Tangkoko-Batuangus than outside. Elevation may also affect population densities in primary forest as reported by Merker and Muehlenberg (2000) and Yustian *et al*. (2008).

Little information is available on the distribution, population, behaviour, habitat preference and ecology of *T. dentatus* (Yustian *et al*., 2008). It is normally nocturnally active and adapted to an arboreal habitat but can also be found on the ground searching for food. On any flat surface they can also leap frog-like and they can walk on all fours with tails hanging down. They have small territories that are actively defended and marked by urine and the scent of various glands (Supriatna & Hendras, 2000).

Conservation strategies for these unique and endemic species should consider the different effects of various human activities. Although some land use types seem to be less detrimental to tarsiers than others, conservation of intact forest is still the best bet. More detailed research is needed to assess the impacts of human activities on tarsiers. According to IUCN criteria (IUCN, 2015), the conservation status of *Tarsius lariang*, *T. wallacei*, and

T. pumillus are data deficient (DD), which means there should be more data collected for categorizing this species as critical, vulnerable, or at high risk of extinction. For now, increasing forest clearing is a serious threat to the continuing present of these island endemic primates.

The Endemic Macaques of Sulawesi: Macaques are the most widespread genus of monkeys with a total of 22 species found from African deserts to the snowy mountains of Japan (Ankel-Simmons, 2000). In Indonesia, 11 species are distributed across Sumatra, Kalimantan, Java, Sulawesi, and islands as far east as Timor (Supriatna & Hendras, 2000). The long tail macaque, *Macaca fascicularis* is distributed widely throughout Thailand, Malaysia, the Philippines, and Indonesia, while the Pig tail macaque (*Macaca nemestrina*) is found only in Malaysia, Kalimantan and Sumatra (Supriatna & Hendras, 2000). The Pagai island macaque (*Macaca pagensis*), shares many characteristics with the pig tail macaque but is smaller and genetically different. Sulawesi macaques have distinctive forms in comparison to the rest of the macaque genus (Supriatna & Hendras, 2000). In the past, the Sulawesi macaques have been assigned to two genera, *Macaca* and *Cynopithecus*. Fur colors of the seven species vary from brown *Macaca maura* in the south to dark black of *Macaca nigra* in the north Sulawesi.

Seven out of a global total of 19 species of the genus *Macaca* are endemic to Sulawesi (Fooden, 1969: *Macaca nigra*, *M. maura*, *M. tonkeana*, *M. hecki*, *M. ochreata*, *M. brunnescens*, and *M. nigrescens*). Figure 3 (pl. 11) maps their distribution, including a possible eighth species, *M. togeanus*, which has been proposed as a separate species (Froelich and Supriatna 1996). It is for high levels of endemism such as this that Wallacea has been recognised as one of the 25 global hotspots for biological conservation (Myers *et al*., 2000). Although the evolution, population genetics, and morphological variation of the Sulawesi macaques have been the focus of a considerable amount of research (for example, Bynum *et al*., 1997; Evans *et al*., 1999, 2001, 2003; Abegg & Thierry, 2002; Bynum, 2002; Schillaci & Stallman, 2005), the behavioural ecology and conservation of these species remain relatively understudied. Figure 4 (pl. 11) maps the remaining habitat available to Sulawesi macaques, showing the extent of the reduction that has occurred.

Long-term ecological and behavioural research with conservation implications has only been conducted on wild populations of three species; *M. nigra* (Lee, 1997; O'Brien & Kinnaird 1997), *M. nigrescens* (Kohlhaas, 1993) and *M. tonkeana* (Riley, 2005). The remaining species have been the subjects of short-term observations on aspects of social organization and behavior (Watanabe & Brotoisworo, 1982; Reed *et al*., 1997; Matsumura, 1998; Kilner, 2001). With such limited data, our understanding of their habitat needs, current conservation threats, and their ability to respond to these threats, remains unclear (Bynum *et al*., 1999).

Sulawesi macaques show degrees of overlap among species, sometimes occurring in mixed-species groups that may be hybridization zones. Riley *et al*. (2007) observing mixed-species groups and individuals with similar traits of both species (black forelimbs, but grey/white hind limbs) suggested that hybridization is occurring in the areas of overlap between *M. tonkeana* and *M. ochreata*.

Based largely on the sampling of pet macaques, along with occasional observations of wild groups, Watanabe *et al.* (1991) suggested that the distribution of *M. ochreata* extended north-northwest of the provincial boundary between South and Southeast Sulawesi. Riley *et al*. (2007) confirmed that *M. ochreata* inhabits forests

around the Matano, Towuti, and Mahalona lake system and that the distribution of *M. ochreata* extends as far north-northwest as the Faruhumpenai Nature Reserve at the border of South and Central Sulawesi, in addition to two other protected areas in Southeast Sulawesi: Rawa Aopa National Park (105,000 ha) and Tanjung Peropa Game Reserve (38,937 ha). Riley *et al*. (2007) suggested that *M. tonkeana* may extend further southeast than was previously believed (see Watanabe *et al*., 1991). In Buton, *Macaca brunnescens* has been listed as a subspecies of *ochreata* (IUCN 2015). *M. brunnescens* lives in lowland primary and secondary forest 0-200 m above sea level. They are often seen on the periphery of plantations or agricultural areas (Supriatna & Hendras, 2000; Riley 2010).

