Conservation ecology of the golden monkeys *Cercopithecus mitis kandti* and their habitats in Rwanda

By

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Declaration

I, Tuyisingize Deogratias, declare that this thesis is the result of my own work, and has not been submitted for any other degree at the University of Rwanda or any other institution. All information herein contained is based on my observations and conclusions unless otherwise stated.

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Dedication

To my family and friends.

ABSTRACT

Habitat loss and fragmentation are major threats to primate populations globally. Many primate species exhibit great flexibility to adapt to habitat change through alterations in multiple aspects of their behavioral ecology. The Endangered golden monkey (*Cercopithecus mitis kandti*) is an example of this, as it has suffered a series of major habitat loss events across its entire range between 1950s and 1990s. Consequently, golden monkeys only subsist in two forest fragments in the Albertine Rift region, the Virunga massif (Uganda, Rwanda, and Democratic Republic of the Congo) and Gishwati-Mukura National Park (Rwanda) where they mainly inhabit the bamboo zone and tropical montane forest, respectively. Their long-term survival will depend on effective conservation management strategies. However, little is known about the feeding and reproductive behaviors and the conservation status of golden monkeys in their distinct habitats. This doctorial work aimed to provide more information on the above-mentioned knowledge gaps.

I used scan and *ad libitum* sampling to record data on feeding and ranging behavior, as well as on demography and reproductive behavior (births and mating events) of two golden monkey groups (groups K~150 individuals and M~60 individuals) in Volcanoes National Park (VNP) and one group (group G~30 individuals) in Gishwati forest for 24 months from January 2017 and 2018. I also examined the phenology of key foods (bamboo shoot in VNP, and fruit trees in the Gishwati forest). Surveys of golden monkeys and illegal human activities in the two fragments were conducted. I used a 13-year data set from group K (2004-2016) and an 8-year data set for group M (2004-2012) acquired from the Dian Fossey Gorilla Fund for assessing birth seasonality in golden monkeys. I also assessed the contribution of forest landscape restoration to primate conservation in the Gishwati-Mukura landscape. All data contributed to the development of the first golden monkey conservation action plan.

Results revealed that golden monkeys fed on more than 110 plant species. The VNP groups were mostly folivorous (between 72.8% and 87.16% of the diet) and fed mostly on young bamboo leaves and bamboo shoots, while 48.69% of the diet of the Gishwati group consisted of fruit from 22 different tree and shrub species. Bamboo shoots and fruit are seasonally available foods. Like other blue monkey subspecies, golden monkeys appear to have a flexible dietary strategy and adjust their diet and monthly average home range size to local habitats and available food resources. Food availability strongly determines golden monkey birthing seasons, even at a small spatial scale. The golden monkey reproduction pattern was linked to differences in the timing of bamboo shoot availability and consumption in the Virunga groups, and to fruit availability and consumption in the Gishwati group. Births occurred prior or during the peak of key food availability and consumption periods. Interestingly, the two VNP groups had different birthing seasons despite both groups ranging only a short distance (16 km) apart. Females from group K gave birth from September to December, while females from group M gave birth from February to April, which could be explained by spatiotemporal variation in bamboo shoot availability in VNP mainly determined by elevation.

Surveys showed that the golden monkeys in VNP almost exclusively range in the bamboo zone, while in Gishwati-Mukura National Park, they mainly occur in the remnant tropical montane forest patch (Gishwati forest) within this park. The 2017-2018 survey estimated 5.47 (95% CI: 3.68-8.14) groups per km^2 in VNP, which corresponds to an estimated population size of 4,626 (95% CI: 4,165-5,088) individuals. In the Gishwati forest, group density was much lower and averaged 1.98 (95% CI: 1.27-3.16) per km^2, corresponding to 172 (95% CI: 154-190) individuals in 2017-2018. Limited habitat, along with illegal human activities such as bamboo and firewood harvesting, the presence of feral dogs, and cattle grazing, threaten golden monkeys in Rwanda and require continued monitoring and increased protection measures. The forest landscape restoration project which aimed to restore Gishwati provided additional habitat for primates, and the restoration efforts in this forest appear to have reduced conflicts between local communities and primates around the protected area. The golden monkey population in VNP is stable, but its habitat is under high pressure from the poor and dense human population living adjacent to the park, and long-term bamboo phenology data indicate a reduction in the regeneration of bamboo, their key habitat and food. Current changes in key food regeneration, potentially driven by climate change, need to be closely monitored to inform golden monkey conservation management. Despite continued protection efforts, including the recent creation of the Gishwati-Mukura National Park, illegal human activities persist throughout the distribution range of golden monkeys in Rwanda. Habitat loss and degradation, human-wildlife conflict, and limited ecological information are major threats to the golden monkey survival. We developed a five-year conservation action plan (2022-2027) aiming to have viable golden monkey populations thriving across their range by 2027 with targeted actions including reducing anthropogenic threats to the species. This will depend on community engagement and development, community sensitization, tourism, and research, as well as improving protection and law enforcement.

Key words: Bamboo, conservation action plan, diet, forest landscape restoration, forest fragmentation, golden monkeys, population density, reproduction.

List of papers

TUYISINGIZE, D., W. ECKARDT, D. CAILLAUD, and B. A. KAPLIN. 2021. High flexibility in diet and ranging patterns in two golden monkey populations in Rwanda. American Journal of Primatology. 84: e23347. https://doi.org/10.1002/ajp.23347

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List of symbols and acronyms

RDB: Rwanda Development Board

VNP: Volcanoes National Park

IUCN: International Union for Conservation of Nature

IGCP: International Gorilla Conservation Programme

UR: University of Rwanda

CoEB: Centre of Excellence in Biodiversity and National Resource Management

NGS: National Geographic Society

DFGFI: Dian Fossey Gorilla Fund International

MGVP: Mountain Gorillas Veterinary Project

ICCN: Institut Congolais Pour la Conservation de la Nature

UWA: Uganda Wildlife Authority

MGNP: Mgahinga Gorilla National Park

WCS: Wildlife Conservation Society

FHA: Forest of Hope Association

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CHAPTER ONE

GENERAL INTRODUCTION

Knowledge of critical threats to a species and its habitat are important in designing species conservation strategies (IUCN, 2017). Land use change is a critical challenge for tropical forest-dwelling species such as nonhuman primates (Arroyo-Rodríguez *et al.*, 2013). Land use change reduces and alters tropical forests and exposes primate species to critical threats and conflicts with humans (Hill, 2000; Rylands *et al.*, 2008; Estrada *et al.*, 2017). Changes in suitable habitats for primates impacts their food availability, reproduction, and may increase distribution (Korstjens and Hillyer, 2016; Nunn and Gillespie, 2016) and may predation risk (Irwin, 2008) as well as conflicts with surrounding human population (Hill, 2000; Ries *et al.*, 2004). As a result of anthropogenic activities, nonhuman primates are declining globally, and approximately 60% of all primate species are threatened with extinction (Rylands *et al.*, 2008; Estrada *et al.*, 2017). For example, habitat loss has resulted in a rapid decline of population size of Cross River gorillas, *Gorilla gorilla diehli* (Bergl et al., 2008), and in low genetic diversity of pied tamarins, *Saguinus bicolor* (Farias *et al.*, 2015). Primates living in fragmented forests can also experience increased exposure to diseases, such as shown in red colobus, *Procolobus rufomitratus*, and black-and-white colobus, *Colobus guereza* (Gillespie and Chapman, 2008).

Many primate species exhibit flexibility to adapt to land use changes through alterations in multiple aspects of their daily life (Garber, 1987; Chapman *et al.*, 2013; Tesfaye *et al.*, 2013; Estrada *et al.*, 2017). For example, some primates are able to shift their diet or may adjust their group size, daily travel distances and ranging patterns to cope with available resources (Butynski 1990; Chapman et al. 2007; Clutton-Brock and Harvey 1977; Fairgrieve and Muhumuza 2003; Irwin et al. 2014; Mekonnen et al. 2018; Reyna-Hurtado et al. 2018). Furthermore, primates may also expand to new habitats, such as regenerating logged forests (e.g., *Colobus guereza*, *Cercopithecus mitis*, *Cercopithecus ascanius,* and *Pan troglodytes schweinfurthii* (Chapman *et al.*, 2000; Plumptre and Reynolds, 2006; Marsh and Chapman, 2013)) or previously fragmented and degraded forests (e.g. *Pan troglodytes verus,* and *Allochrocebus lhoesti* (Marchesi *et al.*, 1995; Ukizintambara, 2008)). Habitat loss coupled with climatic change can lead to reduced habitat quality with limited food resources, resulting in stronger negative effects on the availability of important food resources and on reproduction in primates (Wright, 1999; Ratsimbazafy, Ramarosandratana and Zaonarivelo, 2002; Brockman and van Schaik, 2005; Lewis and Kappeler, 2005; Estrada *et al.*, 2017), leading to alteration in the timing of the energetically demanding periods of the reproductive cycle (e.g. lactation) to coincide with the availability of high-quality food sources rich in needed energy and protein (Dufour and Sauther, 2002; Cords and Chowdhury, 2010; Emery Thompson, 2017). As an alternative strategy, primates living in habitats with unpredictable availability of high-quality food resources may store energy (e.g. fat) to be used during highly demanding reproductive stages (Butynski, 1988; Brockman and van Schaik, 2005; Emery Thompson, 2017). However, it is not well known how these adjustments affect their fitness and survival rates.

Primate species have been increasingly affected by the growing pressure from the human populations surrounding their habitats. Understanding how primates cope with remnant forest fragments can provide both theoretical understanding of primate behavioral ecology and practical responses. The golden monkey (*Cercopithecus mitis kandti*) lives in the remnant forest fragments of Virunga massif, and Gishwati-Mukura landscape in Rwanda, has been affected by habitat degradation and loss, and ongoing human pressures.

Ecology and conservation of *Cercopithecus* species

Cercopithecus species (also called guenons) are endemic to sub-Saharan Africa, and their populations are declining as a result of habitat degradation, loss, fragmentation, and hunting (Grubb *et al.*, 2003; Butynski and de Jong, 2020a; IUCN, 2021). Most *Cercopithecu*s species are highly arboreal, and have evolved to live in primary forests that range from sea level up to 4500m a.s.l (Gauthier-Hion, 1980; Ukizintambara and Thébaud, 2002). *Cercopithecu*s species generally live in one adult male-multifemale groups with few species or populations characterized by multimale–multifemale groups (Glenn and Cords, 2002). Their home ranges range between 0.03 km^2 and 52 km^2 (Glenn and Cords, 2002). The preferred diet of most *Cercopithecus* species is fruit (typically 40–70% of the diet), however, they include fallback food items like leaves, flowers, pith, small vertebrates, and arthropods (Kaplin, Munyaligoga and Moermond, 1998; Glenn and Cords, 2002; Lambert, 2002; Tashiro, 2006). Therefore, fragmented and degraded forests often characterized by fewer indigenous fruiting trees are thought to be poor quality habitats for these primates (Tutin, 1999; Worman and Chapman, 2006).

The blue monkey *Cercopithecus mitis* is a group of 17 subspecies, including one Critically Endangered, four Endangered, and three Vulnerable subspecies (IUCN, 2021). It is the most widely distributed guenon, occupying a wide variety of forested habitats and feeding on a fairly wide variety of available food (Butynski, 1990; Fairgrieve and Muhumuza, 2003; Tesfaye *et al.*, 2013). In addition to dietary shifts, blue monkeys seem to have strategies for breeding to cope with a changing environment (Gevaerts, 1992). Timing of mating and birthing might be related to maternal energy demand (Cords and Chowdhury, 2010), which is directly driven by food availability and possibly indirectly by rainfall (Omar and De Vos, 1971). Despite having a great flexibility in habitat and diet, this species is experiencing population and habitat decline primarily due to habitat loss and fragmentation (Butynski and de Jong, 2020b; IUCN, 2021).

The Albertine Rift spans from the northern end of Lake Albert to the southern tip of Lake Tanganyika, and is a highly fragmented biodiversity hotspot (Plumptre *et al.*, 2016), including around 40 forests (protected areas and sites) surrounded by a matrix of cultivated lands and settlements (Salerno *et al.*, 2018). The Albertine Rift also has a higher human density than found elsewhere in Africa, which places a particularly high pressure on protected forests (Fisher and Christopher, 2007; Ryan *et al.*, 2017). This ecoregion contains many endemic and threatened species that cannot be found in any other region in Africa (Plumptre *et al.*, 2016). Three blue monkey's subspecies live in the Albertine Rift region: the golden monkey *Cercopithecus mitis spp. kandti*, Stuhlmann's blue monkey *Cercopithecus mitis spp. stuhlmanni*, and the Doggett's blue monkey *Cercopithecus mitis spp. doggetti.* The target species of this dissertation, the golden monkey, is the only endemic subspecies of blue monkey found in the Albertine Rift. Golden monkeys live in very small and isolated forests (often less than 5,000 km^2), in a high elevational range (from 2100 up to 3500m of elevation) compared to other closely-related species; these forests are surrounded by high human density and large settlements, with an average of 458 people per km^2 and up to 1,000 people per km^2 around protected areas (NISR, 2012; Plumptre *et al.*, 2016; Ayebare *et al.*, 2018; Butynski and de Jong, 2020b). Given that the golden monkey is a highly isolated and endemic subspecies, it represents a highly important species for conservation, and the study of this species can contribute to deeper understanding of behavioral ecology and conservation of primate species living in highly fragmented landscapes.

Ecology and conservation of golden monkey

The golden monkey is a guenon or African forest monkey (genus *Cercopithecus*; Linneas 1758). There is lack of consensus about whether the golden monkey should be classified as a distinct guenon species (Groves, 2006) or as a subspecies of the blue monkey, *Cercopithecus mitis kandti* (Grubb *et al.*, 2003; Butynski and de Jong, 2020a). Regarding its conservation status, the International Union for Conservation of Nature (IUCN) has categorized the golden monkey as an Endangered subspecies due to habitat fragmentation, loss, and degradation, and its population is thought to be declining (Twinomugisha and Chapman, 2006; Butynski and de Jong, 2020a).

The golden monkey is restricted to highland forests, and only two populations of golden monkeys remain. These two forest fragments are composed of different vegetation cover yet are only 26 km apart: the Virunga massif (which spans three parks including Volcanoes National Park (VNP) in Rwanda, Virunga National Park (ViNP) in DR Congo and Mgahinga Gorilla National Park (MGNP) in Uganda) and the remnant component of Gishwati forest which is part of the Gishwati-Mukura National Park (GMNP) in Rwanda. A study on golden monkeys in MGNP conducted between 1998 and 2003 found that bamboo is a major food item and key habitat for golden monkeys. This study also revealed alarming results suggesting that the Virunga population is declining (by 59%) due to habitat loss (Twinomugisha and Chapman, 2006; Twinomugisha *et al.*, 2007).

In Rwanda's VNP, the golden monkey is the only other primate species besides the mountain gorilla (*Gorilla beringei beringei*) which is the flagship species for Rwanda's wildlife tourism sector. The GMNP in Rwanda hosts three primates species, including the golden monkey, the eastern chimpanzee (*Pan trogrodytes schweinfurthi*), and the l'Hoest's monkey (*Allochrocebus lhoesti*) (Chancellor *et al.*, 2012). I chose these two forested landscapes in Rwanda to explore how the golden monkey, as an endemic primate species with very limited range, adapts to fragmentation and forest loss, including foraging behavior, diet composition, reproductive strategies, and distribution in contrasting remnant habitats.

Before the 1950s, both Virunga massif and Gishwati forest were connected (Spinage, 1972) but became separated by the intense agriculture cultivation in the 1950s which led to clearing of nearly 50% of the forest of VNP, the Rwandan side of the Virunga massif. This forest clearance resulted in the loss of most of the mixed forest zone, which was the only vegetation zone containing fruiting trees in VNP (Spinage, 1972). Similarly, the Gishwati forest went through a series of forest cover losses and associated fragmentation, initially due to animal husbandry and pine plantation projects funded by the World Bank in the 1980s, followed by further forest conversion to farm land in the 1990s (Plumptre, Masozera and Vedder, 2001). As a result, the forest cover dramatically dropped from 280 km^2 in the 1970s to less than 10 km^2 in 2003 (Nyandwi and Mukashema, 2011). The Gishwati forest together with the Mukura forest remnant, forms Gishwati-Mukura National Park.

As a result of habitat loss, the extant VNP and Gishwati golden monkey populations inhabit unconnected forest island habitats with very different habitat types. The golden monkeys in VNP inhabit vegetation zones covering elevational ranges (between 2500 and 3300m asl) above the cleared mixed forest, dominated by bamboo, *Yushania alpina* (Aveling, 1984; Tuyisingize, 2016). The population in Gishwati forest fragment inhabits a predominantly afromontane forest (between 2100 and 2500m asl) with very small patches of bamboo.

Context of this research

Though the vast majority of golden monkeys are currently found in protected habitats, illegal activities, such as bamboo harvesting, firewood collection, snaring, and grazing are still present (Hickey *et al.*, 2019). Consequently, golden monkey populations throughout their range in Rwanda must adapt to the loss of key habitats under intense human pressure. There is a need for more documentation to improve our understanding of behavioral ecology of the golden monkey.

My research aimed to understand how the Endangered golden monkey copes within forest fragments of different habitat types. In this study, I examined the dietary regimes of golden monkeys, namely, how golden monkeys cope with food resource seasonality and adjust their ranging patterns in relation to habitat and available key food resources. I also explored the implications of key food availability on reproductive strategies in these animals. Next, I describe current golden monkey density, population size, and conservation status in Rwanda. In addition, I documented how forest landscape restoration contributes to primate conservation in the Gishwati-Mukura Landscape. Lastly, I present a conservation action plan for the species to guide threat reduction strategies and conservation planning that benefit both the golden monkeys across their entire distribution range and the local communities (which represent the main sources of threats to the golden monkey habitats).

The research in this thesis is guided by five objectives and associated research questions as detailed below:

Objective 1: Assess and compare dietary variation and monthly group home range size of remnant golden monkey populations in Rwanda.
Research questions: (1) What is the golden monkey diet composition and how does it vary between the populations and groups? (2) How do group ranging patterns differ across their habitats?

Objective 2: Identify factors determining golden monkey reproductive patterns.
Research question: How do golden monkeys adjust their reproductive patterns in different habitats with differing food resources?

Objective 3: Identify the spatial-temporal density and distribution of the golden monkeys as well as the potential threats to their survival in their habitats.
Research questions: (1) Does golden monkey density and population size differ between habitats? (2) What are major threats to each population?

Objective 4. Assess the contribution of forest landscape restoration to the conservation of primates in the Gishwati-Mukura landscape.
Research questions: (1) How do primates respond to forest restoration? (2) Does forest restoration reduce human-primate conflicts?

Objective 5: Design a golden monkey conservation action plan to address threats to the golden monkeys across their entire distribution range.

The data for this thesis provides information about golden monkey behavioral ecology, habitat requirements, reproductive strategies, and a baseline population estimate. These data were used to design the conservation action plan for this subspecies across its distribution range. The process of developing the conservation action plan represents the first collaborative project to bring together conservation managers, local leaders, and local communities to discuss the management and conservation of the golden monkey and their habitats. The resulting conservation action plan recommends community engagement, reinforcement, and initiation of conservation education where it does not exist, enhancement of revenue sharing and reinforcement of protection in collaboration with local communities, and reinforcement of laws while ensuring benefits of living near the parks through reducing human-wildlife conflicts.

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CHAPTER TWO

HIGH FLEXIBILITY IN DIET AND RANGING PATTERNS IN TWO GOLDEN MONKEY (CERCOPITHECUS MITIS KANDTI) POPULATIONS IN RWANDA

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INTRODUCTION

Land use and land cover changes linked to anthropogenic activities are primary drivers of biodiversity loss in tropical regions (Basnet & Vodacek, 2015; Fritz, Bininda-Emonds, & Purvis, 2009; Hilton-Taylor, & Stuart, 2009). Habitat specialists and endemic species are particularly vulnerable to deforestation and degradation (Arroyo-Rodríguez et al., 2013; Ayebare et al., 2018; Davies et al., 2000; Fahrig, 2003). The ability to adapt to changing environments and resource availability are critical attributes for species persistence in the face of tropical deforestation and degradation.

Most primate species exhibit behavioral flexibility and are able adapt to environmental changes by altering aspects of their daily life (Chapman et al., 2013; Estrada et al., 2017; Irwin, 2016; Isabirye-Basuta & Lwanga, 2008; Kaplin, Munyaligoga, & Moermond, 1998). This includes shifts in ranging (e.g., collared lemur, *Eulemur collaris,* Campera et al., 2014; Eppley, Verjans, & Donati, 2011; Boutourlini's blue monkeys, *Cercopithecus mitis boutourlinii*, Tesfaye, Fashing, Bekele, Mekonnen, & Atickem, 2013), group size (e.g, Tana river red colobus (*Procolobus rufomitratus*), Tana crested mangabey (*Cercocebus galeritus),* Wahungu *et al.*, 2005), and diet (e.g., bale monkeys, *Chlorocebus djamdjamensis*; Mekonnen *et al.*, 2018; diademed sifakas, *Propithecus diadema,* Irwin, 2008; southern bamboo lemurs, *Hapalemur meridionalis*, Eppley *et al.*, 2015; Eppley *et al*. 2017). Guenons are typically frugivorous, and leaves have been described as fallback food (Beeson et al., 1996; Chapman et al., 2002; Chapman, Struhsaker, & Lambert, 2005; Gauthier-Hion, 1980; Kaplin et al., 1998; Lambert, 2002; Tesfaye et al., 2013). However, some guenons such as the blue monkey (*Cercopithecus mitis*), have been observed to live permanently or temporarily in forest areas where density of fruit trees and thus fruit availability is low (Chapman et al., 2002; Fairgrieve & Muhumuza, 2003; Onderdonk & Chapman, 2000). There is little information about how frugivorous guenons adapt in habitats with low fruit availability. Yet it is known that diet composition has a strong influence on group size and ranging: primates with a frugivorous diet are expected to form smaller groups and have larger home range sizes compared to primates with a more folivorous diet (Clutton-Brock, 1975, 1977; Clutton-Brock & Harvey, 1977; Lambert, 2011).

The golden monkey (*Cercopithecus mitis kandti*), a subspecies of the blue monkey, lives in high-elevation forest remnants in the Virunga massif in Uganda, Rwanda and Democratic Republic of the Congo, and in the tropical montane forest of Gishwati, Rwanda. It is classified as Endangered by the World Conservation Union (IUCN) due to its small population size and decreasing remaining habitat (Butynski & de Jong, 2020a). In the Virunga massif golden monkeys range primarily in the bamboo forest where fruit trees are rare (Aveling, 1984; Tuyisingize, 2017; Tuyisingize et al., 2021; Twinomugisha et al., 2007); bamboo accounts for the majority of their diet (Tuyisingize, 2016; Twinomugisha et al., 2007), while fruits represent a small component compared to other *Cercopithecus mitis* populations (Chapman et al., 2002). The Gishwati population ranges in tropical montane forest dominated by fruiting trees and few bamboo stands (Tuyisingize et al., 2021; Twinomugisha & Chapman, 2006). Our knowledge of golden monkey seasonal and spatial variation in diet and ranging pattern given these differences is still limited.

To shed light on how the endangered golden monkey copes with low fruit availability and degraded forests, we compared dietary variation, food availability and ranging patterns of two large groups ranging in the fruit-scarce bamboo forest of the Virunga massif, one at higher elevation and another at lower elevation, and one small group ranging in the Gishwati afromontane forest, which is richer in fruit. We expected the Virunga massif population to be mainly folivorous, with bamboo the main food plant item in the diet, while in the Gishwati population, we expected fruit to be the main food resource. We also predicted that these differences would be associated with differences in home range size, with the more frugivorous group having a larger home range. This study helps to understand ecological and dietary constraints affecting population dynamics, management and conservation.

METHODS

Study site

The study took place in the two protected tropical montane forests where golden monkeys occur in Rwanda. Volcanoes National Park (VNP) is part of the Virunga massif, a forested landscape shared between Uganda, the Democratic Republic of the Congo and Rwanda. The Virunga massif ranges from 2000 to 4507 m above sea level (ASL) with a total surface area of 443 km^2. The VNP (1°21'-1°35'S, 29°22'-29°44'E) at 2300m to 4507 m ASL, has a surface area of 160 km^2. The park is divided into eight vegetation zones, including mixed semi-deciduous forest (hereafter, mixed forest), bamboo (*Yushania alpina*), *Hagenia* forest, brush ridge (dominated by *Hypericum revolutum*), herbaceous, meadow, subalpine, and alpine zone (McNeilage, 1995). Fruit trees are mainly found in the mixed forest (Plumptre et al., 2001; Spinage, 1972; Weber, 1987), and almost all of the mixed forest zone was lost in the 1950s due to agricultural activities; golden monkeys now exclusively live in the bamboo forest of VNP.

The Gishwati forest, located between 2000 and 2300 m ASL, is a remnant tropical montane forest, which together with the Mukura forest remnant, forms Gishwati-Mukura National Park. The Gishwati forest (1° 49´ S, 29° 22´ E) is ~16 km^2 and is located approximately 26 km from the southernmost border of VNP. It is characterized by fruit producing tree species, including *Symphonia globulifera*, *Alangium chinense*, *Polysias fulva*, *Maesa lanceolata*, *Albizia gummifera*, and *Ilex mitis*, and a few bamboo (*Yushania alpina*) stands (Figure 2.1). Most of the bamboo forest in Gishwati was removed in the 1990s due to human activities (Nyandwi & Mukashema, 2011; Plumptre et al., 2001). VNP and Gishwati-Mukura National Park were previously connected, but became separated in the late 1950s due to agricultural-related activities (Spinage, 1972).

Both forest areas have clearly experienced a series of land-use changes and forest cover loss. VNP has been protected since 1925 as a national park, while the Gishwati forest together with the Mukura forest was declared a national park in 2016. The parks are characterized by four seasons: the short dry season (SD; December- February), long rainy season (LR; March- May), long dry season (LD; June-August), and short rainy season (SR; September- November).

