Designation of a New Subspecies of Angola Colobus *Colobus angolensis* Sclater, 1860 (Primates: Cercopithecidae) Endemic to the Mahale Mountains of Western Tanzania

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Abstract: The polytypic Angola colobus *Colobus angolensis* is a widespread species that, in eastern Africa, is often restricted to small, highly isolated, areas. In 1966, evidence for an undescribed subspecies of *C. angolensis* was obtained in Mahale Mountains National Park, central west Tanzania. Mahale *C. angolensis* has only been observed twice by scientists (1976 and 1979) and remained unnamed. In April 2022, 43 years after the last published observation, we observed, heard, and photographed a group of Mahale *C. angolensis*. Given the considerable current geographic isolation (~100 km across L. Tanganyika; ~330 km across land) of this monkey from its conspecifics, together with the distinctive coloration and pattern of its pelage, we here designate this as a new subspecies. We also describe the environment in which Mahale *C. angolensis* lives, discuss its paleobiogeography, taxonomic arrangement, and threats, and provide recommendations for conservation and research. Mahale *C. angolensis* is endemic to the montane forests of Mahale Mountains National Park where it has been observed at only two sites, the south slope of Mt. Ihumo (~1,970 m asl) and on the ridge between Mt. Nkungwe and Mt. Kahoko (~2,350 m asl). In addition, bouts of 'roar' loud calls were heard on nearby Mt. Mhensabantu (~2,050 m asl) on two occasions. The geographic distribution of Mahale *C. angolensis* is likely between 10 km² and 50 km². The size of this population is probably <400 individuals, with <200 adults. This monkey appears to occur wholly within a remote and rugged part of Mahale Mountains National Park where agricultural encroachment and poaching are not major concerns at this time. The primary threats are habitat loss due to fire, and to a warming climate. With its small population and severely restricted geographic distribution, Mahale *C. angolensis* qualifies as a 'Critically Endangered' subspecies under current IUCN Red List degree of threat criteria.

Key Words: Albertine Rift, climate change, *Colobus angolensis langheldi*, primate biogeography, primate conservation, primate taxonomy, Mahale *Colobus angolensis*, Mahali, Mahari, Mount Ihumo, Mount Mhensabantu, Mount Nkungwe

Introduction

Reliable information on the taxonomy, geographic distribution, abundance, and conservation status of populations is not only of scientific interest, but also critical to setting science-based priorities for actions for the conservation of biodiversity (Mace 2004; Grubb *et al.* 2003; Zinner and Roos 2016; Gippoliti *et al.* 2018).

The polytypic Angola colobus *Colobus angolensis* Sclater, 1860, is a widespread species, occurring from northeast Angola northwards through the Congo Basin, then eastwards to the Indian Ocean coasts of southeast Kenya and northeast Tanzania (Fig. 1; Table 1). In eastern Africa, *C. angolensis* is often restricted to highly isolated and small areas on mountains. This medium-sized, arboreal folivore lives in several evergreen and semi-deciduous forest types, including coastal, swamp, groundwater, riparian, gallery, lowland, mid-altitude (= transitional), and montane, from

sea-level to 3,100 m asl (Schouteden 1944; Rahm and Christiaensen 1960; Rahm 1966, 1970; Dandelot 1974; Colyn 1991; Colyn *et al.* 1991; Oates 1994; Bocian and Anderson 2013; Kingdon and Groves 2013; De Jong *et al.* 2020; Butynski and De Jong 2022; De Jong and Butynski 2023).

The classification of *C. angolensis* is predominantly founded on the coloration and pattern of the pelage, craniometrics, and geographic distribution. Recent ecological and genetic studies examined the subspecies-level taxonomy of *C. angolensis* in Kenya and Tanzania (McDonald and Hamilton 2010; McDonald *et al.* 2019, 2022). Here we follow the taxonomic arrangement of De Jong *et al.* (2020), Butynski and De Jong (2022), and McDonald *et al.* (2022) in recognizing eight subspecies (Table 1). This arrangement is largely based on Schwarz (1929), Rahm (1970), Dorst and Dandelot (1972), Dandelot (1974), Hull (1979,
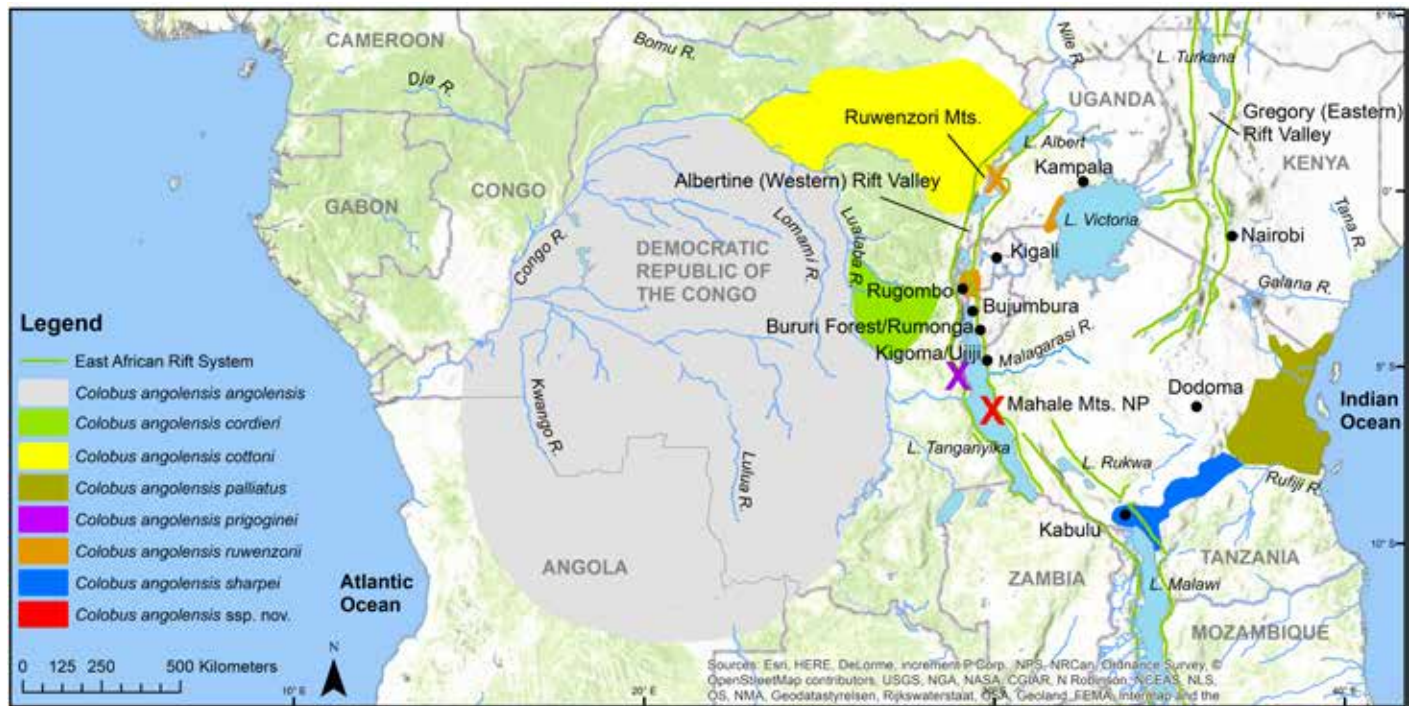
Figure 1. Geographic distribution of the subspecies of Angola colobus *Colobus angolensis*. Map based on Rodgers (1981), Colyn (1991), Bocian and Anderson (2013), De Jong and Butynski (2018, 2020, 2023), Butynski and De Jong (2020b, 2022), Cunneyworth *et al*. (2020), De Jong *et al*. (2020), Maisels (2020a, 2020b, 2020c), Rovero *et al*. (2020), and this study.

Table 1. Latin name, vernacular name, and distance to Mahale Mountains National Park of the eight subspecies of Angola colobus *Colobus angolensis* recognized in this article.

Subspecies	*C. a. angolensis* Sclater, 1860	*C. a. cordieri* Rahm, 1959	*C. a. cottoni* Lydekker, 1905	*C. a. palliatus* Peters, 1868	*C. a. prigoginei* Verheyen, 1959	*C. a. ruwenzorii* Thomas, 1901	*C. a. sharpei* Thomas, 1902	*C. a.* ssp. nov.
Vernacular	Sclater's Angola colobus	Cordier's Angola colobus	Powell-Cotton's Angola colobus	Peters' Angola colobus	Prigogine's Angola colobus	Rwenzori Angola colobus	Sharpe's Angola colobus	Mahale Angola colobus
Shortest distance to Mahale NP (km)	310	300	620	770	100	315	525	0
Shortest distance over land to Mahale NP (km)	630	420	620	770	560	330	525	0

~1996), Napier (1985), Colyn (1991), Groves (2001, 2005, 2007), Grubb *et al*. (2003), Bocian and Anderson (2013), and Kingdon (2015). These taxonomies primarily differ in three respects: (1) whether *C. a. adolfi-friederici* Matschie, 1914, is recognized or treated as a synonym of *C. a. ruwenzorii*; (2) whether *C. a. sharpei* is recognized or treated as a synonym of *C. a. palliatus*; and (3) whether a putative taxon of *C. angolensis* in the Mahale (= Mahari = Mahali) Mountains of central west Tanzania is recognized. The latter, often referred to as "*Colobus angolensis* ssp. nov." (Groves 2001, 2007; Grubb *et al*. 2003; Bocian and Anderson 2013; De Jong and Butynski 2018; De Jong *et al*. 2020; Butynski and De Jong 2022) was discovered in 1966 and proposed as a distinctive population (Nishida 1968; Nishida *et al*. 1981)

but has not been formally named. The published English vernaculars applied to this monkey are "Nkungwe's Angolan colobus" (Nishida *et al*. 1981; Groves 2007; Groves and Ting 2013), "Mahale Mountains Angola colobus" (Grubb *et al*. 2003; Bocian and Anderson 2013; Butynski and De Jong 2022), and "Mahale Angola colobus" (De Jong and Butynski 2023).

Colobus angolensis ssp. nov. is currently listed as 'Data Deficient' on The IUCN Red List of Threatened Species because of its poorly known geographic distribution and population size (Butynski and De Jong 2020a). 'Data Deficient' taxa are of great conservation concern as they are often considered to be non-threatened when, in fact, sufficient data might indicate that they are threatened (Parsons

2016). Borgelt *et al.* (2022) found that a higher portion of 'Data Deficient' taxa are threatened with extinction than are data-sufficient taxa.

The aim of this article is to formally describe and name *Colobus angolensis* ssp. nov. and present what is known concerning its geographic distribution, abundance, ecology, and threats. Finally, we give criteria for an updated assessment for The IUCN Red List of Threatened Species and present priorities for research and science-based conservation actions.

Discovery of the Mahale Angola Colobus

The Mahale Angola colobus was discovered on 29 September 1966 by Toshisada Nishida and Junichiro Itani (Nishida 1968, 1972; Kano 1971; Nishida *et al.* 1981; Itani 1990). This discovery is described by Nishida (1972, p.61; Fig. 2), "…found some food remnants of a leopard, comprising a bundle of black and white hair and the lower jaw of a primate, in the montane forest near the summit of Mt. Nkungwe (2500 m a.s.l.). This primate is very possibly a black and white colobus (*Colobus angolensis*), which is called Nkamba in Kitongwe. According to native information, the species is confined to montane forests more than 1800 m above sea level (Mt. Sibindi etc.) …". Itani (1990, p.46) states, "We collected the mandible." "…on the basis of what we learned later, it is also possible that it was killed by chimpanzees." Also on 29 September 1966, they heard "loud goat-like sneeze of alarm" calls (see Methods) that they thought, "…were probably emitted by Angolan colobus at the col between Mt. Ihumo (ca. 1,900 m a.s.l.) and Mt. Mhensabantu (ca. 2,050 m a.s.l.)…". (Nishida *et al.* 1981, p.558). This event is also reported by Itani (1990, p.46) as follows, "On the saddle point between Mhensabantu and Humo, we heard strange calls, which the Tongwe guides told us were those of nkama (*Colobus angolensis*)."

The first published record for *Colobus* in the Mahale Mountains (hereafter, 'Mahale') is that of Nishida (1968) where *C. polykomos* (= *C. angolensis*) is listed among prey of leopard *Panthera pardus* (Linnaeus, 1758) and said to live only in the high-altitude forest. The next published record of *Colobus* in Mahale is that of Kano (1971). He states the following (p.295), "Itani and Nishida, however, heard its vocalizations near the peak of Mt. Kungwe on an early morning in October, 1965, and they also found hair and a mandible of a black and white guereza which had probably fallen victim to a leopard, the only large carnivore in that area. The mandible, which Nishida brought in, is so far the only evidence that the black and white guereza occurs in this area." "Information was obtained from most of the villagers of the Mahali Range to the effect that a primate called 'Kamba' lives in the montane forests on or near the peak of Kungwe Mountain, which is the highest peak of the Mahali Mts. (Fig. 9). Judging from their descriptions this primate is apparently a black and white guereza." "In spite of extensive inquiry, no information on 'Kamba' was obtained outside of Mt. Kungwe." "As a result, the black and white guereza

of this area, if any, appear to be extremely local, restricted to the montane forest of Mt. Kungwe, and on the verge of extinction, which may be a result of competition with the other leaf-eater, the red colobus, which extensively inhabits the montane forest region south of the Lugugu Basin." Note that the date of discovery given here (October 1965) differs from the September 1966 date provided by Nishida *et al.* (1981) and Itani (1990).

