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Research Article

Geographic range, taxonomy, and conservation of the Mount Kilimanjaro guereza colobus monkey (Primates: Cercopithecidae: *Colobus*)

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This paper is dedicated to Colin Groves who died on 30 November 2017. He was Professor Emeritus of Biological Anthropology at the Australian National University where he served for 40 years and became a noted primate and ungulate taxonomist. Colin was the best of colleagues and a dear friend. As a leading proponent of the "Phylogenetic Species Concept", he encouraged the publication of this paper.

Abstract

The Mount Kilimanjaro guereza colobus monkey is endemic to northern Tanzania and southern Kenya, occurring on and near Mount Kilimanjaro/Mount Meru. Currently referred to as "*Colobus guereza caudatus* Thomas 1885", this monkey is geographically very isolated, and phenotypically distinct from all other taxa of guereza monkeys. As such, application of the "Phylogenetic Species Concept" resurrects the Mount Kilimanjaro guereza to specific rank as *Colobus caudatus*. The geographic range of *C. caudatus* is small (ca. 4030 km^2) and in decline, as is the number of individuals and area of habitat. *Colobus caudatus* qualifies as an IUCN Red List globally "Endangered" species, as a nationally "Endangered" species in Tanzania, and as a nationally "Critically Endangered" species in Kenya. *Colobus caudatus* is Kenya's most threatened species of primate. Recommendations for research and conservation actions are provided.

Introduction

Reliable information on the taxonomic status of populations is critical to setting priorities and to making decisions for the conservation of species (Zinner and Roos, 2016). Primates represent one of Africa's best-studied groups of mammal. Nonetheless, the taxonomic status of many of the continent's primates is under debate, and the geographic range, abundance, and conservation status of most primate taxa remain poorly understood. This is especially the case in recent decades, given the rapid degradation, loss, and fragmentation of primate habitats, and increase in hunting. One genus for which the taxonomy has been particularly unstable and contentious is *Colobus* Illiger 1811 — the "black-and-white colobus monkeys" (Elliot, 1913; Allen, 1925, 1939; Schwarz, 1929; Pocock, 1936; Dandelot, 1968, 1974; Rahm, 1970; Hull, 1979; Oates and Trocco, 1983; Oates et al., 2000; Groves, 2001, 2007; Grubb et al., 2003; Ting, 2008).

Eight subspecies of guereza monkey *Colobus guereza* Rüppell, 1835 are recognized at this time (Hull, 1979; Napier, 1985; Groves, 2001, 2005, 2007; Grubb et al., 2003; O'Leary, 2003; Fashing and Oates, 2013; Groves and Ting, 2013; Kingdon, 2015). Four of these occur in Kenya (*C. g. caudatus* Thomas, 1885; *C. g. matschiei* Neumann, 1899; *C. g. kikuyuensis* Lönnberg, 1912; *C. g. percivali* Heller, 1913) and two occur in Tanzania (*C. g. caudatus*; *C. g. matschiei*; De Jong and Butynski, 2012). All four have allopatric distributions, each on its own set of mountain forest islands and adjacent forests (Schwarz, 1929; Rahm, 1970; Groves, 2001, 2007; Fashing and Oates, 2013; Butynski and de Jong, 2015).

The aim of this paper is to assess the geographic range and conservation status of *C. g. caudatus*, the Mount Kilimanjaro guereza (Fig. 1), and to reassess the taxonomic position of this monkey.

Methods

The information presented in this paper is based on a long-term field study of the biogeography, taxonomy, and conservation status of the primates of eastern Africa. This study involved foot and vehicle surveys in hundreds of sites in eastern Africa [Uganda (>40 sites); Kenya (>150); Tanzania (>50); Ethiopia (>5); Eritrea (>10); eastern Democratic Republic of Congo (>30)] to determine which primate species/subspecies are present and their relative abundance. Details of the field methods are presented in Butynski and de Jong (2015). Research at some sites was conducted for up to 11 years, while other sites were visited for less than a day. TMB began this study in 1978, and YDJ in 2001. To the findings of this field study we added information from a detailed review of the literature and from extensive correspondence with colleagues.