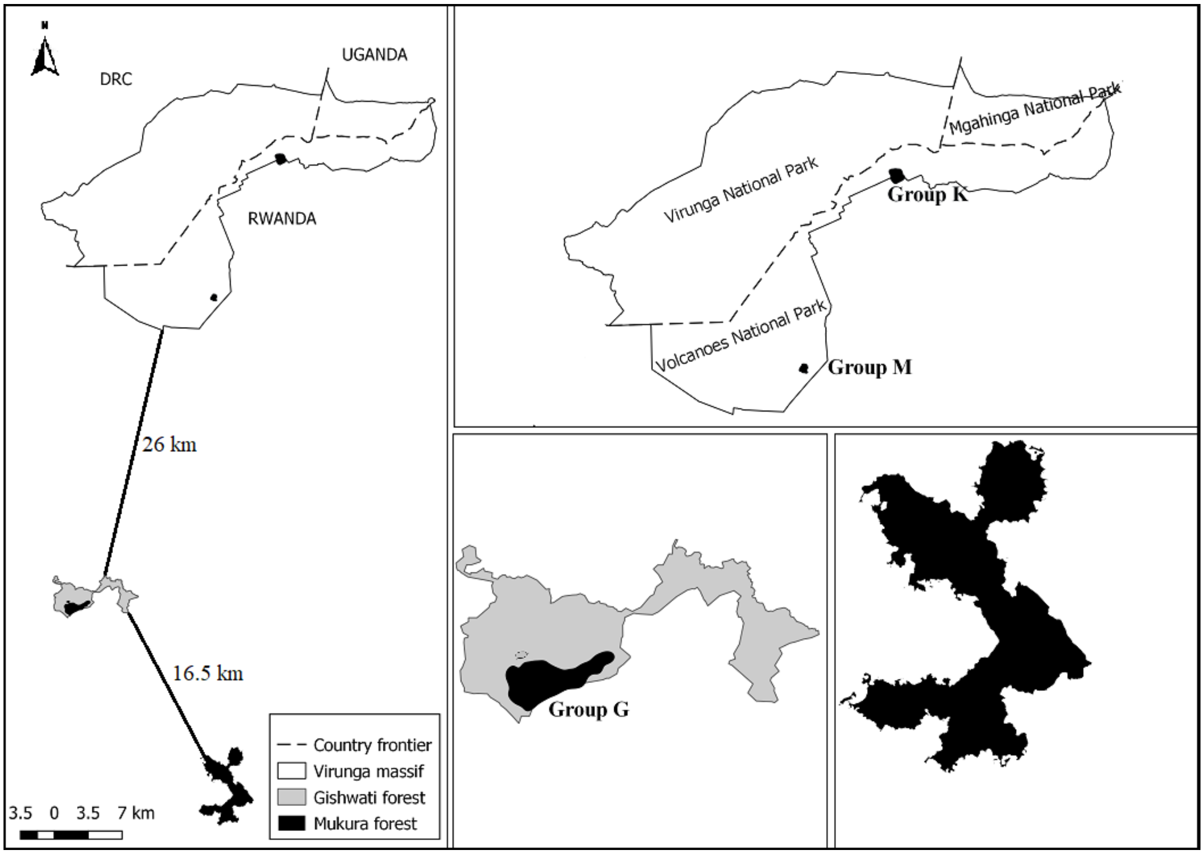

Figure 2. 1. Location of the three study groups (group K, M, and G) in the study areas, Volcanoes National Park and the Gishwati-Mukura National Park in Rwanda in 2017 and 2018

Study species

We studied two habituated golden monkey groups from VNP: the Kabatwa group (hereafter group K) with ~150 individuals (75 females, 5 males, 52 juveniles and 18 infants) located between 2520 m-2640 m ASL, and the Musonga group (hereafter, group M) with ~60 individuals (31 females, 4 males, 18 juveniles and 7 infants) at 2950 m -3200 m ASL (Figure 2.1). We also studied one habituated group in the Gishwati forest, composed of ~30 individuals (14 females, 1 male, 10 juveniles and 5 infants) (hereafter, group G) (Figure 2.1). Individuals were identified by age-sex classes: adult males, adult females, juveniles, and infants. Adult females were easily identified from visible elongated nipples, and males had larger body size and visible testicles. Juveniles had middle size and independent from their mothers, while infants were characterized by their small size and constant presence next to their mothers.

Data collection

Phenology of key foods

We sampled bamboo phenology in VNP and fruit availability in Gishwati to understand the relationship with diet and home range. The bamboo stands were too small (< 1% of home range size) to monitor in the home range of the Gishwati group, and fruit trees were very rare (< 5% of home range size) in the home ranges of the VNP groups. Therefore, we did not carry out bamboo phenology in the Gishwati forest nor fruit phenology in VNP.

Bamboo shoot phenology

We monitored bamboo shoots, defined as newly emergent bamboo culms that regenerate from rhizomes during the rainy seasons and have not started developing branchlets (Sheil et al., 2012), in VNP during two rainy seasons in 2017 and in 2018 because they have been shown to be an important resource for the golden monkeys in this park. Using a Global Positioning System (GPS) unit and a measuring tape, we established 4 x 4m^2 plots every 200 m along four line-transects of 0.6-1 km, each separated by 200 m, in the home range of group K (15 plots) and group M (13 plots). Plots were visited at two-week intervals from March to May during the heavy rainy season and from September to early December during the short rainy season, as soon as the first shoots were sighted. For each plot, we counted the number of bamboo shoots and marked them with a permanent maker pen to recognize new bamboo shoots during subsequent visits.

Fruit tree phenology

In the Gishwati forest, we selected six tree species (representing ~50% of all feeding records on food type) from a total of 22 fruit tree species used by group G based on prior feeding observations to sample fruit availability over time.

We monitored a total of 82 mature trees with a diameter at breast height greater than 10 cm, a good crown visibility, and located close to a trail (15 individuals of *Symphonia globulifera, Alangium chineunce, Polysias fulva,* and *Maesa lanceolata*; 13 individuals of *Albizia gummifera*, and 10 individuals of *Ilex mitis*). The selected trees were located within the 50% kernel home range of group G. Phenology data were collected at two-week intervals from March 2017 to December 2018. We scored each tree according to the estimated percentage of the canopy crown occupied by fruit : score 1=1-25%, 2=26-50%, 3=51-75%, 4=76-100% (Sun et al., 1996). For the data analysis, we treated trees with a score of 1 or more as trees providing fruits, and a score of 0 as trees without fruits.

Behavioral data

Diet composition and ranging patterns

From January 2017 to December 2018, we collected feeding data two weeks per month in the VNP groups (K and M) and on a daily basis in the Gishwati group, except for January to May 2018, when data were only collected two weeks a month due to logistical constraints. A feeding score was only made when an animal was observed to put a food item into its mouth. We collected ranging and feeding data for 3-5 hours per day, between 8:00 to 14:00, using scan sampling (Altmann, 1974). Due to National Park regulations, we were not able to collect data past 14:00. It is possible that the percentage of time spent feeding varies throughout the day. Dietary composition (i.e., the proportion of the total feeding time spent feeding on different food plant items), however, is less likely to vary in a systematic way during the day. Since our analyses focused on dietary composition and diversity, our results can likely be safely extrapolated to time periods after 14:00. Variation in the daily duration of data collection varied depending on how long it took to find the group, tourism activities, and rainfall. No data were collected in July 2017 and July 2018 in group M due to logistical constraints.

During each scan, we walked among the group in a direction opposite to the group's movement to observe as many individuals as possible. We recorded each individual's activity and age-sex class (adult males, adult females, juvenile or infant) over a period of 5-minute. Scans were repeated every 20-minute. If the monkey was feeding (i.e., putting food in the mouth), we also recorded the food type (plant species, insect, milk in case of infants) and food plant items consumed (leaves, bamboo shoot, fruit, flowers, stem, tree bark, rhizomes, pith, or tendril). At the beginning of each scan, we recorded the GPS waypoint of the group to calculate the home range size.

Data analysis

Feeding behavior

To determine diet composition, we calculated the percentage of each food type and food plant item consumed per group and observation day. We then averaged the daily data for each group and observation month. To assess diet diversity, we calculated the monthly Shannon-Wiener diversity index, H´, and the corresponding Evenness index, J, using the proportion of food species consumed by each group (Krebs, 1989). We assessed the seasonal variation in dietary diversity by combining all monthly diversity indices for each season across the two years and compared first all seasons within a group and then each season between groups using Kruskal-Wallis tests, with 95% confidence intervals for percentages of feeding records and monthly home range variation using base R.

Key food availability

For each month, we calculated the mean number of bamboo shoots per square meter for the VNP groups K and M, and the mean number of tree species providing fruit expressed (scores >0) as a percentage of the total sample for the Gishwati group. Using monthly food availability, we compared seasonal variation in key food availability for each group using Kruskal-Wallis tests, and Dunn-Bonferroni post hoc method for pairwise comparisons. To investigate the relationship between monthly availability of key food plant items (bamboo shoots and fruits) and their consumption within each group, we used Spearman's rank correlation.

Ranging patterns

To calculate monthly home range sizes, we used the GPS coordinates to estimate the 95% kernel density outline using the 'adehabitatHR' package in R version 3.6.1 (R Core Team, 2019). We compared monthly home range sizes across groups using the Kruskal–Wallis test. To investigate the relationship between monthly key food availability (bamboo shoots or fruits) and monthly home range size, we used Spearman's rank correlations.

RESULTS

Over the study period, we obtained a total of 2,694 scans in 319 days for group K, 2,125 scans in 233 days for group M, and 4,879 scans for 362 days in group G. Golden monkeys fed on a total of 111 plant species, including 59 plant species for group K, 29 plant species for group M (both in VNP), while group G (in Gishwati forest) fed on 60 plant species (see supplementary material).

Food availability

The main seasonally available food plant items in VNP and Gishwati were bamboo shoots and fruit, respectively. In VNP, seasonal variation in bamboo shoot availability differed in the habitats of the two study groups (Figure 2.2). In the home range of group K, bamboo shoot availability peaked once a year during the short rainy season, with very few shoots emerging during the long rainy season and this difference was significant statistically (Pairwise Dunn's tests, $Z=-3.07$, $p=0.006$). In contrast, we observed two small peaks in bamboo shoot availability in the home range of group M, coinciding with the two rainy seasons, which were not statistically different (Pairwise Dunn's tests, $Z=0.416$, $p=0.677$).

Fruit availability in Gishwati was less seasonal than bamboo shoot production in VNP. Elevated fruit availability was observed between January and August during the dry seasons and long rainy season (Figure 1.2). Pairwise Dunn's tests showed a significant difference in fruit availability between the short rainy season and long dry season ($Z=2.447$; $p=0.043$), and between short and long rainy seasons ($Z=2.981$; $p=0.017$).

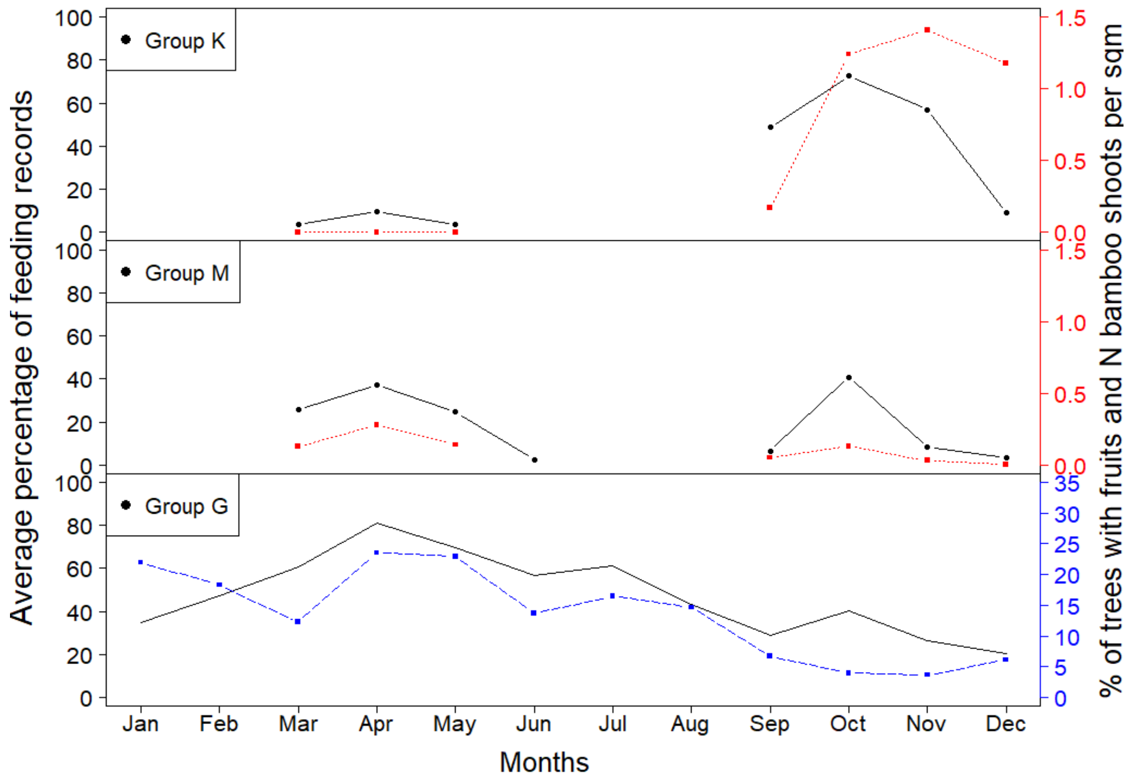

Figure 2. 2. Monthly average percentage of bamboo shoot consumption (points connected by black lines) and fruit consumption (black line); and key food availability in the home ranges of the study groups (Top row=Group M, middle row=group K, lower row=Group G) in 2017 and 2018 combined; points connected by dotted red lines denote bamboo shoots density (number/area); points connected by long dashed blue lines denotes average percentage of fruiting trees.

Diet variation

The top six species consumed by golden monkeys in the VNP groups made up a larger portion of the diet (82.28% at K and 95.39% at M) than the top six species in the Gishwati group (67.2%). The primary food type in VNP for both groups was bamboo. Bamboo accounted for 59.27% (95% CI: 37.77-85.84) of the diet in group K and 78.49% (95% CI: 55.95-93.39) of the diet in group M. In Gishwati, the key food plant species were *Acacia mearnsii* at 18.47% (95% CI: 0.19-50.96), *Symphonia globulifera* at 17.72% (95% CI: 0.32-60.66).

The diet of all the study groups included small animal prey, primarily insects (larvae, caterpillars and mature insects). While insects only accounted for 5.63% (95% CI: 0.21-32.54) of feeding records in group K and 1.16% (95% CI: 0-3.9) in group M in the VNP, they were among the six most important food types of group G in Gishwati at 20.04% (95% CI: 9.34-37.61) of the diet (Table 2.1, Figure 2.3–2.5).

Table 2. 1. Average daily percentage of scans spent feeding on the top six food species of each study group. (+) and (-) indicate the presence or absence of other plant species in groups K, M and G in 2017 and 2018. CI: Confidence Interval.

#	Scientific name	Part eaten	Plant form	K (95% CI)	M (95% CI)	G (95% CI)
1	*Yushania alpina*	Leaves, shoots	Tree	59.27 (37.77-85.84)	78.49 (55.95-93.39)	+
2	*Urera hypselodendron*	Leaves, flowers	Vine	5.54 (1.74-9.67)	+	+
3	*Mikania capensis*	Leaves, flowers, stems	Vine	5.07 (0.31-10.55)	3.94 (0-11.82)	+
4	Insects (unidentified)	All		5.63 (0.21-32.54)	1.16 (0-3.9)	20.04 (9.34-37.61)
5	*Solanum tuberosum**	Tubers	Tuber	4.07 (0-17.58)	-	-
6	Terrestrial ferns (unidentified)	Leaves	Herb	2.7 (0.15-6.67)	+	+
7	*Hypericum revolutum*	Leaves, flowers, stems	Tree	+	5.39 (0-13.97)	-
8	*Mimulopsis solmsii*	Leaves, flowers	Herb	+	3.72 (0-11.16)	+
9	*Plectranthus sp*	Leaves, flowers, stems	Herb	+	1.83 (0-4.08)	+
10	*Acacia mearnsii*	Fruits, flowers, leaves	Tree	-	-	18.47 (0.19-50.96)
11	*Symphonia globulifera*	Fruits, flowers, leaves	Tree	-	-	17.72 (0.32-60.66)
12	*Albizia gummifera*	Fruits, flowers, leaves	Tree	-	-	4.14 (0-11.89)
13	*Alangium chinense*	Fruits, flowers, leaves	Tree	-	-	3.87 (0.35-10.79)
14	*Ilex mitis*	Fruits, flowers, leaves	Tree	-	-	2.96 (0-14.26)

* food acquired during crop foraging out of the park

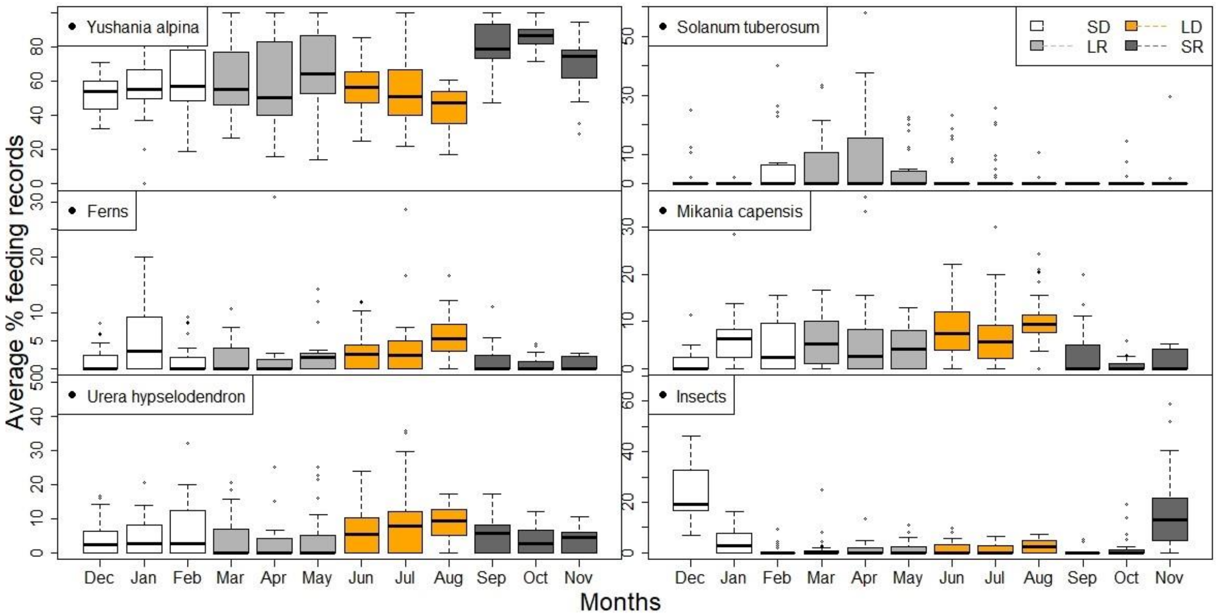

Figure 2. 3. Monthly average of daily percentages of golden monkeys consuming the top six food species in group K (N=319) during the short dry season (SD) in white, the long rainy season (LR) in grey, the long dry season (LD) in orange, the short rainy season (SR) in dark, in 2017 and 2018 combined in Volcanoes National Park, Rwanda.

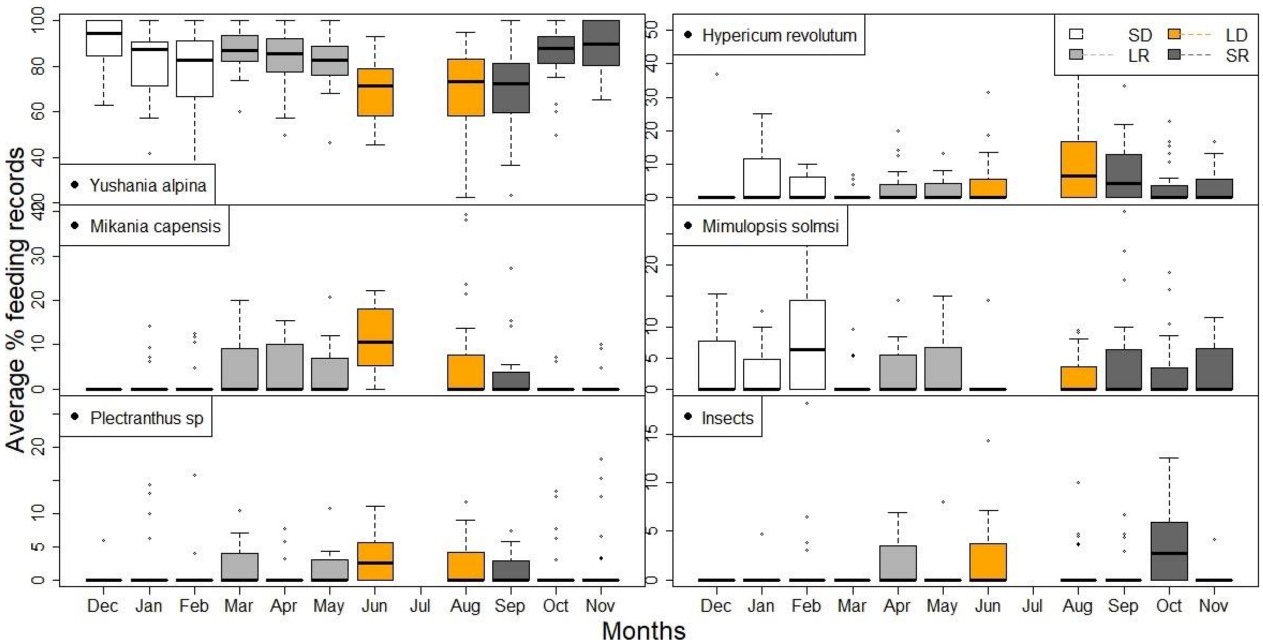

Figure 2. 4. Monthly average of daily percentages of golden monkeys consuming the top six food species in group M (N=233) during the short dry season (SD) in white, the long rainy season (LR) in grey, the long dry season (LD) in orange, the short rainy season (SR) in dark, in 2017 and 2018 combined in Volcanoes National Park, Rwanda.

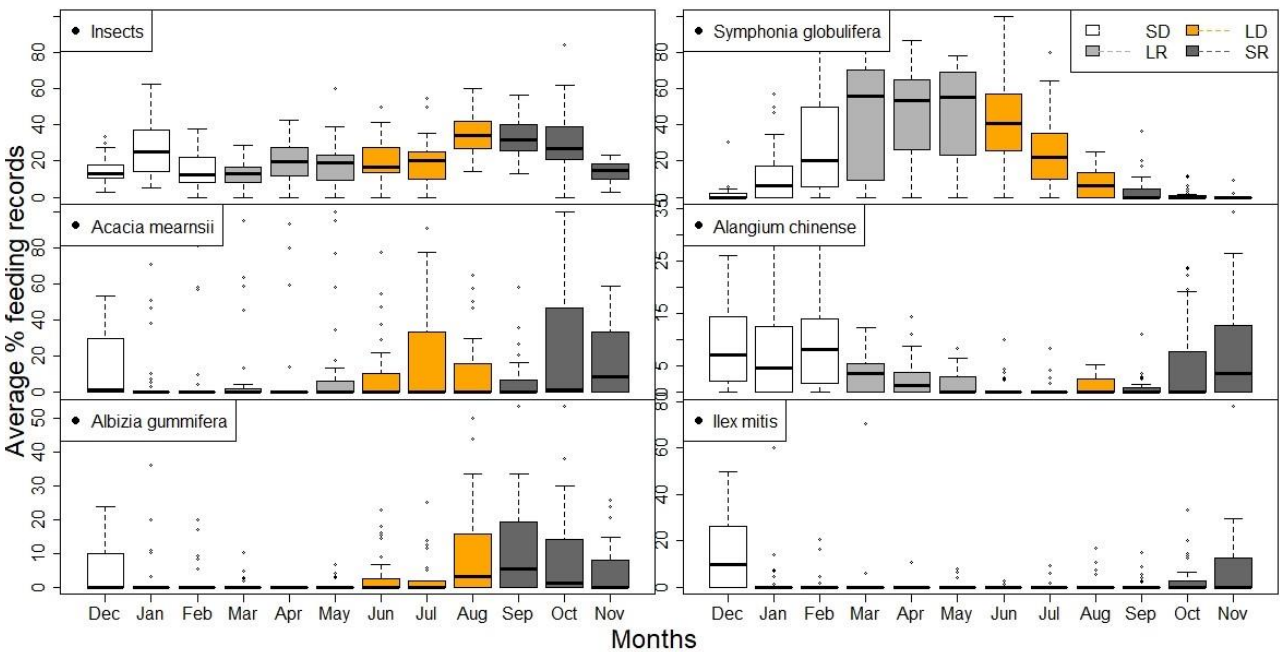

Figure 2. 5. Monthly average of daily percentages of golden monkeys consuming the top six food species in group G (N=362) during the short dry season (SD) in white, the long rainy season (LR) in grey, the long dry season (LD) in orange, the short rainy season (SR) in dark, in 2017 and 2018 combined in Gishwati-Mukura National Park, Rwanda.

Food plant items in VNP included leaves (mainly tips of young bamboo leaves), bamboo shoots, and other items: flowers, tendrils, fruits, pith, tree bark, stems (Table 2.2, Figure 2.6). In Gishwati, the diet consisted of fruit, leaves, and other items (flowers, tendrils, and tree back) (Table 2.2, Figure 2.6). Group K and M consumed bamboo shoots twice a year during both rainy seasons with peaks in short rainy season in group K and long rainy season in group M. Bamboo shoot consumption was significantly correlated with shoot availability in group K (rho=0.773, N=14, p=0.001) and in group M (rho=0.601, N=14, p=0.023). Leaves were consumed by all the groups year-round but made up a lower percentage of the diet when bamboo shoots (for groups K and M) or fruits (for group G) were available. Group G consumed fruit year-round with annual peaks in fruit consumption between January and July, and fruit availability was significantly correlated with fruit consumption (rho=0.491, N=22, p=0.02).