Since 1987, the moor macaque, *Macaca maurus* has been listed as Endanger by the IUCN/SSC Primate Specialist Group. This Sulawesi endemic was protected by a ministry of Forestry declaration on 10 June 1991 No. 301/Kpts-II/1991. The moor macaque is facing extinction due to habitat loss and hunting by the community due to it being an agricultural pest (Supriatna *et al*., 1992). Forest conversion has led to the loss of 88% of its habitat, from 23,000 km^2 to only 2,800 km^2. There are likely to be no more than 4,000 individuals remaining (Supriatna & Hendras, 2000).

Presumably *M. maurus* is currently the most threatened among the Sulawesi's macaques. The IUCN/SSC Primate Specialist Group (Eudey, 1987), lists this species as Endangered but protected by the Indonesian government under the Ministry of Forestry. Because of its preference for secondary forest where it is often in areas of human habitation, this macaque is well known as a crop raider and is killed by villagers (Supriatna *et al*., 1992). Habitat destruction is the main threat to this species so the remaining forest available in southwest Sulawesi is critical to its future conservation (Supriatna *et al*., 1992).

The crested macaque, *Macaca nigra*, is protected by the government of Indonesia with the Ministry of Agricultural decree 29 January 1970 No 421/Kpts/um/8/1970, the Ministry of Forestry decree 10 June 1991 No 301/Kpts-II/1991 and UU No. 5 1990. It is categorized as "Critically Endangered" by IUCN (IUCN, 2015) and listed in Appendix II of CITES. Its habitat has been shrinking due to deforestation and the opening up of land for agriculture and plantations. The crested macaque has lost 60% of its original habitat with 12,000 km^2 becoming 4,800 km^2, part of which is a conservation area of 2,750 km^2 (Sugandjito *et al*., 1989). Another threat comes from the Minahasa people, especially during religious ceremonies, during which they consume many wild animals including crested macaques. This macaque has also become a favorite pet. Sugardjito *et al*. (1989) predicted that the population would be no more than 2000 individuals by the year 1991. The current threat status of this macaque is Critically Endangered (IUCN, 2015). The protected area available for the crested macaque is the Tangkoko Batuangus Nature Reserve and Dua Saudara, which is 60 km from Manado, North Sulawesi (16,000 ha). It can also be seen at Gunung Lokon Nature reserve, Gunung Ambang Nature Reserve and Tangale Nature Reserve, approximately 100 km toward the west of Manado (Rosenbaum *et al*., 1998).

The Gorontalo macaque, *Macaca nigrescens* occurs in northern Sulawesi just south of *M. nigra* and north of *M. hecki*. They commonly can be found in the highlands and mountainous areas between 400–600 m above sea level. Gorontalo macaques are locally called 'Dihe'. They are known to eat at least 69 different kinds of fruit. Approximately 70% of their diet consists of fruit, and the rest is other parts of plants, insects, molluscs and other small

invertebrates (Kohlhaas, 1993). Like other species of macaque, the Gorontalo macaque also has a special pouch on the cheek for storing food. They live in groups of around 20 individuals. Sometimes there are smaller groups of 2–5 individuals, but also there may be large groups of up to 60 individuals (Kolhass, 1993; Kohlhaas & Southwick, 1996). This Sulawesi endemic has been protected but due to a rapidly increasing indigenous population, together with the influx of transmigrants and the logging that has occurred, the area of habitat now available has been reduced to only 4,800 km^2 (Supriatna *et al*., 2001).

Heck's macaque, *Macaca hecki*, is considered to be Vulnerable (IUCN, 2015). It is both semi-arboreal and terrestrial. At Panua Nature reserve, the heck's macaque can be a pest in corn plantations and is often destroyed by the villagers. When a group enters a plantation the leading male usually observes from a tree, while the rest stay on the ground. After entering the plantation, the dominant male will come down to eat. In the neighbourhood of other species, such as *M, tonkeana* in the south and *M. nigrescens* in the north, the species often hybridize (Supriatna & Hendras 2000). The offspring are slightly different from the parents, as seen on the growth of the ischial callosity, the thickening skin on the bottom (Groves, 2004).

Like the other Sulawesi macaques, the heck's macaque is faced with habitat loss. Potential available habitat has been reduced from 67,000 km^2 to 38,500 km^2. However, the only known population occupies an area of no more than 1,055 km^2 in a protected area (Supriatna & Hendras 2000). According to IUCN, the conservation status is Vulnerable (IUCN, 2015) and is listed in Appendix II of CITES (Supriatna *et al*., 2001). The increasing human pressure and lack of available habitat are the primary threats to their continued existence in the wild. The problem for conservation of this species is similar to *M. nigrescens*. Forest conversion to shifting cultivation, influx of transmigration and logging operations are the main factors threatening the future of this species.