The first observation of the Mahale Angola colobus was on 18 May 1976 by T. Nishida. This encounter is described in Nishida *et al.* (1981, pp.557–558; Fig. 2) as follows, "Then he observed a great number of monkeys all jumping up and down at once in the canopy of the montane forest which covers the narrow ridge extending from the summit of Mt. Nungwe to Mt. Kahoko. It was the same narrow ridge where the mandible and hair were found in 1966 (Fig. 1). Although the excited monkeys were about 200 m away from him, he could recognize with the aid of binoculars that they had long, white cheek hair, long white epaulettes, and long tails with white tips. Otherwise, their coats were all black in color. These animals were undoubtedly Angolan black-and-white colobus monkeys. Nishida was able to count 16, but he estimated that there must have been more than 30 animals in all. Then the troop gradually moved through the trees from the ridge to the Kasiha Valley. One red colobus monkey (*Colobus badius tephrosceles*) was noticed travelling with it. At 15:28, a troop of red colobus monkeys appeared from the south and descended the ridge and proceeded to follow the previous troop of Angolan colobus monkeys."

The second observation of Mahale Angola colobus was made by J. Itani, M. Hiraiwa, and T. Hasegawa on 22 August 1979. This encounter is described by Nishida *et al.* (1981, p.558), "From the summit, they observed about 30 Angolan colobus monkeys completely mingling with about 20 red colobus monkeys in the montane forest at a spot very close to the place where Nishida had observed them three years earlier. They could see that the shoulder-cape of the Angolan colobus was very long and that the tail was greyish only at the very tip. Its white cheek hair was long and there was no white band on the forehead. Its buttocks were totally black except for a pink patch at the root of the tail (Fig. 3)." "Judging from the close proximity between their observation site and Nishida's, it is likely that they were observing the same troop of monkeys. The observation time was 103 min (13:35–15:18)." Their Figure 3 presents two drawings of Mahale Angola colobus. Itani (1990, p.53) recorded this encounter as follows, "On the peak to the south across a deep gap, there was a mixed group of about 30 *Colobus angolensis* and 12–15 *C. badius*."

The above are the only five published accounts of the first two observations of Mahale Angola colobus by scientists. To the best of our knowledge, there is no specimen or photograph of this monkey, nor recordings of its vocalizations. However, based on their field observations, Nishida *et al.* (1981, p.557) noted that, "This may very well be a heretofore undescribed, and distinctive subspecies."
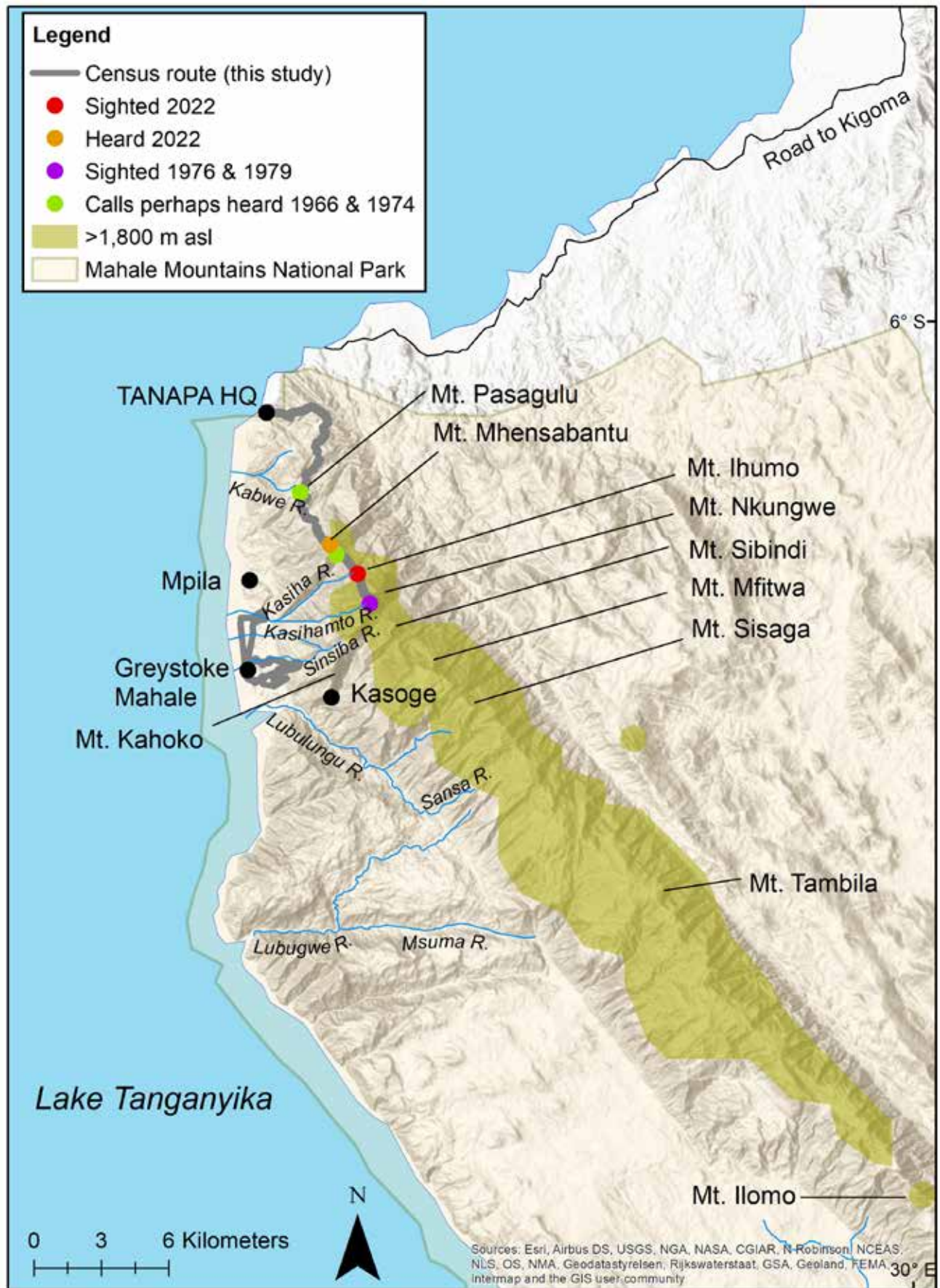
Figure 2. Localities of the three Mahale Angola colobus *Colobus angolensis* ssp. nov. sightings. Note that the location of Mount Kahoko provided by Nishida *et al*. (1981, Fig. 1) differs from other sources (Google Earth; Peakery.com; PeakVisor.com). For the sake of compatibility, the location provided by Nishida *et al*. (1981; Fig. 1) is presented here.
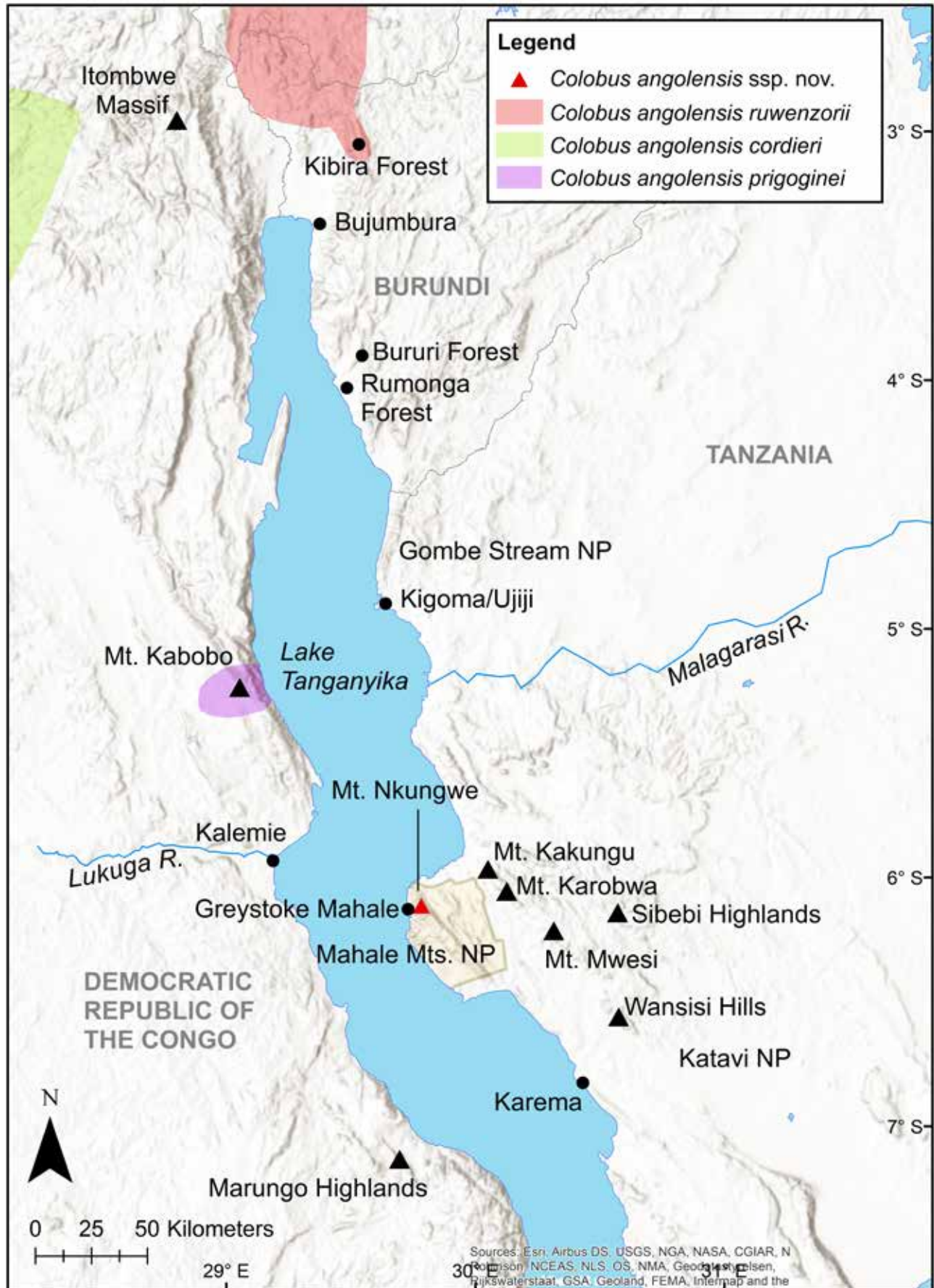
Figure 3. Mahale Mountains National Park and the geographic distributions of the three nearest subspecies of Angola colobus *Colobus angolensis*. Map based on Nishida *et al*. (1981), Colyn (1991), Butynski and De Jong (2020b, 2022), De Jong and Butynski (2020, 2023), De Jong *et al*. (2020), Maisels (2020b), and this study.

On 21 April 2022, 43 years after the last published observation, we encountered a group of Mahale Angola colobus, heard the 'roar' loud call (see Methods), and obtained the first photographs of this monkey. Below, based on the descriptions provided in Nishida *et al.* (1981), and on our observations and photographs, we designate a formal name for the Mahale Angola colobus.

Albertine Rift

The Albertine (Western) Rift, the west branch of the East African Ridge, extends from the north end of L. Albert, northwest Uganda, southwards through west Rwanda, west Burundi, and west Tanzania to the south end of L. Tanganyika in northeast Zambia (ca. 300,000 km²; 900–5,110 m asl; Fig. 1). This region, recognized as the 'Albertine Rift Biodiversity Hotspot', supports extremely high levels of species diversity and endemism (Moreau 1943, 1966; Carcasson 1964; Omari *et al.* 1999; Fishpool and Evans 2001; Plumptre *et al.* 2003, 2004, 2007). For example, as of 2007, 402 mammal species, of which 35 are endemic, are known to occur in the Albertine Rift. This is approximately 39% of the mammal species in Africa (Kityo *et al.* 2003). Of the 1,061 bird species, 41 are endemic. Of the 5,793 plant species, 567 are endemic. Butterflies are represented by 117 endemic species. The species lists for all four of these taxonomic groups are, however, far from complete.

The forests of the Albertine Rift are threatened by habitat loss because of agricultural expansion, human-caused fire, logging, mining, and other human activities. Poaching, civil war, and general insecurity are major problems over large areas (Butynski 1984; Omari *et al.* 1999; Plumptre *et al.* 2004, 2021; Owiunji and Plumptre 2010).

Mahale Mountains National Park

The Mahale Mountains, an outlier relict of the Albertine Rift, are located along the Albertine Rift on the east shore of L. Tanganyika, central west Tanzania (Figs. 1 and 3). Mahale Mountains National Park (1,613 km²; hereafter, 'Mahale NP'), gazetted in 1985, includes all of the Mahale Mountains and represents the western limit of the 'Greater Mahale Ecosystem/Landscape' (~18,200 km²; Kano 1971; Moyer *et al.* 2006; TANAPA 2006; Piel *et al.* 2013; McLester *et al.* 2019; Bonnin *et al.* 2020). Mahale NP is also an 'Important Bird Area' (Fishpool and Evans 2001; Baker and Baker 2002). Overviews of the history, geography, vegetation, and biodiversity of Mahale NP are presented in Moreau (1943), Ulfstrand and Lamprey (1960), Nishida (1968, 1972, 1990, 2012), Kielland (1978), Itani (1990), Anderson and Baker (2003), Moyer (2006), Moyer *et al.* (2006), TANAPA (2006), Itoh and Nakamura (2015), and Nakamura and Itoh (2015). Moyer (2006) and Nakamura *et al.* (2015b) review the biodiversity surveys and other studies conducted there.

