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Case Study:

Forest Fragmentation: A Probable Cause for Two Cases of Natural Primate Hybridization in the Midlands of KwaZulu-Natal, South Africa

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INTRODUCTION

Hybridization in primates is no longer considered a rare phenomenon. It has been estimated that more than 10% of all primate species hybridize (Arnold & Meyer 2006; Zinner *et al.* 2011). Hybridization is well documented within most lineages of Old World monkeys (e.g., *Papio, Macaca, and Cercopithecus*), supporting the growing consensus that this phenomenon is an important evolutionary mechanism driving speciation processes (Detwiler *et al.* 2005; Zinner *et al.* 2011). However, cases of natural hybridization between sympatric, intergeneric species are considered rare, such as reported crosses between olive baboons (*Papio anubis*) and gelada baboons (*Theropithecus gelada*) (Dunbar & Dunbar 1974) and gelada baboons and hamadryas (*Papio hamadryas*) (Jolly *et al.* 1997). The first records of hybridization in the wild between blue monkeys (*Cercopithecus mitis*) and vervet monkeys (*Chlorocebus pygerythrus*) were recorded in Kenya (de Jong & Butynski 2010).

Here I report two new probable cases of sympatric, intergeneric hybridization between two guenons, the samango monkey (*Cercopithecus mitis labiatus*) (Figure 1) and the vervet monkey (*Chlorocebus pygerythrus*) (Figure 2) from the midlands of KwaZulu-Natal, South Africa.

Following the advice of the African Primate Group, Grubb *et al.* (2003) kept vervets within the genus *Cercopithecus*, although Groves (2001, 2005) placed them in the genus *Chlorocebus*. Subsequently, this latter classification has been followed by most others (e.g., Butynski & de Jong 2019b) and is followed here. The taxonomy of the polytypic *Cercopithecus nictitans* group is inconsistent, with 2-3 species recognized: *C. nictitans, C. mitis* and sometimes *C. albogularis*. Based on pelage colourations, Groves (2001, 2005) recognised *C. albogularis* as a separate species. However, Grubb *et al.* (2003) do not recognise *C. albogularis* as a separate taxon and classify it as *C. mitis*. The samango monkey is listed as a subspecies of *C. mitis* in Lawes *et al.* (2013) as well as on the IUCN Red List (Butynski & de Jong 2019a). Therefore, for the purposes of this field study, *C. mitis labiatus* is used.

C. mitis exists in isolated or semi-isolated forest fragments with a suspected low rate of dispersal (Lawes *et al.* 2000; Linden *et al.* 2016). The aim of this study is to assess whether hybridization has occurred because of forest fragmentation and degradation combined with the samango monkey's poor dispersal ability (Lawes *et al.* 2000), and whether further research and greater conservation management for the forests and samango monkeys is needed.

METHODS & OBSERVATIONS

The Study Area

The study area lies between Dargle and Balgowan in the midlands, KwaZulu-Natal (Figure 3) and is primarily comprised of guest houses, large residential gardens with exotic plant species, and livestock farms against a backdrop of fragmented

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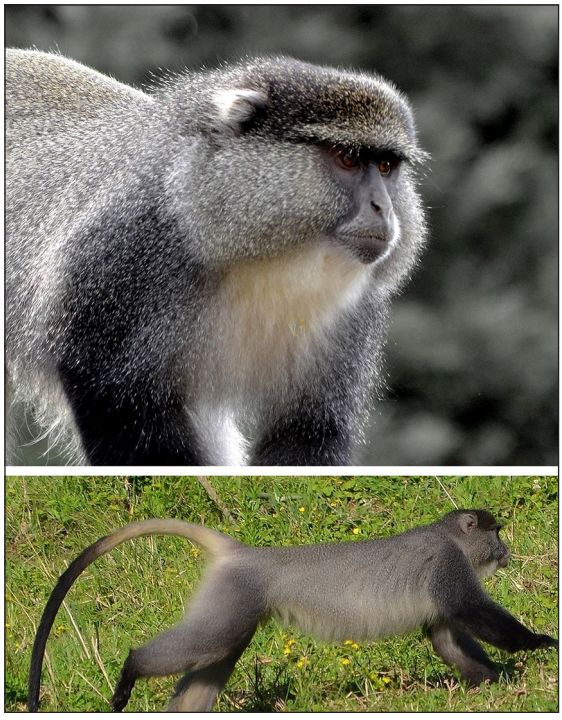