The distribution of the Tonkean macaque, (*M. tonkeana*), is quite wide compare to other Sulawesi macaques. This species is found in Central Sulawesi. In the north the distribution is limited by the lowlands of Siweli-Kasimbar, in the southwest by the narrowing of Tempe Lake, and in the south east by Matana and Towuti lakes (Groves, 2004; Froehlich *et al*., 1996). It has been found up to 1300m at Fehrumpenai nature reserve. Apart from that, the species occurs in agricultural areas, plantations, and coastal areas (Supriatna & Hendras, 2000). The tonkean macaque eats many plant parts, especially fruit, about 57% of the diet and leaves, about 17%. They also consume sprouts, grasses, insects, molluscs and small vertebrates. In the wild, tonkean macaques live in large groups of between 25–40 individuals (Supriatna *et al*., 1992; Supriatna & Hendras, 2000). Tonkean macaques on the eastern peninsula of Central Sulawesi and the Togean islands have been proposed as separate species; *M. togeanus* (Froehlich & Supriatna, 1996) or *M. balantakensis* (Supriatna & Hendras, 2000).

Primates of Wallacea outside of Sulawesi: It is thought that the islands of Sundaland and Wallacea have never been connected although Sulawesi may have been connected to Borneo during the Pliocene and Early Pleistocene (Whitten *et al*., 2002, Harrison et al. 2006). Some species such as birds and primates can cross the sea barrier from Bali to Lombok and other islands of Nusa Tenggara. Lombok and Bali are separated by deep water but only a narrow channel (32 km) and they share the same species of primates, the leaf monkey or Javan langur, *Trachypithecus auratus* and the long tailed macaque, *Macaca fascicularis* (Groves, 2004). It is an unresolved

question whether these species occur on Lombok naturally or were brought there by people.

T. auratus exhibits clinal variation from west to east Java and Bali in terms of coloration and morphology (Maryanto *et al*., 1997). Rossenbaum *et al*. (1997) also found high mitochondrial DNA diversity with little structure within and among populations in this leaf monkey. Until recently Roos (2014) separated this leaf monkey into two species, the western Java species *Trachypithecus margaritus* and the eastern Java, Bali and Lombok species *Trachypithecus auratus.* In west Java, there are many national parks and protected areas that constitute the habitat of *T. margaritus* (from West to central Java) while in east Java, Bali and Lombok, the areas of available habitat are mostly small national parks such as Bali Barat National Park in Bali and Rinjani National Park in Lombok. In east Java there are some large national parks such as Meru Betiri, Baluran, Bromo-Tengger Semeru and Alas Purwo (Supriatna, 2014).

The long-tailed macaque, *M. fascicularis*, is distributed widely in western Indonesia from Thailand, Sumatra, Kalimantan, Jawa, and Bali. Research on distribution, genetic diversity and evolution of this macaque in Sumatra, Java, Bali, Lombok and Nusa Tenggara was carried out by a Japanese team, which began working in 1983 (Aimi *et al*., 1982; Kawamoto *et al*., 1982, 1984, 1991). This research found that the genetic and morphological diversity of the long tail macaque in Lombok and elsewhere in Nusa Tenggara was high, indicating that they may have been in the area for quite long time. Since these primates are very widely distributed and have even become farm pests, they have never been categorized as threatened species (Supriatna *et al*., 1996).

The primate in Bacan, *Macaca nigra*, was probably introduced by the King of Ternate (Froehlich *et al*., 1996). This monkey was already in Bacan by the time that Wallace (1876, 1989) and van Bemmelen (1895) visited the island. *M. nigra* has occupied almost all of the forest areas on Bacan Island and is now numbered in the hundred thousands (Rossenbaum *et al.*, 1998). This is even larger than the population of this macaque in its original habitat in North Sulawesi, where there are now approximately only a few thousand individuals (Sugardjito *et al*., 1989; Froehlich *et al*., 1996).

Primate habitat and loss of Forest: The impacts of biodiversity loss on ecosystem goods and services are felt most at the local level by poorer communities dependent on biological resources for livelihoods and welfare. Millions of Sulawesians are directly dependent on forest resources, and many others benefit indirectly. Global interest in the wise use of Sulawesi's biological resources has grown during the past 15 years. Indonesian and international NGOs have become effective partners. Human capacity and environmental awareness in government has increased substantially, with more Indonesian scientists getting into the field in the major national parks and elsewhere.

Notable conservation milestones for Indonesia during this period include: 48% increase in protected areas, including large marine ecosystems; publication of the Biodiversity Action Plan, now under revision; revision of conservation policy and regulation; ratification of the Ramsar Convention; ratification of the Convention on Biological Diversity and more than 60 major international cooperation programs to support biodiversity conservation (Supriatna *et al*., 2001).