Mahale NP supports both savanna-adapted species of eastern Africa and southern Africa, and forest-adapted species of western Africa and central Africa (Carcasson 1966; Kielland 1978; Moyer 2006; Nishida 2012; Ihobe 2015a,

2015b). Moyer (2006) provides preliminary lists of the species of plants and animals in Mahale NP, while more recent lists of the plants and mammals are given in Itoh (2015a, 2015b) and Ihobe (2015a, 2015b), respectively. Of the 355 species of bird known for Mahale NP, 11 are endemic subspecies. There are no known endemic bird species (Fishpool and Evans 2001; Baker and Baker 2002; Moyer 2006; Moyer *et al.* 2006). At least 70 species in 11 orders of mammals are listed for the park (Ihobe 2015a), a few of which are endemic.

The terrestrial part of Mahale NP (~1,500 km²) ranges in altitude from the shore of L. Tanganyika at 773 m asl to the top of Mt. Nkungwe at ~2,530 m asl. The altitude of Mt. Nkungwe has been variously reported as 2,460 m asl (Nishida 1990), 2,462 m asl (Nishida 1968; Nishida *et al.* 1981; Nakamura and Itoh 2015; TANAPA visitor sign on the peak), 2,473 m asl (Peakery 2023), 2,490 (Itani 1990), 2,500 m asl (Kano 1971; Nishida 1972), 2,515 m asl (Moreau 1943); 2,520 m asl (Itani 1990; PeakVisor 2023), 2,525 m asl (Baker and Baker 2002), 2,576 m asl (Procter 1958), and 2,597 m asl (Grant 1949). In agreement with Stevens (1958), we recorded ~2,530 m asl twice on a GPS (Garmin GPSMAP 65) and twice with the Gaia GPS app on an iPhone X.

Mahale forms a large peninsula that extends westward into L. Tanganyika (773 m asl) and is, therefore, isolated by water and low ground to the north, south, and west (Fig. 3). Lake Tanganyika, formed during the Late Miocene (12–9 million years ago), is the longest (676 km), second deepest (1,471 m; mean depth 570 m), and second oldest major lake in the world. It ranges in width from 18 km to 70 km. Covering 32,900 km², L. Tanganyika is the biggest lake in Africa by volume, holding about 17% of the world's fresh water (Moreau 1943; Cohen *et al.* 1997; O'Reilly *et al.* 2003; Nevado *et al.* 2013; Hunink *et al.* 2015; Wikipedia 2023).

To the east and south, Mahale NP is isolated by a vast semi-arid region of low ground (<1,300 m asl) that is mostly covered by 'Central Zambezian Miombo Woodland' (Olson *et al.* 2001; Foley *et al.* 2014) where the dominant trees are *Brachystegia* spp., *Julbernardia* spp., and *Isoberlinia angolensis* (Moreau 1943; Kano 1971; Nishida 1972, 1990, 2012; Nishida and Uehara 1981; White 1983; Itani 1990; Moyer *et al.* 2006; Hunink *et al.* 2015; McLester *et al.* 2019; Bonnin *et al.* 2020). Photographs of the major habitat types of Mahale NP are presented in Nishida (2012).

Mean annual rainfall in Mahale NP on the lakeshore (773 m asl) is ~142 cm at Bilenge Camp (1978–1982) and ~177 cm at Myako Camp (1976–1984), and ~184 cm at Kansyana Camp (1973–1988) approximately 1 km inland at 820 m asl (Takasaki *et al.* 1990; Moore 1992; Hunink *et al.* 2015). Mean annual rainfall at Kansyana Camp during 1983–2013 was 175 cm (Itoh 2015a). There are no rainfall data for the higher altitudes of Mahale NP, but models predicting mean annual rainfall are available (see below). The one dry season lasts about 6 months (May–October; Seismon and Picton Phillips 2012; Itoh 2015a).

Annual mean minimum and maximum daily temperatures are as follow: Bilenge Camp (1977–1984) 20°C and 30°C; Myako Camp (1977–1984) 21°C and 30°C; Kansyana Camp (1973–1988) 18°C and 29°C. Annual mean minimum and maximum daily temperatures at Kansyana Camp during 1983–2013 were 18°C and 29°C. The three coolest months are June, July and August, while the two warmest months are September and October (Takasaki *et al.* 1990; Itoh 2015a).

In Mahale NP, closed montane forest occurs from ~1,800 m asl to ~2,350 m asl (Nishida 1972, 2012; Nishida and Uehara 1981; Nishida *et al.* 1981; Itani 1990; T. Butynski and Y. de Jong pers. obs.). This forest is often shrouded in clouds, particularly at higher altitudes where it might be better described as 'cloud forest' (Figs. 4 and 5; Nishida 1990; Hemp 2005; Owiunji and Plumptre 2010).

The interior of Mahale NP is extremely rugged with six closely packed peaks >2,000 m asl (Fig. 2) and many cliffs and steep-sided valleys (Figs. 4 and 5). The only other site in the Greater Mahale Ecosystem with montane forest appears to be Mt. Mwesi (1,921 m asl) ~60 km east-southeast of Mt. Nkungwe (Fig. 3). The area of montane forest on Mt. Mwesi is, however, only ~40 ha. Although the two nearest mountains to the east of Mahale, Mt. Kakungu (1,747 m asl) and Mt. Karobwa (1,879 m asl), are within 25 km of L. Tanganyika, they lie in the rain-shadow of Mahale (Fig. 3). They are also far inland from the Indian Ocean, ~960 km to the east. These two mountains are, therefore, likely too dry to support montane forest. In addition, any montane forest on these two mountains is probably greatly suppressed by frequent fire.

From Mahale NP, the nearest sites with large areas of montane forest, Mt. Kabobo (= Misotshi-Kabogo) and Itombwe Massif, are on the opposite (west) side of L. Tanganyika (Fig. 3). Mt. Kabobo (2,750 m asl) is ~115 km to the northwest and holds ~800 km² of forest, roughly 120 km² of which is montane forest (Plumptre *et al.* 2008; A. Plumptre pers. comm.). The Itombwe Massif (3,475 m asl, ~15,000 km²) is ~200 km to the north-northwest and supports well over 4,000 km² of montane forest (Doumenge 1998; Omari *et al.* 1999; Fishpool and Evans 2001). All the forest-dependent species of Mahale are, therefore, extremely isolated (Moreau 1943, 1966; Kano 1971). This is especially the case for those many species that are dependent on montane forest, such as *C. angolensis* ssp. nov.

Mahale NP has been a major research site for primates, particularly eastern robust chimpanzee *Pan troglodytes schweinfurthii* (Giglioli, 1872), since 1965 (Nishida 1968, 1990, 2012; Itani 1990; Uehara and Ihobe 1998; Uehara 2003; Nakamura *et al.* 2015b). Eleven species of primate are confirmed present in Mahale NP: miombo silver galago *Otolemur crassicaudatus monteiri* (Bartlett in Gray, 1863), Thomas' dwarf galago *Galagoides thomasi* (Elliot, 1907), an unidentified dwarf galago *Paragalago* [perhaps Mozambique dwarf galago *P. granti* (Thomas and Wroughton, 1907)]*,* eastern vervet *Chlorocebus pygerythrus centralis* Neumann, 1900, Mahale silver monkey *Cercopithecus*

mitis ssp.? Wolf, 1822, Schmidt's red-tailed monkey *Cercopithecus ascanius schmidti* Matschie, 1892, southern yellow baboon *Papio cynocephalus cynocephalus* (Linnaeus, 1766), Kinda baboon *Papio kindae* Lönnberg, 1919, Mahale Angola colobus *Colobus angolensis* ssp. nov., ashy red colobus *Piliocolobus tephrosceles* (Elliot, 1907)*,* and *P. t. schweinfurthii* (Nishida 1968, 2012; Kano 1971; Moyer 2006; TANAPA 2006; Butynski and De Jong 2009, 2023; Ihobe 2015a, 2015b). This is more species of primate than for any protected area in Tanzania except for the Udzungwa Mountains National Park (13 species; Rovero *et al.* 2009; Davenport *et al.* 2013). Nishida (1968, 1990) and TANAPA (2006) also list Tanzania lesser galago *Galago senegalensis sotikae* Hollister, 1920, and olive baboon *Papio anubis* (Lesson, 1827). While *G. senegalensis* is likely present in the lowlands of Mahale NP, *P. anubis* is almost certainly absent (Kano 1971; Moyer *et al.* 2006; T. Butynski and Y. de Jong pers. obs.). The presence of southern lesser galago *Galago moholi* is mentioned (Kano 1971; Moyer 2006; Ihobe 2015a, 2015b), but this requires confirmation. If present, this would be a range extension of ~750 km to the northwest of the known geographic distribution (De Jong and Butynski 2023).

Methods

Primate censuses

From 12–23 April 2022, we conducted a training course on natural history and large mammal monitoring in Mahale NP for eight guides and trackers from Greystoke Mahale camp (hereafter, 'Greystoke') and five Tanzania National Park (TANAPA) rangers. We were also asked to find the most appropriate three or four campsites for tourists wishing to spend nights in the more remote parts of Mahale NP (Butynski and De Jong 2023). This course built upon those that we conducted for Greystoke guides and trackers during 22 November–22 December 2008 and 5–19 November 2009. During the 2022 course, 52 km of trail were walked by census teams that ranged in size from three to eight people. Existing trails were used to climb to Mfiga Camp on the Ntale R. to the east of Greystoke (1 day and night), Mt. Pasagulu (1 day and night), Mt. Mhensabantu (1 day and night), and Mt. Nkungwe (3 days and nights) (Fig. 2). Each team walked at an average speed of approximately 1 km/h, looking and listening for primates and other mammals, and stopping at viewpoints to scan the forest with binoculars. Information collected for each census included date, weather, start time, end time, places surveyed (GPS, e.g., Garmin GPSmap 60Cx), walking speed, and distance walked (GPS). Each encounter with primates was given a unique identification code. Information collected during each encounter included time, coordinates (GPS), altitude (GPS), vegetation type, species/subspecies, minimum group size, and group composition. Particular attention was given to obtaining descriptions and photographs of adult males. Observations were made with binoculars (e.g., Zeiss Dialyt

Figure 4. North slopes of Mount Ihumo and Mount Nkungwe as seen from Mount Mhensabantu. Note the dense cloud cover, the rugged terrain, the fire-maintained grassland on and to the left (east) of the ridge, and the closed montane forest to the right (west) of the ridge. Photograph by Yvonne de Jong and Tom Butynski.

Figure 5. Mount Sibindi (in the distance) as seen from the top of Mount Nkungwe. The patch of montane forest in the middle of this photograph is where the first two observations of *Colobus angolensis* ssp. nov. occurred (Nishida *et al*. 1981; Itani 1990). Note the dense cloud cover, the rugged terrain, the fire-maintained grassland on the left (east) slope of Mount Sibindi, and the closed montane forest on the right (west) slope. This amount of cloud cover is typical for the peaks of the Mahale Mountains and is related to the presence of Lake Tanganyika to the west. Photograph by Yvonne de Jong and Tom Butynski.

7x42B, Zeiss Victory 10x42). YDJ took photographs with a Canon EOS 5D Mark III digital camera fitted with a Canon 100–400 mm lens and with an iPhone X.

Census routes were saved by GPS and downloaded into an Asus Latitude notebook using Garmin MapSource and ESRI ArcMap (Version 10.8.1) software. The number of primate groups encountered per kilometer and per hour were the indices used to assess relative abundance (e.g., Butynski and Koster 1994; White and Edwards 2000). Locations of all primate groups were plotted on a map using ArcGIS.

Describing pelage coloration and pattern for Colobus angolensis

Comparisons of pelage coloration and pattern among subspecies of *C. angolensis* were conducted using photographs of live animals, examinations and photographs of museum specimens, and descriptions from the literature, including those of the holotypes. Many terms have been used to describe the coloration of the hair of *C. angolensis*. Some terms often used in the literature have several definitions, and the colors are often interpreted differently. This being the case, we strove to limit the number of terms and colors used for our descriptions. In particular, we adopted the word 'flecked' over 'agouti' and 'grizzled', both of which have multiple meanings, some of them strongly associated with the color grey. The 'epaulette' is the patch of long white hair on the shoulders and upper arms. The 'pubic-band' (= 'perineal-band') is the band of white hair that runs medially from the anus to the external genitalia. The 'pubic-patch' (= 'perineal-patch') is the oval patch of grey and black hairs between the anus and the genitals in the adult male. This patch has, sometimes, been incorrectly termed the 'pygal-patch'.

Call terminology for Colobus angolensis

Nishida *et al.* (1981) reported hearing two calls emitted by Mahale *C. angolensis*: 'grunts', and a call that they believed to be the "loud goat-like sneeze of alarm" that Kingdon (1971, p.166) described for *C. angolensis* and *C. guereza*. We suspect that this second call is the same as the 'snort'. The snort is probably only emitted by adult males and can be evoked by surprise or by a potential predator, including humans (Marler 1972; Walek 1978; Bocian and Anderson 2013; Poirier-Poulin and Teichroeb 2020). In April 2022, we heard two bouts (= sequences) of 'roar' calls. The roar is emitted only by adult males and appears to serve at least three roles: maintain intergroup spacing, predator alarm, and predator intimidation (Kingdon 1971; Marler 1972; Walek 1978; Oates and Trocco 1983; Poirier-Poulin and Teichroeb 2020).