Table 2. 2. Average daily percentage of each food plant item (all leaves, bamboo leaves only, bamboo shoots, fruits and other: flowers, tendrils, pith, back of trees, stems) in the diet of the three study groups (groups K, M (VNP) and G (Gishwati)) in 2017 and 2018. CI: Confidence Interval.

Food item/studied groups	K (95% CI)	M (95% CI)	G (95% CI)
All leaves	72.8 (17.68-96.62)	87.16 (59.5-99.11)	21.61 (5.62-43.41)
Bamboo leaves	**43.95** (6.74-65-58)	**69.46** (47.07-89.37)	0.98 (0-7.73)
Bamboo shoots	19.26 (0-78.86)	9.89 (0-40.49)	0.31 (0-3.12)
Tubers (potatoes)*	4.25 (0-17.13)	-	-
Stems	1.14 (0-5.51)	0.57 (0-3.17)	4.36 (0-13.04)
Flowers	0.95 (0-3.34)	2.18 (0-14.05)	6.35 (0.37-26.28)
Fruits	0.42 (0-1.24)	0.11 (0-0.92)	**48.69** (17.33-79.97)
Tendrils	0.26 (0-1.07)	0.01 (0-0.15)	5.58 (1.59-11.53)
Pith	-	-	12.6 (3.5-26.04)
Others (rhizomes and tree back)	0.92 (0-3.29)	0.08 (0-0.8)	0.5 (0-3.02)

* food acquired during crop foraging out of the park

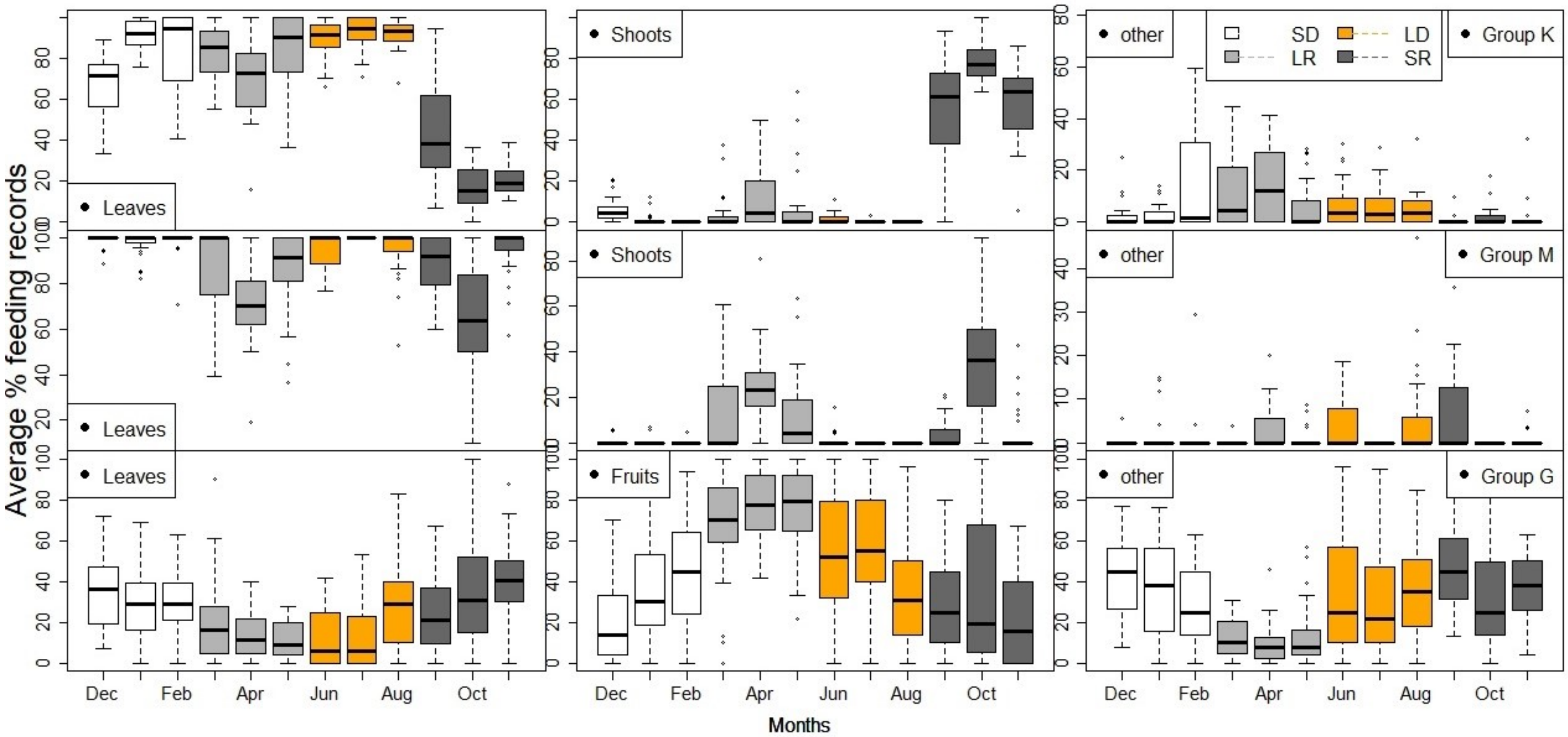

Figure 2. 6. Daily percentages of food plant item (leaves, bamboo shoots, fruits and other: flowers, tendrils, pith, back of trees, stems) in the diet of each group (N=319 in group K, N=233 in group M, N=362 in group G), averaged for each month. Data from 2017 and 2018 are combined. The short dry season (SD) in white, the long rainy season (LR) in grey, the long dry season (LD) in orange, the short rainy season (SR) in dark.

Dietary diversity

Diet diversity, estimated by calculating Shannon-Wiener indices, varied across groups. Group M had a lower diet diversity (0.77-1.14) in each season compared to group K (1.10-1.56) and G (1.33-1.46) (Table 2.3). The diet diversity also varied within each of studied groups across seasons.

There was a significant seasonal difference in diet diversity in group K (Kruskal-Wallis chi-squared=15.133, df=3, p=0.001). Diet diversity and evenness were high during the short dry, long rainy, and long dry season from December to August compared to the short rainy season from September to November, when bamboo shoots were highly available and became the main food plant item (Table 2.3). Pairwise Dunn's tests showed a significant difference in diet diversity between the short rainy season and long dry season (Z=3.756; p=0.001), and between short rainy season and long rainy season (Z=2.735; p=0.018), as well as between short rainy season and short dry season (Z=2.327; p= 0.039).

There was a significant difference in diet diversity across seasons in group M (Kruskal-Wallis chi-squared=8.477, df=3, p=0.037). Pairwise Dunn's tests only showed a significant difference between short rainy season and long dry season (Z=2.346; p=0.037), and between long rainy season and long dry season (Z=2.447; p=0.043). Group M consumed mainly bamboo shoot during the two rainy seasons and dietary evenness was low as found in group K also, and diet diversity was also relatively low. However, the lowest diet diversity occurred during the short dry season in both groups.

In group G, diet diversity was overall high compared to VNP groups. Diet diversity and evenness were lower during the long rainy season and long dry season when fruit availability was high (Kruskal-Wallis chi-squared=11.327, df = 3, p = 0.01) (Table 2.3). Significance. Pairwise Dunn's tests revealed that diet diversity differed between the long rainy season and short dry season (Z=2.531; p=0.034), and between the long rainy season and short rainy season (Z=3.143; p=0.01).

Table 2. 3. Seasonal Shannon–Wiener diversity index (H′) and evenness index (J) for golden monkey groups K, and M in VNP and group G in Gishwati forest, Rwanda during the short dry season (LR), the long rainy season (LR), the long dry season (LD), and the short rainy season (SR). Low diet diversity coupled with low evenness in each group coincided with high availability of seasonal key food (bamboo shoots in VNP and fruits in Gishwati) in 2017 and 2018.

	Group K		Group M		Group G	
Seasons	H′	J	H′	J	H′	J
SD	1.42	0.53	0.77	0.41	1.46	0.73
LR	1.47	0.55	0.88	0.35	1.33	0.51
LD	1.56	0.60	1.14	0.50	1.43	0.67
SR	1.10	0.36	0.92	0.37	1.46	0.75

Ranging patterns

To analyze ranging patterns, we collected 2,541 GPS waypoints for group K, 1,882 GPS points for group M, and 4,509 GPS points for group G. Monthly home range sizes varied among study groups, with group G having a larger home range compared to the VNP groups (Table 2.4, Figure 2.7). There was a significant difference in monthly home range size across groups (Kruskal-Wallis chi-squared = 47.469, df=2, $p < 0.001$) with group G having larger monthly home range sizes than groups M ($Z=6.652$, $p<0.0001$) and K ($Z=1.687$, $p=0.091$) (Table 2.4). Group K had significantly larger monthly home range sizes than group M ($Z=5.001$, $p<0.0001$).

Table 2. 4. Overall monthly mean (95% confidence interval) home range sizes in golden monkey groups studied in the Volcanoes National Park (groups M and K), and in Gishwati forest (group G), Rwanda, between 2017 and 2018.

Studied groups	Monthly home range size (95% KDE*) in hectares		
Group	Min	Mean	Max
K	64.37	91.3 (74.91-103.19)	130.34
M	13.9	25.24 (15.79-30.99)	35.38
G	38.52	150.07 (98.09-226.28)	321.99

*KDE: kernel density estimation

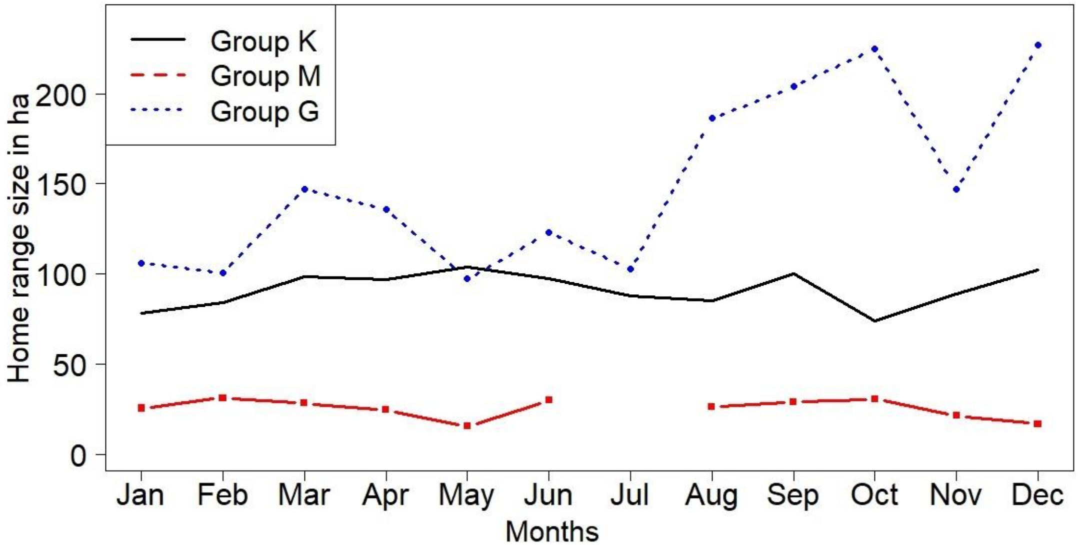

Figure 2. 7. Monthly average home range sizes in 2017 and 2018 combined, in golden monkey group K (black line, N=2541), group M (points connected with red lines, N=1882) in Volcanoes National Park and group G (points connected with dotted blue lines, N=4509) in the Gishwati forest, Rwanda.

Relationship between home range size, key food availability and consumption

In VNP, monthly bamboo shoot availability in group K and M did not significantly correlate with monthly home range size (K: rho=-0.324, N=14, p=0.257; M: rho=0.281, N=14, p=0.331), nor was bamboo shoot consumption correlated with monthly home range size (K: rho=0.099, N=24, p=0.644; M: rho=-0.051, N=24, p=0.822). In Gishwati forest, monthly fruit consumption was not correlated with monthly home range size (rho=-0.251, N=24, p=0.236).

DISCUSSION

Dietary variation in relation to habitat sites

The diets of the different golden monkey groups in this study differed, and together they fed on a diversity of food types (including 111 plant species in total), indicating that golden monkeys have different diets in the different habitats, which is typical in the *Cercopithecus* genus (Butynski, 1990; Chapman & Chapman, 2002; Takahashi et al., 2019). This dietary flexibility allowed golden monkeys in our study populations to adapt to the different types of food available in their respective habitats. The VNP groups have a folivorous diet, mostly feeding on leaves and on seasonally available bamboo shoots. In contrast, the Gishwati group had a frugivorous diet supplemented with leaves and insects in months with reduced fruit availability.

The frugivorous diet as observed in the Gishwati group is characteristic of the *Cercopithecus* genus (Beeson et al., 1996; Butynski, 2002; Chapman et al., 2005; Chapman et al., 2002; Fairgrieve & Muhumuza, 2003; Gauthier-Hion, 1980; Kaplin & Moermond, 2000; Twinomugisha et al., 2007; Worman & Chapman, 2006). There are only a few populations which exhibit a folivorous diet (i.e., over 50% folivory), such as *Cercopithecus ascanius* in the Budongo forest (Chapman et al., 2002). The diet of blue monkeys generally only includes 20-45% leaves, consumed when preferred foods are scarce (Beeson et al., 1996; Coleman & Hill, 2014; Lawes, 1991; Takahashi et al., 2019).

The deforestation of the Virunga massif in the past decade included the near total loss of the mixed forest, which formerly covered the landscape up to the bamboo zone in VNP and MGNP. The golden monkeys from MGNP in Uganda rely on bamboo leaves and shoots (Chapman et al., 2002) like their counterpart from VNP, but they incorporate more fruit in their diet (26.3% on average) compared to the VNP subpopulation (average <1%). This may be due to the presence of regenerated mixed-forest remnants in MGNP. Gishwati golden monkeys consume twice as much fruit as golden monkeys from MGNP, a level of frugivory similar to blue monkeys from Kibale National Park (Uganda) and Kakamega forest (Kenya) (Coleman & Hill, 2014; Cords, 1986). These comparisons across sites highlight the great dietary flexibility of golden monkeys, which enables them to survive in fragmented and degraded habitats.

To our knowledge, owl-faced monkeys (*Cercopithecus hamlyni*) from Nyungwe National Park located in Rwanda and Kahuzi-Biega National Park in the Democratic Republic of the Congo are the other guenon populations which heavily rely on bamboo as a key food (Colyn & Rahm, 1987; Tumwesigye et al., 2018). Bamboo is an important part of the diet of a few other primate species, including the bale monkey (*Chlorocebus djamdjamensis*) in Ethiopia (Mekonnen et al., 2010, 2018). Bamboo shoots are important sources of protein, fiber, carbohydrates and minerals (Calcium, Magnesium, Potassium and Phosphorus) and thus appear to be a suitable alternative key food where fruits are absent (Karanja et al., 2015). Though bamboo is a great source of protein for the golden monkeys of the Virunga massif (Twinomugisha et al., 2007), further studies need to document levels of cyanide in bamboo, and how golden monkeys cope with bamboo cyanide.

The study groups in both populations increased their consumption of alternative food resources that are lower in energy (young leaves and insects) when their key foods (bamboo shoots in VNP and fruit in the Gishwati forest) are absent or scarce. Since these alternative food sources cover a substantial proportion of the groups' diet year-round, leaves and insects can be categorized as staple foods for golden monkeys. Young leaves and insects are relatively high in protein and constitute good alternatives when bamboo shoots and fruits are unavailable, as shown in other primates (Lambert & Rothman, 2015).

Bamboo shoots are available twice a year in the ranges of our two VNP study groups. In group K, which was at lower-elevation, bamboo shoot availability was the highest during the short rainy season (September-December). In contrast, in group M which was at higher-elevation range, the availability of bamboo shoots was the greatest during the long rainy season (March-May). These findings largely match elevational differences in bamboo regeneration intensities reported in a long term study in VNP, which revealed that bamboo phenology depends on elevational gradient (van der Hoek et al., 2019). Future studies should investigate the extent of temporal and spatial dietary variation within this population by including more groups and determine how spatial differences in bamboo shoots affect monkey reproduction patterns.

The difference in elevation observed between the home ranges of groups K and M may also explain the wider variety of foods consumed by group K (the group at lower elevation) compared to group M, where plant species diversity declines with increasing elevation (Gentry, 1988; Vázquez & Givnish, 1998). This is supported by the fact that the diversity of the diet of group M is comparable to observations from golden monkeys from MGNP (33 plant species) which range at a comparable elevation (Twinomugisha et al., 2007). In addition, field observations suggest that less light penetrates the bamboo cover in the home range of group M compared to group K where the bamboo forest is more heterogeneous and includes small patches of other vegetation. Future studies will clarify if this small-scale habitat variations influence the feeding behavior of golden monkeys.

Determinants of ranging patterns

Primate ranging behavior is strongly related to food resource availability and distribution (Lambert & Rothman, 2015; Reyna-Hurtado et al., 2018). Frugivorous primates travel longer distances to acquire their food and generally exhibit larger home range sizes than folivorous species (Clutton-Brock & Harvey, 1977; Newton, 1992). Associations between large home range sizes and frugivory have been reported in spider monkeys (*Ateles geoffroyi yucatanensis*), gray-cheeked mangabeys (*Lophocebus albigena*) (Butynski, 1990; Reyna-Hurtado et al., 2018), chimpanzees (*Pan troglodytes*), gray-cheeked mangabeys (*Lophocebus albigena),* and Japanese macaques (*Macaca fuscata*) (Lambert & Rothman, 2015). Similarly, in our study, the Gishwati group, which fed mainly on fruit that is distributed in discrete patches, was smaller in group size but had a larger home range size compared to the VNP groups, which fed mostly on leaves and bamboo shoots that were more evenly distributed in their habitat. The lack of significant relationship between bamboo shoot availability and monthly home range size in the VNP groups also suggests that food distribution rather than food availability determine monthly home range sizes. The Gishwati group increased its home range size in periods of relative fruit scarcity when fruit remained the majority of the diet, possibly to search for the rare remaining trees providing ripe fruit. This relationship has been found in blue monkeys, in which predominantly folivorous groups tend to have smaller home ranges than predominantly frugivorous groups (Butynski, 1990; Coleman & Hill, 2014; Kaplin et al., 1998)

Due to within-group scramble competition, large groups are predicted to have larger home ranges (Isbell, 1991). Consistent with this hypothesis, group K (~150 individuals) had a larger home range than the smaller group M (~60 individuals). A larger number of groups need to be studied to draw stronger conclusions. The considerably larger monthly home ranges found in the Gishwati group G, and the fact that it only included 30 individuals, may indicate that the bamboo habitat has a higher carrying capacity than the mixed forest from Gishwati. Indeed, previous studies suggest that the bamboo zone of the Virunga massif supports higher monkey densities than the Gishwati forest (Tuyisingize, Kaplin, et al., 2021; Twinomugisha & Chapman, 2006). The golden monkeys in Gishwati may face inter-specific feeding competition with the other primate species in the forest, such as chimpanzees and L'Hoest's monkeys (*Allochrocebus lhoesti*).

Common illegal human activities such as firewood collection and bamboo harvesting, as well as the presence of feral dogs, in both parks, may also affect golden monkey ranging patterns. The impact of predation (e.g., chimpanzee in Gishwati) is also not understood. Detailed information on daily travel distances and travel paths would help gain insights into the respective roles of illegal activities, food resource distribution and predation in both populations. Like golden monkeys, most large mammals such as the mountain gorillas (*Gorilla beringei beringei*), African elephant (*Loxodonta africana*), buffaloes (*Syncerus caffer*), bush buck (*Tragelaphus scriptus*), and black fronted duiker (*Cephalophus nigrifrons*) of the Virunga massif feed on bamboo shoots when available (Andrew J Plumptre, 1991; Sheil et al., 2012).

Conservation implication and conclusions

Golden monkeys in VNP and the Gishwati forest have recently been through a series of habitat changes and loss. This study demonstrated the flexibility of golden monkey diet to adapt to habitat changes, but the long-term survival of the golden monkey is uncertain. The main conservation concern is continued habitat loss and degradation caused by illegal activities. In the Gishwati forest, firewood collection and tree cutting remain the biggest threats to golden monkeys (REMA, 2015). In VNP, bamboo is illegally cut for handicrafts, construction and firewood throughout the year (Bitariho & McNeilage, 2008; Munanura et al., 2018; Sheil et al., 2012).

In addition, evidence of an ongoing decline in bamboo regeneration possibly due to the proliferation of herbivores in the region, or to climate change, are projected to affect the golden monkeys in the near future (Ayebare et al., 2018; Hemp, 2006; van der Hoek et al., 2019). The decline in bamboo availability may lead golden monkeys to expand their range and time spent outside the park boundaries to feed on crops such as carbohydrate-rich potatoes, as is already observed in group K. In VNP, golden monkeys are already considered the second most impactful species foraging on crops after forest buffalo (Mispiratceguy, 2019). Continued conservation efforts will be essential to protect both golden monkey populations and their habitats, as they face new challenges in Gishwati-Mukura National Park and Volcanoes National Park.

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SUPPLEMENTARY MATERIALS

Supplement: Golden monkey food plant species

#	*Plant species*	Family	Plant form	Group	Food plant item
1	*Acacia mearnsii*	Leguminosae	Tree	G	Fl,Fr,Lv
2	*Acacia montigena*	Leguminosae	Tree	G	Fl,Lv
3	*Acalypha racemosa*	Euphorbiaceae	Shrub	G	Fl,Fr,Lv,Pi
4	*Alangium chinense*	Cornaceae	Shrub	G	Bk,Fl,Fr,Lv,St
5	*Albizia gummifera*	Leguminosae	Tree	G	Bk,Fl,Fr,Lv,Pi,St
6	*Arisaema mildbraedii*	Araceae	Herb	K	Lv
7	*Asplenium sp*	Aspleniaceae	Herb	K	Lv
8	*Basella alba*	Basellaceae	Vine	K, G	Lv,Ten
9	*Begonia pulcherrima*	Begoniaceae	Shrubs	G	Lv
10	*Beilschmiedia rwandensis*	Lauraceae	Shrubs	G	Fr,Pi
11	*Bersama abyssinica*	Melianthaceae	Shrub	G	Lv,Pi,St,Ten
12	*Carapa grandiflora*	Meliaceae	Tree	G	Ste
13	*Carduus leptacanthus*	Asteraceae	Herbs	K	Bk,Lv
14	*Carduus nyassanus*	Asteraceae	Herb	K, M	Fl,Lv
15	*Carex bequaertii*	Cyperaceae	Herb	K	Lv
16	*Cassipourea ruwensorensis*	Rhizophoraceae	Shrubs	G	Bk,Fl,Fr,Lv,Pi
17	*Chrysanthemum sp*	Asteraceae	Herb	K	Lv
18	*Chrysophyllum gorungosanum*	Sapotaceae	Tree	G	Bk,Fl,Fr,Lv
19	*Cineraria deltoidea*	Asteraceae	Herb	K	St
20	*Clematis hirsuta*	Ranunculaceae	Vine	K, M	Fl,Lv
21	*Clerodendrum johnstonii*	Lamiaceae	Shrub	K, G	Fl,Lv,Pi
22	*Crassula granvikii*	Crassulaceae	Herb	K	Lv
23	*Croton megalocarpus*	Euphorbiaceae	Tree	G	Bk,Fr,Lv,Pi,
24	*Cupressus sp*	Cupressaceae	Tree	K	Bk,Lv
25	*Cyathea manniana*	Cyatheaceae	Tree	G	Lv,Pi,Ste
26	*Cyathula cylindrica*	Amaranthaceae	Herb	G	Lv,Ten
27	*Cynodon dactylon*	Poaceae	Grass	K	Lv,Rh,St

28	*Discopodium penninervium*	Solanaceae	Shrub	K, M	Fr,Lv,St
29	*Dombeya goetzenii*	Malvaceae	Tree	G	Bk,Fl,Fr,Pi,St
30	*Droguetia iners*	Urticaceae	Herb	K, M	Lv,St
31	*Eucalyptus sp*	Myrtaceae	Tree	K	Bk,Bk,Lv,St
32	*Fern*		Herbs	K, G	Lv,St
33	*Ficus thonningii*	Moraceae	Tree	G	Lv
34	*Galiniera coffeoides*	Rubiaceae	Tree	M	Lv
35	*Galiniera saxifraga*	Rubiaceae	Shrub	K	Fr,Lv,St
36	*Galium sp*	Rubiaceae.	Herb	K, M	Fr,Lv,St
37	*Girardinia bullosa*	Urticaceae	Shrub	K, M	Fl,Lv,St
38	*Gouania longispicata*	Rhamnaceae	Shrubs	G	Lv,Pi,Ste,Ten
39	*Gynura scandens*	Asteraceae	Herb	K, M	Fl,Lv
40	*Hagenia abyssinica*	Rosaceae	Tree	G	Fl,Lv,
41	*Helichrysum globosum*	Asteraceae	Herb	G	Lv,Ten
42	*Hypericum revolutum*	Hypericaceae	Tree	K, M	Fl,Lv,St
43	*Ilex mitis*	Aquifoliaceae	Tree	G	Fl,Fr,Lv,
44	*Impatiens burtonii*	Balsaminaceae	Herbs	K, M, G	Fl,Fr,Lv,St
45	*Impatiens stuhlmannii*	Balsaminaceae.	Herbs	K, M	Lv
46	*Ipomoea involucrata*	Convolvulaceae	Herb	G	Fl,Lv,Pi,Ten
47	*Ipomoea pileata*	Convolvulaceae	Herbs	K	Fl
48	*Jaundea pinnata*	Connaraceae	Shrub	G	Pi,Ste
49	*Keetia gueinzii*	Rubiaceae	Shrub	G	Fr,Lv
50	*Kyllinga appendiculata*	Cyperaceae	Herbs	K	Lv,Rh,St
51	*Lagenaria sphaerica*	Cucurbitaceae	Herb	K, M	Lv,Ten
52	*Laportea alatipes*	Urticaceae	Herbs	K, M	Lv
53	*Lobelia giberroa*	Campanulaceae	Shrub	G	Pi
54	*Lycopodium sp*	Lycopodiaceae	Herb	G	Lv,Ten
55	*Lycopodium clavatum*	Lycopodiaceae	Herbs	K, M	Lv
56	*Macaranga kilimandscharica*	Euphorbiaceae	Tree	G	Bk,Fl,Fr,Lv,Pi
57	*Maesa lanceolata*	Primulaceae	Tree	K, M, G	Bk,Fr,Lv,Pi,Fl
58	*Markhamia lutea*	Bignoniaceae	Shrub	G	Lv,Pi,Ste