Human invasion of primate habitat has also become one of several important factors affecting the existence of primates especially the endemic and restricted range primates. Human activities are considered

to be the main cause of forest fragmentation and the loss of orangutan habitat (Meffe & Carroll, 1994). Fragmentation will affect the dispersal of primates; hence their home range or territory will be limited and furthermore, increase isolation of sub-populations and competition for habitat. Habitat isolation caused by forest fragmentation will speed up local extinction and the formation of metapopulations (Monaghan *et al*., 2001). Limited home range and isolation of populations will reduce the population size and ability to survive (Cowlishaw & Dunbar, 2000). Sulawesi, the major island in Wallacea, is at high risk of habitat loss in the remaining lowland tropical forests due to deforestation (FWI/GFW, 2002). The species that may suffer most from this fragmentation are those that have limited ranges, endemics and species dependent on the forest for their food such as frugivores and seed eaters, which include most of the Sulawesi macaques. Sulawesi macaques have become easy targets for poachers in the open spaces between habitat fragments. Many studies have found that once their habitat becomes fragmented, they become very easy targets for hunting (Riley 2008, Riley & Priston 2010).

Some macaques use forest patches and more heavily disturbed forests, and even cacao plantations that still include some of the original forest trees, triggering human-primate conflict. Many agricultural crops have been reported to be raided by *M. maurus* and *M. tonkeana* (Supriatna *et al*. 1992) where corn and bananas were the main targets. Riley (2008) suggested that the range of *M. tonkeana* includes cacao and coffee agroforest where crops are not raided. Habitat disturbance and logging were observed in virtually every forest (Supriatna, 1988; Supriatna *et al*., 1992). The interface between humans and primates has been known for a long time, which in some parts of the region is in the form of pet ownership and overlapping resource use which causes crop raiding. In Buton, subsistence crops are the most vulnerable to crop raiding (Riley & Priston, 2010).

Without protection, much of the remaining tropical forest and its biodiversity will be lost (Jepson *et al*., 2001). Protected areas can significantly mitigate logging, land clearing, hunting, burning, and grazing in tropical areas. Endemism on Sulawesi is partitioned (Figs. 2, 3: pls. 10, 11). Because of this, to best preserve biodiversity, areas with complementary, non-redundant diversity should be prioritised for protection (Vane-Wright *et al*., 1991; Margules & Pressey, 2000; Margules & Sarkar, 2007). Unfortunately, the current distribution of protected areas indicates that some large conservation areas such as Lore Lindu and Morowali National Parks are restricted to a single area of genetic endemism (West Central) while other areas of genetic endemism such as East Central, Northwest, and Southwest Sulawesi are poorly protected (IUCN, 1992; Whitten *et al*., 2002). However, substantial portions of each of these regions have been proposed for protection including Bakiriang in East Central Sulawesi; Mt. Lompobatang in Southwest Sulawesi; the Palu Mountains, Mt. Sojol, Mt. Dako, the Toli-Toli Mountains, and the Marisa complex in Northwest Sulawesi (Whitten *et al*., 2002). Recently, a national park in Southeast Sulawesi has also been proposed (Mekongga, 258,000 ha) (Gunawan, 2014). Protection of those sites would better complement the protection of primates achieved in existing reserves. All of the Sulawesi primates are protected by Indonesian law, but most of them are still threatened because of their shrinking habitat. Efforts by Indonesian and international organizations, including international financial support, to protect and manage each area of endemism would make significant strides toward preserving much of the remaining biodiversity on Sulawesi.

The first commercial logging operation in Wallacea began in the early part of the century, and forests have been cleared for agriculture, for industrial timber plantations, and for land settlement schemes like the infamous transmigration program that resettled hundreds of thousands of people from densely populated Java moving to other less inhabited (but much less productive) corners of Indonesia (Whitten *et al*., 2002). This has greatly reduced the amount of forest habitat, particularly in the lowlands, and has caused dramatic and severe declines in the populations of many forest species (many by as much as 90%) such as in Central, North and Southeast Sulawesi (Supriatna, 2008). Much of the remaining forest is now given out in timber concessions of various kinds then turned it into palm oil plantations (Supriatna, 2008).

As a result of the different human impacts on the Sulawesi environment, there has been a substantial decline in forest cover, though less than that in most of the other hotspots. What remains is also partly a function of dryness and altitude. Drier areas have generally been more impacted than the wetter portions of the region, and lowland areas more so than the upper reaches of mountains. Dry forest types in general have only about 10−20% of their area remaining, moist and wet forest types substantially more. Looking at particular sub-regions of Wallacea for which information is available, the Lesser Sundas are thought to have only about 7% forest cover remaining, whereas the wetter islands of the Moluccas still have some 74%; Sulawesi is still about 42% covered in original forest (FWI/GFW, 2002). Overall, about 45% of Wallacea still has some forest cover; however, if one considers forest that is still in more or less pristine condition, the percentage drops to only 15%, or about 50,774 km².

One of these is in the 300,000 ha Bogani Nani Wartabone National Park (previously Dumoga-Bone National Park) in north Sulawesi, the single most important conservation area on the entire island. In the early 1980s, the World Bank made one of its first links between a development project (in this case, irrigation) and conservation when it helped WWF to encourage establishment of this park. The reason behind the Bank's interest was protection of the upper watershed of the Dumoga River, which was to be used to irrigate 11,000 ha of rice fields. Although the park enjoyed serious and sustained support from provincial and district officials for many years, recently the park has suffered from large numbers of small-scale gold miners, who have poisoned the river with mercury and cleared forest (Bigford *et al*., 2008).