Figure 1. Adult male samango monkey (*Cercopithecus mitis labiatus*) on a cattle farm in Dargle Valley in the midlands of KwaZulu-Natal, 2018. Photograph by Karin Saks.

mistbelt forest, *Pinus elliottii* plantations, *Eucalyptus globulus* plantations, and grasslands. Three of South Africa's five primate species occur in the midlands, KwaZulu-Natal: chacma baboons (*Papio ursinus*), vervet monkeys, and samango monkeys.

Risks from natural predators are relatively low due to human-induced changes to the natural habitat and the trapping and killing of predators by cattle and poultry farmers. Species sighted in the area include forest buzzard (*Buteo trizonatus*), crown eagle (*Stephanoaetus coronatus*), caracal (*Caracal caracal*), serval (*Leptailurus serval*), bushbuck (*Tragelaphus scriptus*), grey duiker (*Sylvicapra grimmia*), reedbuck (*Redunca arundinum*), porcupine (*Hystrix africaeaustralis*), scrub hare (*Lepus saxatilis*), and bushpig (*Potamochoerus larvatus*). Anthropogenic risks to monkeys are high; they are killed by dogs, shot at by residents (for their eating planted crops), trapped for traditional medicine, hit by vehicles, and electrocuted on pylons. Getting close to the study group was challenging; thus, camera traps were used to collect additional data.

Data Collection

This report focuses primarily on Study Site 1, a 56 hectare forest patch in Balgowan where the vervet monkey/hybrid study group resided. Fieldwork at Study Site 1 was conducted between October 2017 and October 2018. At the time of these observations, the study group included several vervet monkeys (two adult males, three subadult males, seven adult females, three subadult females and 12 juveniles) and two hybrids (one subadult male and one juvenile male). Comparisons were made with Study Site 2, where vervet monkey and samango monkey groups coexisted. The vervet monkey group of seventeen individuals at Site 2 consisted of two adult males, five adult females and ten juveniles at the time of these observations. The samango monkey group consisted of 29 individuals: one adult male with females and juveniles. At Study Site 3, a private property occupied by a vervet monkey group and single male samango monkey, the habitat was dominated by exotic plant species and was approximately 1 km away from mistbelt forest.

Figure 2. Subadult male vervet monkey (*Chlorocebus pygerythrus*) in residential garden in Dargle Valley in the midlands of Kwazulu Natal, 2018. Photograph by Karin Saks.

Observational data were collected using *ad libitum* sampling (Altmann 1974) during 150 visits to the study site with each visit taking between 2 h and 11 h. During these visits, observers walked through the mistbelt forest and on private agricultural and residential land to look for signs of the vervet monkey/hybrid study group as well as signs of samango monkeys. On 15 of these occasions, the study group was sighted and photographed when possible. *Ad libitum* notes were also drawn from trail camera footage (18 videos captured), which included 64 sightings of the group with one or both of the hybrids visible. The trail cameras were placed at two separate locations at Site 1 in Balgowan for 120 days. We recorded activity patterns and the