Site names, maps, and distances

In this article we attempt to apply the most used name and spelling for each site. Here are some alternative names/spellings for six sites mentioned in this article: Mt. Ihumo = Mt. Humo; Mt. Mwesi = Mt. Mwese = Mt. Mezi; Mt. Sibebi = Mt. Sitebi; Mt. Sisaga = Mt. Sisaba; Ujiji = Udjidji; Mt. Wansisi = Mt. Warisisi. Mt. Kakungu, Mt. Karobwa, and Mt. Mwesi are sometimes jointly referred to as the 'Mwesi Mts.'.

We found that the most useful maps for Mahale NP and for the Greater Mahale Ecosystem to be those presented in Kano (1971), Nishida (1972, 1990, 2012), Kielland (1978), Nishida *et al.* (1981), Uehara and Ihobe (1998), Moyer *et al.* (2006), TANAPA (2006), Nakamura and Itoh (2015), and Bonnin *et al.* (2020).

Unless otherwise stated, all distances present in this article are straight-line distances.

Use of photographs to designate holotypes and type series

For rare species and subspecies that are, or are expected to be, listed as 'threatened' (i.e., 'Critically Endangered', 'Endangered', 'Vulnerable') on The IUCN Red List of Threatened Species, it is now widely considered to be unethical and unjustifiable for individuals to be killed in order to serve as holotypes or as other members of the type series. As such, the use of a live specimen in photographs is taken to be an adequate alternative to a physical voucher specimen (Wakeham-Dawson *et al.* 2002; Jones *et al.* 2005; Polaszek *et al.* 2005; Donegan 2008; Minteer *et al.* 2014a, 2014b; Pape *et al.* 2016). The use of individuals in photographs to form type series is expected to increase as the vast majority of rare species and subspecies have yet to be described and named (Ceballos and Ehrlich 2009).

It should also be noted that many species and subspecies have been given acceptable scientific names without the benefit of a voucher specimen (Wakeham-Dawson *et al.* 2002), and that many holotypes are based on incomplete specimens, some being comprised of but a small part of the body (e.g., the head, arms, and legs are missing). While complete physical dead specimens are undeniably important as they offer information that photographs cannot provide (e.g., precise and accurate measurements of body parts and samples for molecular study), photographs of live specimens hold some advantages over physical specimens. One advantage is that photographs can be reproduced, distributed, viewed, and stored in many places, making them readily and widely available. For mammals, other advantages of photographs of specimens include: (1) retention of the original colors of the pelage, bare skin, and eyes; (2) demonstration of how the pelage lies on the body; (3) shape of the body in real life; and (4) indications of how the animal moves and behaves. One simply needs to compare drawings that are based on voucher specimens against drawings based on photographs of the living animal to appreciate some of the advantages presented by photographs. We are aware of cases where long-time debates over the validity of species and subspecies, based solely on study skins, would never have occurred had live animals in photographs been compared (e.g., Is *C. a. sharpei* a synonym of *C. a. palliatus*?).

Results

During the 2008 and 2009 courses, we recorded all groups of diurnal primates seen during nature walks and censuses. These were limited to the region on the west side of Mahale NP between L. Tanganyika (773 m asl) and 1,500 m asl. This is a region of lowland and mid-altitude closed-canopy moist forest. The following groups of primates were observed: *C. ascanius* (35 groups), *P. tephrosceles* (14), *P. kindae* (8), *C. mitis* (5), and *P. troglodytes* (2). *Chlorocebus pygerythrus* was only seen in and around Greystoke. *Colobus angolensis* was neither seen nor heard.

Table 2 summarizes our visual encounters with diurnal primates in Mahale NP from 13–22 April 2022. These censuses lasted 31.8 hours and covered 52 km of transect. A total of 19 groups were observed. The most common primate observed was *P. tephrosceles* (8 groups), followed by *C. ascanius* (7 groups). In addition, 10 groups of monkeys were observed off censuses and 17 groups were heard but not seen. In interpreting these results, much consideration needs to be given to the fact that the altitudinal range over which each species occurs differs greatly and that we did not census all altitudes equally. For example, while *C. mitis*, *P. tephrosceles*, and *P. troglodytes* all occur from 773 m asl up to 2,358 m asl, *C. pygerythrus* is confined to the lakeshore (773 m asl), and *C. angolensis* has not been confirmed to occur below 1,800 m asl. *Cercopithecus mitis* is, surprisingly, patchy in its distribution and low abundance. Overall, it appears that *P. tephrosceles* is the most common and widespread monkey in Mahale NP, but *C. ascanius* is the more abundant monkey below 1,600 m asl. There can be no doubt that, among the monkeys of Mahale NP, *C. angolensis* has the most limited altitudinal range and geographic distribution, as well as the smallest population. Although our census data are limited, they are corroborated by the much more extensive research of others (e.g., Kano 1971; Nishida 1972; Nishida *et al*. 1981; Uehara and Ihobe 1998; Uehara 2003; Moyer 2006).

Two groups of *C. angolensis* were heard during this exercise and one group was observed. At ~09:00 h on 18 April 2022, B. Nyundo, M. Nelson, A. Twalib, S. Masalu, and B. Rehani (pers. comms.) heard one bout of three roars at ~1,800 m asl on Mt. Mhensabantu (~6.08ºS; ~29.75ºE). The group was only ~100 m away, but reaching it was not practical due to the extremely rugged terrain and absence of a trail.

Only one group of *C. angolensis* was observed during this exercise. On 21 April 2022, at 07:45 h, we located a group of at least seven *C. angolensis* (Fig. 6). The group was ~300 m from us across a forested valley on the steep south slope of Mt. Ihumo (6.100ºS; 29.767ºE) at ~1,970 m asl (Fig. 2). We observed this group with binoculars for ~20 minutes before dense clouds moved between us and the group and it began to rain. During our observations, the group was feeding, and one bout of two roars was given.

Geographic distribution of Mahale Colobus angolensis

Our encounter with Mahale *C. angolensis* on 21 April 2022 appears to be only the third observation of this taxon by scientists. This group was ~1.6 km north of where this subspecies was observed on Mt. Nkungwe in 1976 and 1979 (Nishida *et al*. 1981; Itani 1990). The two nearest subspecies of *C. angolensis* are in eastern Democratic Republic of Congo (DRC; Figs. 1 and 3; Table 1). These are *C. a. prigoginei*, ~100 km to the northwest across L. Tanganyika on Mt. Kabobo, and *C. a. cordieri*, ~300 km to the northwest across L. Tanganyika on the Itombwe Massif (Verheyen 1959; Rahm and Christiaensen 1960; Rahm 1966, 1970; Colyn 1991; Omari *et al*. 1999; Plumptre *et al*. 2008). The shortest distance from Mahale across L. Tanganyika to DRC is ~45 km. The distances over-land, however, around the north end of L. Tanganyika, to *C. a. prigoginei* and *C. a. cordieri,* are ~560 km and ~420 km, respectively (Table 1). The third nearest subspecies is *C. a. ruwenzorii,* ~330 km to the north in Kibira Forest, extreme northwest Burundi (see below). Over-land, *C. a. ruwenzorii* is the subspecies nearest to Mahale *C. angolensis*.

Pelage characters of Mahale Colobus angolensis

The assessment of the pelage coloration and pattern of Mahale *C. angolensis* is based on observation with binoculars of seven individuals in the group encountered on 21 April 2022 (Fig. 6), examination of the many photographs taken of these individuals, and the description and drawing

Table 2. Visual encounters with groups of diurnal primates in Mahale Mountains National Park, 13–22 April 2022. The altitudinal range is based on both visual encounters and vocalizations.

Species	Groups/km (n)	Groups/hour (n)	Encounters off census	Altitudinal range (m asl)*
Chlorocebus pygerythrus	0.00	0.00	2	773 (n = 2)
Cercopithecus ascanius	0.13 (7)	0.22 (7)	2	773–1,595 (n = 12)
Cercopithecus mitis	0.00	0.00	1	1,103–2,350* (n = 7)
Papio kindae	0.06 (3)	0.09 (3)	2	773–1,100 (n = 9)
Piliocolobus tephrosceles	0.15 (8)	0.25 (8)	3	790–2,358* (n = 12)
Colobus angolensis	0.02 (1)	0.03 (1)	0	1,800–1,968 (n = 2)
Pan troglodytes	0.00	0.00	0	1,103–2,300* (n = 5)

* Known to occur on the shore of Lake Tanganyika at 773 m asl.

Figure 6. Group of Mahale Angola colobus *Colobus angolensis* ssp. nov. in pristine montane forest at ~1,970 m asl on Mount Ihumo, Mahale Mountains National Park, west Tanzania, on 21 April 2022. To the best of our knowledge, this is the first photograph of this taxon. Photograph by Yvonne de Jong and Tom Butynski.

provided by Nishida *et al*. (1981). The coloration and pattern of the pelage of all seven individuals seen by us were similar.

Given the geographic isolation, together with the distinctive coloration and pattern of the pelage, we agree with Nishida *et al*. (1981) that Mahale *C. angolensis* is a new subspecies that requires formal classification. Here we designate this new subspecies.

The Mahale Angola Colobus Monkey

Order Primates Linnaeus, 1758
Family Cercopithecidae Gray, 1821
Subfamily Colobinae Jerdon, 1867
Genus *Colobus* Illiger, 1811
Species *Colobus angolensis* Sclater, 1860

***Colobus angolensis mahale*, ssp. nov.**

Holotype. Live monkey in the photographs in Fig. 7. Based on its relatively large size, this is almost certainly an adult male.

Type locality. South slope of Mount Ihumo, Mahale Mountains National Park, Kigoma Region, central west Tanzania; 6.100ºS, 29.767ºE, ~1,970 m asl (6,460 ft asl).

Paratopotypes 1, 2, and 3. Live monkeys in the photographs in Figs. 8, 9, and 10, respectively. South slope of

Mount Ihumo, Mahale Mountains National Park, central west Tanzania; 6.100ºS, 29.767ºE, ~1,970 m asl (6,460 ft asl). Based on their large size, all four individuals in this type series are, almost certainly, adults. Photographs taken on 21 April 2022 by Yvonne de Jong and Tom Butynski.

Description. Entirely black *Colobus angolensis* except temples, cheeks, and epaulettes white, ischial callosities pink, and distal ~10% of tail dirty white with off-white tip. Compared to other subspecies of *Colobus angolensis*, cheek whiskers are moderately long and marginally connected to the epaulettes, and the epaulettes are moderately long and full, extending to about the elbows (Fig. 11).

Diagnosis. One hundred percent diagnosable from the seven other currently recognized subspecies of *Colobus angolensis* when the following three pelage characters are applied: white brow-band absent; white pubic-band absent; tail black with distal ~10% dirty white with off-white tip.

Sexual dimorphism. No sexual dimorphism detected in coloration or pattern of the pelage among the seven individuals seen in one group on 21 April 2022, the 16 individuals observed in one group on 18 May 1976, nor the about 30 individuals seen in one group on 22 August 1979 (Nishida *et al.* 1981). As for other subspecies of *C. angolensis*, adult females are expected to weigh approximately 20% less than adult males (Napier 1985; Bocian and Anderson 2013).

Figure 7. Holotype. Mahale Angola colobus *Colobus angolensis mahale*. Photographs by Yvonne de Jong and Tom Butynski taken on 21 April 2022.

Figure 10. Paratopotype 3. Mahale Angola colobus *Colobus angolensis mahale*. This individual shows that neither a white pubic-band nor a greyish pubic-patch is present.

Figure 8. Paratopotype 1. Mahale Angola colobus *Colobus angolensis mahale*. This individual shows the absence of a white brow-band, moderately long cheek whiskers, moderately long and full epaulettes, and a mostly black tail with distal ~10% dirty white.

Figure 9. Paratopotype 2. Mahale Angola colobus *Colobus angolensis mahale*. This individual shows the absence of a white brow-band, moderately long cheek whiskers, moderately long and full epaulettes, and a mostly black tail with distal ~10% dirty white.

Body size. No measurements available. Body size is likely nearly the same as for other subspecies of *C. angolensis* as there does not seem to be much difference in body size among the adults of each of the eight subspecies. For example, the geographic distribution of *C. a. mahale* is found between *C. a. cordieri* and *C. a. palliatus*. These two subspecies are located ~1,000 km apart and on opposite sides of the Albertine Rift (Figs. 1 and 3). Here are the means for three body measurements for three adult male *C. a. cordieri* (Rahm and Christiaensen 1960) and 17 adult male *C. a. palliatus* (Bocian and Anderson 2013), respectively: length of head + body = 678 mm vs 665 mm; length of tail = 794 mm vs 810 mm; length of hindfoot 175 mm vs 172 mm. The above measurements yield a tail length that is 54% of the total body length for both subspecies. Mean body weight for 16 adult male *C. a. cordieri* is 8.9 kg.

Variation. No intra-subspecific variation in coloration or pattern of the pelage of adults detected or reported in the three groups observed.