Conservation Status and Efforts: Preventing rapid biodiversity loss requires efficient allocation of conservation efforts (Pimm *et al*., 2001) within biodiversity hotspots; those areas where concentrations of endemic species clash with high levels of human activity (Myers *et al*., 2000). One hotspot, Wallacea, encompasses Sulawesi, the Lesser Sunda Islands, and the Moluccas. As with many large islands, the biota of Sulawesi is highly distinctive, but this island is too large to protect in its entirety. Therefore, designation of conservation areas requires a detailed understanding of patterns of endemism on it. Macaque monkeys, for example, have diversified into seven endemic allopatric species (Fooden, 1969), and the central Sulawesi species *Macaca tonkeana* is further divided into two genetically distinct sub-populations (Evans *et al*., 2003a, b; Froehlich *et al*., 1996).

According to the IUCN/SSC Primate Specialist Group (IUCN/SCC 2008) over 70% of Asian primate species area threatened with extinction. Up to 80% of the over 40 Indonesian primate species are threatened (Grow *et al*., 2010). Four species from Indonesia have been listed

among the 25 most endangered primates globally, the Sumatran orangutan (*Pongo abelli*), the Mentawai pigtailed langur (*Simias concolor*), the Javan Slow loris (*Nycticebus javanicus*) and the Siau Island tarsier (*Tarsius tumpara*) (Mittermeier *et al*. 2009). The Siau tarsier, first found in 2008, occurs on Siau Island, a small volcanic island of 116 km^2 and more than 28,000 people (Shekelle & Salim, 2008) located off north-eastern Sulawesi.

Tonkean macaques are probably more secure than other Sulawesi macaques because their habitat is wide and the most extensive in Sulawesi, although their status is Vulnerable (IUCN 2015). Much of their habitat has been protected within nature reserves such as Lore Lindu, Morowali and Fehrumpeni with good forest, with more than 550,000 ha in total (Supriatna *et al*., 1992). For other macaque species there is not enough information to accurately determine their conservation status. According to IUCN, the status of the Buton macaque, *Macaca brunescens* or *M. ochreata brunescens*, is data deficient. On the other hand, populations of the Booted macaque, *Macaca ochreata ochreata* remain widespread and extensive, although habitat destruction now looms as a danger. Conservation of small island macaques is at a critical stage. The Buton macaque has lost more than 37% of its habitat, from 29,500 km^2 to 18,500 km^2. According to IUCN, this species is vulnerable to extinction, and also on Appendix II of the Cites list. They now occupy a forest area of only 1,420 km2 in a conservation area. In Sulawesi, this macaque can be seen in Rawa Aopa (Supriatna & Hendras, 2000; Supriatna, 2000).

Besides extending protection to species not currently found in protected areas (Table 3), we also need to conserve habitat in areas of identified hybridisation. Hybrid zones provide excellent opportunities to study animal genetics, molecular biology and even the social behavior of mixed species. For example, Batu Mila, where *Macaca maura* and *Macaca tonkeana* hybrids flourish, is a valuable field laboratory for studying genetic composition, gene flow and evolution of speciation (Supriatna, 1991). The mating behaviour of those two Sulawesi macaques is different, with multiple matings between females and males in one, while females mate only with one dominant male in the other. In the hydrid animals this varies between many different groups (Supriatna, 1991).

There are only two places in the world where primates are known to hybridise. One is in Africa and other in Sulawesi. Some hybridisation has also been detected in Kalimantan gibbons, but in only a few populations (Mather, 1992). Therefore, the Sulawesi macaques are of great scientific interest. It is very imporant to preserve these natural examples of the evolution of speciation. Two such places are the Batu Mila area noted above, where *M. Maura and M. tonkeana* hybridise (Groves, 1984, Supriatna 1991) and a very thin strip of forest in northern Palu that has been identified as hybrid zones between *M. tonkeana* and *M. hecki* (Bynum, 2002). Both of these sites would be good places to conserve in order to save hybrid zones as natural laboratories (Fig. 5: pl. 12). Other proposed conservation areas are Nantu Wildlife Reserve which is an important area for *M. nigra*, Tompotika, which has a population of *M. tonkeana* which will probably be recognized as a separate species or sub-species, *M. togeanus*, and Sorowako for M. ochreata, where there is Nickel mining concessions . This rich diversity is especially important to our quest to understand genetic variation and speciation. For Tarsier conservation, a Global Tarsier Action Plan conference was conducted in November 2008, in Manado, North Sulawesi. Results from this conference such as supporting taxonomic work, improvement of Red List assessment, investment in ex-site

conservation and emulation of successful tarsier conservation programs elsewhere in Sulawesi, need to be implemented (Shekelle & Salim, 2008). As envisioned by Shekelle & Leksono (2004), developing a tarsier sanctuary in North Sulawesi may not be too difficult to implement. Combining ecotourism and research side-by-side can help to promote effective conservation for Sulawesi primates.