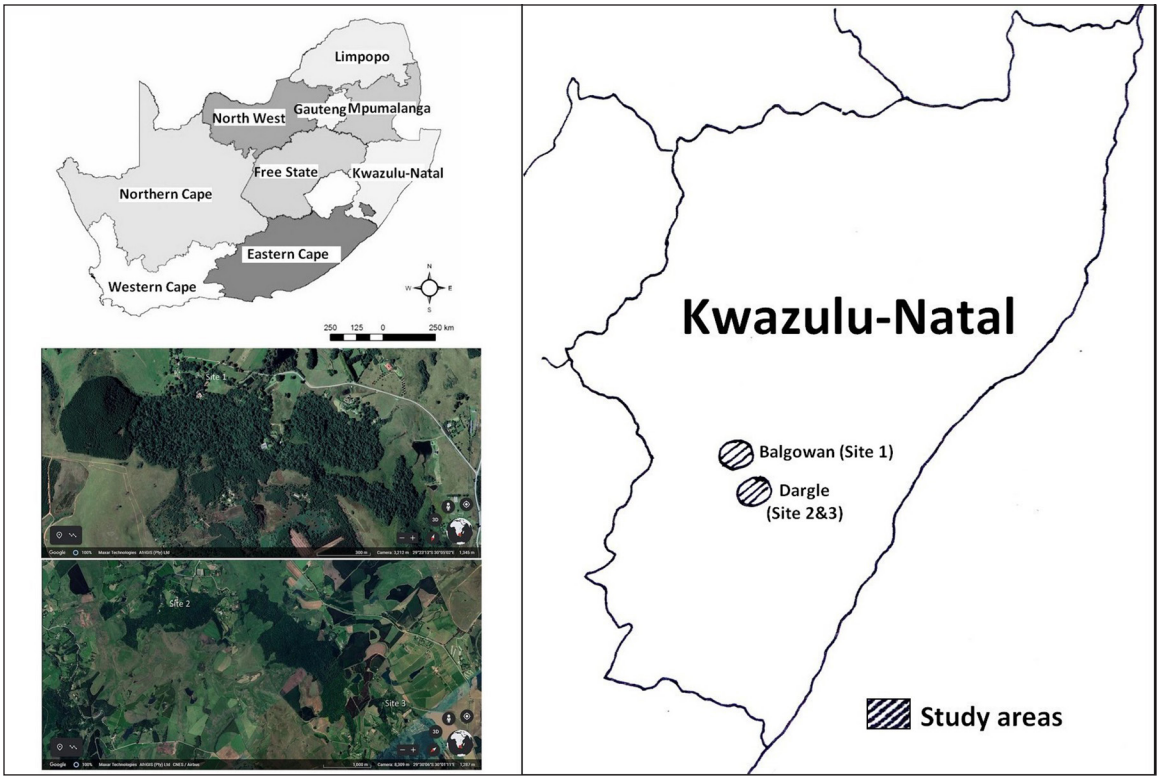

Figure 3. Location of Study Sites 1, 2, and 3 in the midlands, KwaZulu-Natal, South Africa.

presence or absence of samango monkeys and hybrids. Samango monkey individuals were not captured on trail camera footage between October 2017 and October 2018. Local residents reported that only solitary male samango monkeys had been sighted in the area; no groups were observed.

Observation of Probable Hybrids

On 26 November 2017, we came across two unusually marked monkeys with a group of vervet monkeys: a juvenile male (named JJ) estimated to be about two years old and a subadult male (named JA) estimated to be around five years old (Figures 4, 5, and 6). Because only two species of guenon exist in the study area, the intermediate phenotypic characters of the two guenons led us to suspect that the two individuals were crosses between samango monkeys and vervet monkeys.

The most prominent morphological characteristics distinguishing the hybrids from their parent species are their white hands and feet, full length white tail with dark area at the base and the white band (in an inverted "v" shape) around the nose. The older hybrid had a very pale grey scrotum that was intermediate in size contrasting with the large blue scrotum of vervet monkeys and smallish dark grey scrotum of samango monkeys. Like samango monkeys, the back legs of the hybrids were longer than those of vervet monkeys.