59	*Mikania capensis*	Asteraceae	Shrub	K, M	Fl,Lv,St
60	*Mimulopsis sp*	Acanthaceae	Herb	G	Lv
61	*Mimulopsis solmsii*	Acanthaceae	Herb	K, M	Fl,Lv,St,Rh,
62	*Myrianthus holstii*	Urticaceae	Shrub	G	Fr,Lv,Pi
63	*Neoboutonia macrocalyx*	Euphorbiaceae	Tree	K, G	Lv,St,Pi
64	*Panicum hymeniochilum*	Poaceae	Herb	K, M	Lv
65	*Parinari excelsa*	Chrysobalanaceae	Tree	G	Fr,Lv,Pi
66	*Passiflora edulis*	Passifloraceae	Vine	G	Fl,Fr,Lv
67	*Pavetta rwandensis*	Rubiaceae	Trees	G	Fl,Fr,Lv
68	*Pennisetum purpureum*	Poaceae	Grass	G	Bk,Pi,St
69	*Pentarrhinum insipidum*	Apocynaceae	Vine	K, M	Lv
70	*Persea americana*	Lauraceae	Tree	G	Bk,Pi
71	*Pilea johnstonii*	Urticaceae	Herb	K	Lv
72	*Plectranthus sp*	Lamiaceae	Herb	K, M	Fl,St,Lv
73	*Plectranthus ferrugineus*	Lamiaceae	Shrub	K	Lv,St
74	*Plectranthus luteus*	Lamiaceae	Shrub	K	Lv,St
75	*Polygonum nepalense*	Polygonaceae	Herb	K	Lv,St
76	*Polyscias fulva*	Araliaceae	Tree	G	Bk,Fr,Lv,Pi,St
77	*Prunus africana*	Rosaceae	Tree	M	Lv
78	*Psychotria mahonii*	Rubiaceae	Tree	G	Fr,Lv
79	*Pycnostachys goetzenii*	Lamiaceae	Shrub	K, G	Fl,Lv
80	*Rubus kirungensis*	Rosaceae	Shrub	K	Fr,Lv
81	*Rubus runssorensis*	Rosaceae	Shrub	K, G	Fr,Lv,St
82	*Rumex abyssinicus*	Polygonaceae	Shrub	G	Lv
83	*Rumex bequaertii*	Polygonaceae	Herb	K, M, G	St,Fl,Lv
84	*Sagina abyssinica*	Caryophyllaceae	Herbs	K	Fr,Lv,St
85	*Senecio mariettae*	Asteraceae	Shrub	K, M	Lv,St
86	*Senecio maranguensis*	Asteraceae	Shrub	K	Lv
87	*Senecio subsessilis*	Asteraceae	Shrub	K	Lv
88	*Setaria megaphylla*	Poaceae	Grass	G	Lv,Pi
89	*Solanecio mannii*	Asteraceae	Shrub	K	St

90	*Solanum aculeastrum*	Solanaceae	Shrub	K	Lv,St
91	*Solanum nigrum*	Solanaceae	Herb	K	Lv
92	*Solanum plousianthemum*	Solanaceae	Shrub	K	Lv
93	*Solanum tuberosum**	Solanaceae	Shrub	K	Lv,St,Tub
94	*Solenostemon silvaticus*	Lamiaceae	Herb	G	Lv
95	*Stephania abyssinica*	Menispermaceae	Vine	G	Fr,Lv,Ten
96	*Symphonia globulifera*	Clusiaceae	Tree	G	Bk,Fl,Fr,Lv
97	*Syzygium guineense*	Myrtaceae	Tree	G	Fr,Lv
98	*Tabernaemontana stapfiana*	Apocynaceae	Tree	G	Fl,Fr
99	*Thalictrum rhynchocarpum*	Ranunculaceae	Herb	G	Lv
100	*Uebelinia kiwuensis*	Caryophyllaceae	Herb	K	Fl,Lv
101	*Urera hypselodendron*	Urticaceae	Shrub	K, M, G	Fl,Lv,Fr,Pi
102	*Urtica massaica Mildbr*	Urticaceae	Herb	K	Lv
103	*Vernonia myriantha*	Asteraceae	Shrub	G	Lv,Pi,St
104	*Vernonia abbotiana*	Asteraceae	Shrubs	K	Lv
105	*Vernonia adolfi-friderici*	Asteraceae	Shrub	M	Fl,Lv,St
106	*Vernonia auriculifera*	Asteraceae	Shrub	G	Lv,Pi
107	*Vernonia kirungae*	Asteraceae	Shrub	G	Lv,Pi
108	*Viola eminii*	Violaceae	Herb	G	Lv
109	*Xymalos monospora*	Monimiaceae	Tree	G	Bk,Fr,Pi
110	*Yushania alpina*	Poaceae	Bamboo	K, M, G	Lv,St,Bsh,Pi
111	*Zehneria scabra*	Cucurbitaceae	vines	K, M	St,Ten,Lv

+Lv: Leaves; Bsh: Bamboo shoots; Fr: fruits; Fl: Flower; St: Stem; Ten: Tendril; Rh: Rhizomes; Pi: Pith. * food acquired during crop foraging out of the park

CHAPTER THREE

FOOD AVAILABILITY INFLUENCES BIRTHING SEASONALITY AT A SMALL SPATIAL SCALE IN ENDANGERED GOLDEN MONKEYS (CERCOPITHECUS MITIS KANDTI)

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INTRODUCTION

The energetically demanding periods of pregnancy and lactation influence reproductive strategies of primates and other mammals, female primates need energy and protein to conceive, be pregnant and lactate (Cords & Chowdhury, 2010; Dufour & Sauther, 2002; Emery Thompson, 2017). Increased consumption of high-energy and protein-rich food as well as reduction in physical activities have been linked to reproductive stages in both humans, such as in the Lese women of Ituri in the Demographic Republic of the Congo, and non-human primates (Brockman & van Schaik, 2005a; Dufour & Sauther, 2002; Ellison et al., 1989; Emery Thompson, 2017). Since lactation is the most energetically demanding stage of reproduction, timing birth before or during periods of high-quality food availability can increase female primates' reproductive success, in particular in species with short interbirth interval period and gestation (Brockman & van Schaik, 2005a; Clutton-Brock, 2006; Emery Thompson, 2013). Primates exhibiting this strategy are referred to as classic breeders or income breeders (Brockman & van Schaik, 2005b; Stephens et al., 2009). For example, most guenons give birth shortly before or during the annual peak in key food resource availability (Butynski, 1988; Cords & Chowdhury, 2010).

In some primates, such as human, chimpanzees (*Pan troglodytes schweinfurthii*), Sanje mangabeys (*Cercocebus sanjei*), and orangutans (*Pongo sp*), dietary quality predicts hormonal balance and the probability of conception (Ellison, 2003; Emery Thompson et al., 2007; Emery Thompson, 2017; Knott et al., 2009; Mccabe et al., 2013). Notably, conception may critically depend on female energy balance even in species traditionally categorized as income breeders (Emery Thompson, 2017). As female energy balance varies in relation to within-group feeding competition, and feeding competition often increases with group size, several studies also found that females living in larger groups have a lower fertility (Majolo et al., 2008; Roberts & Cords, 2013).

The golden monkey, *Cercopithecus mitis kandti,* is an endangered subspecies of the blue monkey. It occurs in two small forest fragments in the Albertine Rift region: the Virunga massif (Democratic Republic of the Congo, Uganda, and Rwanda) and the Gishwati forest in Gishwati-Mukura National Park, Rwanda (Butynski & de Jong, 2020). The populations were separated due to rapid deforestation between 1958 and 1973 in Volcanoes National Park (VNP), the Rwandan side of the Virunga Massif. Intense deforestation between 1980 and 2000 further shrunk the Gishwati forest. Overall, the forest cover was reduced by 50% in VNP and by 98% in the Gishwati forest (Nyandwi & Mukashema, 2011; Plumptre, Masozera, & Vedder, 2001; Spinage, 1972). Golden monkeys have a flexible diet, which allow them to use different types of habitat and food resources (Tuyisingize et al., 2021). In VNP, golden monkeys range almost exclusively in the bamboo forest where fruit trees are absent (Tuyisingize et al., 2022). This population is mainly folivorous, and bamboo shoots are their preferred food (hereafter, "key food") (Tuyisingize et al., 2021; Twinomugisha et al., 2007). Bamboo phenology in VNP is markedly seasonal, and shoots are only produced during the two annual rainy seasons: March-May and September-November (van der Hoek et al., 2019). Interestingly, bamboo growth also varies at a small spatial scale, with high altitude bamboo from the southern sector of VNP producing shoots mostly during the first rainy season, while lower-altitude bamboo located farther north produce bamboo shoots mostly during the second rainy season (van der Hoek et al., 2019). As golden monkeys from VNP occur throughout the bamboo altitudinal range, from 2540 to 3100m (Tuyisingize et al., 2022), we expect bamboo phenology to affect the timing of golden monkey reproduction.

In contrast, bamboo is scarce in the Gishwati forest, located 26 km from VNP at ca. 2300m above sea level (ASL) elevation. Bamboo only represents less than 1% of the golden monkey feeding time (Tuyisingize et al., 2021). Fruit trees are abundant compared to VNP, and ripe and unripe fruit is the golden monkeys' preferred food (Tuyisingize et al., 2021). Leaves and insects function as fallback foods in both VNP and Gishwati (Tuyisingize et al., 2021; Twinomugisha et al., 2007).

This study examines the seasonality in mating and birthing in VNP and the Gishwati forest. We hypothesized that in VNP, females should give birth during or short after the two bamboo growth seasons. Due to small scale spatial variations in bamboo shoot seasonality, we also expected female monkeys to give birth during different seasons depending on the timing of the main bamboo shooting season within their home range. Finally, we expected female monkeys from Gishwati to give birth during periods of high fruit availability.

METHODS

Study sites and animals

We collected data on three habituated golden monkey groups ranging in two national parks in Rwanda between 2004 and 2018. Two groups lived in the Rwandan part of the 443-km^2 Virunga massif, VNP (1°21'-1°35'S, 29°22'-29°44'E). The Musonga group (hereafter, group M) ranged between 2,915-3,150 m above sea level (ASL) and the Kabatwa group (hereafter, group K) ranged 16 km away from group M, between 2,540-2,660 m ASL (Figure 3.1). The third group, the Gishwati group (hereafter group G), lived in the Gishwati forest, which is part of Gishwati-Mukura National Park (1°49´S, 29°22´E). It ranged at an elevation of 2,216-2,480 m ASL. Both VNP groups had relatively small home range sizes of 0.25 km^2 for group M, 0.91 km^2 for group K, and a narrow elevational range (235 m for group M and 120 m for group K). The Gishwati group had also a narrow elevational range (264 m), with a home range size estimated to be 1.5 km^2 (Tuyisingize et al., 2021).

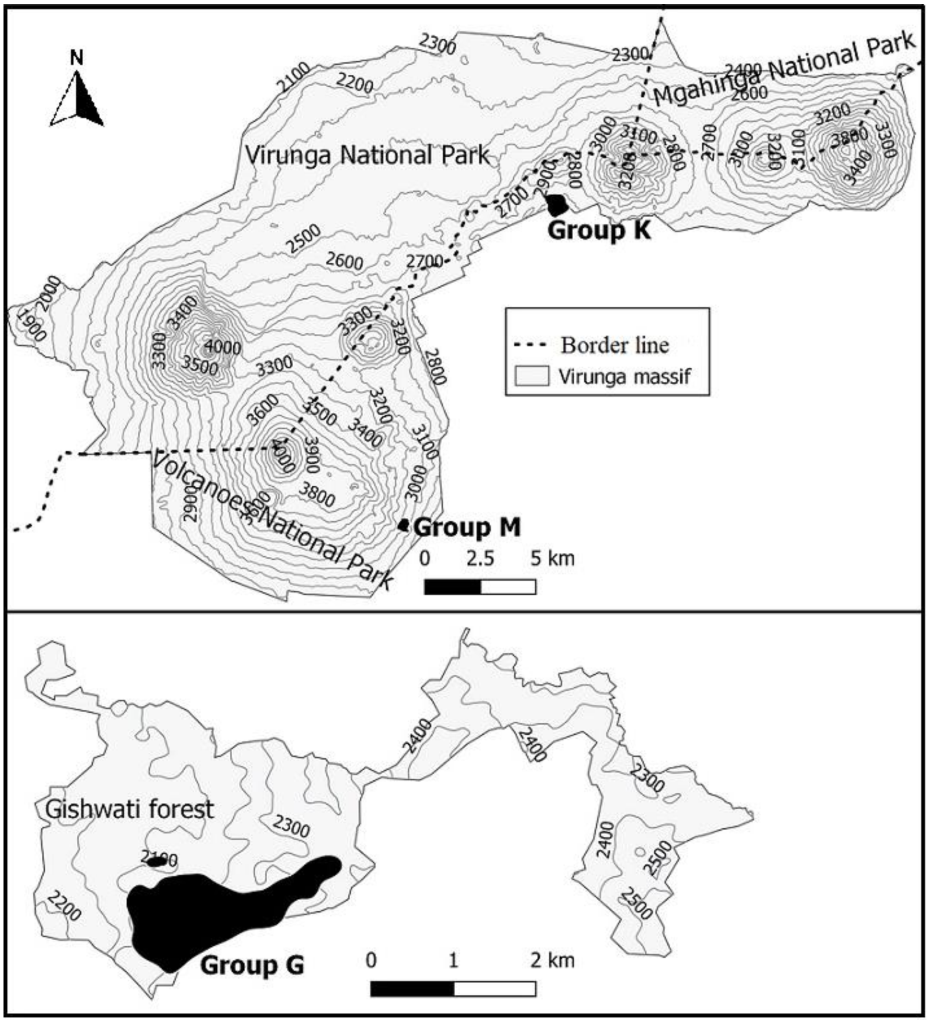

Figure 3. 1. Location of the 95% kernel home ranges of the study groups (groups M, K, and G) in Volcanoes National Park and the Gishwati forest in Rwanda. The contour lines correspond to elevation, in meters.

VNP covers 160 km^2 of afromontane forest, at an elevation ranging between 2,300-4,507 m. It includes eight vegetation zones: mixed semi-deciduous forest, bamboo, *Hagenia* forest, brush ridge, herbaceous, meadow, subalpine and the alpine zone (McNeilage, 1995). Golden monkeys in VNP are found almost exclusively in the bamboo zone (Aveling, 1984; Tuyisingize, 2016; Tuyisingize et al., 2021; Twinomugisha & Chapman, 2006). The Gishwati forest is located approximately 26 km from the southernmost border of VNP at an elevation of 2200-2500 m ASL and covers ~16 km^2 of afromontane mixed forest with a few small bamboo patches (Figure 3.1). The climate in this equatorial region is characterized by a short dry season (December - February), a long rainy season (March- May), a long dry season (June-August), and a short rainy season (September- November) (Seimon & Phillips, 2012).

Groups M and K were both multimale-multifemale groups, as is typical for golden monkeys, and unlike most blue monkey populations, which generally only have one-male groups (Glenn & Cords, 2002; Tuyisingize, 2016). Group size estimates varied during our study period. Group M comprised an estimated ~50-110 individuals depending on the study period, including 2-6 resident adult males, ~20-50 adult females, and their offspring. Group K was composed of ~80-150 individuals, including 2-8 resident adult males, ~30-60 adult females, and their offspring. Group G was a one-male group with ~12-17 adult females and their offspring, totaling ~28-32 individuals. Non-resident adult males (~4-10 males in group M, ~5-12 males in group K, two males in group G) joined the study groups occasionally for mating (Tuyisingize, 2016). Mature females were easily identified from their elongated nipples, and males had a larger body size and conspicuous testicles. Newborns (hereafter new infants) aged between 0-1 month were identified from their small body size, their greyish and blackish body color, and reddish face, palms, and feet. They also had a thin tail with little hair on it and were always carried ventrally by their mothers.

Data collection

We recorded phenology, feeding, demographic and mating data in group M for 11 years over two periods (2004-2012 and 2017-2018), and in group K for 15 years from 2004-2018. Group G, where behavioral observations started only recently, was monitored for two years, from January 2017 to December 2018.

Phenology of key foods

In 2017 and 2018, we collected phenology data on key food plants in VNP (bamboo shoot) and in the Gishwati forest (fruit). Because bamboo only regenerates during the rainy seasons in VNP (van der Hoek et al., 2019), we collected data on bamboo phenology within the home range of the two study groups (M and K) at two-week intervals starting as soon as the first shoots were observed during each rainy season (March-May and September-December). In the home range of group M, we established 13 (4x4 m^2) plots, placed every 200 m, along four parallel line transects separated by 200 m. Similarly, we established 15 plots along four parallel line transects in the home range of group K. Every two weeks, we counted bamboo shoots in each plot, measured their height, and marked them to avoid counting them again during subsequent visits.

In the Gishwati forest, we monitored fruit tree phenology at two-week intervals from March 2017 to December 2018. We collected data on 82 individual fruiting trees belonging to the six most important species (representing ~50% of feeding records) in group G's diet (15 individuals of *Symphonia globulifera, Alangium chineunce, Polysias fulva, and Maesa lanceolata*; 13 individuals of *Albizia gummifera,* and 10 individual trees of *Ilex mitis)* (Tuyisingize, Eckardt, et al., 2021). We selected mature trees with high crown visibility and diameter at breast height over 10 cm, which were mature enough to produce fruit (Mekonnen et al., 2018; Morellato et al., 2000). All phenology trees were located within the 50% kernel home range of group G. Given that phenophases of individual trees of a given species are synchronized in Gishwati (Chancellor, pers. comm), we assumed that our selected trees represented the phenology patterns within the entire home range of group G. We estimated the percentages of the crown occupied with fruit by using scores from zero to four (0 = 0%, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%) (Kaplin & Moermond, 2000). Since monkeys consume both unripe fruit and ripe fruit, we only considered two categories of trees in our statistical analyses: fruiting (scores > 0) vs. non-fruiting (score = 0).

Key food consumption, mating and birthing

Data about key foods were collected using scan sampling (Altmann, 1974). As National Park regulations only allowed us to conduct observations until 14:00, scan data were recorded at 20-minute intervals over three to five hours between 0800 and 1400. Observation time could vary depending on how long it took to find the group, tourism activities, and rainfall. Dietary composition and diversity did not vary in a systematic way during the day, which limits the risk of bias due to our limited observation period. Each scan lasted five minutes, during which we moved slowly through the group and recorded the age-sex class (adult females, adult males, juveniles, old and new infants) and main activity of each visible monkey. If the activity was feeding-related (harvesting and ingesting food), we also noted the food species and plant part consumed. We obtained a total of 20,687 scans for group M, 33,763 scans for group K, and 4,864 scans for group G. Mating events were recorded *ad libitum*, over a total duration of 6,895 hours (1,720 days) in group M, 11,254 hours (3,308 days) in group K, and 1,623 hours (362 days) in group G.

Bamboo phenology can vary depending on elevation (van der Hoek et al., 2019). Golden monkeys from VNP live at an elevation ranging from 2540 to 3100 m (Tuyisingize et al., 2021). We hypothesized that spatial variations in the seasonality of bamboo shoot production could influence the timing of golden monkey reproduction in VNP. To determine whether golden monkey birthing season varied spatially within VNP, we compiled data from a golden monkey survey conducted from October 2017 to September 2018 (Tuyisingize et al., 2021) and added data from additional observations conducted in November 2019. During the 12-month survey, observers walked seven times, at regular time interval, along 20 line transects (separated by a minimum 1 km interval) placed along the Rwandan border of VNP, from DR Congo to Uganda. Along transects, monkeys were detected from their movements, feeding signs, noise and vocalizations but only confirmed sightings of golden monkeys were recorded. Upon visual detection of one or more monkeys, the observer recorded their GPS location on the transect, elevation, and the number and age-sex class (adult males, adult females, new infants, others) of sighted individuals. Special attention was paid to the detection of new infants aged between 0-3 months old, which we used as a proxy to estimate the birthing season for these groups. Infants in this age range were similar or slightly larger to the <1mo infants observed in groups K, M and G. They were systematically carried ventrally by their mother when the group moved away from the observers. Within this age range, new infants under 1 months of age were probably very rarely detected due to their small size and the distance between observers and animals. It is therefore likely that most new infants observed along transects were close to 2-3 months of age.

Because mating events are often difficult to detect, and only part of the females can be monitored at a given time, we likely missed some mating events and could not reliably calculate a precise mating rate (i.e., number of matings/female/hour). However, we expected this bias to be relatively constant over time for a given monkey group, and we considered the number of observed mating events per observation hour to be proportional to the actual mating rate. We calculated the average value of this metric for each month of observation and each monkey group and named it "relative mating frequency".

Every month, we counted individuals in each study group at least once, including new infants aged approximately 1 month or younger, when a group crossed an open area, such as a riverbed, a clearing or a trail, or when a group was foraging in crop fields (Struhsaker et al., 2004; Wich &

Marshall, 2016). Intervals between consecutive counts occurring during the birthing season were always under 35 days, so all the individuals categorized as new infants were under 35 days old. Monthly counts in groups M and K were subject to some variation as these groups were particularly large and some individuals could occasionally be missed. We calculated birth rates every month as the ratio of observed new infants (aged < 1 month old) to the number of observed adult females that given month. This ratio was not biased by the fact that number of females could be underestimated in some months.

Data analysis

All statistical analyses were performed using R version 3.6.1 (R Core Team, 2019) with significance level $p \leq 0.05$. As Shapiro-Wilk tests indicated that the residuals of linear models were not normally distributed, we used non-parametric tests.

Relationship between key food availability, consumption, mating, and births rates

For each month, we calculated the mean number of bamboo shoots per square meter for groups M and K, and the mean percentage of trees that were fruiting in the range of group G. For each study group, we calculated the percentage of leaves, bamboo shoots, and fruit in the diet of female monkeys using scan data, as the ratio between the number of scanned individuals that were feeding on a particular food item, divided by the number of scanned individuals that were feeding on any food item. For each VNP group, we conducted Wilcoxon's signed ranks tests to assess whether there was a significant difference between bamboo shoot consumption during the early bamboo growing season (bamboo shoots produced during the long rainy season, from March to early June) and the late bamboo growing season (bamboo shoots produced during the short rainy season, from September to early December).

Relative mating frequencies were calculated for each month, and we used Spearman's rank correlations to investigate the relationship between monthly relative mating frequencies and the consumption of key foods in each studied group. We calculated monthly birth rates as the number of < 1 month old infants observed in a given month, divided by the total number of observed adult females in the group. We assessed the relationship between birth rate and key food consumption using Spearman rank correlation tests. We observed graphically whether the peak in birth rate corresponded to the period when key food availability was the highest, but we did not conduct a statistical analysis due to the absence of bamboo phenology data outside of rainy seasons in VNP.

As we did only observe two golden monkey groups in VNP, we did not investigate the effect of group size on birth rate and seasonality.

Spatial and elevational distribution of birth events

We plotted the location and elevation of groups sighted each month during the population-wide surveys conducted in VNP, along with the number of new infants aged 0-3 months old observed in each group using QGIS version 3.6.2. We expected to observe new infants during two distinct periods corresponding to peaks in bamboo shoot availability. We also expected to observe two gaps in the temporal distribution of new infant sightings, corresponding to low bamboo shoot availability periods occurring in January-February and July-August. The presence of these gaps was used to determine if the sighted new infants were born around the early or the late bamboo shooting season.

RESULTS

Key food availability

A total of 356 bamboo shoots were counted in the 13 quadrats placed in group M's home range, over a two-year period, corresponding to 0.07 new bamboo shoots per m^2. In group K's home range, a total of 1,922 bamboo shoots were counted in 15 quadrats, over the same period, corresponding to 0.32 bamboo shoots per m^2. In the home range of group M, bamboo shoot availability was almost similar between the early (0.093 bamboo shoots per m^2) and the late growing season (0.065 bamboo shoots per m^2) in 2017, while bamboo shoot availability was slightly higher (0.27 bamboo shoots per m^2) during the early growing season than during the late growing season (0.044 bamboo shoots per m^2) in 2018 (Figure 3.2). The difference between early and late growing season was not tested statistically as we only had data for four growing seasons. The pattern of bamboo shoot availability was very different in group K's home range, where the late growing season peaked between September and December with 0.93 and 1.07 bamboo shoots per sq-m observed in 2017 and 2018 respectively.

Fruit availability in the home range of group G did not show a clear seasonal pattern in 2017 and in 2018, although there seemed to be a slightly greater fruit availability between January and August (Figure 3.2). Between 11% and 32% of the observed trees produced unripe or ripe fruit during that period. Fruit production dropped between September and December (Figure 3.2).