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PLATE 10

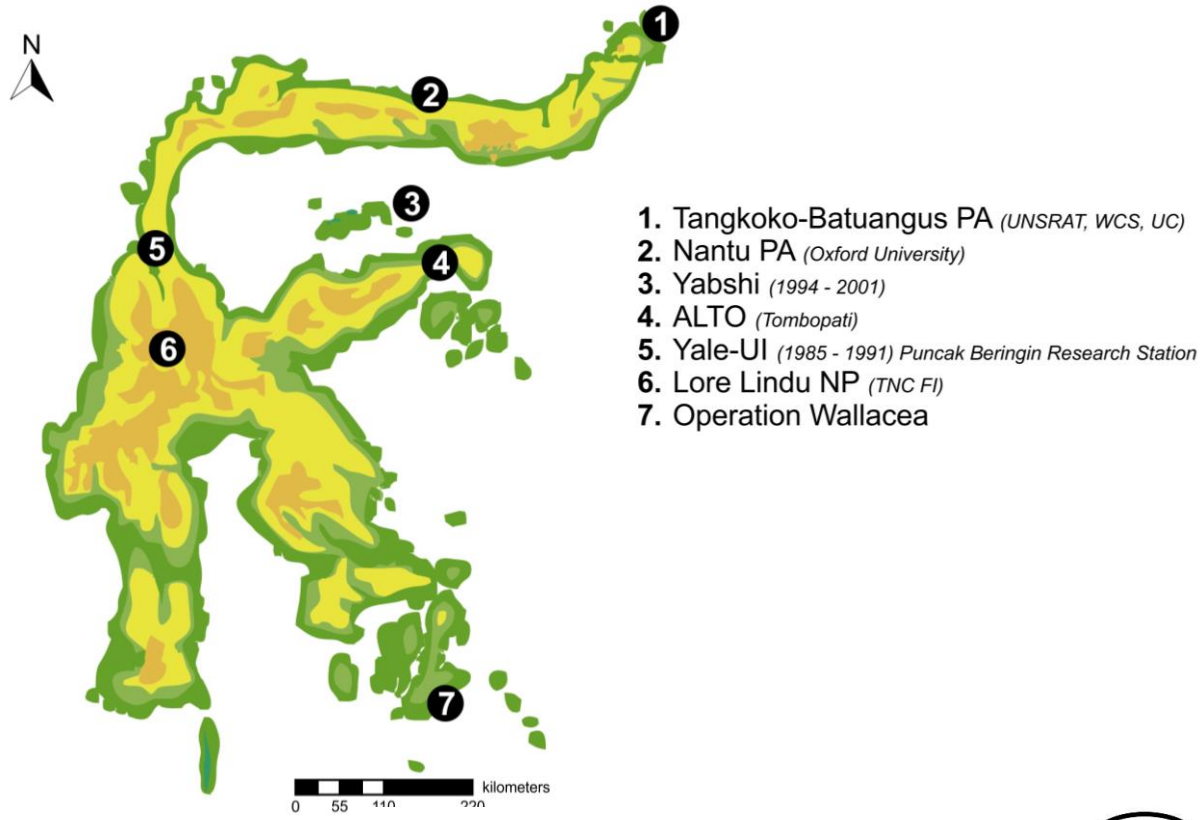

Figure 1: Field stations established for biological research.