The hybrids' overall pelage had a grey tone without the yellow hues seen in vervet monkeys but not in samango monkeys. The hair of the hybrids was the same length as that of vervet monkeys, while samango monkeys have longer hair. There was a rust tinge along the side of the hybrids' bodies which was not obviously present in either parent species but is noticeable in another subspecies, Stairs' white-collared monkey (*Cercopithecus mitis erythrarchus*), which does not exist in the study area. The present distribution of these two C. mitis subspecies is closely correlated with the distribution of Afromontane, Scarp, and Indian Ocean coastal belt forests in southern Africa and the two subspecies do not overlap in their distribution (Lawes 1990a).

On the 15 December 2017, soon after sunrise, we heard a male samango monkey "pyow" vocalization next to the vervet monkey/hybrid group's sleeping site. The "pyow" vocalization was heard again at other times on at least five occasions while walking through the forest. These vocalizations confirmed the presence of at least one male samango monkey in the area.

When an adult male vervet monkey moved into the study group during April 2018, and JA was no longer present, this suggested that JA had dispersed

Figure 4. One-eyed, juvenile vervet monkey with hybrid JJ, December 2017. The two hybrids and this vervet monkey were often seen together during the first months of 2018. Photograph by Dave Brammage.

from the group. Vervet monkey breeding season usually begins around May and Young *et al.* (2019) found that dispersal in vervet monkeys was seasonal. Indeed, ad libitum notes made from trail camera footage and direct observations suggested that the breeding season at KwaZulu-Natal coincided with the immigration of new males and the dispersal of males.

On 21 May 2018, we observed a solitary adult male samango monkey within 10 m of the vervet monkey/hybrid study group.

Mixed-species Association Between Samango Monkey and Vervet Monkey Groups

At Study Site 2, on at least eight occasions, we observed a mixed-species association between vervet monkey and samango monkey groups. Our most prominent direct sightings occurred during October 2017 and October 2018 when a Ficus craterostoma was in season. Trail camera footage captured in October 2018 showed individuals from each species grooming each other and vervet monkey males mounting samango monkey females. Trail camera footage captured on the 26 October 2018, showed the mixed-species group chasing off what appeared to be an outsider samango monkey group at the site where the mixed-species group

Figure 5. Subadult hybrid JA in Cape Chestnut (*Calodendrum capense*), January 2018. Both vervet monkeys and samango monkeys eat the fruit and seeds of this tree. Photograph by Carol Brammage.

was feeding. A group of monkeys from the mixed-species group had left the *Ficus craterostoma* then approached a group at the edge of the field which contained about 10-15 samango monkeys. The two groups lunged at each other until the outsider group moved off. Hybrids were absent at this site.

At Study Site 3, a solitary adult male samango monkey was regularly observed in close proximity to a vervet monkey group between 2015 and 2018. Hybrids were absent at this site.

DISCUSSION

Because of population decline when suitable habitat was lost throughout the samango monkey's highly fragmented range, and an inferred continuing population decline, this species is listed as Vulnerable on the IUCN Red List (Lawes & Masters 2020). Generally absent from small forest patches less than 150 ha (Lawes *et al.* 2000; Lawes 2004), with 45 ha estimated to be the minimum critical patch area (Lawes *et al.* 2000), samango monkeys exist in temporary or declining metapopulations (Lawes 2004). Hybridization in this case, where solitary male samango monkeys exist in the primary study forest patch without conspecifics, and have mated with heterospecific females, appears to be the result of forest fragmentation combined with the overall poor dispersal ability of blue monkeys (Lawes *et al.* 2000). Possible causes for their poor dispersal ability are group dynamics that limit the feasibility of movement between patches (Lawes 2000) as well as large body size, low population density, and specialized diet, all factors negatively affected by fragmentation (Laurence 1990, 1991).