Geographic distribution. Endemic to the montane forests of Mahale Mountains National Park, central west Tanzania (Figs. 2 and 3). The known geographic distribution is based on the group observed on the south slope of Mt. Ihumo at ~1,970 m asl (6.100ºS, 29.767ºE; T. Butynski and Y. de Jong pers. obs.), on the group observed on the ridge between Mt. Nkungwe and Mt. Kahoko at ~2,350 m asl (Nishida *et al*. 1981; Itani 1990), and on the groups heard calling on Mt. Mhensabantu at ~1,970 (Nishida *et al*. 1981; Itani 1990) and at ~1,800 m asl (~6.08ºS, 29.75ºE; B. Nyundo, M. Nelson, A. Twalib, S. Masalu and B. Rehani pers. comm.). Limits of the known geographic distribution are north 6.088ºS, east 29.782ºE, south 6.113ºS, and west 29.765ºE. This is an area <7 km². Known altitudinal range is 1,800–2,350 m asl.
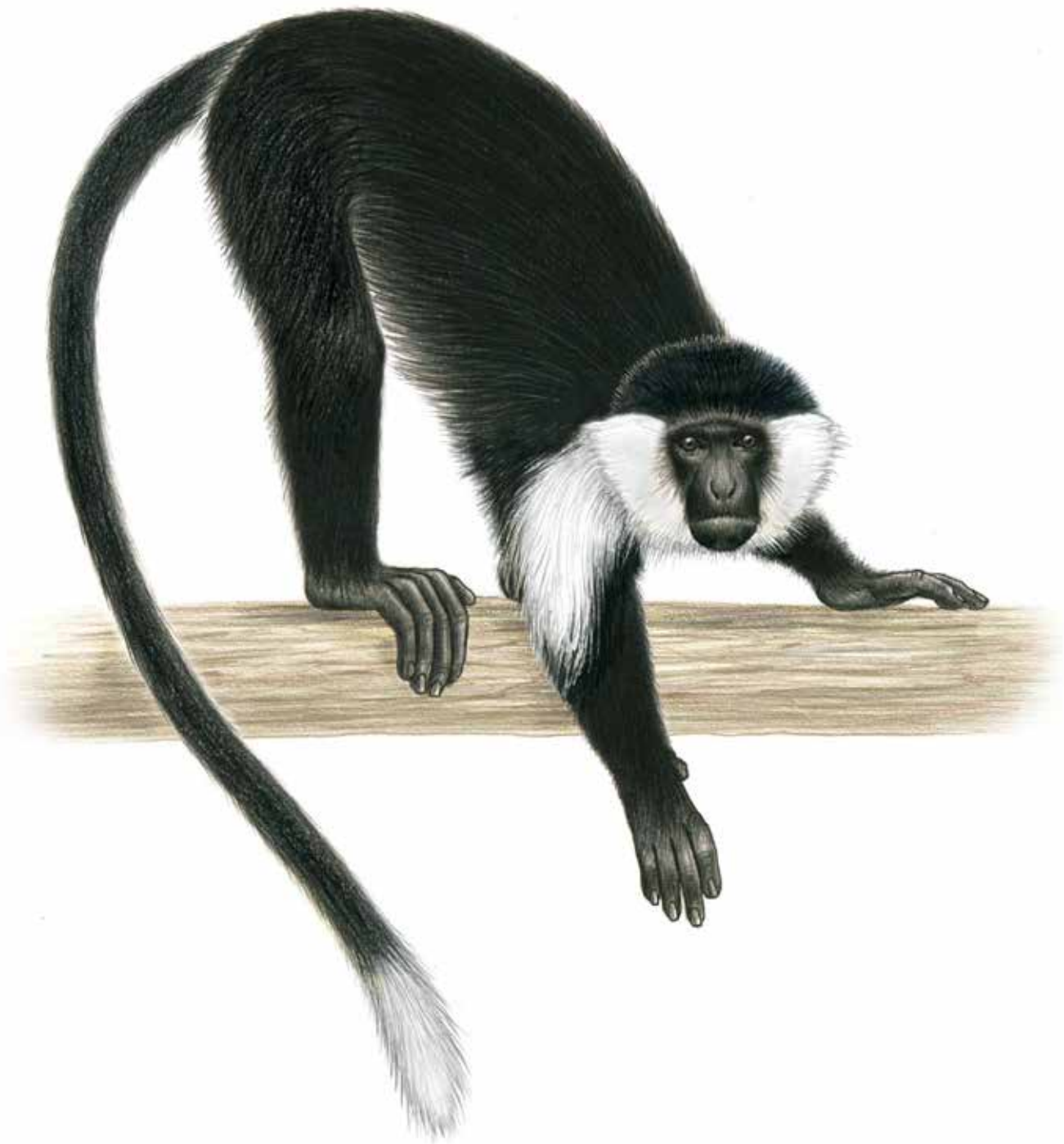
Figure 11. Adult Mahale Angola colobus *Colobus angolensis mahale*. Illustration by Stephen D. Nash.

The limits of the area >1,800 m asl in Mahale Mountains National Park are north 6.080ºS, east 30.008ºE, south 6.355ºS, and west 29.765ºE (Fig. 2). This is an area of roughly 145 km², of which about 50 km² is montane forest. Since *C. a. mahale* appears to be dependent on montane forest, it is unlikely to have a geographic distribution greater than 50 km² or an altitudinal range greater than 1,800–2,350 m asl.

Climate. Mean annual rainfall in the montane forest of Mahale Mountains National Park is high, ranging from ~123 cm at 1,800 m asl to ~148 cm on the peak of Mt. Nkungwe (WorldClim 2.1 Bioclimatic variable 12, resolution 30 arc-second; WorldClim 2016; Fick and Hijmans 2017). Located on the east side of the Albertine Rift, with L. Tanganyika (see above) immediately to the west, much of the rain and

mist is probably due to the orographic lift of moist air off L. Tanganyika by the eastward winds.

Mean annual temperature is ~20°C at 1,800 m asl and ~16°C on the peak of Mt. Nkungwe (WorldClim 2.1 Bioclimatic variable 1, resolution 30 arc-second; WorldClim 2016; Fick and Hijmans 2017). The nearest sites where mean annual rainfall is this high and mean annual temperature is this low are Mt. Kabobo (~181 cm, ~14°C at 2,600 m asl) and Itombwe Massif (~205 cm, ~10°C at 3,400 m asl) to the west across L. Tanganyika.

The high ground of Mahale Mountains National Park holds, by far, the wettest and coolest climate in the Greater Mahale Ecosystem and is the only place able to support a significant area of montane forest. The orographic clouds and mist on the windward (west) side (Figs. 4 and 5) must play a significant role in the maintenance of this montane forest and, thus, in enabling *C. a. mahale* to survive there.

Ecology and behavior. Although there is little information concerning the ecology and behavior of *C. a. mahale,* its ecology and behavior are expected to be similar to other taxa in the genus *Colobus*, particularly the other subspecies of *C. angolensis* living in montane forest. All are diurnal, arboreal, group-living folivores. This monkey appears to be restricted to montane forest in the most rugged, coolest, and wettest, part of the Mahale Mountains [Figs. 4, 5 and 6; see also Fig. 1.2 and Plates 1.2 and 1.6 in Nishida (2012)]. The montane forest of the Mahale Mountains lies in the 'Afromontane-Afroalpine Biotic Zone' (White 1983; Happold and Lock 2013) and in the 'Albertine Rift Montane Forests Ecoregion' (Olson *et al*. 2001). *Parinari excelsa* is a readily recognized dominant emergent tree that can likely serve as a good indicator of suitable habitat for *C. a. mahale*. Other common, relatively easy to identify, trees include *Bersarma abyssinica, Celtis africana, Gambeya gorungosana (Chrysophyllum gorungosanum), Croton megalocarpus, Diospyros abyssinica, Faurea rochetiana, Ficalhoa laurifolia, Ficus thonningii, Harungana madagascariensis, Macaranga kilimandscharica, Markhamia lutea, Nuxia congesta, Olea welwitschii, Podocarpus latifolius, Polyscias fulva, Prunus africana, Spathodea campanulata, Tabernaemontana pachysiphon, Vepris nobilis*, and *Trema orientalis* (T. Butynski pers. obs.). Alpine bamboo *Oldeania alpina* is also common here. Nishida and Uehara (1981), Nishida *et al*. (1981), and Itoh (2015b) mention additional species of trees for Mahale's montane forest. Many of these tree species are present, and often common, in all the montane forests of the Albertine Rift, and beyond, where *C. angolensis* occurs. Indeed, it is surprising how similar the communities of montane forest trees are across the mountains of Equatorial Africa, from the Horn of Africa and East Africa westward to Cameroon and Bioko Island, Equatorial Guinea.

Three vocalizations are reported for *C. a. mahale*: 'grunt', 'snort', and 'roar'. All three of these vocalizations are well known for *Colobus* (Marler 1972; Groves 1973;

Walek 1978; Bocian 1997; Poirier-Poulin and Teichroeb 2020).

Colobus a. mahale is sympatric with *Galagoides thomasi, Otolemur crassicaudatus monteiri, Piliocolobus tephrosceles, Cercopithecus mitis, Pan troglodytes schweinfurthii* and, perhaps, a *Paragalago* sp.? Sometimes, perhaps often, *C. a. mahale* is in polyspecific association with *P. tephrosceles* (Nishida *et al*. 1981). It is likely that polyspecific associations also occur with *C. mitis* as is the case for *C. angolensis* at other sites (e.g., Diani on the south coast of Kenya, and Ituri Forest in northeast DRC; Bocian and Anderson 2013). None of the other species of diurnal primate in Mahale reach the lower known altitudinal limit of *C. a. mahale* (1,800 m asl; Kano 1971; Butynski and De Jong 2009; T. Butynski and Y. de Jong pers. obs.).

Etymology. The name '*mahale*' acknowledges the Mahale Mountains, Tanzania, the type locality.

English vernacular name. Mahale Angola colobus.

Local vernacular name. Nkamba or kamba (Kitongwe).

Discussion

Characters distinguishing Colobus angolensis mahale *from other subspecies of* Colobus angolensis

The combination of characters of the pelage that distinguish *C. a. mahale* from the other seven subspecies of *C. angolensis* are the absence of a white brow-band, absence of a white pubic-band, and a black tail with distal ~10% dirty white and off-white tip. Drawings comparing the coloration and pattern of the pelage of some or all subspecies of *C. angolensis* are presented in Rahm (1970), Dorst and Dandelot (1972), Colyn (1991), Gautier-Hion *et al*. (1999), Bocian and Anderson (2013), Groves and Ting (2013), Kingdon (2015), Fashing (2016), Burgin *et al*. (2020), and De Jong and Butynski (2023). Here are the one, two, or three characters of the pelage that, taken alone or together, most readily distinguish each of the other currently recognized seven subspecies of *C. angolensis* from *C. a. mahale*.

Taxonomy and distribution of Colobus angolensis *on the northeast and north shores of Lake Tanganyika*

There is confusion, and some mystery, concerning the taxonomy and distribution of *C. angolensis* in the vicinity of the northeast and north shores of L. Tanganyika. It has also been unclear as to which population and subspecies of *C. angolensis* is geographically closest to Mahale. These matters are summarized and addressed in this section.

Records for Colobus angolensis *on the northeast shore of Lake Tanganyika*. According to current taxonomy, *C. a. sharpei* is recognized (Rahm 1970; Kingdon 1971; Napier 1985; Groves and Ting 2013; Foley *et al*. 2014; McDonald *et al*. 2019, 2022; Butynski and De Jong 2022), *C. a. adolfi-friederici* is a synonym of *C. a. ruwenzorii* (Dorst and

C. a. angolensis.   Distal ~30–70% of tail dirty white transitioning to off-white towards tip.

C. a. cordieri.   Distal ~70–80% of tail brownish-grey.

C. a. cottoni.   Distal ~30–60 % of tail greyish, dusky, or pale brown. Some with pure white tip.

C. a. palliatus.   White brow-band. White pubic-band. Coloration of tail highly variable; on average, distal ~50% greyish (~33%) grading into off-white (~17%).

C. a. prigoginei.   Middle ~80% of tail flecked pale grey, distal ~10% pale grey or white.

C. a. ruwenzorii.   White brow-band. Greyish pubic-patch. Distal ~26% of tail dark grey (~21%) grading into pale grey (~5%).

C. a. sharpei.   White brow-band. White pubic-band. Distal ~35% of tail greyish (~28%) grading into off-white (~7%).

Dandelot 1972; Dandelot 1974; Groves 2001, 2005, 2007; Grubb *et al.* 2003; Bocian and Anderson 2013; Butynski and De Jong 2022), and *C. a. langheldi* Matschie, 1914, is a synonym of *C. a. sharpei* (Schwarz 1929; Allen 1939; Rahm 1970; Napier 1985; Butynski and De Jong 2022).

Many authors indicate that *C. a. ruwenzorii* occurs, or occurred, in the Ujiji/Kigoma/Gombe region on the northeast shore of L. Tanganyika (Figs. 1 and 3; Schwarz 1929; Rahm and Christiaensen 1960; Rahm 1970; Kano 1971; Dandelot 1974; Nishida 1981; Rodgers 1981; Oates and Trocco 1983; Colyn 1991; Groves 2007; Kingdon *et al.* 2008; Fashing 2016; De Jong and Butynski 2018; De Jong *et al.* 2020; Butynski and De Jong 2022; McDonald *et al.* 2022). Kigoma is ~130 km from Mahale. To the best of our knowledge, however, there are no confirmed records for *C. angolensis* in this region. The Museum für Naturkunde Berlin has three *C. angolensis* skins for which the tags indicate were obtained in Ujiji (ZMB_Mam_086958/A111.09; ZMB_Mam_086827/31919/A4086; ZMB_Mam_086992/A24.00.211). We examined these three skins. The hands and feet are missing from the latter two skins and there are no skulls. This strongly suggests that all are 'trade skins.'