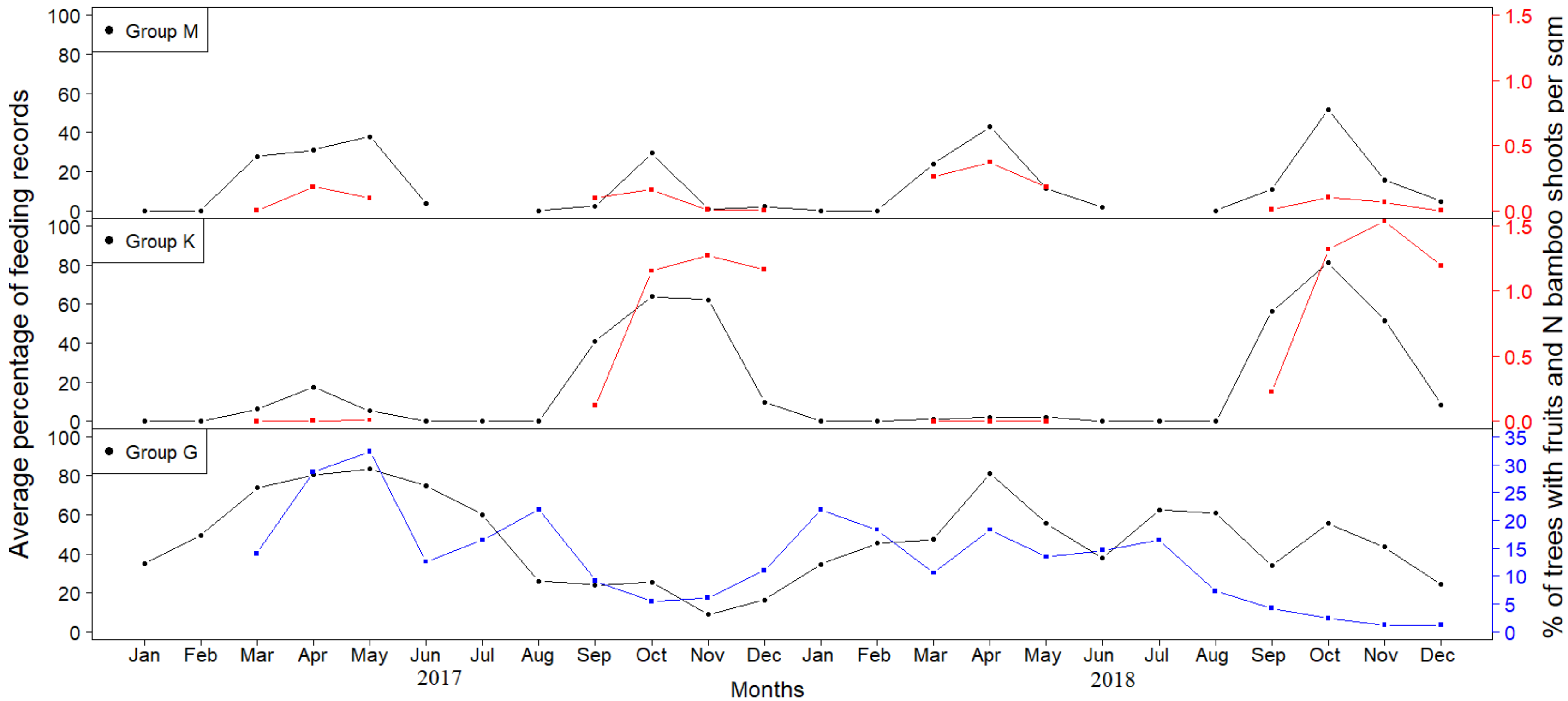

Figure 3. 2. Monthly average percentage of feeding records with bamboo shoot consumption in groups M and K (black dashed lines) and fruit consumption in group G (black line) from January 2017 to December 2018; dotted red lines denote bamboo shoots density (number/area): blue dashed line denotes percentage of fruiting trees. Top row=Group M, middle row=group K, lower row=Group.

Seasonality in key food consumption

Due to the limited availability of fruit in VNP, fruit consumption was marginal in groups M and K (Supplementary figure 3.1). Similarly, group G consumed very little bamboo shoots (Supplementary figure 3.1). Group M and group K both fed on bamboo shoots during both the early and late bamboo growing seasons. In both group M and group K, peaks in bamboo shoot availability were associated with peaks in bamboo shoot consumption (Figure 3.2). Although this could not be tested statistically, it is very likely that seasonal variations in bamboo shoot consumption reflects variations in bamboo shoot availability. The monthly diet of adult females' golden monkey from groups M and K included an average of 17% (range: 0-51%) and 22% (range: 0-78%) of bamboo shoots, respectively. The monthly diet of adult females from group G included on average 53% (range: 26-85%) of fruit.

The highest peak in bamboo shoot consumption was observed during the early bamboo growing season in group M and during the late bamboo growing season in group K (Figure 3.2-3.3, and Supplementary figure 3.2). For group M, bamboo consumption was on average 2.3 times greater during the early growing season than during the late growing season (Wilcoxon signed-rank test, N=120 months, V=49, $p=0.02$). By contrast, in group K, bamboo shoot consumption was on average 5.1 times greater during late bamboo growing season than during the early bamboo growing season (Wilcoxon signed-rank test, N=173 months, V=1, $p<0.001$). If we assume that bamboo shoot consumption tracks bamboo shoot availability, this result suggests that bamboo shoot availability is the highest during the early growing season in group M's range and during the late growing season in group K's range. Golden monkeys from the Gishwati forest consumed both ripe and unripe fruit year-round, with annual peaks occurred between March and June in 2017 (over 80% of the diet) and in April 2018 (83% of the diet). As expected, fruit consumption was positively correlated with fruit availability (Spearman rank correlation, N=22, rho=0.523, $p=0.012$).

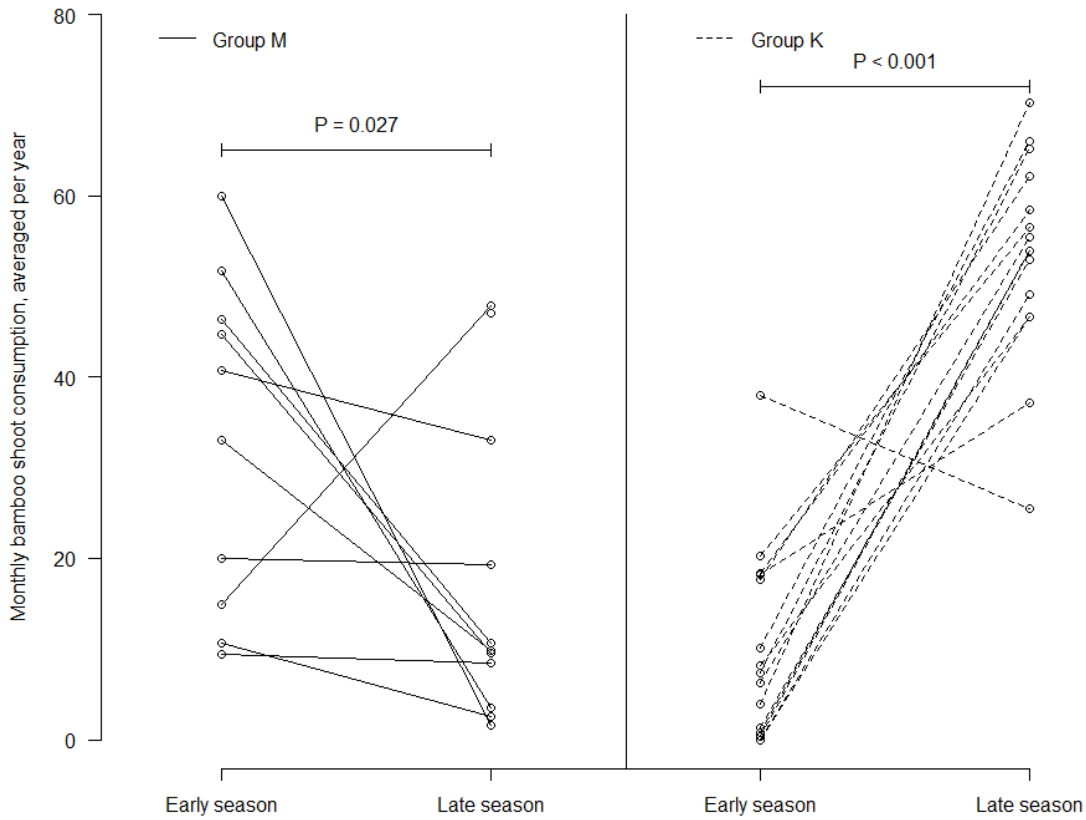

Figure 3. 3. Comparison of bamboo shoot consumption (the ratio between the number of scanned individuals that were feeding on bamboo shoots) in the early (March-June) and late (September-December) bamboo shoot growing seasons in in group M (between 2004 to 2012 and 2017 to 2018) and group K (between 2004 and 2018) in Volcanoes National Park. P values denote Wilcoxon signed rank test.

Seasonality in mating and births

We recorded an average of 13 mating events per year in group M over 11 years from 2004 to 2012 and from 2017 to 2018, 31.2 mating events per year in group K over 15 years from April 2004 to December 2018, and 18.5 mating events per year in group G over two years from January 2017 to December 2018. The average monthly relative mating frequencies was 0.015 (varied between 0.001 in March and 0.036 in October) in group M. In group K, average monthly relative mating frequencies was 0.065 (varied between 0.003 in December and above 0.160 in March-May), while the average monthly relative mating frequencies in group G was 0.025 (varied between 0.008 in May and 0.074 in October). In group G, the highest number of mating events was observed in October 2018 (0.142), although this observation is only based on two years of data (Figure 3.4, and Supplementary figure 3.3). Although golden monkeys did mate year-round in VNP and the Gishwati forest, relative mating frequencies increased between four and six months prior to the birthing period, when females became pregnant. The mean operational sex ratio (average number of adult females per adult male) was 9.34 (95%CI:7.20-11.48) in group M, 9.60 (95%CI:8.05-11.14) in group K, and 12.40 (95%CI:11.39-13.41) in group G.

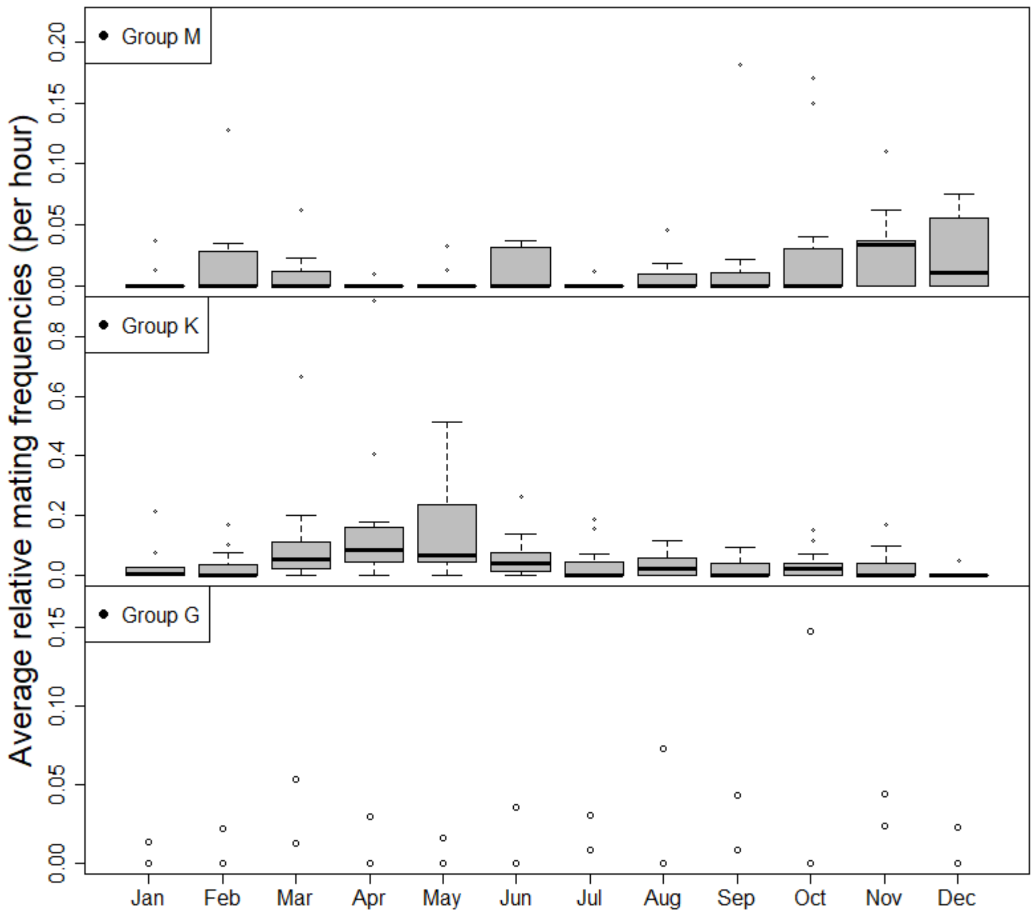

Figure 3. 4. Boxplot of monthly average of daily relative mating frequencies (per hour) in group M (data from 2004 to 2012 and 2017 to 2018, N=120) and group K (data from 2004 to 2018, N=173) in VNP, and group G (data from 2017 to 2018, N=14) in the Gishwati forest.

In VNP, relative mating frequency in group M did not significantly correlate with bamboo shoot consumption (Spearman rank correlation test, N=120, rho=0.081, p=0.377). In group K, relative mating frequency also was not significantly correlated with bamboo shoot consumption (Spearman rank correlation test, N=173, rho=-0.088, p=0.244). We also found no evidence for a relationship between mating events and fruit consumption in group G (Spearman rank correlation test, N=24, rho=-0.050, p=0.816). However, mating events negatively correlated with fruit availability in group G (Spearman rank correlation test, N=22, rho=-0.463, p=0.03).

We recorded an average of 6 births per year in group M over 11 years, and 12 births per year in group K over 15 years, and 5 births per year in group G over two years. The average annual birth rate was 0.093 (range: 0.048-0.135) and 0.115 (range: 0.06-0.223) births per female in group M and K respectively, and 0.176 (range: 0.156-0.197) births per female in group G. All adult females in group M gave birth between January and April with 94% of observed new infants occurring in February and March. Females in group K gave birth between August and December with 99% of observed new infants occurring between September and November. All observed new infants in group G occurred between March and May with 93% of new infants observed in March and April.

Peaks in birth rate coincided with peaks in key food consumption in all groups (Figure 3.5). In VNP, birthing seasons occurred around or just before the period when bamboo shoot consumption was the greatest (i.e., the early bamboo shoot growing season for group M and the late growing season for group K). In the Gishwati forest, births also occurred at the time when fruit consumption peaked (Figure 3.5, and supplementary figure 3.4). Birth rates significantly correlated with bamboo shoot consumption in group K (Spearman rank correlation test, N=173, rho=0.686 p<0.001), and with fruit consumption in group G (Spearman rank correlation test, N=24, rho=0.596, p=0.005), as well as fruit availability in G (Spearman rank correlation test, N=22, rho=0.496, p=0.03). The relationship between bamboo shoot consumption and birth rate was not statistically significant in group M (Spearman rank correlation test, N=120, rho=-0.096, p=0.456). This last result is not surprising though, as group M exhibits two small annual peaks in bamboo shoot consumption, and only a single annual birthing peak. Looking at the ten years for which we have food consumption and birth data for both the early and late growing season, we observed that births occurred at the beginning of the season when bamboo consumption was the highest (i.e., the early growing season), nine out of ten times (binomial test, p = 0.021).

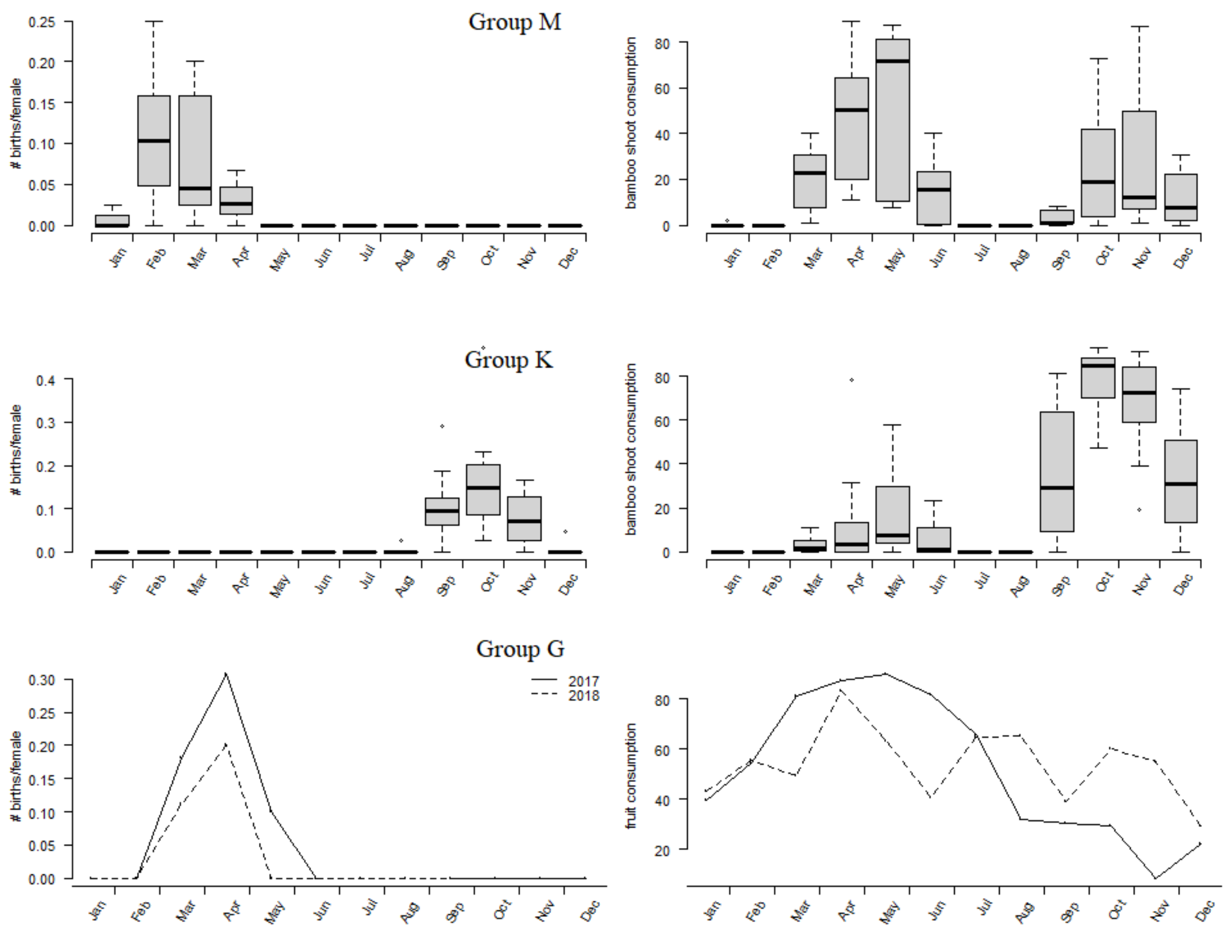

Figure 3. 5. Average monthly birth rates (number of births per female) and average monthly bamboo shoot consumption (proportion of feeding scans corresponding to bamboo shoots) observed every month in group M (between 2004 to 2012 and 2017 to 2018) and group K (between 2004 and 2018) in Volcanoes National Park and fruit consumption (proportion of feeding scans corresponding to fruit) in group G in the Gishwati forest between 2017 and 2018.

Seasonality of new infant sightings at different elevations

A total of 118 monkey groups were sighted during the golden monkey survey conducted in VNP in 2017-2018 and additional observations conducted in 2019. New infants (aged 0-3 mo) were observed in 11 of these groups. Given the small size of golden monkey home ranges, the location and elevation where new infants were sighted likely reflects the location where births occurred, up to 3 months earlier. Most of the groups with new infants were observed at lower elevations. Only three groups with infants were observed above 2900 m, all between May and July, which likely corresponds to the early birthing season. Seven groups with new infants were observed between November and January (late birthing season), below 2900 m (Figure 3.6 and Figure 3.7). One group was observed with a single new infant in February. Although this infant was likely born during the late birthing season, we cannot rule out that it was born in the early birthing season and categorized it as "undetermined". Two clusters of observations of groups with new infants (including two and three observations) occurred around the same two locations and may correspond to the same two groups. Since the total number of observations was 11, this means that our data included at least eight independent observations.

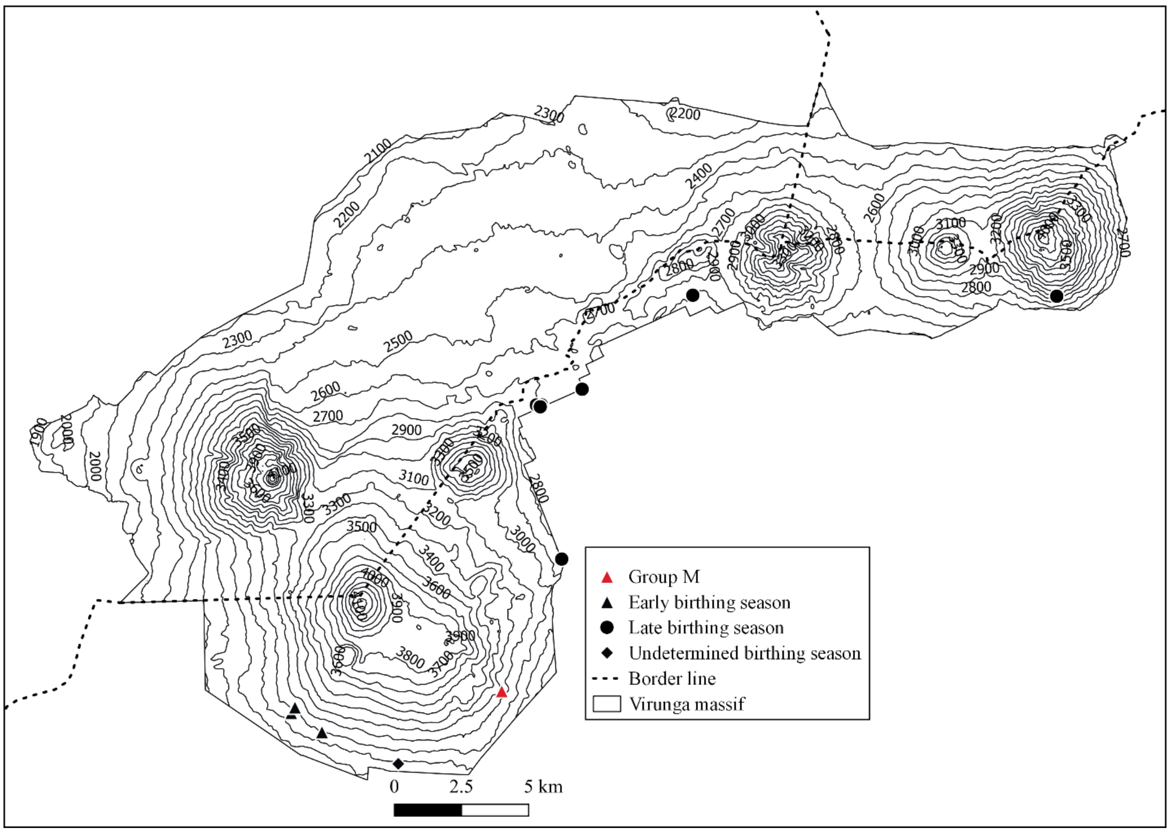

Figure 3. 6. Locations of groups observed with infants (0-3 months) during the 2017-2018 golden monkey survey and additional observation in 2019 in Volcanoes National Park, Rwanda. The contour lines correspond to elevation, in meters. Group M (early birthing season) was not found during the survey and was added to the map (red triangle).

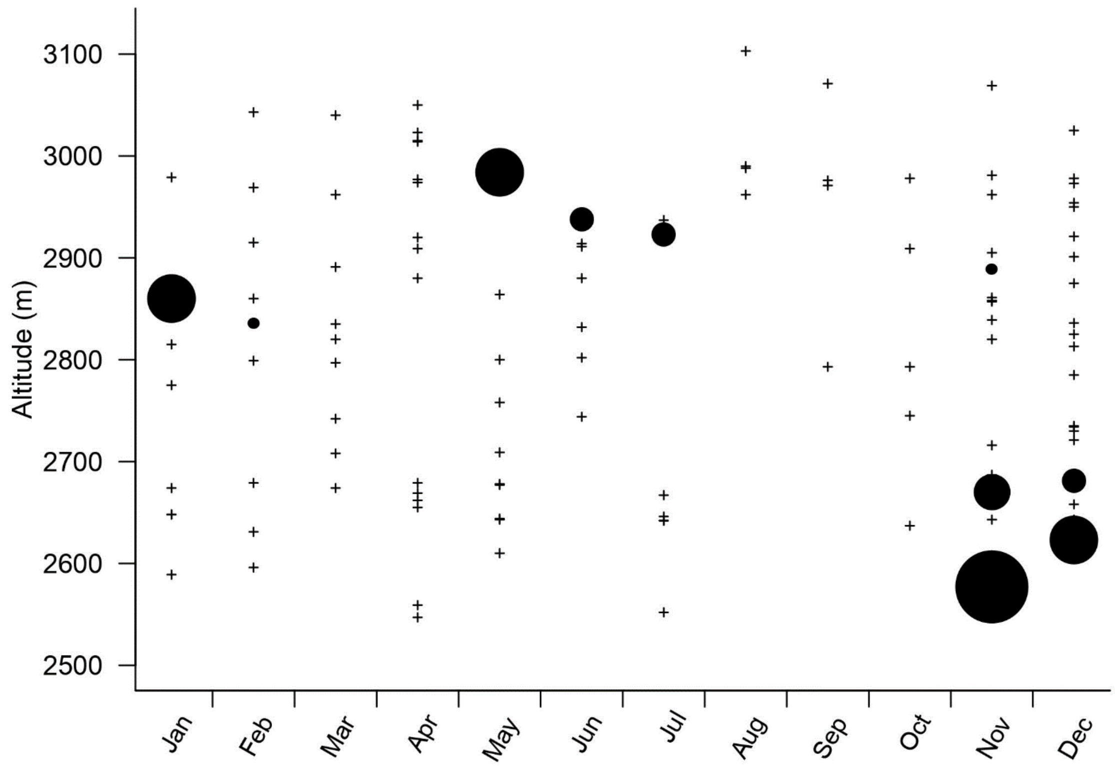

Figure 3. 7. Elevational distribution of observations of groups with infants (0-3 months) (black circles) across months in Volcanoes National Park, in 2017 and 2019. Circle diameter is proportional to the number of 0-3 mo individuals observed, per group (range: 1-6). Plus, signs (+) indicate observations of groups without infants (0-3 months). Note that in February, a group was observed with a single infant. Whether this individual was born during the early or late birthing season could not be determined.