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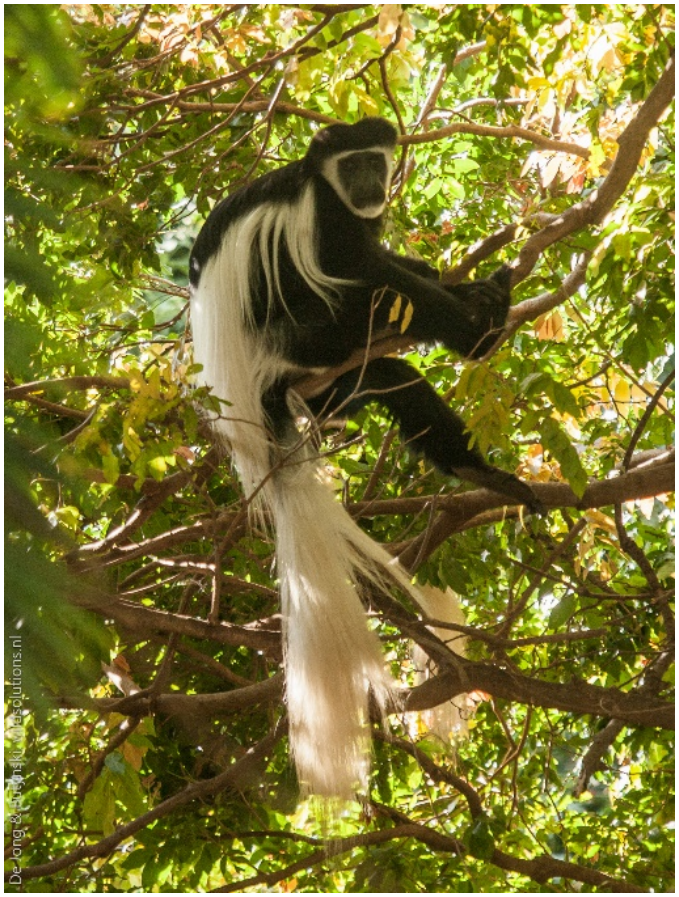

Figure 1 – Adult male Mount Kilimanjaro guereza colobus monkey, Kitobo Forest Reserve, southeast Kenya. Photograph by Yvonne de Jong and Tom Butynski.

Geographic range of the Mount Kilimanjaro guereza

The current geographic range of *C. g. caudatus* is limited to the slopes of Mount Kilimanjaro (5895 m above sea level; asl) and Mount Meru (4566 m asl), and to several nearby forest fragments (Fig. 2). This is the southeastern-most guereza. About 98% of the geographic range is in extreme northern Tanzania, with but ca. 2% of the range in extreme southern Kenya. The altitudinal range of *caudatus* is ca. 660–3050 m asl, and the geographic range is ca. 4030 km^2 (Butynski and de Jong, 2015). There is nothing in the literature or in museum collections to indicate that this monkey had a geographic range at the end of the 19th Century that was much greater than at present (Thomas, 1885; True, 1892; Schwarz, 1929; Napier, 1985). "Area of Occupancy" (IUCN, 2001) has, however, been much reduced as a result of considerable habitat degradation, loss, and fragmentation, and extirpations due to hunting.

Isolation of the Mount Kilimanjaro guereza

At the present time in eastern Africa, all taxa of guereza mainly occupy transition forest (i.e., mid-altitude forest) and montane forest on large mountains and massifs (map p. 9 in Kingdon, 1971; map p. 71 in Hamilton, 1982; map p. 112 in Fashing and Oates, 2013; de Jong and Butynski, 2017, in press). These sites are isolated by lower, dryer, and hotter ground where forest is absent — except along perennial rivers, lakes, and wetlands in the vicinity of the large mountains and massifs. The non-forested areas are often large (map p. 30 in Kingdon, 1971). Guereza at sites in eastern Africa probably represent relictual populations of a species that was once very widespread in the region. The present discontinuous distribution likely reflects the retraction and restriction of moist forest to refugia during the cooler and dryer periods that began to occur ca. 125000 BP (Late Pleistocene; Trauth et al., 2015). The resultant physical barriers, particularly the expansive areas of unfavourable arid habitat (map p. 65 in Kingdon, 1971; maps p. 5 in Colyn, 1991), would have prevented genetic exchange among populations (Kingdon, 1971, 1990; Hamilton, 1982, 1988; Colyn, 1991; Kamilar et al., 2009; Morley and Kingdon, 2013). During periods of isolation, these allopatric populations continued to adapt to ever-changing local conditions, including geology, climate, availability of resources, competition, predators, and pathogens.