Skin 086958 appears to be *C. a. ruwenzorii* (the tag indicates *C. a. adolfi-friederici*, a synonym of *C. a. ruwenzorii*).

Skin 086827 appears to be *C. a. sharpei*. This agrees with Schwarz (1929). Interestingly, this skin is the holotype for *C. a. langheldi*, which is now a synonym of *C. a. sharpei*. Kano (1971) suggests that skin 086827 came from Mahale as this is the nearest population of *C. angolensis* to Ujiji. Matschie (1914) states, however, that it came from Manyema Province, central east Belgian Congo (now DRC). In any case, we now know that the Angolan colobus in Mahale is not *C. a. sharpei*.

Skin 086992 appears to be *C. a. cordieri*. The tag indicates that this skin came from "Congo" (presumably Belgian Congo, currently the DRC).

We suspect that the belief that *C. angolensis* occurred in the Kigoma/Ujiji/Gombe region and, therefore, that the Angolan colobus in Mahale is likely *C. a. ruwenzorii* or *C. a. sharpei* (Kano 1971; Nishida *et al.* 1981), is based on the above-mentioned three skins, none of which seem to have originated from this region.

Records for Colobus angolensis *on the north shore of Lake Tanganyika.* Schwarz (1929), Schouteden (1944), Rahm and Christiaensen (1960, 1963), Dandelot (1974), Verschuren (1978), Oates and Trocco (1983), Wolfheim (1983), Colyn (1991), Groves (2001, 2007), Kingdon *et al.* (2008), Bocian and Anderson (2013), Kingdon (2015), Fashing (2016), De Jong and Butynski (2018), De Jong *et al.* (2020), Butynski and De Jong (2022), and McDonald *et al.* 2022, indicate that *C. a. ruwenzorii* occurs in southwest Burundi off the north end of L. Tanganyika (3.36°S, 29.36°E; ~300 km north of Mahale and ~170 km north of Kigoma/Ujiji). We have not found specimens or photographs of *C. a. ruwenzorii* that are, without doubt, from this region; no specimens are listed in VertNet.org or GBIF.org, and no records are presented on iNaturalist.org or observation.org. Specimen ZMB_Mam_087018 in the Museum für Naturkunde Berlin is that of *C. a. adolfi-friederici*. This skin, obtained in 1903, has "Usumbura?" on the tag (Usumbura = Bujumbura). Bujumbura, central west Burundi, is on the extreme northeast corner of L. Tanganyika. The question mark on the tag indicates that the provenance of this skin is uncertain. That the hands and feet are missing, and that there is no skull, suggests that this is a trade skin purchased in Bujumbura. This is the only record that we have that indicates that *C. a. adolfi-friederici* 'might' have occurred at the north end of L. Tanganyika within the past 120 years (perhaps in Bururi Forest, 230 km north of Mahale). As concerns Mahale, it appears that the nearest confirmed record for *C. a. ruwenzorii* is for Kibira Forest, northwest Burundi. Kibira Forest is ~330 km north of Mahale.

Taxonomic history of Colobus angolensis langheldi

That *C. a. sharpei* skin 086827, which is the *C. a. langheldi* holotype, was moved at least 650 km from the range of this subspecies in south Tanzania to Manyema Province, central east DRC, and then purchased to the east of L. Tanganyika in Ujiji in 1900, is extremely surprising, especially given the difficulty of transport through this remote region at

that time (Fig. 1; Ingham 1962). We believe that it is highly likely that skin 086827 was never in Manyema or Ujiji, and that there is at least one error concerning its recorded history.

Of further interest is that skin 086992 appears to be that of *C. a. cordieri*, a subspecies not described until 1959 by Rahm. Matschie described *C. a. langheldi* in 1914 but seems to have over-looked skin 086992, although both this skin and the *C. a. langheldi* holotype (skin 86827) are recorded as being acquired by Major Wilhelm Langheld in Ujiji on the same day (10 April 1900), both probably arrived at the Museum für Naturkunde Berlin at the same time, and they differ considerably from one another in their appearance. Suspecting that Matschie might have made a mistake in the designation of the *C. a. langheldi* holotype, we examined both skins. The *C. a. langheldi* holotype (skin 086827) is as described in Matschie (1914), indicating that there was no mistake in the designation of the holotype.

Which subspecies of Colobus angolensis *is geographically closest to Mahale?*

Kano (1971) and Nishida *et al*. (1981) state that the two nearest populations of *C. angolensis* to Mahale are those of *C. a. ruwenzorii* at the northeast end of L. Tanganyika to the north and of *C. a. sharpei* at the north end of L. Malawi, ~525 km to the southeast. Nishida *et al*. (1981) also mentions the proximity of Sango Bay-Minziro, ~590 km from Mahale on the central west shore of L. Victoria. Kano (1971) suggests that the Mahale Angola colobus is *C. a. sharpei* based on the proximity of its range (Fig. 1) to Mahale, and on a skin (086827) of *C. a. sharpei* said to have been purchased in Ujiji (Schwarz 1929). This taxonomy is adopted by Nishida *et al*. (1979). Kano (1971, p.295) states, "Though its exact locality is unknown, Kungwe is the only possible locality of the black and white guereza near Ujiji, so Kungwe's guereza may be *Col. polykomos sharpei* rather than *Col. polykomos adolfi-friederici*, though it is impossible to express any implication about its systematic position there being no specimen available." Note that, in 1971, *angolensis* was recognized as a subspecies of *Colobus polykomos*.

Based on the information presented above, the population of *C. a. ruwenzorii* in Kibira Forest is the nearest (~330 km) known population of *C. angolensis*, overland, to Mahale NP, either historically or at present. Across L. Tanganyika, the nearest population (~100 km) is that of *C. a. prigoginei* on Mt. Kabobo, but this subspecies is ~560 km overland from Mahale NP. The second nearest population (~300 km), also across L. Tanganyika, is that of *C. a. cordieri* in the lowlands to the west of the Itombwe Massif. This subspecies is ~420 km overland from Mahale NP (Figs. 1 and 3; Table 1).

Geographic distribution of Colobus angolensis mahale

Kano (1971) and Nishida *et al*. (1981) estimate the geographic distribution of *C. angolensis* in Mahale to be no less than 10 km² and no more than 50 km². Based on the three visual records and two vocal records, *C. a. mahale* has an 'Area of Occupancy' (IUCN 2012) of ~3 km² and an 'Extent of Occurrence' (IUCN 2012) of ~7 km².

Although the area above 1,800 m asl is ~145 km², of which about a third is montane forest, the many researchers studying and surveying *P. troglodytes* over large parts of Mahale NP since 1965 have not reported additional visual or vocal encounters with *C. a. mahale*, nor have those exploring Mahale or surveying other species (Grant 1949; Procter 1958; Stevens 1958; Ulfstrand and Lamprey 1960; Simkin and Juniper 1961; Anderson and Baker 2003; Moyer 2006; Moyer *et al*. 2006).

There are, however, several records for *C. a. mahale* that we have not included in our estimate of the geographic distribution as it seems prudent to first confirm the presence of *C. a. mahale* at these sites. These records are summarized in the following three paragraphs:

(1) In January 1974, J. Itani and S. Uehara, while climbing Mt. Pasagulu (~1,600 m asl; Fig. 2), heard the loud call of what they took to "probably" be that of *C. angolensis* in isolated montane forest to the southwest of the summit (Nishida *et al*. 1981). This encounter was also described by Itani (1990, p.50), "On the summit we heard a *Colobus angolensis* call from the forest at the source of the Kabwe River. The altitude was estimated at 1,350 m, which is probably the lowest recorded for the habitation of *C. angolensis*." The relatively low altitude of this record brings it into question, as does the fact that none of the rangers, guides, trackers, or porters that we asked had encountered *C. a. mahale* on Mt. Pasagulu. We walked on Mt. Pasagulu while moving to and from Mt. Nkungwe and camped there for one night. We did not detect *C. angolensis* there.

(2) Nishida *et al*. (1981, p.558) stated that, "A village woman of Kasoje said that she had observed nkamba at the higher altitude of the Mpila Valley in the early 1960's…" (Mpila Valley is on the west slope of Mt. Mhensabantu). "Also, Mr. Sadi Katensi of Kasoje village once observed a group of nkamba jumping at the proximity of the summit of Mt. Sibindi, the adjacent peak to the south of Mt. Nkungwe in the late 1950's." (Fig. 2).

(3) During our first and second visits to Mahale NP (22 November–22 December 2008 and 5–19 November 2009), we asked the trackers, guides, and other staff at Greystoke whether they had ever encountered Mahale Angola colobus. Only one person had a record; guide G. Lazaro said that, on two occasions, he heard the 'roar' call of this species up the valley of the Lubulungu R. This river drains the west slopes of Mt. Sibindi, Mt. Mfitwa, and Mt. Sisaga (Fig. 2).

Colobus a. mahale appears to have the smallest geographic distribution of any extant taxon of African colobine. It is followed by the 'Critically Endangered' Bioko (= Pennant's) red colobus *Piliocolobus pennantii* (Waterhouse, 1838) at ~160 km², and the 'Critically Endangered' Tana River red colobus *Piliocolobus rufomitratus* (Peters, 1879) at ~200 km² (Butynski and De Jong 2022). Given that *C. a. mahale* is a montane forest-dependent subspecies, and that

the climate and altitudinal gradient of Mahale can only support a small area of montane forest, the geographic distribution of *C. a. mahale* has probably been small for thousands of years.

Altitudinal limits of Colobus angolensis mahale

As mentioned above, the known altitudinal range for *C. a. mahale* is 1,800–2,350 m asl. The lower limit is probably the lower limit of the montane forest in Mahale at ~1,800 m asl. The upper limit is marked by the upper limit of montane forest which reaches almost to the tops of the highest peaks. If the lower altitudinal limit is correct, the altitudinal gradient for this monkey is only ~550 m. Of the eight subspecies of *C. angolensis*, four occur above 2,350 m asl, but none has such a limited altitudinal gradient (Butynski and De Jong 2022).

Population size of Colobus angolensis mahale

There has been considerable exploration and research in Mahale by professional botanists and zoologists since 1939 (e.g., Grant 1949; Procter 1958; Stevens 1958; Ulfstrand and Lamprey 1960; Simkin and Juniper 1961; Kielland 1978; Moyer 2006; Moyer *et al.* 2006; Nakamura *et al.* 2015a; Kerbis Peterhans *et al.* 2020). Research on primates in Mahale began in 1961, and one or more primatologists have been active there most of the time since 1965 (Nishida 1990, 2012; Nakamura *et al.* 2015b). Despite this presence of professional scientists, there are only three published reports of visual encounters with *C. a. mahale,* and none prior to 1976. These encounters were with groups estimated to comprise at least 30 individuals (18 May 1976; Nishida *et al.* 1981), about 30 individuals (22 August 1979; Nishida *et al.* 1981; Itani 1990), and at least seven individuals (21 April 2022; this study). *Colobus* often feed in the canopy where the white of their pelage is readily detected against the green foliage and shadows. In montane forest it is often possible to visually detect *Colobus* at >1 km. During our 8 days in the montane forest of Mahale, we, and the 13 rangers, guides, and trackers in our training course, spent most of the day-light hours searching for primates, particularly *C. a. mahale*. We spent about half of the day-light hours scanning roughly 20 km² of montane forest canopy from high ridges and mountain-tops and were always alert to their loud call. Large areas of montane forest were scanned several times by multiple observers (Butynski and De Jong 2023).

The roar loud call of *Colobus* is given by group-living adult males (Marler 1972; Walek 1978; Bocian 1997; Oates *et al.* 2000; Bocian and Anderson 2013; Poirier-Poulin and Teichroeb 2020). The roar of *C. angolensis* is not as loud as that of *C. guereza* (T. Butynski and Y. de Jong pers. obs.). In *C. angolensis*, the human ear can typically hear this call at ~1.0 km (Poirier-Poulin and Teichroeb 2020), and we estimate it to farther than 1.5 km under ideal conditions. In the Ituri Forest, *C. angolensis* typically roar after dawn and, rarely, during the night. In contrast to *C. guereza*, and except for *C. a. ruwenzorii* in Nyungwe NP, southwest

Rwanda (Fimbel *et al.* 2001), the roar of *C. angolensis* is not a common vocalization as it is emitted on less than a daily basis (Groves 1973; Walek 1978; Bocian 1997; Oates *et al.* 2000). In Ituri Forest, where *C. guereza* and *C. angolensis* are sympatric, roars in study groups of *C. guereza* were emitted about once/day (n=60 days), while roars in study groups of *C. angolensis* were emitted only about once every six days (n=58 days; Bocian 1997; Oates *et al.* 2000). The frequency at which the roar is given might be positively correlated to population density in some regions (Groves 1973; Walek 1978), although the density of *C. guereza* in Ituri Forest was less than half that of *C. angolensis*. There are no recordings or published accounts of the roar of *C. a. mahale*. During the 3.5 days that our team of 16 people spent on Mt. Nkungwe (within hearing distance of the south slope of Mt. Ihumo) we only heard one bout of roars. That our team heard only two bouts of roars during 8 days in montane forests suggests that *C. a. mahale* roars infrequently or that groups are at low density or, most likely, both.