DISCUSSION

We studied reproduction in relation to key food availability for both remaining endangered golden monkey populations in Rwanda. Key food availability was seasonal in both populations, and key food consumption varied according to availability. Although golden monkeys were observed mating year-round, increased mating behavior occurred four to six months prior to the birthing season. Golden monkeys in both populations were seasonal breeders with distinct birthing seasons as described in other guenons (Butynski, 1988; Cords & Chowdhury, 2010; Gevaerts, 1992; Heldstab et al., 2021). Births were observed right before or during the period when key food availability and consumption was the highest. Importantly, the timing of the mating and birthing seasons differed between both populations and even within the VNP population, likely as a result of the observed fine-scale differences in the phenology of key food plant species.

Food availability is a crucial driver of female reproductive strategies in mammals (Clutton-Brock, 2006; Dufour & Sauther, 2002). Bamboo shoots are rich in protein, fiber, and minerals (Calcium, Magnesium, Potassium, and Phosphorus) but low in fat and carbohydrates (Grueter et al., 2016; Karanja et al., 2015; Rode & Robbins, 2000; Rothman et al., 2007), while fruit is rich in carbohydrates and fats (Lambert & Rothman, 2015). In VNP, golden monkeys consume highly nutritious bamboo shoots during the wet seasons, and they consume leaves, in particular young bamboo leaves, and a small amount of insects and fruit, when bamboo shoots are unavailable. The Gishwati population has a frugivorous diet supplemented with leaves and insects (Tuyisingize et al., 2021). In group K's low-elevation range, bamboo shoots production almost exclusively occurred during the late bamboo growing season. At higher elevation, where group M ranges, bamboo shoot regeneration was observed during both the early and the late growing season but was higher during the early growing season. This difference in bamboo phenology is consistent with a previous bamboo phenology study, which showed that bamboo regeneration in VNP is higher at high elevation during the early bamboo growing season and is higher at low elevation during the late bamboo growing season (van der Hoek et al., 2019). Even if we could not test this statistically, we observed that bamboo shoot consumption tracked bamboo shoot availability, and was the highest between March and June for group M and between September and December for group K. This study only includes simultaneous bamboo shoot production and consumption data for four rainy seasons. However, our limited observation is further supported by six years of published bamboo phenology data which indicate that bamboo shoots are strictly available during the rainy seasons, at the same time when our 15 years of feeding behavior data show a peak in bamboo consumption.

Relative female mating rates differed among groups, with the Gishwati group exhibiting the highest rate. However, since this rate was calculated using ad libitum data, between-group differences may be caused by between-group differences in the visibility of animals. The larger VNP groups appear to have lower birth rates than the smaller study group from Gishwati. An inverse relationship between group size and female fertility has been previously reported in primates, including guenons (Dunbar & Shultz, 2021). Given that only three groups are included in the current study, and the Gishwati group has only been studied for two years, we cannot establish whether the observed between-group variation in female fertility is due to group size variation, diet, or other socio-ecological factors. We have observed aggressive interaction among females feeding on bamboo shoots and fruit (DT pers. obs.), so it is possible that feeding competition affects female fertility in both populations. Future behavioral and hormonal studies may investigate the level of feeding competition among adult females in groups varying in size and habitat type.

The VNP bamboo zone hosts larger groups compared to the Gishwati forest (Tuyisingize et al. 2021). In particular, the density of the terrestrial herbaceous vegetation in the Gishwati forest is lower than in VNP, which likely translates into a higher detection of mating events in group G compared to groups M and K. Our personal observations also show that the terrestrial vegetation is denser in group M's range compared to group K's, which could also explain why our estimated relative mating rate is higher in group K than in group M. However, this detection bias may not explain all the differences in relative mating rates that we observed among groups. Future studies based on a larger focal-follow dataset will allow us to estimate unbiased mating rates and provide a more definitive answer. Given that we only conducted observations on three groups, our ability to investigate relationships between group-specific demographic variables such as group size and operational sex ratio, and female reproduction (fertility, birthing season), are limited. Future studies including a larger number of groups are needed to address these questions.

Females in our study groups M, K, and G consistently conceived when key food consumption was not at its highest, while birthing and early lactation occurred just before and during the highest peak in key food consumption. The availability of high-quality food seems to be more important for birth and lactation than for conception and pregnancy, as commonly observed in other mammals (Clutton-Brock, 2006; Dufour & Sauther, 2002), including closely related blue monkeys (Cords & Chowdhury, 2010; Gauthier-Hion, 1980). Notably, bamboo shoot consumption also increased to a lower extent during the conception period in group M. This observation could either reflect a higher need for energy and protein during the conception period, or, alternatively, it could simply be a coincidence since in group M's home range, the interval between bamboo growing seasons is similar to the duration of pregnancy. The fact that conception periods in groups K and G do not coincide with periods of high key food availability suggests that golden monkeys meet their energy requirements during the conception period even in the absence of high-quality food. Some primates, especially those living in seasonal habitats can also meet their energy requirements by storing energy (i.e., fat) to cope with variation in energetic food resources (Emery Thompson, 2017). Female golden monkeys have access to a reliable source of high-quality food during at least three months a year and may be able to store energy during this period that they can use to conceive during the next mating season. Hormonal studies would be necessary to evaluate the energy balance of female golden monkeys throughout their reproductive cycle.

The relationship between elevation, bamboo phenology, and birthing season in VNP was also supported by sightings of 0-3 mo infants in at least eight non-habituated groups. Because these observations are based on non-habituated groups, sometimes at a long distance, it was not possible to precisely determine the age of the observed new infants. However, most of them were likely around 2-3 months old though, as younger individuals are usually very difficult to see. Our observations are therefore consistent with a September-December birthing season below 2900 m, and a February-April birthing season above 2900 m. Periods with no infant sightings, in March-April and August-October, likely correspond to gaps between the two distinct birthing seasons that we also observed in groups M and K, with a 2–3-month lag because most detected new infants were 2-3 months old. Bamboo shooting seasons coincide with raining seasons throughout the park (van der Hoek et al., 2019), and rainy seasons do not change with elevation, so we would not expect the birthing peak to gradually move up along the altitudinal gradient.

The mechanism causing the relationship between elevation and bamboo phenology was not identified in this study. Notably, the park boundary in the southwest sector of VNP is at an elevation of 2800 m, so there are no bamboo patches below this elevation. The park boundary is significantly lower in the northeast sector of VNP, where bamboo patches can be found from around 2,500 m up to about 3,100 m. We did not observe monkey groups with new infants (0-3 month) ranging at high elevation in this northeast sector, so the breeding season for these animals remains unknown. Because the data we collected at different elevations also come from different sectors of VNP, we cannot exclude the possibility that the seasonality of bamboo shoot growth and the breeding season of golden monkey, depend on the region of the park (northeast vs. southwest) rather than on elevation. Future research should focus on the northeast of VNP, and investigate the link between elevation, bamboo shoot seasonality and monkey birthing season.

This study shows that the reproduction of golden monkeys is flexible and responds to small-scale variations in key food availability. Recent studies have pointed out a recent decline in bamboo shoot regeneration in VNP (van der Hoek et al., 2019), and fluctuation in fruit availability in neighboring tropical forests in Uganda (Babweteera et al., 2018; Chapman et al., 2005), possibly as a consequence of climate change. Changes in bamboo shoot and fruit availability and seasonality may affect the energy balance of golden monkeys and may subsequently impact their reproduction. Additional studies focusing on fluctuations in the energy balance of golden monkeys during the reproduction cycle, and in response to long-term changes in key food availability, are needed to assess the viability of golden monkey populations.

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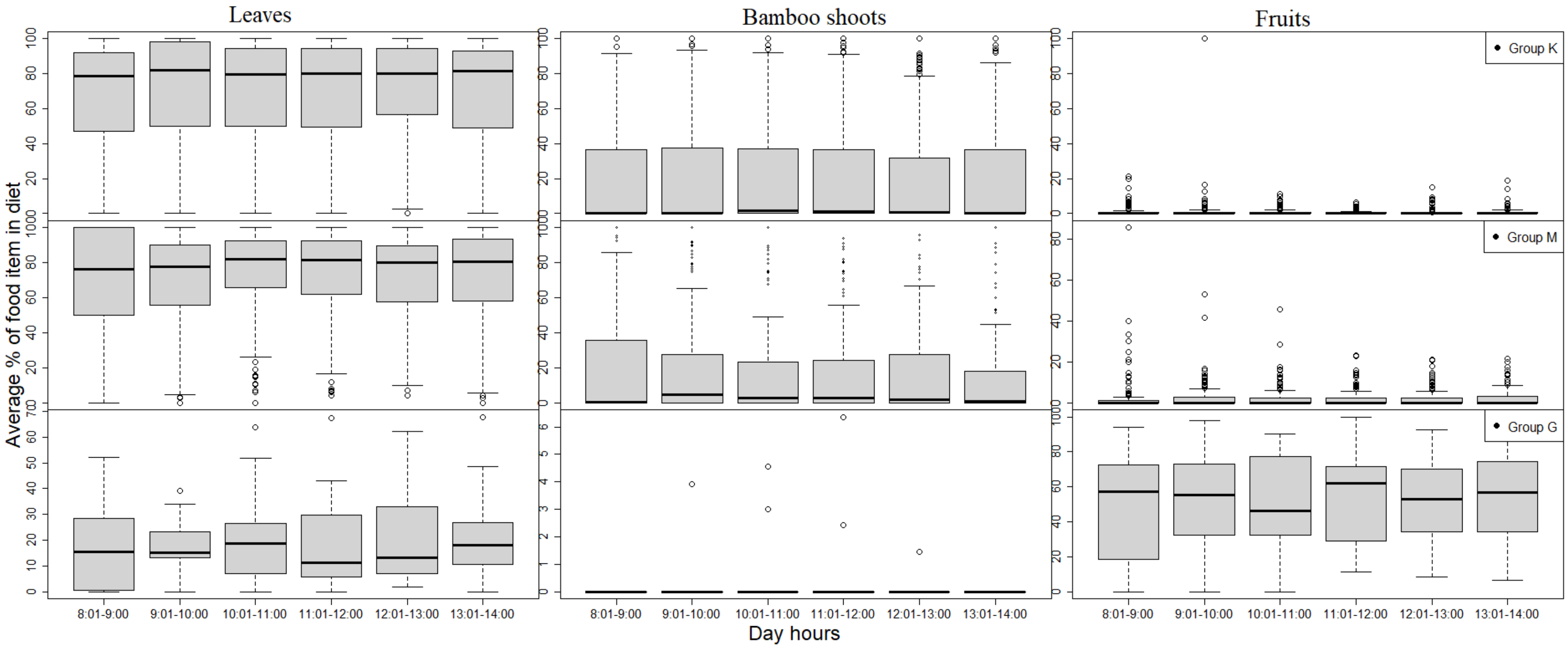
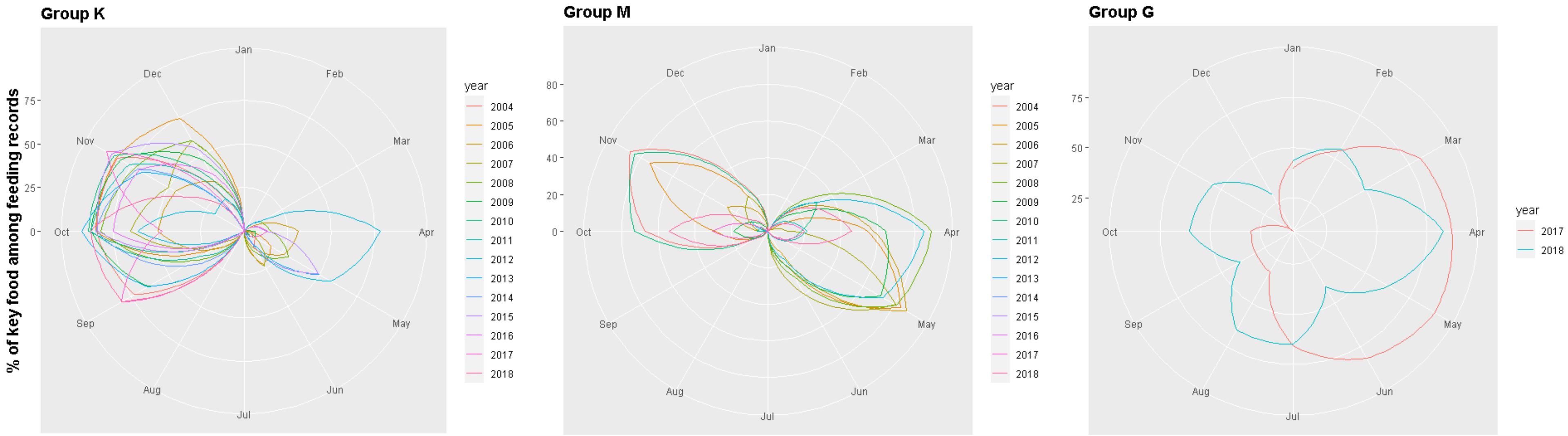
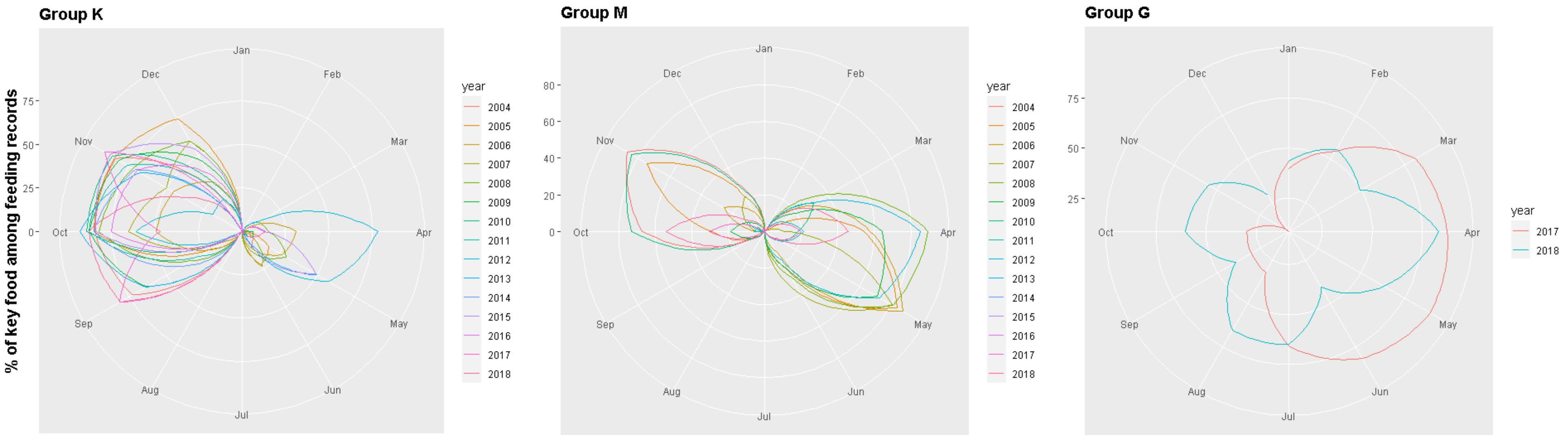
SUPPLEMENTARY MATERIALS



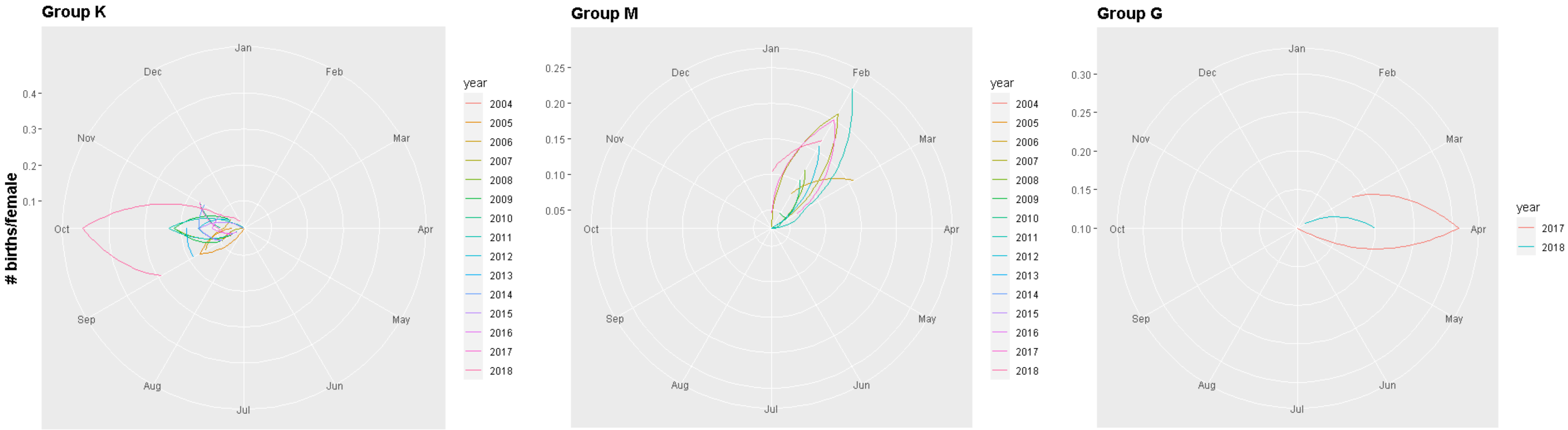
Supplementary figure 3.1. Percentage of food plant item (leaves, bamboo shoots, and fruits) in the diet of each group (Top row=Group K, middle row=group M, lower row=Group G), for each hour from 8:00 to 14:00. Data for groups K and M were collected between 2004 and 2018, and data for group G were collected between 2017 and 2018.



Supplementary figure 3.2: Daily percentage of bamboo shoots in the diet of groups K and M, averaged per month, between 2004 and 2018, and fruit in group G between 2017 and 2018.



Supplementary figure 3.3: Relative mating frequencies in groups K and M between 2004 and 2018, and in group G between 2017 and 2018



Supplementary figure 3.4: Birth rates in groups K and M between 2004 and 2018, and in group G between 2017 and 2018.

CHAPTER FOUR

DISTRIBUTION AND CONSERVATION STATUS OF THE GOLDEN MONKEY CERCOPITHECUS MITIS KANDTI IN RWANDA

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INTRODUCTION

Habitat loss and fragmentation, mainly because of land-cover change driven by agricultural intensification and urbanization, are major threats to biodiversity (Arroyo-Rodríguez et al., 2013; Hilton-Taylor, 2000; Lambin et al., 2001). Over 75% of non-human primate species are declining in numbers and range because of human activities, and c. 60% are threatened with extinction (Estrada et al., 2017; Rylands et al., 2008). Urgent action is needed, including the examination of population trends and threats to survival, to design effective management plans (Estrada et al., 2017; Rylands et al., 2008).

Many forest primate populations now live in isolated forest patches surrounded by human-dominated landscapes and high density of human settlements (Estrada et al., 2017; Marsh & Chapman, 2013). Forest habitat loss and fragmentation have resulted in a rapid decline of primate populations (Cowlishaw, 1999). Guenons (genus *Cercopithecus*) are endemic to Africa, and of the 20 extant species, eight are threatened with extinction, mainly as a result of habitat loss (IUCN, 2021). The blue monkey *Cercopithecus mitis* is the most widely distributed guenon, occupying a variety of forested habitats. It is experiencing population and habitat decline primarily because of habitat loss and fragmentation (Butynski & de Jong, 2020b; IUCN, 2021). There are 17 subspecies of the blue monkey, one of which is categorized as Critically Endangered on the IUCN Red List, four as Endangered and three as Vulnerable (IUCN, 2021).

Primates often respond to changes in their habitat by adapting their range and foraging behaviour to follow resource availability (Chapman et al., 2013; Eppley et al., 2011) Blue monkeys are omnivorous, with a preference for fruit, which enables them to cope with fluctuating resource availability in fragmented habitats (Butynski, 1990; Lawes et al., 2013). For example, the group size and density of Boutourlini’s blue monkey *Cercopithecus mitis* *boutourlinii* and Stuhlmann's blue monkey *Cercopithecus mitis stuhlmanni* vary depending on the habitat quality in the forest fragments they inhabit (Mammides et al., 2008; Tesfaye et al., 2013).

The golden monkey *Cercopithecus mitis kandti* is a forest-dwelling subspecies occurring in the centre of the Albertine Rift, in Uganda, the Democratic Republic of the Congo and Rwanda(Butynski & de Jong, 2020a). Although currently classified as a subspecies of the blue monkey, taxonomists have argued that it could be a separate species (Butynski & de Jong, 2020a). It is categorized as Endangered on the IUCN Red List because of its small population size, shrinking habitat, and threats posed by poaching and diseases (Butynski & de Jong, 2020a). Its distribution is restricted to two isolated forest fragments surrounded by areas with high human population densities (up to 1,000 people/km^2) (NISR, 2012). One of these forests is the 450-km^2 Virunga massif, comprising three contiguous national parks: Volcanoes National Park in Rwanda, Virunga National Park in the Democratic Republic of the Congo and Mgahinga Gorilla National Park in Uganda. The second is the c. 16-km^2 Gishwati forest remnant (hereafter, Gishwati forest), part of Gishwati-Mukura National Park in Rwanda (Butynski & de Jong, 2020a).

Within this limited geographical range, golden monkeys occur at an altitude of 2,100–3,550 m (Butynski & de Jong, 2020a; Tuyisingize, 2016). Previous studies in Uganda showed they prefer bamboo *Yushania alpina* and mixed tropical montane forest (Twinomugisha & Chapman, 2006). Golden monkeys share their habitats with other primates, including mountain gorillas *Gorilla beringei beringei* in Volcanoes National Park, and L'Hoest's monkeys *Allochrocebus lhoesti*, eastern chimpanzees *Pan troglodytes schweinfurthi* and bushbabies *Galago* sp. in Gishwati forest (Chancellor et al., 2012).

Estimates from Mgahinga Gorilla National Park showed a 59% decline in the golden monkey population during 1998–2003, probably linked to habitat loss resulting from bamboo harvesting (Twinomugisha & Chapman, 2006). A recent survey conducted in Gishwati forest resulted in approximate population estimates without confidence intervals, because of low sampling effort (Siegel et al., 2020). Here we report results of population surveys in both Volcanoes National Park and Gishwati forest conducted during 2007–2018, and provide individual density, group density, distribution and population size estimates for golden monkeys in Rwanda. We also examine the relationship between golden monkey distribution and the spatial-temporal distribution of human disturbances. Our findings provide baseline information for future studies.

Study area

Volcanoes National Park and Gishwati forest were connected until the 1950s by continuous forest habitat. Volcanoes National Park spans altitudes of 2,400–4,507 m. During 1958–1973 the total area of the Park was reduced by c. 50%, from 328 to 160 km^2, as a result of agricultural expansion (Spinage, 1972). The Park comprises eight vegetation zones: mixed tropical montane, bamboo and *Hagenia–Hypericum* forest, brush ridge, meadows, and herbaceous, subalpine and alpine zones (McNeilage, 1995). The majority of habitat loss occurred in the mixed tropical montane forest zone, the only vegetation zone in Volcanoes National Park containing a significant number of fruiting trees (Spinage, 1972). Only c. 5 km^2 of mixed tropical montane forest remain.

Gishwati forest lies at 2,100–2,500 m altitude and has also been subject to land conversion and habitat loss. Forest cover dropped from 280 km^2 in the 1970s to <10 km^2 in 2003 (Nyandwi & Mukashema, 2011). Restoration efforts have led to a 5.6 km^2 increase in forest cover since 2016. The current tropical montane forest is dominated by fruiting trees (e.g. *Symphonia globulifera* and *Syzygium guineense*) and a few bamboo stands, and the restored montane forest patch is dominated by bamboo, *Xymalos monospora* and *Hagenia abyssinica*. The two forest patches are connected by a narrow corridor. In 2016, the government of Rwanda gazetted Gishwati forest and Mukura forest, 16 km apart, to form Gishwati–Mukura National Park (Fig. 1). Illegal activities such as bamboo and firewood harvesting, grazing and presence of feral domestic dogs are common in both Volcanoes National Park and Gishwati forest (Hickey et al., 2019).