Blue monkey groups are philopatric and live in multifemale groups led by a single adult male (Cords 2000). Upon reaching sexual maturity, males disperse and typically spend a long time alone or in bachelor groups before moving into a group with females (Henzi & Lawes 1987). When leaving their forest patches to cross human-modified landscapes, dispersing males risk being killed by dogs, hit by vehicles, trapped or shot at by people, and electrocuted on pylons. These are all factors exacerbating samango monkeys' poor dispersal ability. The challenges faced by samango monkeys in the midlands appear to have resulted in alliances formed with vervet monkeys. Vervet monkeys have a wide habitat tolerance, are both terrestrial and arboreal, inhabit savanna, riverine woodland, coastal forest mountains (Butynski & de Jong

Figure 6. Hybrid JJ in 2020, a few months before he dispersed. Photograph by Karin Saks.

2019b), and are normally absent from deserts and deep forest (Isbell & Jaffe 2013). In the midlands, vervet monkeys are commonly seen on the edge of indigenous forest where their range may overlap with the range of samango monkeys.

Utilising the canopy of evergreen forests, blue monkeys are essentially arboreal and have a broad forest habitat tolerance (Lawes 1990a). The diets of the two species of monkey differ considerably (Bruorton *et al*. 1991). Blue monkey diet is primarily frugivorous (Lawes 1990b; Linden *et al*. 2015) and includes cellulose-rich leaf material, reflected in the microflora as a significant component (Bruorton *et al.* 1991). Despite the differences between the two species, the tendency for blue monkeys to associate with other primate species in other parts of Africa has been well documented (Rudran 1978; Cords 1990). Such an alliance may help the group to form coalitions against other conspecific groups, provide protection against predators, and increase the ability to locate food sources (Cords 1990).

Samango monkeys have a uni-male, polygynous social system, while vervet monkeys have a multimale-multifemale, promiscuous social system. During this field study, solitary male samango monkeys have been seen on the periphery of the vervet monkey/hybrid study group. It is therefore likely that the samango monkey males are sneaking copulations with vervet monkey females in the study group. Elsewhere, solitary *C. mitis* males or males from bachelor groups have been found to sneak copulations with group females during breeding season (Henzi & Lawes 1987; Macleod *et al.* 2002; Roberts & Cords 2015). Although there have been multiple reports of sympatric hybridization in guenons, mostly between the closely related (intragenus), *Cercopithecus mitis* and *C. ascanius* taxa, hybridization is rare, with most hybrids disappearing within a generation or two (Aldrich-Blake 1968; Struhsaker *et al.* 1988; Detwiler 2002; Detwiler *et al.* 2005). The two hybrids recorded here are likely F1 monkeys and, along with the three Kenyan hybrids recorded by de Jong and Butynski (2010), are the only records of any blue monkey x vervet monkey hybrids in the wild. No sign of backcrossing was recorded in the study groups. Vervet monkey x blue monkey hybrids appear to be exceptionally rare, thus it is unlikely that hybridization will have any significant evolutionary effect on the parent populations in the study area. Further observation may assess whether the hybrids are fertile and, if they are, how gene flow from a vulnerable taxon into an abundant, adaptable taxon could impact both populations in the future. Differences in diet, ecology, and behavior of the hybrids from the parent species and whether the hybrids have a wider habitat tolerance than blue monkeys raises further questions that could be studied.

The IUCN Red list assessment classifies samango monkeys as Vulnerable and acknowledges that populations continue to decline with forests being poorly managed and fragmented (Lawes & Masters 2020). Forest management principles suggested by Lawes (1990b) included: separate management for samango monkeys and Stairs' white-collared monkeys as well as for forest subtypes. Additionally, Lawes (1990b) suggested movement corridors as a short-term management strategy to improve the gene flow between otherwise isolated populations. The presence of hybridization in this case study, as a probable result of forest fragmentation, supports the Vulnerable status of the samango monkey, suggesting that further research and conservation management of South African forests – and this species – are needed.

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