Based on the above, the density of *C. a. mahale* over the northern montane forest of Mahale is low, perhaps in the range of 5–10 individuals/km². *Colobus angolensis* densities elsewhere vary between 2.9 and 31.0 individuals/km² (Bocian and Anderson 2013; Araldi *et al.* 2014). Thus, the density of *C. a. mahale* in the region surveyed is at the low end of the reported estimates for this species. It remains to be determined whether this low density persists throughout this subspecies' geographic distribution, but that seems likely to be the case given the scarcity of reports of sightings and roar loud calls. Assuming a density of 5–10 individuals/km² and a geographic distribution of 10–50 km², the number of *C. a. mahale* is likely within the range of 50–400 individuals, or <200 mature individuals.

Paleobiogeography of Colobus angolensis mahale

Molecular phylogenetic evidence indicates that the five extant species of *Colobus* began to diverge ~3.5 million years ago (Ma; mid-Pliocene), with the emergence of *C. angolensis* ~2.1 Ma (early Pleistocene; Ting 2008). The subsequent subspeciation within *C. angolensis* (Fig. 1), and the current distribution and ecology of its subspecies, is the outcome of many factors, particularly Plio-Pleistocene geologic changes and climatic fluctuations related to at least some of the about 21 high-latitude glacial or near-glacial periods of the past 2.3 Ma (Van Donk 1976; Hamilton 1988). These factors combined to make the late-Pliocene and Pleistocene environments of eastern Africa variable, unstable, and extreme, both temporally and spatially, one result being the relatively frequent expansion, contraction, and isolation of forests (Hamilton 1988; Kingdon 1990, 2013; Morley and Kingdon 2013; Pozzi 2016). These are the circumstances under which the subspecies of *C. angolensis* evolved and which led to the situation that we see today where several subspecies in eastern Africa are isolated on widely scattered mountains.

Based on current species and subspecies distributions, together with molecular data, it is hypothesized that *Colobus* evolved in the forests of central Africa and radiated eastward (Schwarz 1919; Rahm 1970; Kano 1971; Ting 2008; McDonald *et al.* 2022). When, and by what route, did *C. a. mahale*, or its ancestor, reach Mahale? In assessing the many possible scenarios, here are two important considerations:

(1) The *C. angolensis* that moved eastwards from central Africa to the Albertine Rift was a lowland forest monkey (e.g., *C. a. angolensis, C. a. cottoni, C. a. cordieri*) while the present subspecies living along the Albertine Rift are restricted to montane forest (i.e., *C. a. ruwenzorii, C. a. prigoginei, C. a. mahale*). We do not know where this transition from lowland forest-dependence to montane forest-dependence occurred but, presumably, somewhere along the west side of the Albertine Rift during glacial periods when climates were 'typically' arid and cool. Each glacial resulted in the retreat of lowland forest and in the down-slope movement of montane forest. For early lowland *C. angolensis* on the west edge of the Albertine Rift, it was either adapt to life in montane forest or perish. Each subsequent inter-glacial brought a wet and warm climate and the return of the lowland forest. They may also have brought lowland-adapted arboreal folivorous primates (e.g., *Piliocolobus*) against which a montane *C. angolensis* could no longer compete in the lowland forest environment. If valid, this scenario, repeated several to many times over the last 2 million years, would have resulted in some subspecies of *C. angolensis* being both increasingly adapted to life in montane forest and increasingly dependent upon montane forest.

(2) Of the mountains of the Albertine Rift, Mahale is one of the lowest and probably the smallest and driest. This means two things. First, that the area of montane forest on Mahale has always been relatively small (~50 km² today, even though this is a moist period in the region's climatic history) and second, that there were likely several extended periods during glacials when Mahale held no montane forest. About 1.1 Ma the water level of L. Tanganyika was 650–700 m lower than at present. Lake Tanganyika dropped 250–350 m below its present level 390–360 ka (thousand years ago), 290–260 ka, and 190–170 ka, followed by additional 600 m declines 135–127 ka and 93–75 ka. Near modern lake levels were reached 60 ka and have persisted to the present except for the aridity of the Last Glacial Maximum (35–15 ka) when lake levels were 30–200 m lower than at present. The periods of extreme aridity since 390 ka were long, ranging from 8 to 30 thousand years. Subjected to a mean annual rainfall of <40 cm during the driest periods, L. Tanganyika was surrounded by semi-desert vegetation during the most severe of these megadroughts and probably by semi-arid vegetation during the less severe droughts (Scholz and Rosendahl 1988; Lezzar *et al.* 1996; Cohen *et al.* 1997, 2007; Scholz *et al.* 2007; Nevado *et al.* 2013; McDonald *et al.* 2022). Under these conditions, all montane forest-dependent species were likely extirpated from Mahale multiple times, and those montane forest-dependent species there today are

probably relatively new colonists. This view of unstable, oscillating, plant and animal communities on Mahale is supported by the relatively small number of endemic montane forest-dependent taxa of bird (Moreau 1943; Fishpool and Evans 2001; Baker and Baker 2002, Moyer 2006), mammal (Moyer 2006; Ihobe 2015a, 2015b; Kerbis Peterhans *et al.* 2020), reptile (Spawls *et al.* 2018; S. Spawls per. comm.), amphibian (Channing and Howell 2006; S. Spawls pers. comm.), and butterfly (Kielland 1990; Congdon and Collins 1998; S. Collins pers. comm.).

Although most of the middle of the glacial periods of the past 2.3 Ma were marked by arid and cool climates, the periods of deglaciation were wet and cool (Pokras and Mix 1985). In addition, the glacials centered on 220 ka and 176 ka were exceptional in that they were probably wet and cool (Rossignol-Strick *et al.* 1983; Hamilton 1988). It was during periods of deglaciation and, perhaps particularly, around 220 ka and 176 ka, that conditions were most conducive for the spread and reconnection of montane forest. Forests are also reported to have expanded and reconnected 1.9–1.7 Ma, 145–120 ka, 110–95 ka, 80–65 ka, 55–50 ka, 35–30 ka, and after 12 ka (Hamilton 1982; 1988; Colyn *et al.* 1991; deMenocal 1995; Maley 1996; Morley 2000; Trauth *et al.* 2005; Anhuf *et al.* 2006; Blome *et al.* 2012; Morley and Kingdon 2013).

When might *C. angolensis* have reached Mahale? It is likely that the movement of *C. angolensis* eastwards across the Albertine Rift to Mahale occurred at a time when there was montane forest across the floor of the Rift. This may have occurred during the wet and cool climates of deglacials, and 220 ka and 176 ka. The montane forest of Mahale may have come and gone multiple times over the past 1 million years, perhaps together with one or more populations of *C. angolensis*. The montane forest and population of *C. angolensis* on the Mahale Mountains today are likely to have been present since at least 30 ka but it is unlikely that they were present prior to 70 ka due to the severe 93–75 ka arid period. Alternatively, if all montane forest was lost at Mahale during the Last Glacial Maximum (35–15 ka), then *C. angolensis* must have colonized (or recolonized) Mahale sometime during the subsequent deglacial (i.e., 12–10 ka) when conditions were wet and cool. At that time, with good rainfall and temperatures depressed ~6°C, montane forest to the west of the Albertine Rift moved >1,000 m down-slope on sites such as Mt. Kabobo and the Itombwe Massif and, again, crossed the Rift to Mahale (Hamilton 1982; 1988; Morley and Kingdon 2013).

Colobus a. mahale is geographically nearest to, and phenotypically most like, *C. a. cordieri* and *C. a. prigoginei*. It seems most probable that *C. a. mahale,* or *C. a. cordieri,* or *C. a. prigoginei*, or a now extinct common ancestor, reached Mahale via forest around the north end of L. Tanganyika. The montane forest-dependent *C. a. ruwenzorii* occurs to the north, but the coloration and pattern of its pelage is least like that of *C. a. mahale*.

Taxonomic arrangement of Colobus angolensis mahale

As indicated above, the Mahale *C. angolensis* is both phenotypically distinct and highly isolated from other populations of *C. angolensis*. We here describe this monkey as a subspecies—*C. a. mahale*. This is, however, a conservative assessment of its taxonomic status as, following a taxonomic revision of *C. angolensis*, applying the 'Phylogenetic Species Concept' (Cracraft 1983, 1992; Groves 2001, 2004; Groves and Happold 2013), this monkey might merit recognition as a species—*Colobus mahale*.

Nishida *et al*. (1981, p.561) found that, when all external phenotypic traits are considered, Mahale Angola colobus "presents a curious cross" between *C. a cottoni*, *C. a. cordieri*, and *C. a. prigoginei*, and *C. a. angolensis*, *C. a. palliatus*, *C. a. sharpei*, and *C. a ruwenzorii*. Our comparison of the pelage coloration and pattern of the other seven recognized subspecies of *C. angolensis* indicates that *C. a. mahale* is most similar to *C. a. prigoginei* and *C. a. cordieri* as all three of these subspecies lack a white brow-band, white pubic-band, and greyish pubic-patch. The major difference among these three subspecies relates to the color of the tail: black with distal ~10% dirty white with off-white tip in *C. a. mahale*; middle ~80% flecked pale grey with distal ~10% pale grey or white in *C. a. prigoginei*; distal ~70–80% brownish-grey in *C. a. cordieri*. *Colobus a. prigoginei* and *C. a. cordieri* are also the geographically closest subspecies to *C. a. mahale* (100 km and 300 km, respectively), albeit across L. Tanganyika. Another important difference is that *C. a. cordieri* is a lowland species at 400–1,000 m asl, whereas *C. a. prigoginei* (1,800–2,400 m asl), like *C. a. mahale* (1,800–2,350 m asl), is a montane forest species.

That *C. a. mahale* is phenotypically more similar to the subspecies to the west of the Albertine Rift (i.e., *C. a. prigoginei*, *C. a. cordieri*, *C. a. angolensis*, *C. a. cottoni*), than to subspecies to the east (i.e., *C. a. palliatus*) and southeast (*C. a. sharpei*), is to be expected given that the vast majority of species in other taxonomic groups, such as other mammals, birds, and plants, have affinities to the north and west (Moreau 1943, 1966; Ulfstrand and Lamprey 1960; Rahm 1966; Vollesen and Bidgood 1997; Plumptre *et al*. 2003, 2007; Moyer 2006). Four of the other five forest-dependent primate taxa in Mahale NP do not have populations east of the Greater Mahale Ecosystem/Landscape or east of the forests close to the east shore of L. Tanganyika (i.e., *G. thomasi*, *C. a. schmidti*, *P. tephrosceles*, *P. t. schweinfurthii*: Swynnerton and Hayman 1951; Rahm 1970; Kano 1971; Butynski *et al*. 2013; Foley *et al*. 2014; De Jong and Butynski 2023). In the case of *C. mitis* ssp.?, it appears to be more closely related to Mweru monkey *Cercopithecus mitis opisthostictus* Sclater, 1894, across L. Tanganyika to the west, and/or to Doggett's silver monkey *Cercopithecus mitis doggetti* Pocock, 1907, to the north, than to any of the 12 subspecies found to the east or south (Lawes *et al*. 2013; Butynski and De Jong 2020c; De Jong and Butynski 2023). What is unexpected is that *C. a. ruwenzorii*, a montane subspecies found to the north of Mahale, is the subspecies with a phenotype that differs most from *C. a. mahale*.

Conservation of *Colobus angolensis mahale*

Primate diversity

Tanzania is one of the most important countries in Africa for primate conservation (De Jong and Butynski 2012, 2021; Davenport *et al*. 2013) given its large number of non-human primates—14 genera, 29 species, and 46 taxa. Of these, seven species and five subspecies are endemic to Tanzania. One genus and eight species are monotypic (De Jong and Butynski 2023). Seventeen taxa are classified as threatened on The IUCN Red List of Threatened Species (IUCN 2023): three species and five subspecies are 'Vulnerable'; five species and three subspecies are 'Endangered'; and one species is 'Critically Endangered'. *Colobus angolensis* ssp. nov. (now *C. a. mahale*) is the only 'Data Deficient' primate in Tanzania (Butynski and De Jong 2020a).

Human population growth

The rate of natural increase of the human population in Tanzania is high at ~2.9% per year (PRB 2021). There were 65.5 million people in Tanzania in 2022. This is projected to increase to 90.4 million by mid-2035, and to 129.4 million by 2050 (worldpopulationreview.com 2022). Given this trend, it is inevitable that Tanzania will continue to lose large areas of forest. As most primates in Tanzania are forest-dependent, this means that Tanzania is in danger of soon losing several primate taxa. The primates of the Greater Mahale Ecosystem are under threat as here the annual human population growth rate is especially high (~4.2% during 2002–2012; Tanzania National Bureau of Statistics 2012), enhanced by movement into the area of more 100,000 refugees from DRC and more than 62,000 refugees from Burundi in the 1990s (Moyer *et al*. 2006, Piel *et al*. 2013; Nakamura and Itoh 2015). This rapid human population growth has been accompanied by an increase in poaching and extensive habitat degradation, loss, and fragmentation due to removal of forest products, forest clearance, and fire (Kielland 1978; Moyer 2006; Moyer *et al*. 2006; Hosaka and Nakamura 2015; McLester *et al*. 2019; Bonnin *et al*. 2020).

Until 2021, Mahale NP could only be reached by foot or boat. The new road from Kigoma to the north edge of the park will further increase the rate of growth of the human population around it, put added pressures on its natural resources, and further isolate its species. As the natural resources of the Greater Mahale Ecosystem are exploited and degraded, the threats to Mahale NP increase (Nishida 2012; Hosaka and Nakamura 2015).