Geographically, the nearest guereza to *caudatus* is the Mau Forest guereza *C. g. matschiei* [ca. 155 km to the northwest at Shompole on the floor of the Eastern (Gregory) Rift Valley west of Lake Magadi, Kenya; W. Knocker, *pers. comm.*, 2015; Q. Luke, *pers. comm.*, 2015] and the Mount Kenya guereza *C. g. kikuyuensis* (ca. 175 km to the north-northwest in the Ngong Hills southwest of Nairobi, Kenya; Groves, 2001, 2007; D. Martins, *pers. comm.*, 2015; P. Kahumbu, *pers. comm.*, 2015; Fig. 2). To the north and northwest of Mount Kilimanjaro/Mount Meru, in their rain shadow, lies the Taru Desert (which includes the Amboseli Basin and Tsavo West National Park, and extends westward towards Lake Magadi and northward to the Athi River near Nairobi). This expanse, at 1100–1500 m asl, has a mean annual rainfall of ca. 300 mm and no perennial rivers. The Taru Desert is covered by grassland and *Acacia-Commiphora* thicket and bushland — habitats that cannot support guereza (map p. 13 and map p. 30 in Kingdon, 1971; Butynski and de Jong, 2015). The Taru Desert serves as a vegetational barrier that isolates *caudatus* both from *C. g. matschiei* and *C. g. kikuyuensis*. Another contiguous, large, arid region lies west of Mount Kilimanjaro/Mount Meru up to Lake Natron and Lake Manyara in the Eastern Rift Valley (Fig. 2).

The Eastern Rift Valley is a geological barrier for many primates and other taxa (Butynski and de Jong, 2007; Livingston and Kingdon, 2013; Aghová et al., 2017). The floor of the Eastern Rift Valley at Lake Magadi (to the west of which is Shompole, the nearest site for *C. g. matschiei*) is low (<600 m asl), wide (>32 km), dry (mean annual rainfall ca. 400 mm), and hot (mean maximum temperature ca. 35 °C; Bennun and Njoroge, 1999). Thus, the Eastern Rift Valley isolates *C. g. kikuyuensis* from *C. g. matschiei* and, together with the Taru Desert, isolates *caudatus* from *C. g. matschiei*. As such, gene-flow between *caudatus* and other populations of guereza is not possible at this time. It