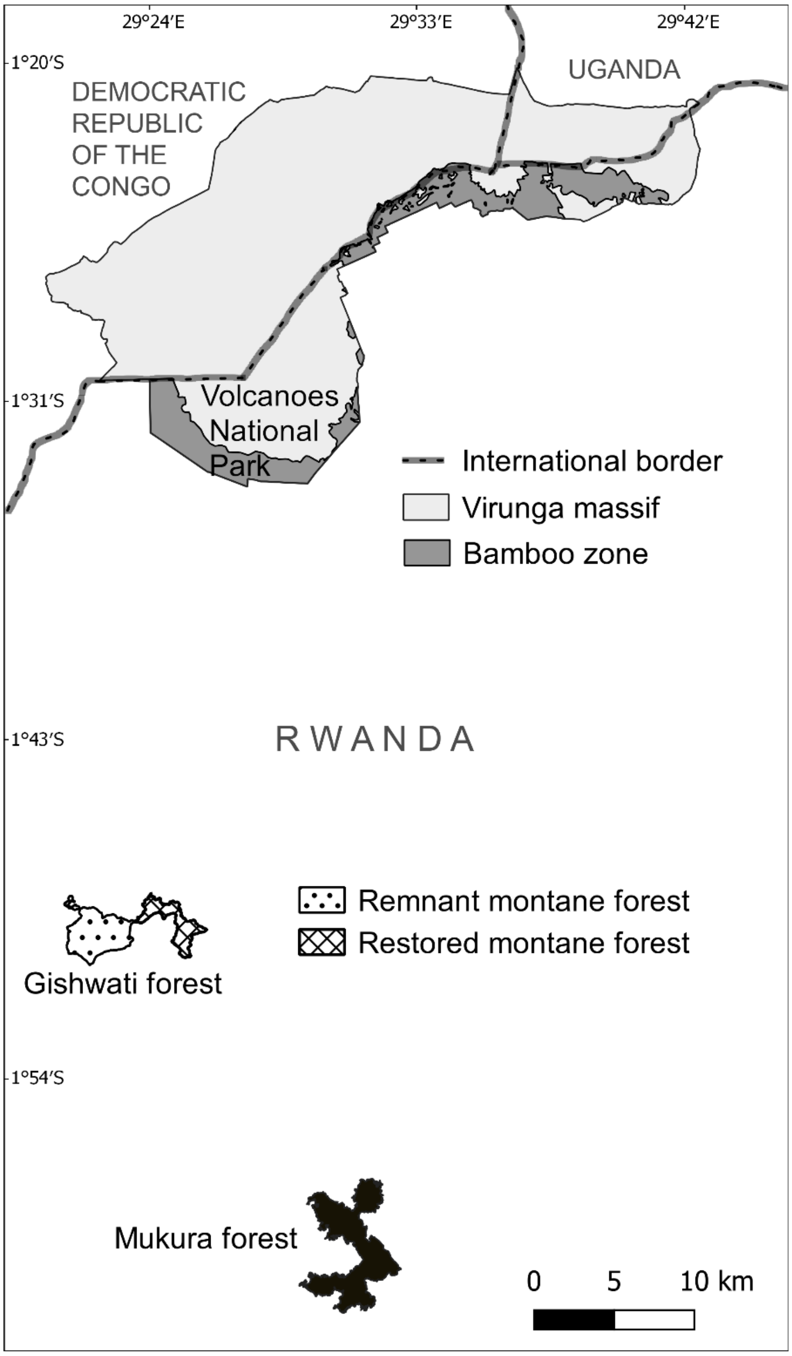

Figure 4. 1. The study sites in Rwanda, where we carried out surveys of the golden monkey Cercopithecus mitis kandti during 2007–2018.

METHODS

Data collection

Line and recce transect surveys

We used both line transects and reconnaissance walks (hereafter recce walks) to survey golden monkey populations at both study sites and across four time periods (Table 4.1). Line transect surveys provide accurate animal density estimates but can be time consuming and costly to implement, whereas recce walks facilitate quick monitoring of large areas, without the need to cut new trails, as is necessary for line transect surveys (Fashing & Cords, 2000; Twinomugisha & Chapman, 2006). We determined line transect starting points, lengths and orientations based on the terrain (e.g. to avoid inaccessible ravines). Daily observations from Park staff and findings from previous biomonitoring surveys in the Virunga massif showed that golden monkeys were almost exclusively found in the bamboo zone in the Virungas (Hickey et al., 2019; Tuyisingize, 2016; Twinomugisha & Chapman, 2006). We surveyed a total of 22 line transects in 2007, 20 in 2011 and 20 in 2017–2018, all in areas dominated by bamboo (Fig. 2). We also collected data outside the bamboo zone along four transects (in 2007 only) and five recce trails (during all study periods) to document presence of golden monkeys there (Figure 4.2). We visited each line transect and recce trail repeatedly (twice in 2007, three times in 2011 and seven times in 2017–2018) to increase the number of detections and thus the accuracy of density estimates (Buckland et al., 2004). The cumulative lengths of these 244 transect surveys and 15 recce trails were 420.7 km and 299.2 km, respectively.

Table 4. 1. Summary of golden monkey Cercopithecus mitis kandti survey efforts (km) in Rwanda, by study period and site (VNP, Volcanoes National Park; GMNP, Gishwati Mukura National Park).

Vegetation zones	Transects	VNP 2007	VNP 2011	VNP 2017–2018	GMNP 2017–2018
Bamboo	Line	64.6	87.45	250.6	
Mixed forest	Recce	4.4	13.2	30.8	
Mixed forest	Line	6.0			
Hagenia forest	Recce	8.0	24.0	56.0	
Hagenia forest	Line	12.0			
Brush ridge	Recce	5.2	15.6	36.4	
Subalpine	Recce	7.6	22.8	53.2	

Vegetation zones	Transects	VNP 2007	VNP 2011	VNP 2017–2018	GMNP 2017–2018
Alpine	Recce	2.0	6.0	14.0	
Afromontane	Recce				55.0
Afromontane	Line				473.0

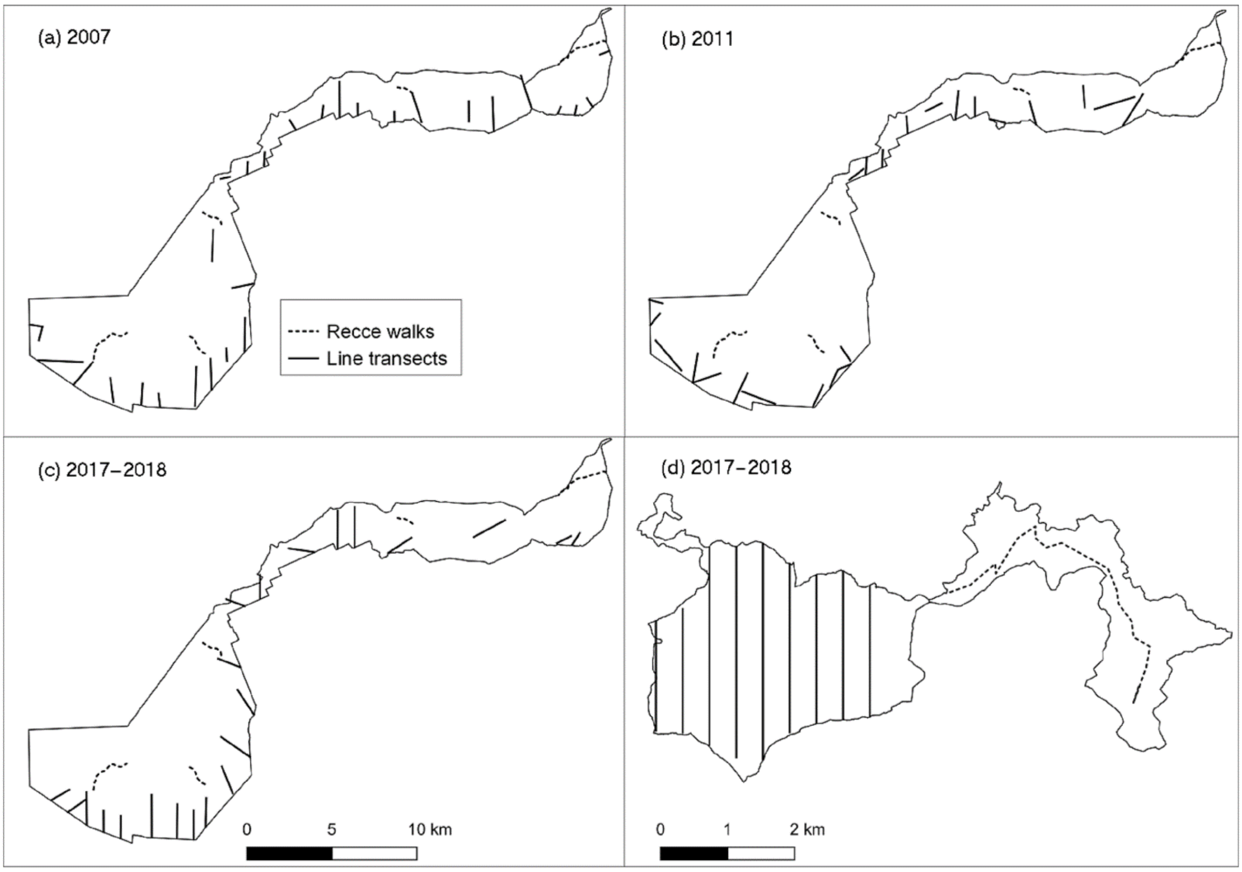

Figure 4. 2. Location of line transects and recce walks at both study sites: in Volcanoes National Park in (a) 2007, (b) 2011 and (c) 2017–2018 and (d) in Gishwati forest in 2017–2018.

Given the small size of the Gishwati forest, we placed nine parallel line transects systematically across the entire remnant, with gaps of 400 m between transects. We also placed a single recce trail across the corridor and restored forest patch to assess the presence of golden monkeys in these areas. We collected data along these transects and recce trail 1–3 times per month for a total of 22 times in 2017 and 2018 (Figure 4.2). The cumulative lengths of transect and recce trail surveys were 473 km and 55 km, respectively.

We collected data along transects and recce trails between 7.00 and 13.00 in Volcanoes National Park and between 7.00 and 16.00 in Gishwati forest. During line transect surveys, a single observer walked at an average speed of c. 1 km/h and stopped every 100 m to listen and look for monkeys ahead of the rest of the survey team, which comprised two people: a park ranger and one observer collecting data on illegal activities (Peres, 1999; Andrew J. Plumptre & Cox, 2006). Monkeys were detected from their movements, feeding signs, noise and vocalizations, but we recorded only confirmed direct sightings. Upon visual detection of one or more monkeys, the observer recorded the geographical location of detection on the transect (using a GPS), the compass bearing of the individual or centroid of the group, the number of sighted individuals and the distance from the transect to the individual or centroid of the group (using a Bushnell Elite 1,500 Golf Laser Rangefinder, Northbrook, USA). Teams of three observers conducted recce walks, recording the location of each monkey group and the number of individuals. We did not collect data during rainy weather, to prevent biases resulting from the lower detectability of monkeys (Peres, 1999).

Illegal activities

We used maps of illegal activities (bamboo cuts, snares, honey and water collection, feral dogs, beehives) produced by Volcanoes National Park rangers. These data were collected during regular law enforcement and monitoring patrols along recce trails over 220 days during October 2017–September 2018. As there was no systematic monitoring by rangers in Gishwati forest at the time of our study, we collected data on illegal activities (such as bamboo cuts, snares, cattle grazing inside the forest, collection of honey or firewood) along recce trails in areas where we suspected illegal activities may occur. The goal of this biased search was to establish a list of illegal activities taking place in the forest. These searches took place 3–4 times per month for 12 months, starting in June 2017. We used *ArcGIS 3.6* (Esri, Redlands, USA) to create maps of frequently occurring (mean frequency >7 records per month) illegal activities in both study areas.

Data analysis

Population density and size

We estimated golden monkey group densities using point process models with the *spatstat* package in *R 3.6.1* (Baddeley et al., 2015; Niemi & Fernández, 2010; R Core Team, 2019). Inhomogeneous Poisson point process models can be fitted to spatial distributions of points to investigate the link between point density and point attributes (e.g. species, sex, group size) or environmental covariates (e.g. vegetation type, terrain, distance to transects). This approach is less commonly used than the distance sampling method but provides more flexibility in handling fine-scale spatial variation in animal density and nested sampling designs (Borchers & Marques, 2017). In the *spatstat* package, the design of inhomogeneous Poisson point process models is similar to the design of generalized linear models; the main difference is that the dependent variable in point process models is a spatial point pattern object as opposed to a numerical variable in generalized linear models. We modelled the natural log of the point density as a linear function of the squared distance to the transect line (denoted as *x*). This implies that the expected sighting density $\widehat{D}$ is:

$$\widehat{D} = exp(\text{ intercept} + b \cdot x) = A \cdot exp(\, b \cdot x)$$

where *A* is the sighting density on the transect line (i.e., for *x*=0), and *b* the negative coefficient denoting the spread of the detection function. This model assumes the detection function has the shape of a half-normal distribution. Visual inspection of the distribution of distances to the transect line confirmed this was a good approximation. Our point process models also included transect identity as a random-effects variable influencing the intercept, to consider our nested design, with each transect repeated 2–7 times in Volcanoes National Park, and 22 times in Gishwati forest. Models were fit using the *mppm()* function from *spatstat* (Baddeley et al., 2015).

Most sighted individuals were within 80 m of a transect line. The few observations that were beyond 80 m were considered outliers and were not used in our statistical analysis. We also excluded the four Volcanoes National Park transects outside the bamboo forest from the analyses, as no golden monkeys were observed there. We fitted mixed-effects point process models to each of the four datasets described in Table 4.1. We estimated the group density for each dataset as the exponential of the model intercept and calculated the 95% confidence interval as exp(intercept±SE×1.96).

The overall individual density $\widehat{D}$ is the product of the mean group density and the mean group size. Both quantities were estimated from our data, together with associated standard errors. We used the delta method (Powell, 2007) to estimate the standard errors of individual densities and to calculate the associated confidence intervals. The coefficient of variation (CV) of the individual density was approximated using:

$$CV(D) = \sqrt{CV^2(G) + CV^2(S)}$$

where *D*, *G* and *S* are the individual density, group density and mean group size, respectively.

The standard error of the individual density was derived as:

$$\mathrm{SE}(D) = CV(D) \cdot \widehat{D}$$

Confidence intervals for individual densities were then calculated for each of the four estimates as $\hat{D} \pm 1.96\ \mathrm{SE}(D)$.

We estimated total population size for both areas by multiplying density estimates for Volcanoes National Park and Gishwati forest with the area of the bamboo zone in Volcanoes National Park (c. 51.2 km^2; McNeilage, 1995) and the area of the remnant tropical montane forest of Gishwati (c. 10 km^2), the only habitats where golden monkeys were found. We extrapolated the confidence intervals for abundance estimates by multiplying the confidence intervals for individual density estimates by total areas.

RESULTS

Golden monkey distribution and population size

In Volcanoes National Park golden monkeys were exclusively observed in the bamboo zone (Figure 4.3a–c), and in Gishwati forest they were restricted to the remnant tropical montane forest (Figure 4.3d). Population sizes were therefore estimated based on the size of these areas.

Social groups sighted in Volcanoes National Park (up to 68 individuals) were larger than those in Gishwati forest (up to 24 individuals). The percentage of observations of solitary males was smaller in Volcanoes National Park (14–17%) than in Gishwati forest (35%; Table 4.2). The sighting rates in Volcanoes National Park varied little across survey periods (0.47–0.54 sightings/km) and were significantly higher than in Gishwati (0.16 sightings/km). The estimated mean group densities were also greater in Volcanoes National Park's bamboo forest than in Gishwati–Mukura National Park's tropical montane forest (Table 4.2).

The 95% confidence intervals of group density in the bamboo forest of Volcanoes National Park overlapped considerably across the three survey periods. The most recent survey (2017–2018) yielded the most precise density estimate: 90.4 individuals/km^2 (95% CI 81.4–99.4), corresponding to a population size of 4,626 individuals (95% CI 4,165–5,088). In the remnant tropical montane forest of Gishwati, individual density was significantly lower (mean 17.90

individuals/km^2, 95% CI 15.48–20.32) and the estimated population size was 172 individuals (95% CI 154–190).

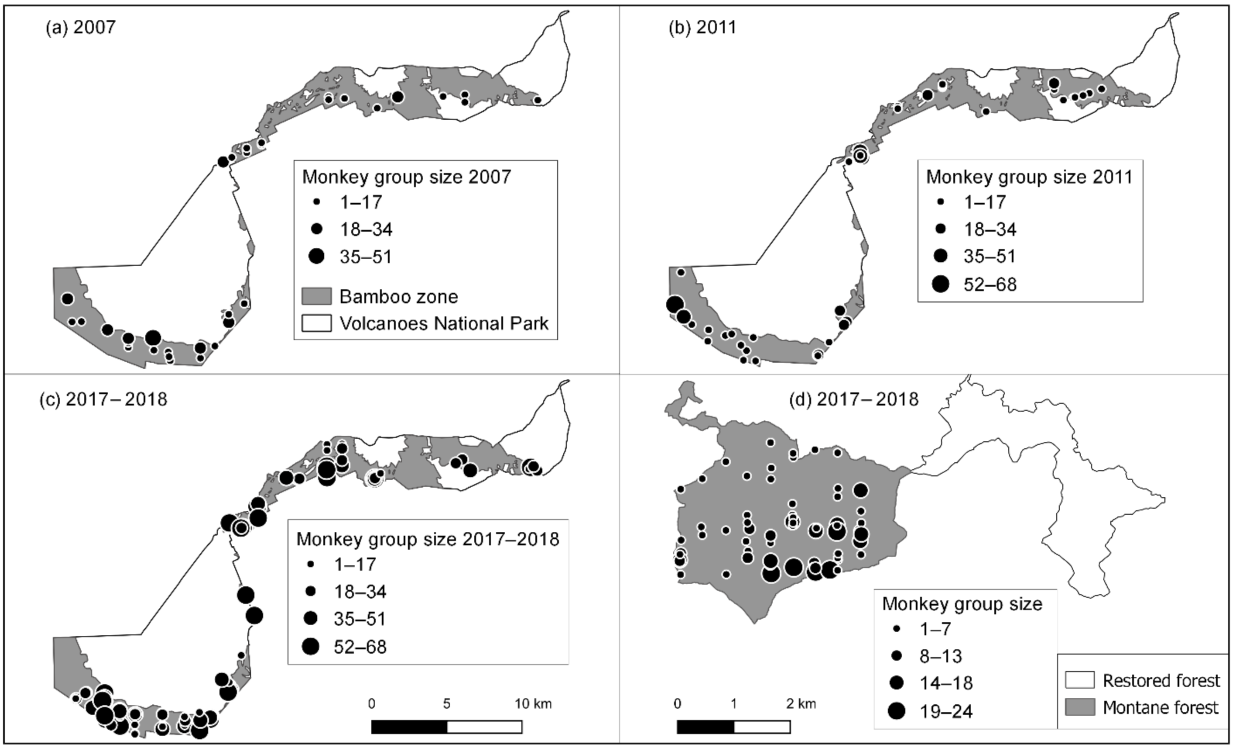

Figure 4. 3. Sightings of golden monkey social units in Volcanoes National Park in (a) 2007, (b) 2011 and (c) 2017–2018 and (d) in Gishwati forest in 2017–2018.

Table 4. 2. Summary of the results of golden monkey transect surveys conducted during 2007–2018 in the bamboo zone of Volcanoes National Park and in the tropical montane forest of Gishwati, part of Gishwati–Mukura National Park, Rwanda.

Description	Volcanoes National Park			Gishwati
	2007	2011	2017-2018	2017–2018
Effort (km walked)	64.6	87.5	250.6	473.0
Sighted social units (groups & solitary males)	35	44	117	75
% of solitary males	17	14	15	35
Group size range	2–45	3–68	2–64	2–24
Sighting rate (social units/km)	0.54	0.50	0.47	0.16
Estimated mean group density/km^2 (95% CI)	7.89 (3.85–16.19)	5.41 (2.64–11.08)	5.47 (3.68–8.14)	1.98 (1.27–3.16)

Description	Volcanoes National Park			Gishwati
	2007	2011	2017-2018	2017–2018
Estimated individual density/km^2 (95% CI)	84.58 (53.19–115.97)	87.64 (56.70–118.58)	90.36 (81.36–99.36)	17.90 (15.48–20.32)
Estimated total population size (95% CI)	4,331 (2,723–5,938)	4,487 (2,903–6,071)	4,626 (4,165–5,088)	172 (154–190)

Illegal activities in golden monkey habitats

In Volcanoes National Park, the major illegal activities recorded during ranger patrols, and believed to significantly affect the monkeys, were bamboo cutting, water collection, feral dogs and snares. Snares primarily target the black-fronted duiker *Cephalophus nigrifrons* and bushbuck *Tragelaphus scriptus* but golden monkeys are occasionally caught, as we have personally observed (DT, pers. obs., 2017). During the most recent survey period (2017–2018), most of the illegal activities recorded were in the bamboo zone, in particular in the south-western sector of the Park (Figure 4.4). Gishwati forest is surrounded by farmland with livestock, pastures, and houses. Cattle grazing, bamboo cutting, and firewood collection were the most common types of human activity recorded in both the remnant and the restored patch (Fig. 5). Bamboo is used by local communities for agriculture (e.g., as bean poles) and weaving material.

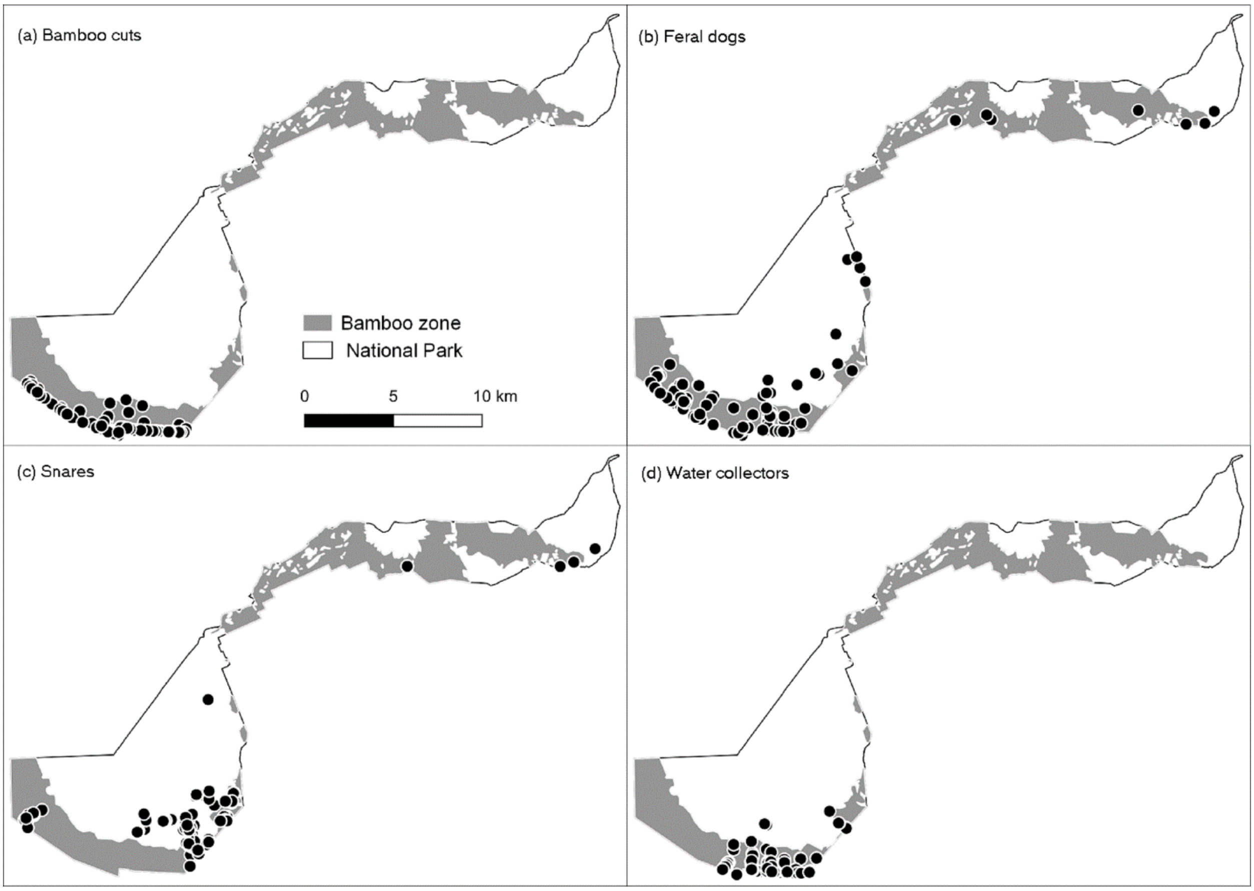

Figure 4. 4. Locations of illegal activities recorded in Volcanoes National Park during October 2017–September 2018: (a) bamboo cutting, (b) feral dogs, (c) snares and (d) water collection.

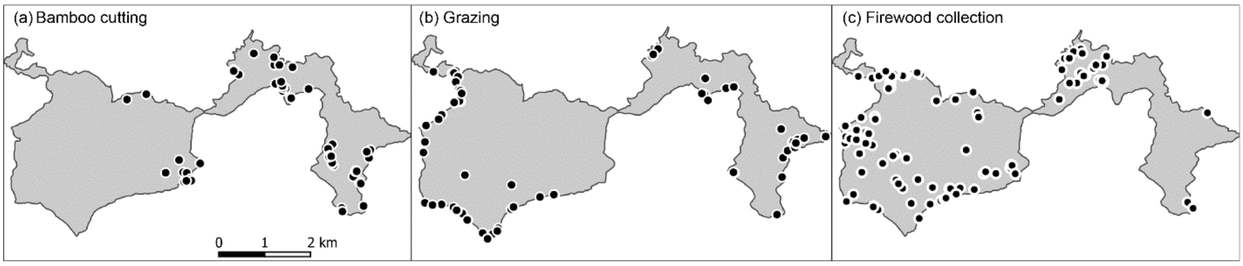

Figure 4. 5. Locations of illegal activities recorded in Gishwati forest during June 2017–May 2018: (a) bamboo cutting, (b) grazing and (c) firewood collection.

DISCUSSION

Population density estimates

In Volcanoes National Park, golden monkeys are restricted to the bamboo zone, although anecdotally Park staff report observations, particularly of solitary males, outside this zone. This population included c. 4,600 individuals in 2017–2018 and did not change significantly over the 12-year study period. In comparison, a previous study from Mgahinga Gorilla National Park, Uganda, suggested a 59% decline in the golden monkey population size during 1998–2003, from 2,438±SD 1,463 to 989±SD 521.5 (Twinomugisha & Chapman, 2006).

In Gishwati forest, an estimated 172 golden monkeys persist in the remnant tropical montane forest, but not in the corridor or the restored forest patch. A brief study conducted in 2019 (Siegel et al., 2020) in Gishwati forest estimated the population size to be 70–211 individuals, but the authors did not provide confidence intervals for their estimates because of methodological limitations.

The Gishwati remnant tropical montane forest includes mature fruit trees such as *S. globulifera, Maesa lanceolata, S. guineense* and *Ilex mitis*, potentially providing a more suitable habitat for golden monkeys than the restored montane forest patch dominated by bamboo stands, young *X. monospora, H. abyssinica* and exotic plant species such as *Acacia mearnsii* and *Alnus* spp. The trees present in the narrow corridor connecting the patches form an open canopy forest with low bamboo stands and *X. monospora*, limiting arboreal movement between the two patches.