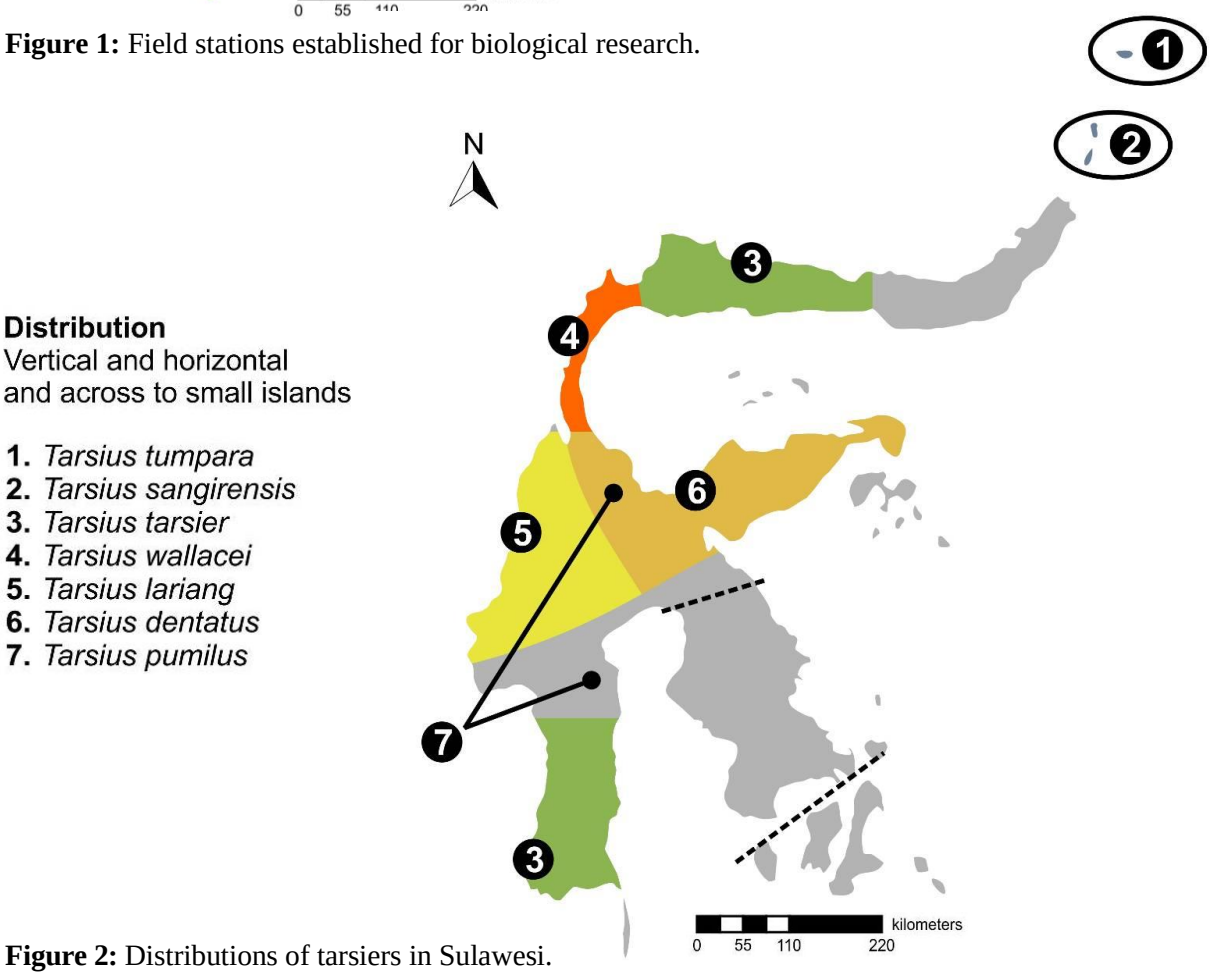

Figure 2: Distributions of tarsiers in Sulawesi.

PLATE 11

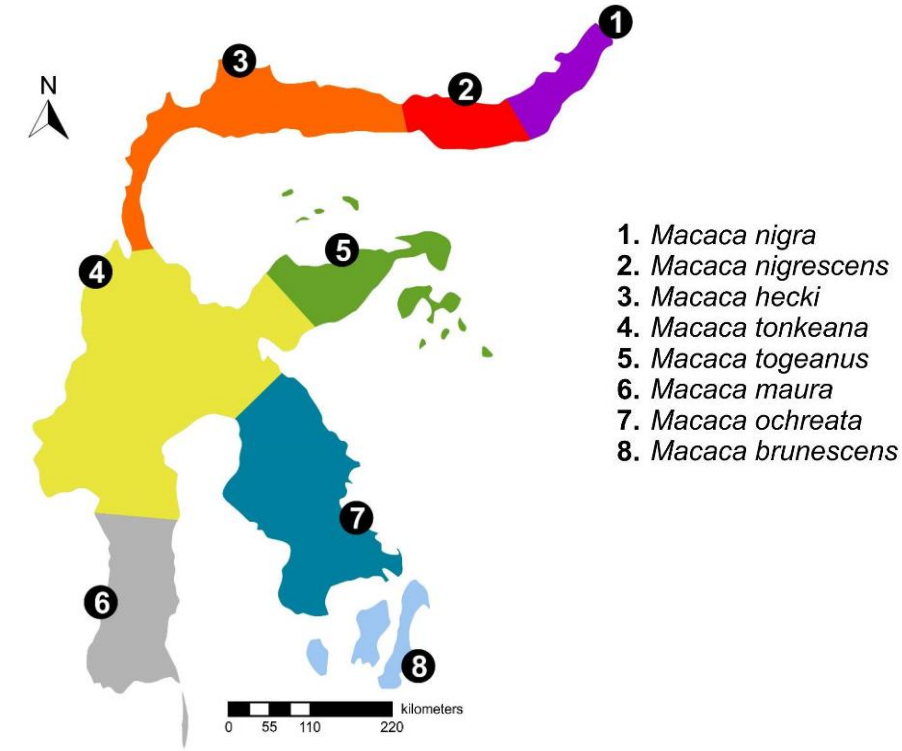

Figure 3: Distribution of macaques in Sulawesi, including *Macaca togeanus*, which has been proposed as a separate species.