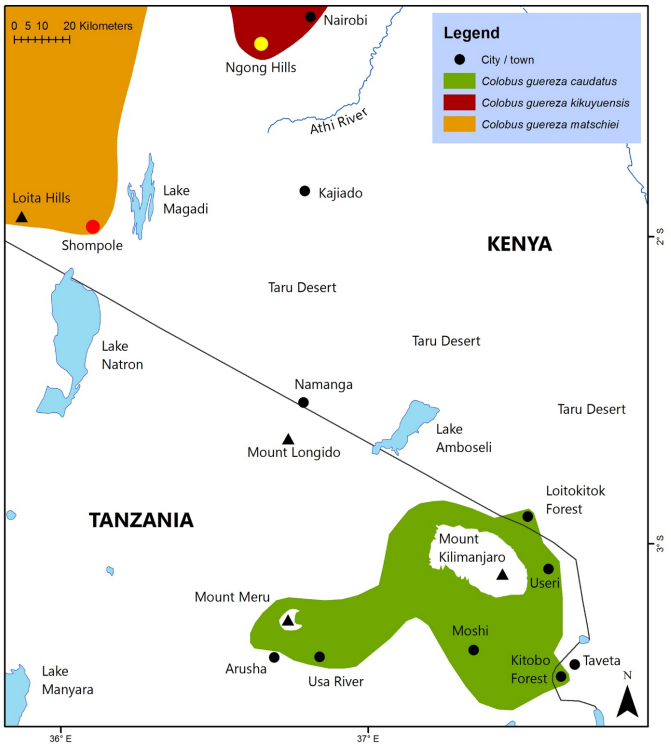

Figure 2 – Localities for the three taxa of guereza colobus monkeys that occur in southern Kenya and northern Tanzania. Geographic range of the Mount Kilimanjaro guereza is depicted in green (ca. 4030 km^2). Nearest population of Mau Forest guereza *Colobus guereza matschiei* is depicted by a red dot. Nearest population of Mount Kenya guereza *Colobus guereza kikuyuensis* is depicted by a yellow dot. Lake Magadi, Lake Natron, and Lake Manyara lie in the arid Eastern Rift Valley and, therefore, between the Mount Kilimanjaro guereza and *C. g. matschiei.* The Taru Desert lies between the Mount Kilimanjaro guereza and *C. g. matschiei* and *C. g. kikuyuensis.*

is important to point out that no guereza occur on the mountains nearest to Mount Kilimanjaro/Mount Meru to the north (Chyulu, 50 km from Mount Kilimanjaro/Mount Meru), east (Taita, 75 km), southeast (North Pare, 10 km), west (Monduli, 15 km; Ngorongoro Crater, 85 km), or southwest (Hanang, 190 km). At this time, all of these sites appear to have habitat capable of supporting guereza (Rodgers, 1981; Y. de Jong and T. Butynski, *personal observation*). Absence of *caudatus* from these sites suggests that the forests of Mount Kilimanjaro/Mount Meru have been long isolated by a major barrier of arid land. If guereza ever occurred at any of these sites, those populations did not survive the vegetation changes (i.e., forest loss) during the most arid period of the Late Pleistocene (see below).

The last interglacial in Africa ended ca. 70000 BP. About 38000–28000 BP, within the subsequent major glacial period (70000–12500 BP), the climate in East Africa was wetter and warmer, and forests expanded somewhat (Kingdon, 1971, 1990; Hamilton, 1982, 1988; Colyn, 1991; Morley and Kingdon, 2013). There appears to be no evidence, however, that forest at that time connected Mount Kilimanjaro/Mount Meru with the Central Kenya Highlands (which comprises the Ngong Hills, Mount Kenya, and Aberdare Range), or that forest connected Mount Kilimanjaro/Mount Meru with the highlands to the west of the Eastern Rift Valley. Forests may have, however, covered some of the floor across the Eastern Rift Valley between the Central Kenya Highlands and the highlands to the west (e.g., Aberdare Range with Mau Escarpment through the Lake Naivasha/Lake Elementeita region where, at ca. 2100 m asl, the floor of the Eastern Rift Valley is at its highest; Butynski and de Jong, 2007), thereby bringing *C. g. kikuyuensis* and *C. g. matschiei* into contact. At present, these two subspecies are separated in this region by only ca. 13 km (Y. de Jong and T. Butynski, *personal observation*).

Subsequently, during the most severe phase (ca. 22000–12500 BP) of the last glacial, the climate was dryer and colder. During the glacial maximum (ca. 18000 BP) in East Africa, temperatures were ca. 6.7 °C–9.5 °C lower than at present, rainfall much less, and forests depressed altitudinally by >1000 m (perhaps downwards to ca. 500 m asl; Hamilton, 1982, 1988 and Colyn, 1991). Under these conditions, the extent of the already isolated forests of Mount Kilimanjaro/Mount Meru, the Central Kenya Highlands, and those west of the Eastern Rift Valley, would have been further reduced. Forest began to expand again at ca. 12500 BP (Kingdon, 1971, 1990; Morley and Kingdon, 2013) but, it seems, not much beyond the extent that we observe today (accounting for human-caused forest removal over the past few hundred years). It appears that these forests, and thus their populations of guereza, have been isolated for at least 22000 years — probably much longer than this in the case of Mount Kilimanjaro/Mount Meru.