Forest loss

Tanzania has one of the highest rates of forest loss in sub-Saharan Africa. During 2002–2021, Tanzania lost 323 km² (4.4%) of its humid primary forest and 28,600 km²

(11%) of its tree cover (Global Forest Watch 2023). The montane forests of Mahale NP, vital for the conservation of *C. a. mahale*, are deep within this large national park and remote, and the terrain is rugged. These montane forests are currently unaffected by agricultural encroachment, mining, logging, or the taking of other forest-products. Hunting also does not appear to be a serious problem there. The population of *C. a. mahale* is, however, small and localized and, therefore, prone to extinction due to loss of habitat because of fire and climate change, and to demographic and genetic stochastic events.

Montane forests and their biodiversity, in particular small forests, are increasingly threatened by fire, deforestation, fragmentation, and climate change (Hemp 2005; Parmesan 2006; Thakur *et al.* 2021). Uncontrolled fires are frequent in the Greater Mahale Ecosystem, including Mahale NP (Kielland 1978; Moyer 2006; Moyer *et al.* 2006). The average 'fire return interval' in the evergreen forests of the Greater Mahale Ecosystem is 8 years. The average fire return interval is, however, much shorter (2–3 years) on the east edge of the current montane forest and over the area where montane forest once occurred on the upper east slopes (Hunink *et al.* 2015). Wildfires, often set by poachers, honey-hunters, and farmers, greatly affect the natural vegetation in and around Mahale NP, destroying both primary forest and regenerating forest. Over parts of the east and south of Mahale NP the frequency of fires is so high (Nakamura and Fukuda 1999; Nakamura *et al.* 2005) that regeneration of forest does not occur, and soil erosion is a severe problem (Hunink *et al.* 2015). Even under the best of circumstances, regeneration of Mahale's montane forest is a very slow process (Kielland 1978).

Climate change

Over almost all of Africa, mean temperatures, as well as hot extremes, are higher than during 1850–1900, with the rate of surface temperature increase more rapid in Africa than the global average (IPCC 2021). A climatological assessment by Seismon and Picton Phillips (2012) predicts the following mean annual changes for the Albertine Rift, including Mahale, during the 100 years from 1990 to 2090: 3.6°C increase in temperature from 22.7°C to 26.3°C; 21 cm increase in rainfall from 120 cm to 141 cm; stable cloud cover at 67%. In Mahale, during 1989–2008, the length of the wet season declined by several weeks and the timing of rainfall shifted; more rain November–December and less rain mid-February–mid-April. Itoh (2015a) found the same shift using a 30-year dataset (1983–2013), as well as trends towards increased temperature and decreased rainfall during this period. Thirty years may be too short, however, to know whether this redistribution of rainfall represents a real climatic change. The predicted 18% increase in rainfall as of 2090 is not expected to dampen the impacts of the predicted 3.6°C increase in temperature (Seismon and Picton Phillips 2012). In the tropics, a change of 5–6°C in mean

annual temperature translates into an upward displacement of montane forest by 1,000 m (Hamilton 1988; Morley and Kingdon 2012). Thus, a 3.6°C thermal increase is expected to displace the montane forests of the Albertine Rift upwards by 600–720 m as of 2090 (Seismon and Picton Phillips 2012). In the case of Mahale, the montane forest cannot advance upwards; the upper limit of the montane forest is already at 2,350 m asl on a mountain that reaches an altitude of only 2,530 m asl. The top 180 m of Mahale not only covers a small area, it is too rocky and windy to support montane forest.

Primates appear to be particularly vulnerable to the adverse impacts of rapid climate change (Estrada *et al.* 2017; Korstjens 2019; Bernard and Marshall 2020; Scheun and Nowack 2023). Meyer and Pie (2022), applying phylogenetic comparative methods, found that, for primates, the projected rates of future climate change are very much faster than the ancestral rates of climatic niche evolution (i.e., *in situ* adaptation to climate change); at least 2,800-fold faster for temperature-related variables and 6,700-fold faster for precipitation-related variables. As concerns *C. a. mahale*, the option to adapt *in situ* to climate change does not exist, nor does the option to shift its geographic distribution as the montane forest on Mahale cannot expand up-slope and the surrounding biogeographic barriers cannot be over-come.

Fire

The continuing warmer temperatures that climate change is predicted to bring, together with a shorter wet season, are expected to enhance the negative impacts of fire on montane forest by creating hotter and drier conditions. Fire and climate change, through their negative impacts on the distribution of montane forest at Mahale (Kielland 1978; Moyer 2006; Moyer *et al.* 2006; Nishida 2012; Seismon and Picton Phillips 2012; Hunink *et al.* 2015), appear to be the biggest threats to the survival of *C. a. mahale*. Priority action for the conservation of *C. a. mahale* is to greatly reduce the incidence of fire in the vicinity of the montane forests of Mahale NP. There may be little that TANAPA, the authority responsible for the protection of Mahale NP and the management of its biodiversity, can do about the growing human population around the park or the changing climate, but it can effectively promote the expansion of the present ~50 km² of montane forest through greatly improved fire suppression. Increasing the area of montane forest will, almost certainly, expand the geographic distribution and increase the abundance of *C. a. mahale*, as well as of the other montane forest-dependent species. This would also enhance the livelihoods of people living in the semi-arid Greater Mahale Ecosystem through improvement of this critical watershed. Among the benefits would be a reduction of soil erosion and sediment yield into L. Tanganyika, one result of which would be enhanced protection of the fishery on which most of the people of the region depend (Cohen *et al.* 2005; Hunink *et al.* 2015).

De Jong and Butynski

Predation

Pan troglodytes preys both on *Piliocolobus* and *Colobus* (Takahata *et al*. 1984; Uehara and Ihobe 1998; Newton-Fisher *et al*. 2002; Uehara 2003; Nishida 2012; Watts and Mitani 2015; Bugir *et al*. 2021; Butynski and De Jong 2022). *Colobus a. mahale* is sympatric with *P. troglodytes*. In Mahale, where *P. tephrosceles* is widespread and relatively common, this species accounted for 70% of *P. troglodytes* prey during 1965–2010 (Hosaka *et al*. 2020). We can assume that *C. a. mahale* is sometimes killed by *P. troglodytes* but we suspect that the incidence is low given that *P. troglodytes* is uncommon in Mahale's montane forest (Kano 1971; Itani 1990).

In addition to humans and *P. troglodytes*, *P. pardus*, and crowned eagles *Stephanoaetus coronatus* (Linnaeus, 1766) are major predators of colobines in Africa (Struhsaker and Leakey 1990; Mitani *et al*. 2001; McGraw *et al*. 2006; Zuberbühler and Jenny 2007; Struhsaker 2010; Butynski and De Jong 2022). Both occur in in the montane forest of Mahale, and both are known to hunt *P. tephrosceles* there (Nishida 1968, 1972, 2012; Nishida *et al*. 1981; Seike 2022). On Mt. Nkungwe we captured a *P. pardus* on a camera trap within 2 km of where we encountered *C. a. mahale,* and we saw *S. coronatus* on 18 April 2022 circling over the site where we found *C. a. mahale* 3 days later. Although all four of these predators are expected to prey on *C. a. mahale,* we suspect that *S. coronatus* is the most important predator for *C. a. mahale* given its ability to hunt arboreal monkeys over large areas of extremely rugged terrain.

Conservation status of Colobus angolensis mahale

Colobus angolensis ssp. nov. (now *C. a. mahale*) is currently listed as 'Data Deficient' on The IUCN Red List of Threatened Species due to its poorly known geographic distribution and population size (Butynski and De Jong 2020a). Based on the above findings, and our review of the literature, *C. a. mahale* meets the criteria for 'Critically Endangered' B1a,b(i,ii,iii,v); B2a,b(i,ii,iii,v) (IUCN 2012). Here are the IUCN (2012) thresholds for assessing a taxon as 'Critically Endangered', followed by our best estimate, within parentheses, for *C. a. mahale*: population size <250 mature individuals (<200); Extent of Occurrence <100 km² (~7 km²); Area of Occupancy <10 km² (~3 km²).

De Jong and Butynski (2021) stated that the southern patas monkey *Erythrocebus baumstarki* Matschie, 1906 (central north Tanzania), Miss Waldron's red colobus *Piliocolobus waldroni* (Hayman, 1936) (south Ghana and southeast Côte d'Ivoire), and the Mount Kenya potto *Perodicticus ibeanus stockleyi* Butynski and De Jong, 2007 (central Kenya) will be among the first three primate extinctions recorded for continental Africa over the coming century. Based on their extremely small geographic distribution, small population, small area of suitable habitat, and the considerable vulnerability of that habitat to climate change and fire, *C. a. mahale* can be added to this list.

Research Priorities

Here are the four priorities for research on *C. a. mahale* and on the montane forest on which it relies.

1. Undertake a comprehensive survey of all closed moist forest above 1,600 m asl in Mahale NP to determine the geographic distribution and abundance of *C. a. mahale.* As pointed out by Nishida *et al*. (1981), the forest around and between Mt. Sisaga and Mt. Mfitwa is the priority for this survey (Fig. 2). Satellite imagery tools (e.g., Google Earth; Peakery; PeakVisor) show that here lies the largest tract of montane forest in Mahale NP. This region includes the Muhela Plateau, a relatively flat area that, until the 1970s, supported a farming community (B. Nyundo pers. comm.). Other priority sites for this survey are Mt. Pasagulu and the gallery forests along the headwaters of the Myako R., Mpila R., Kasiha R., Kasihamto R., and Lubulungu R., as these drain the west catchments of Mt. Mhensabantu, Mt. Ihumo, Mt. Nkungwe, Mt. Sibini, and Mt. Mfitwa. There are reports of *C. angolensis* roars being heard up the valleys of the Mpila R., Kasiha R., and Lubulungu R., perhaps as low as 1,600 m asl. Given the great difficulty of access for much of the proposed survey area, we suggest that the location of *C. a. mahale* groups be undertaken by searching large tracts of forest with binoculars, spotting scopes, and audio recorders (e.g., Audiomoths) from high vantage points on multiple days. Searches using camera-mounted drones might be particularly time- and cost-effective under these challenging conditions. Information obtained from this survey will provide a baseline for the long-term monitoring of this subspecies and serve its next IUCN Red List category of threat assessment.

2. Establish a long-term program to monitor and map the limits of montane forest and the timing and extent of fires within Mahale NP, as well as collect temperature and rainfall data at several sites within the montane forest.

3. Develop a habitat suitability model for *C. a. mahale*. Model the impacts of fire and climate change on the extent and connectivity of montane forest in Mahale NP and, thus, on the distribution of *C. a. mahale*. Together, these two models will help guide recommendations for the long-term, science-based, conservation of *C. a. mahale*.

4. Conduct biogeographical and comparative morphological and molecular research across the geographic distribution of *C. angolensis* to further our understanding of the evolution, phylogeography, and taxonomic arrangement of this species (Grubb *et al*. 2003; McDonald *et al*. 2022). In this regard, the low number of individuals, small geographic distribution, isolation, and vulnerability of *C. a. mahale*, and probably also of *C. a. prigoginei*, dictate that no wild individuals should be 'collected' (Wakeham-Dawson *et al*. 2002; Jones *et al*. 2005; Polaszek *et al*. 2005; Donegan 2008; Minteer *et al*. 2014a, 2014b; Pape *et al*. 2016). Many more photographs should be acquired of wild individuals and made widely available. The mandible and hair of a *C. a.*

mahale obtained in 1966 (Nishida 1968; Nishida *et al.* 1981) are particularly valuable samples. Additional samples might be secured in several ways (e.g., from feces and hairs collection from under sleeping and feeding sites of groups, from body parts obtained from below the nests of *S. coronatus*, and/or from individuals found dead). It is imperative that all physical samples be housed in an internationally recognized safe place, such as a public natural history museum (Gippoliti 2018).

Summary

1. In April 2022, scientists observed the Mahale Angola colobus for the first time in 43 years and obtained the first photographs of this subspecies.

2. The Mahale Angola colobus is phenotypically distinct and geographically isolated from other subspecies of *C. angolensis*: ~100 km across L. Tanganyika and ~330 km overland.

3. This article describes the Mahale Angola colobus and provides the formal name '*Colobus angolensis mahale*'.

4. The entire geographic distribution of *C. a. mahale* lies within the remote and rugged montane forests of Mahale NP.

5. The known 'Area of Occupancy' of *C. a. mahale* is ~3 km², 'Extent of Occurrence' is ~7 km², and geographic distribution is likely between 10 km² and 50 km². The known altitudinal range is 1,800–2,350 m asl. This is one of the world's most severely range-restricted primates.

6. The population size of *C. a. mahale* is probably <400 individuals, with <200 adults. This is one of the smallest populations of any of the world's primates.

7. Given the dependence of *C. a. mahale* on a small montane forest (~50 km²), its geographic distribution and population size have probably been small for thousands of years.

8. The main threats to *C. a. mahale* are fire and climate change, through their negative impacts on the extent of montane forest, as well as demographic and genetic stochastic events related to its small population. This is one of the world's most threatened primates.

9. The priority conservation action is to greatly reduce the incidence and size of fires in Mahale NP.

10. The current IUCN Red List degree of threat category for *C. a. mahale* is 'Data Deficient'. Based on the information provided in this article, this subspecies meets the criteria for 'Critically Endangered'.

11. Research priorities for *C. a. mahale* are to determine its geographic distribution and abundance, develop a habitat suitability model for this subspecies, model the impacts of climate change and fire on the distribution of montane forest in Mahale NP, and undertake biogeographical and comparative morphological and molecular research throughout the geographic distribution of *C. angolensis*.

Acknowledgments

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