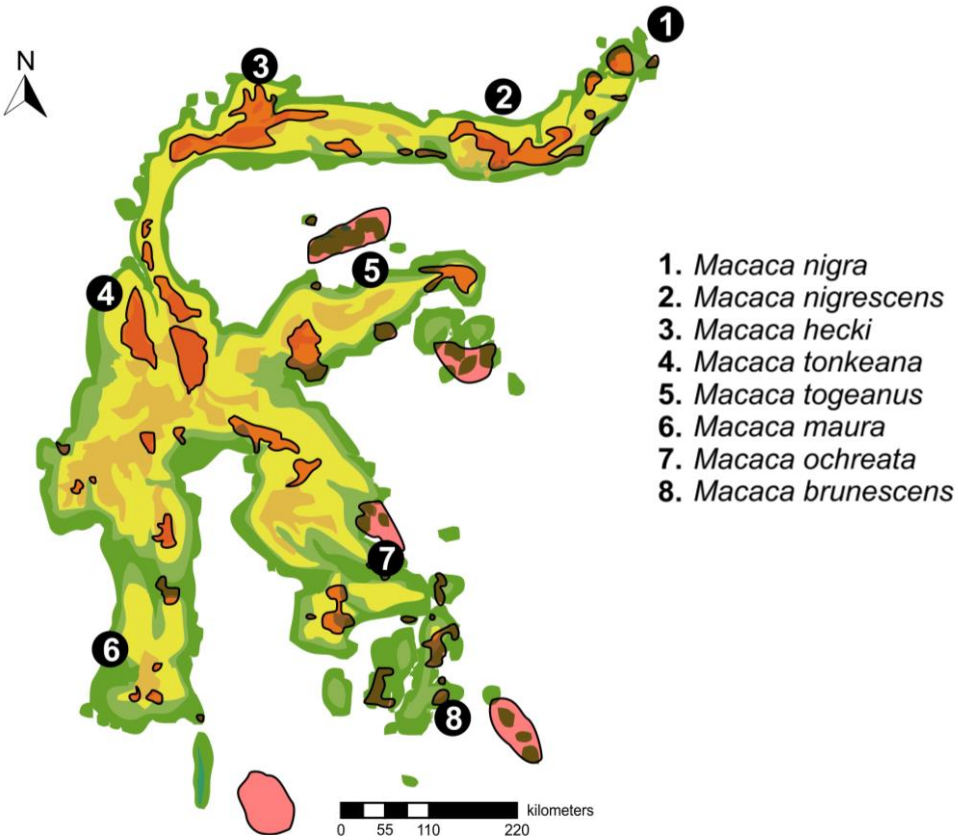

Figure 4: The distribution of habitat remaining for the seven macaque species in Sulawesi, plus *Macaca togeanus*, which has been proposed as separate species.

PLATE 12

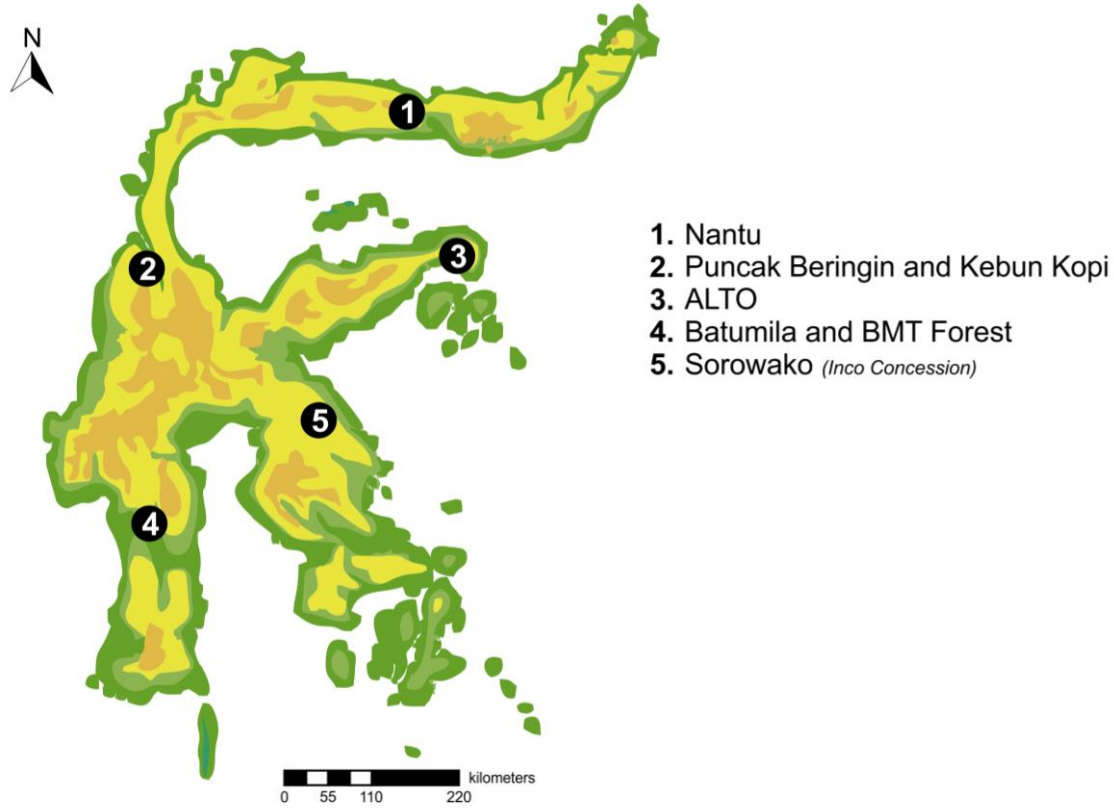

Figure 5: Proposed conservation area to protect hybrid zones.