Conditions wet enough to support a corridor of forest between Mount Kilimanjaro/Mount Meru and the Central Kenya Highlands and/or the highlands to the west of the Eastern Rift Valley have probably not existed for >70000 years. There have been roughly 20 cycles of major forest expansion and contraction in Africa over the last 2.3 Myr (i.e., the Quaternary; Hamilton, 1982, 1988). Of these cycles, the one before the last glacial was probably when forest expansion was most extensive — perhaps extensive enough to connect Mount Kilimanjaro/Mount Meru with the Central Kenya Highlands and/or with the highlands west of the Eastern Rift Valley. In conclusion, the limited information available on the timing and extent of forest expansions in East Africa suggests that *C. g. caudatus* became geographically isolated from *C. g. kikuyuensis* and *C. g. matschiei* at least 70000 years ago. Indeed, the time of isolation may be far greater than 70000 years as preliminary mitochondrial phylogenetic research indicates that *caudatus* split from *kikuyuensis* ca. 230000 years ago, and from *matschiei* ca. 730000 years ago (D. Zinner, *unpublished data*, 2017). It should be noted, however, that mitochondrial information can enlighten only the matrilineal side of the evolutionary history of a taxon. Autosomal and y-chromosomal data are required to obtain a more complete picture.

Taxonomic history of the Mount Kilimanjaro guereza

Two years after being described and named "*Colobus guereza caudatus*" by Thomas (1885), *caudatus* was elevated to species rank by de Rochebrune (1887). Five years later, True (1892, p. 447) wrote, *"This remarkably handsome monkey is regarded by Mr. Thomas as a subspecies of* Colobus guereza*. So far as I know, however, no specimens showing external characters intermediate between those of the two forms have been found, and the skulls which Dr. Abbott brought home are different from that of* C. guereza*. On present evidence it may be affirmed that* Colobus caudatus *is a distinct species, peculiar to the region of Mount Kilima-Njaro"*.

Presumably, it was on this basis that Thomas himself came to treat *caudatus* as a species (Thomas, 1900). Subsequently, Camerano (1909) added specimens to the sample examined by True (1892) and conducted further analyses. He reached the same conclusion — that *caudatus* should be reinstated to species rank — as did Elliot (1913) and Hollister (1924). Elliot (1913, p. 146) pointed out that *caudatus* is, *"Remarkable for its large bushy tail, far exceeding in its brush-like character those of all the members of the genus"*. Hollister (1924, p. 38) stated that, *"Adult male skulls of* C. caudatus caudatus *develop a sharply marked sagittal crest, such as is not found in any of the skulls of much older individuals in our large series of* kikuyuensis *from Kijabe and Mount Kenia"*. Others recognizing *caudatus* as a species include Matschie (1895, 1912), Scott Elliot (1895), de Pousargues (1896), Forbes (1897), Lydekker (1905a,b) and Allen (1909, 1925). A few authors, however, continued to follow Thomas's (1885) initial taxonomy in assigning *caudatus* subspecific rank (e.g., Lönnberg, 1912; Heller, 1913). Roosevelt (1910) variably treated *caudatus* both as a subspecies (*C. abyssinicus caudatus*, p. 538) and as a species (*C. caudatus*, p. 541).

Schwarz (1929) subsumed all black-and-white colobus monkeys under one polytypic species — *Colobus polykomos* (Zimmermann, 1780). Under his taxonomy, *caudatus* became one of 20 subspecies of *C. polykomos*. Schwarz based his taxonomy on the observation that, geographically, there is an "unbroken series" (i.e., there are clinal series links) among several characters of the pelage. He gave little importance to the fact that many of these taxa were diagnosable, geographically isolated, and, in some cases, sympatric. Although Schwarz's taxonomy was widely accepted (e.g., Allen, 1939; Swynnerton and Hayman, 1951; Butler, 1966; Gautier and Gautier-Hion, 1969; Hull, 1978) for about 40 years, his lumping of black-and-white colobus taxa proved to be excessive.

Pocock (1936) was apparently the first to reject Schwarz's (1929) assertion that there is but one species of black-and-white colobus. He did this by reinstating four black-and-white colobus taxa to species rank. It seems, however, that Pocock's important article did not receive much recognition. This may be, at least in part, due to the fact that the wide scope of his article was not made clear by the very specific title; *"External characters of a female specimen of a red colobus monkey"*. This changed with Dandelot's (1965, 1968, 1974) adoption, nearly 30 years later, of Pocock's taxonomy. Today, five of Schwarz's subspecies are widely recognized as species [*Colobus polykomos*, *C. vellerosus* (I. Geoffroy 1830), *C. guereza*, *C. satanas* Waterhouse 1838, *C. angolensis* Sclater 1860] — but not so *caudatus* (Oates and Trocco, 1983; Napier, 1985; Napier and Napier, 1985; Oates et al., 1994; Groves, 2001, 2005, 2007; Grubb et al., 2003; O'Leary, 2003; Ting, 2008; Groves and Ting, 2013; Kingdon and Groves, 2013; Kingdon, 2015).

Taxonomic reassessment of the Mount Kilimanjaro guereza

As stated above, True (1892) and Camerano (1909) found the cranial morphology and pelage of *caudatus* to be diagnosable characters at the species-level. More recent morphometric research supports the uniqueness of the skull of *caudatus*. Hull (1979) conducted a canonical variates analysis on 607 skulls (340 males; 267 females) of adult guereza from 18 populations, applying a series of 76 measurements. He con-

cluded that eight subspecies of *C. guereza* should be recognized. Hull's analysis indicates that the skulls of adult male *caudatus* (n = 23) are the most distinctive of the *C. guereza* subspecies, differing absolutely from those of the other seven subspecies. In addition, the skulls of adult female *caudatus* (n = 23) are different from those of all other guereza except *C. g. matschiei* in the western Kenya population — with which they overlap very slightly. They do not overlap with the skulls of adult females from two other populations of *C. g. matschiei*, nor with those from the three populations of *C. g. kikuyuensis* that were assessed. As concerns pattern of the pelage of *Colobus*, Hull (1978, p. 22) stated, *"These coat colour patterns appear to be remarkably stable. Each species produces its distinctive pattern regardless of the environmental conditions under which it is raised. Furthermore, the patterns seem to be strongly canalized, showing considerable uniformity within the subspecies, and clear distinctions between them (Dandelot, 1971; Rahm, 1970)"*.

It seems that one result of the strong male-male competition in guereza has been the evolution of the loud call ("roar") of the adult male. Oates and Trocco (1983) and Oates et al. (2000) confirmed that the loud call of the adult male guereza, as for the loud call of the adult male of some other primates (e.g., Struhsaker, 1970; Gautier, 1988), can be a reliable taxonomic trait. Oates et al. (2000) found significant difference (p<0.001) in the dominant frequency of the loud call of *caudatus* and *C. g. occidentalis*. They did not compare the loud call of *caudatus* with that of other guereza.

We have made field observations (TMB for 40 years; YDJ for 17 years) on seven of the currently recognized eight subspecies of *C. guereza* (*caudatus*, *kikuyuensis*, *matschiei*, *percivali*, *dodingae*, *occidentalis*, *gallarum*). We believe that *caudatus* is 100% diagnosable in the field from all other guereza on the basis of pelage characteristics, particularly the length and shape of the tail tuft, and the percentage of the tail that is white/cream (Elliot, 1913; Schwarz, 1929; Dandelot, 1968, 1974; Napier, 1985; Groves, 2001, 2007; O'Leary, 2003; Fashing and Oates, 2013; Butynski and de Jong, 2015). Photographs of all currently recognized subspecies are available at: http://www.wildsolutions.nl/photomaps/guereza/ (de Jong and Butynski, 2017).

As indicated above, *caudatus* is geographically very isolated from other guereza both by distance (>155 km) and by geological and arid vegetational barriers (Fig. 2). In addition, *caudatus* is diagnosably distinct from other guereza based on skull morphology and pelage characters, and distinguishable from *C. g. occidentalis* by the loud call of the adult male. These characters are presumed to be based on fixed, heritable, genetic differences. This empirical evidence, and application of the "Phylogenetic Species Concept" (e.g., Cracraft, 1983; Groves, 2001, 2004, 2012; Groves et al., 2013; Cotterill et al., 2014; Rylands and Mittermeier, 2014; Oates and Ting, 2015; Groves et al., 2017), require that this taxon be resurrected from *Colobus guereza caudatus* to *Colobus caudatus*.

Colobus caudatus is not the only species endemic to Mount Kilimanjaro/Mount Meru. Kingdon (1990) and Hemp (2005, 2006) list some of the species of plants and animals endemic to this region, including the Kilimanjaro mouse shrew *Myosorex zinki* Heim de Balsac and Lamotte, 1956. Considering its relatively young age (ca. 1 million years; Hamilton, 1982), Mount Kilimanjaro holds a fair number of endemic species. This too suggests considerable isolation of the forests of Mount Kilimanjaro during much of its existence.

Conservation status of the Mount Kilimanjaro guereza

The human population on the lower slopes of Mount Kilimanjaro/Mount Meru is one of the densest in Tanzania and continues to rapidly grow (1.8% annual population growth rate; NBS/OCGS, 2013). One result is that large areas of indigenous forests within the geographic range of *C. caudatus* have been degraded, lost, and fragmented over the past 100 years, and these processes are ongoing (Grimshaw et al., 1995; Hemp, 2005, 2006; Butynski and de Jong, 2015; de Jong and Butynski, in press).

Colobus caudatus has an "Extent of Occurrence" of <5000 km^2, is comprised of many subpopulations, and is experiencing a continuing decline in Extent of Occurrence, Area of Occupancy, habitat quality, habitat area, and number of mature individuals. As such, applying the current IUCN Red List Categories and Criteria (IUCN, 2001), *C. caudatus* readily meets the criteria of a globally "Endangered" species (de Jong and Butynski, in press). Within Kenya, where *C. caudatus* has an Extent of Occurrence of <100 km^2 and an Area of Occupancy of <10 km^2, it meets the criteria of a nationally "Critically Endangered" species.

The strong-holds for the long-term conservation of *C. caudatus* are Tanzania's Kilimanjaro National Park (1668 km^2) and Arusha National Park (542 km^2) on Mount Meru. In Kenya, *C. caudatus* is known to occur only in two small, degraded, remnant forests; Kitobo Forest Reserve (1.6 km^2) and Loitokitok Forest Reserve (4.2 km^2; Fig. 2). The total number of *C. caudatus* in these two forests is unlikely to be >200 — and might be <100. If additional populations of this monkey occur in Kenya, they will surely be small. At this time, *C. caudatus* is Kenya's most threatened species of primate (de Jong and Butynski, 2012, in press; Butynski and de Jong, 2015).

Recommendations

Additional comparative research on morphology, behaviour, loud call, physiology, and molecular biology should be conducted on all recognized taxa within *Colobus*. This research is expected to: (1) provide insights into the environmental history of eastern Africa during the Pleistocene; (2) reveal additional diagnosable characters leading to an improved taxonomy for this genus; (3) significantly enhance our understanding of the phylogeography of the species and subspecies within *Colobus*; and (4) help in establishing policies, actions, and priorities for their conservation.

Given current environmental trends, Kenya is in danger of losing several primate taxa over the next few decades (de Jong and Butynski, 2012) — perhaps led by *C. caudatus*. The Kenya Forest Department, Kenya Wildlife Service, The National Museums Kenya, Institute of Primate Research, and those international conservation NGOs concerned with maintaining Kenya's biodiversity, should give much more attention to the plight of *C. caudatus* in Kenya. They need to work closely with, and support, the efforts of local communities and local authorities to reverse the continuing degradation and loss of the ca. 5.8 km^2 of *C. caudatus* habitat that remains in Kenya.

The tiny Kitobo Forest Reserve is critical to the survival of *C. caudatus* in Kenya — while also protecting a water supply important to local people and a biodiversity unique in Kenya (Butynski and de Jong, 2015). In this regard, Global Wildlife Conservation is supporting local communities and the Kenya Forest Service in efforts to save the Kitobo Forest Reserve and halt biodiversity loss. The primary activities of this project are reafforestation and conservation training and education.

Conclusions

The Mount Kilimanjaro guereza is endemic to the Mount Kilimanjaro/Mount Meru region. This monkey is geographically isolated and phenotypically distinct. Presently referred to a "*Colobus guereza caudatus*", this study resurrects the Mount Kilimanjaro guereza to specific rank as *Colobus caudatus*. This monkey meets the IUCN Red List criteria of a globally "Endangered" species, as a nationally "Endangered" species in Tanzania, and as a nationally "Critically Endangered" species in Kenya. *Colobus caudatus* is Kenya's most threatened species of primate. *Colobus caudatus* requires more conservation attention than at present if it is going to survive in Kenya.

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