The mean estimates of golden monkey group density in Volcanoes National Park (5.41–7.89 groups/km^2) are close to previous estimates from the subpopulation in Mgahinga Gorilla National Park, which was 6.03 and 4.28 groups/km^2 in 1998 and 2003, respectively (Twinomugisha & Chapman, 2006). They are also similar to density estimates (4.3–6.0 groups/km^2) for Stuhlmann's blue monkey in the intact forest of Kakamega, Kenya (Fashing & Cords, 2000). The group density estimate from Gishwati forest is similar to that of Stuhlmann's blue monkey (1.71–2.06 groups/km^2) in the logged parts of Kibale National Park, Uganda (Chapman et al., 2000), and to that of the Samango monkey *Cercopithecus mitis labiatus* (1.58–3.46 groups/km^2) in a fragmented Afromontane forest in KwaZulu Natal, South Africa (Lawes & Piper, 1992).

Group sizes and densities in each study population probably reflect differences in resource availability at the different sites. The Gishwati population is mainly frugivorous, whereas the Volcanoes National Park population is mainly folivorous (Tuyisingize, Eckardt, et al., 2021). Differences in the spatial and temporal distribution of key food types may drive the differences in group sizes and densities between the sites (Clutton-Brock & Harvey, 1977; Twinomugisha et al., 2007). Leaves are abundant and available year-round in the bamboo forest of Volcanoes

National Park (Tuyisingize, 2016; Twinomugisha et al., 2007), supporting larger group sizes and higher group densities. In contrast, frugivorous primates rely on smaller, scattered, seasonal food patches, which may lead to smaller group sizes and lower densities (Snaith & Chapman, 2007).

The percentage of solitary males was higher in Gishwati than in Volcanoes National Park, which reflects differences in the social organization of the two populations. Golden monkeys in Volcanoes National Park are observed in groups with one male and multiple females or in large multimale–multifemale groups (DT, pers. obs., 2017; Tuyisingize, 2016), whereas in Gishwati forest they only form groups with one male and multiple females (DT, pers. obs., 2017).

Effect of human activities

We observed potential threats to the golden monkey, such as bamboo cutting, collection of firewood and water, cattle grazing inside the forest and presence of feral domestic dogs, during this study. The occurrence of illegal activities in their habitat may limit golden monkey population growth, especially in unmonitored populations, as documented for Virunga mountain gorillas (Granjon et al., 2020). Illegal activities such as bamboo and firewood harvesting are suspected to have contributed to a sharp population decline in the golden monkey population in Mgahinga Gorilla National Park during 1998–2003 (Twinomugisha & Chapman, 2006). Intense bamboo and firewood collection can affect vegetation dynamics and nutrient availability, leading to forest degradation (Sassen et al., 2015; Sheil et al., 2012). Furthermore, cattle grazing and water collection inside golden monkey habitats may also increase the risk of disease transmission between livestock, people and golden monkeys, as reported for mountain gorillas (Hogan et al., 2014). Feral dogs can predate native mammals, including arboreal primates, and should be controlled (Galetti & Sazima, 2006; Soto & Palomares, 2015).

Golden monkeys may also be negatively affected by climate change. A study in Volcanoes National Park reported a decline in bamboo regeneration, possibly the result of an overall decrease in rainfall in the Virunga region (van der Hoek et al., 2019). A simulation study focusing on the Albertine Rift predicted a decrease in the extent of habitats preferred by endemic species, including golden monkeys, because of climate change in the coming 6 decades (Ayebare et al., 2018).

Future research and conservation perspectives

The density of golden monkeys in the bamboo forest in Volcanoes National Park is more than four times higher than in Gishwati tropical montane forest. More research is needed to determine the roles of ecological (e.g. food resource availability and quality) and other factors (e.g. population history and current anthropogenic pressures) on golden monkey demography. People, livestock and feral dogs often use golden monkey habitats and may introduce parasites and other pathogens potentially harmful to the primates. Research is needed to identify pathogens that are likely to be introduced by people and domestic animals, and whether golden monkeys are exposed and susceptible to these pathogens. To examine population trends, regular surveys are needed as part of a long-term conservation management plan for this subspecies.

Given that the Gishwati population is particularly small (172 individuals, 95% CI 154–190) and totally isolated, genetic studies are needed to measure the effects of genetic drift and inbreeding, and to predict possible impacts on population health. If this population shows low genetic diversity, the possibility of translocating animals from Volcanoes National Park to Gishwati forest could be explored.

Our latest survey, from 2017–2018, provides recent and accurate estimates of golden monkey population sizes in Volcanoes National Park and Gishwati forest, and will serve as a baseline to estimate future population trends. Surveys are urgently needed in Mgahinga National Park, Uganda, and in Virunga National Park, Democratic Republic of the Congo, to assess the size and demographic trend of golden monkey populations outside Rwanda. Despite ongoing protection efforts, including the recent creation of Gishwati–Mukura National Park, illegal activities are ongoing throughout the range of the golden monkey in Rwanda. We recommend the development of a comprehensive conservation action plan for the subspecies that incorporates a long-term monitoring programme in all three range countries. This plan should address threats to golden monkeys and their habitats using a participatory approach with local communities, to explore ways to reduce the reliance on forest resources that threatens forest biodiversity.

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CHAPTER FIVE

FOREST LANDSCAPE RESTORATION CONTRIBUTES TO THE CONSERVATION OF PRIMATES IN THE GISHWATI-MUKURA LANDSCAPE, RWANDA

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INTRODUCTION

Ongoing land-use change is leading to loss and fragmentation of habitat for primates worldwide (Cowlishaw, 1999; Estrada et al., 2017; Fahrig, 1997; Marsh & Chapman, 2013; Schwitzer et al., 2011). Land use change results in small and isolated forest fragments, and declines in species diversity and population size (Fahrig, 1997, 2003; Ickes et al., 2012; Irwin, 2006; Laurance et al., 2002). With over 75% of the populations of nonhuman primate species declining due to human activities, and approximately 60% of all primate species in danger of extinction (Estrada et al., 2017; Rylands et al., 2008), land use change is an especially critical issue for primate conservation. Land use and land cover changes can cause primate populations to be more exposed to hunting activity for bushmeat (Bicca-Marques, 2003) and conflicts with humans (Hill, 2000; Mekonnen et al., 2018; Ukizintambara, 2008). Some primate populations have adopted crop foraging behaviors when the surrounding landscape is dominated by agricultural crops, or when there are limited food resources available such as fruit (Baranga et al. 2012; Campbell-Smith et al. 2010; Hill 2018; Naughton-Treves 1998; Newton-Fisher 1999). Indeed, primates must adapt quickly to changing landscape conditions or their populations will decline and eventually go extinct (Estrada et al., 2017; Schwitzer et al., 2011). Forest-associated primates that have the ability to use small fragments of forest and non-forest habitats (e.g., anthropogenic habitats, such as cropland and plantation), are more likely to persist following land use and other environmental changes (Arroyo-Rodríguez et al., 2013; Onderdonk & Chapman, 2000).

Forest landscape restoration is a key approach to return ecological function in deforested or degraded forest landscapes, while also improving human wellbeing. Through emerging global restoration efforts such as the Bonn Challenge (https://www.bonnchallenge.org/), tropical forest cover is being restored as part of national forest landscape restoration initiatives

(Chazdon & Uriarte, 2016). These restoration efforts aim to provide ecological and social benefits, as well as mitigate the effects of climate change, with a common goal of restoring 350 million hectares of forest globally by 2030 (Chazdon & Uriarte, 2016; Mansourian et al., 2017). Since 2011, 74 countries (including 31 African countries) pledged to provide more than 200 million hectares into the forest and landscape restoration efforts (IUCN & WRI, 2014). Forest and landscape restoration initiatives have the potential to support the conservation and recovery of primate populations. Restoring forest functions has already created new opportunities for people and primates (Chazdon et al., 2020; Hanya et al., 2005; Merker et al., 2005). For example, *Cercopithecus* species from Kibale National Park in Uganda and Kakamega forest in Kenya (Chapman et al., 2000; Fashing et al., 2012; Twinomugisha et al., 2007; Vié et al., 2009); chimpanzees (*Pan troglodytes schweinfurthii*) from Gombe National Park, Tanzania (Goodall, 2015); and black-and-white colobus monkey (*Colobus angolensis palliates*) from Diani forest in Kenya (Dunham, 2017) use regenerating or secondary forests and planted forests. Forest restoration has also helped with the recovery of six primate species, including redtail monkeys (*Cercopithecus ascanius*), mangabeys (*Lophocebus albigena*), olive baboons (*Papio anubis*), blue monkeys (*Cercopithecus mitis*), red colobus (*Procolobus rufomitratus*), and black-and-white colobus (*Colobus guereza*) in the Kibale forest in Uganda (Chapman et al. 2018).

In the Albertine Rift region of Central and East Africa, forest loss and fragmentation threaten several primate species, especially endemic species or those that range in small, isolated high-elevation montane forests (Ayebare et al., 2018; Plumptre et al., 2007; Ponce-Reyes et al., 2017; Salerno et al., 2018). These threats are particularly strong in western Rwanda, which has experienced significant forest cover loss due to agricultural transformation (*e.g.,* tea, pyrethrum, pine plantations, pasture land), and pressure due to the very high human population density in this region, with an average of 458 people per km^2 and up to 1,000 people per km^2 around protected areas (NISR, 2012). The Gishwati forest in western Rwanda has suffered substantial forest cover loss and fragmentation, initially due to animal husbandry and pine plantation projects funded by the World Bank in the early 1980s, followed by further forest conversion to farm land in the 1990s (Plumptre et al., 2001). As a result, Gishwati forest cover dropped dramatically from 280 km^2 in the 1970s to ~174 km^2 in early 1980s; forest conversion in the 1990s resulted in further forest cover loss leaving 9.6 km^2 in 2003 (Arakwiye et al., 2021; Nyandwi & Mukashema, 2011). The Government of Rwanda has pledged to restore two million hectares under the Bonn Challenge (MINIRENA, 2014), and to reverse fragmentation and forest cover loss of Gishwati forest, the Government and conservation partners initiated a program in 2014 to restore degraded tropical montane forest (Clay, 2019). This restoration project has the potential to help protect the threatened primate populations residing in the Gishwati forest, but an evaluation is needed to understand how primates use this rehabilitated landscape. A recent study found out that tree species richness, tree density, proportion of native tree species, and diameter at breast height in the montane forest fragment are higher than in the restored forest fragment (Arakwiye, 2020).

In this study, we investigated how primates are responding to landscape restoration in the Gishwati-Mukura landscape of Rwanda, and whether the restoration is benefiting conservation of primates. Specifically, we assessed the distribution of three diurnal primate species, the Endangered and endemic golden monkey (*Cercopithecus mitis kandti*, synonyms: *Cercopithecus kandti*), L'Hoest's monkey (*Allochrocebus lhoesti*), and the Endangered eastern chimpanzee (*Pan troglodytes schweinfurthii*), one remnant tropical montane forest fragment, one restored forest fragment, and several forests fragments planted with exotic species following restoration and conservation initiatives. We addressed the following questions: (i) how do primates respond to forest restoration in the Gishwati-Mukura landscape, and (ii) what is the relationship between forest restoration and crop foraging around the Gishwati-Mukura National Park? We hypothesized that primates would colonize restored forest, and that efforts to restore the degraded forests would increase suitable habitat for primates, leading to a decrease in conflicts between local communities and primates. We predicted that primates would have started using the restored forest fragment.

METHODS

Study site and species

The Gishwati-Mukura landscape includes one remnant tropical montane forest fragment, one restored forest fragment with predominantly native tree species which was previously degraded forest, and several forest fragments planted with exotic species in mid-1980s in areas that had been deforested in early 1980s (Arakwiye et al., 2021; Nyandwi & Mukashema, 2011) (Figure 5.1). These forest fragments are located between 2000 m and 2500 m of elevation, where average annual rainfall is 1884 mm, and temperature ranges between 15.7 °C and 24.2 °C (Chancellor et al. 2012). The remnant tropical montane forest fragment and restored forest fragment were gazetted as the Gishwati-Mukura National Park in 2016 due to their international importance for a number of threatened and endemic species.

The remnant montane forest (9.6 km^2) is characterized by fruit producing tree species typical of afromonontane forest, mainly *Symphonia globulifera*, *Alangium chinense*, *Polysias fulva*, *Maesa lanceolata*, *Albizia gummifera*, and *Ilex mitis.* The restored forest (5.6 km^2) is connected to the remnant tropical montane forest by a narrow corridor of ~ 500 m in length and ~ 50-170 m in width, composed of bamboo stands (*Yushania alpina)* mixed with *Xymalos monospora*, *Maesa lanceolata*, and *Polycias fulva*, and a few exotic tree species including *Acacia mearnsii* (Arakwiye, 2020; REMA, 2015). The planted forest fragments were established in the mid-1980s (~40 km^2) after clearing the native forest in early 1980s. These planted forest patches are dominated by introduced tree taxa, mostly *Pinus* spp., a few *Eucalyptus* spp. and *Cupressus* spp. (Arakwiye, 2020; Ngabikwiye et al., 2019). All forest fragments are separated by farm and pasture lands (Figure 5.1).

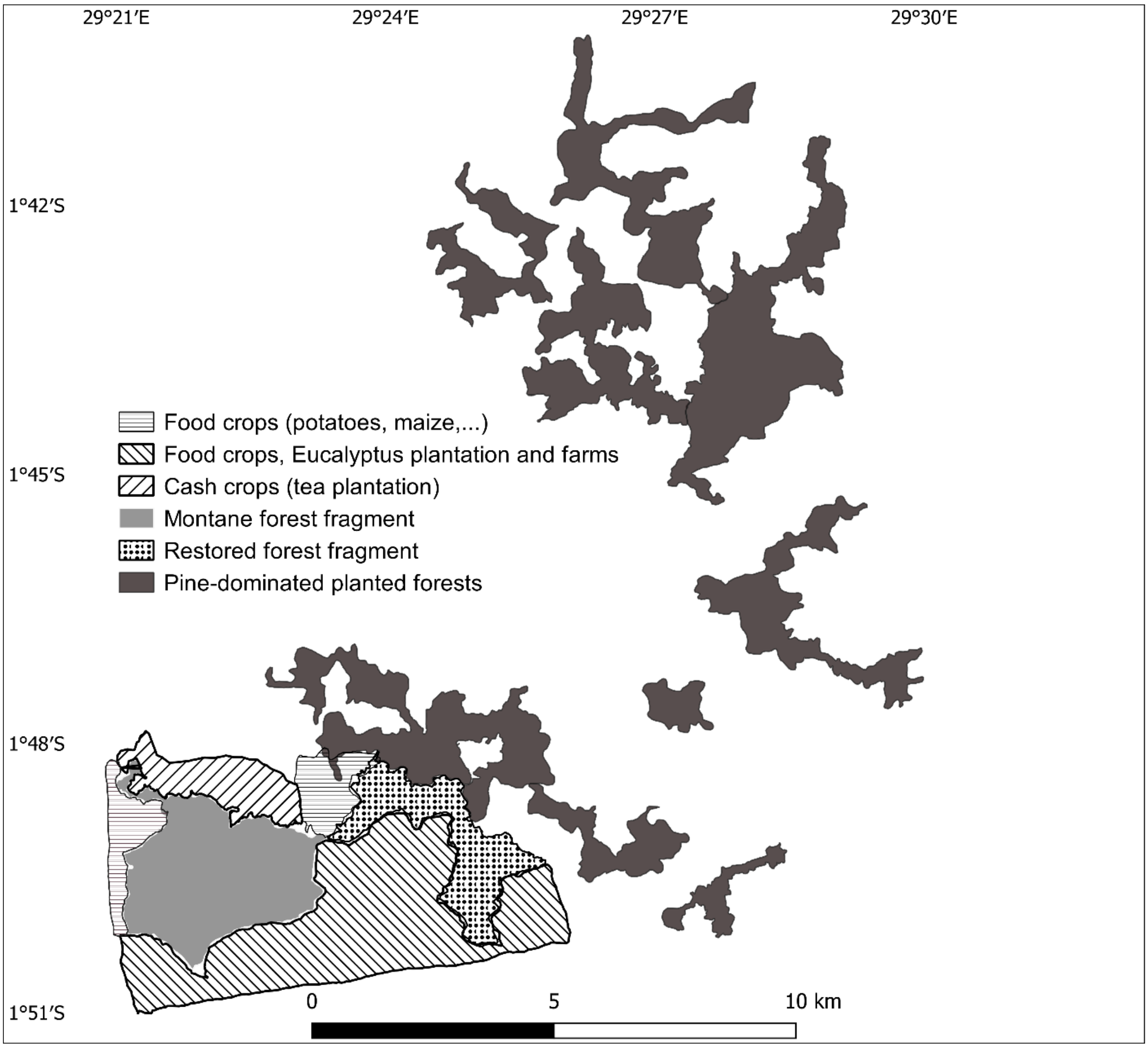

Figure 5. 1. Location of the study areas in the Gishwati-Mukura landscape with one remnant tropical montane forest fragment (grey) and one restored forest fragment (dotted), and several pine-dominated planted forests initiated in mid-1980s (black); both remnant montane and

restored forest fragments are surrounded by agriculture crops (food and cash crops), while the planted forests are surrounded by pasture lands (white).

The remnant tropical montane forest (the Gishwati forest) hosts three diurnal primate species, the golden monkey, the L'Hoest's monkey, the eastern chimpanzee and an unidentified nocturnal bushbaby species (*Galago sp*.) (Chancellor et al. 2012). Only one of several golden monkey groups in the Gishwati population is habituated to human presence (~30 individuals) and had an estimated home range of up to ~151ha (Tuyisingize et al. 2021). A L'Hoest monkey group (~29 individuals) used a home range of ~117 ha (Kaplin, 2001) and a chimpanzee community used a home range of ~4,000 ha (~67 individuals) in a neighboring forest, Nyungwe National Park (Green et al., 2020). Previous studies from 2009 showed that primates were the main crop foraging animals around the Gishwati natural forest (McGuinness & Taylor, 2014).

Data collection

We collected data from June to August 2019. Following the distance sampling method (Buckland et al. 2010a), we surveyed a total of 15 line transects (between 0.75 and 3.2 km in length) three times each during this time period, including nine line transects located at 400 m intervals in the remnant tropical montane forest and six line transects placed at 600 m intervals located in the restored forest (Figure 2a and b). In the planted forests, we surveyed primates using seven existing trails (2-7 km of length) called reconnaissance surveys or recce trails (White and Edward 2000) as a quick method for covering large areas with minimal disturbance (Figure 2c); each of these existing trails was visited three times during the study period.

We moved along transect lines and recce trails at 1 km/hour (Peres 1999), recording the presence of each primate species encountered. At each encounter of a monkey (golden monkey or L'Hoest's monkey), we recorded the GPS location, the detection angles using a Meridian PRO Sighting Compass, the sighting distance from the observer to the individual or the center of the group using a Bushnell 7x26 laser rangefinder, the number of individuals in a group and the vegetation type (Buckland et al. 2010b; Peres 1999). We identified monkeys based on direct sightings and on the golden monkey's "pyow" call, which is not made by the L'Hoest's monkey.

To collect data on the distribution of chimpanzees, we counted all nests (individual nests) and marked them to avoid recounts (Tutin and Fernandez 1984). We also recorded GPS coordinates for all nests. We measured the perpendicular distance from the transect line to the tree trunk hosting each nest. For any direct observations of chimpanzees during transect walks, we counted the observed individuals and collected GPS coordinates.

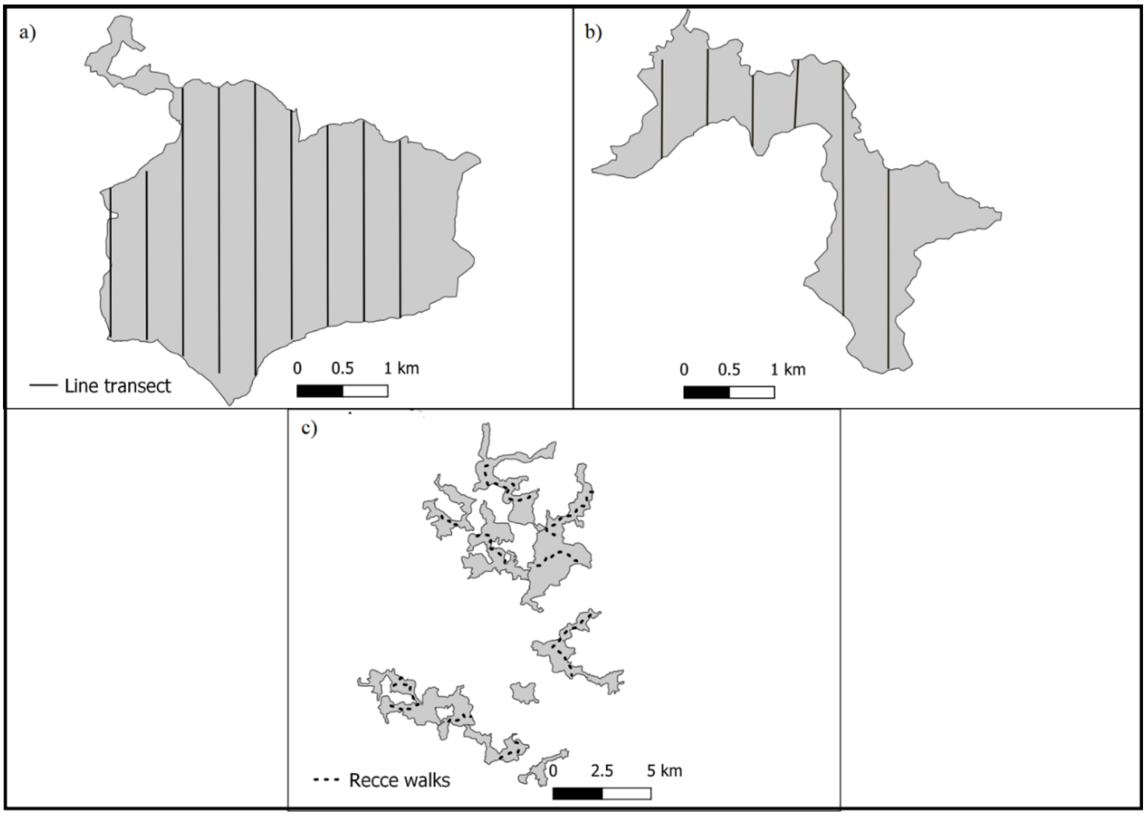

Figure 5. 2. Location of line transects and recce walks in a) the tropical montane forest, b) the restored forest, c) the pine-dominated forest planted in mid-1980s in Gishwati-Mukura landscape, Rwanda.

Crop foraging incidences

As previous studies on crop foraging around the montane and restored forest fragments found that most crop foraging occurs within 200 m of the forest edge (McGuinness & Taylor, 2014; Naughton-Treves, 1998), we collected data about crop foraging incidences (direct observation of presence and absence of primates in people's fields) within 200 m from the remnant tropical montane forest and restored forests. We did not collect crop foraging data around planted forests because no crop foraging incidences were reported near this type of forest (anonymous pasture owners, pers. com). Pasture lands, the dominant land use type around the planted forests, act as a buffer between planted forests and crop fields (Hill, 1997).

To collect crop foraging incidence data, we walked ~31 km around the remnant tropical montane forest and the restored forest counterclockwise starting from the south (at 1° 71´ S, 29° 35´ E) (Figure 5.1). We interviewed any landowners encountered during these walks (above 21 years of age). Landowners could decide whether or not to participate and to which question they wanted to respond. If both a man and woman were encountered together, we allowed them to decide who would respond. We asked whether any primate species had been observed in the field or farm. If any crop foraging incident had occurred during the last 12 months (from July 2018 to June 2019), we asked what species foraged on their crops, if the owners engaged in crop foraging mitigation activities, and how the intensity of crop foraging compared (high=over 60%, medium=between 20-50% and low=below 10%) to the previous three years (between July 2017- June 2018, and between July 2015-June 2017). As respondents remembered better the past two years, our analyses focused on the comparison between July 2017- June 2018 and July 2018-June 2019.

Data analysis

We performed statistical analyses using R package ‘Distance’ to fit detection functions and estimate the abundance and density of primates from measurements of perpendicular distances to the transect lines (Buckland et al., 2010a; Miller et al., 2019). We only calculated density of chimpanzee nests based on individual nests as we had enough field sightings (70 individual nests) to calculate reliable nest density (Buckland et al., 2010a; Furuichi et al., 2001; Plumptre & Reynolds, 1997). We used the ‘ds’ function to fit detection functions. We compared and selected our best models (hazard rate and half-normal) using the Akaike information criterion (AIC). We performed the unweighted Cramér-von Mises test to check whether our models fit the data well (Miller et al., 2019). We used forest type (montane and restored forests) as a covariate and allowed each forest type to have its own detection function. Direct observations of chimpanzees were rare. We only once encountered chimpanzees (five individuals) along line transects in the remnant tropical montane forest, so chimpanzee direct sightings were not included in our analysis. Given that we had few observations of golden monkeys (19 observations) and L’Hoest’s monkeys (12 observations), we only calculated encounter rates (number of groups /km walked), and mean group size.

When fitting the detection functions, we truncated the detections at 20 m for chimpanzee nests. As animal densities cannot be estimated from recce walks data, we only calculated encounter rates, and mean group size for the primates living in planted forests.

To evaluate the incidence of crop foraging, we calculated the percentage of respondents reporting incidents for each species, along with the type of crop foraged on. We ran chi-square tests to determine whether there was a significant difference between participants reporting crop foraging incidences and those who did not report crop foraging incidences between July 2017 and June 2018, and between July 2018 and June 2019.

RESULTS

Primate distribution

We surveyed a total of 88.25 km of line transects, including 63.55 km in the remnant tropical montane forest and 24.7 km in the restored forest. We also collected data along 57 km of reconnaissance walks in forests planted in the mid-1980s. We found all three primate species —chimpanzees, golden monkeys and L'Hoest's monkeys—in the remnant tropical montane forest. We observed only golden monkeys and chimpanzees in the restored forest, and golden monkeys were the only species found in the *Pinus*-dominated planted forest patches (forests planted in the mid-1980s) (Figure 5.3).

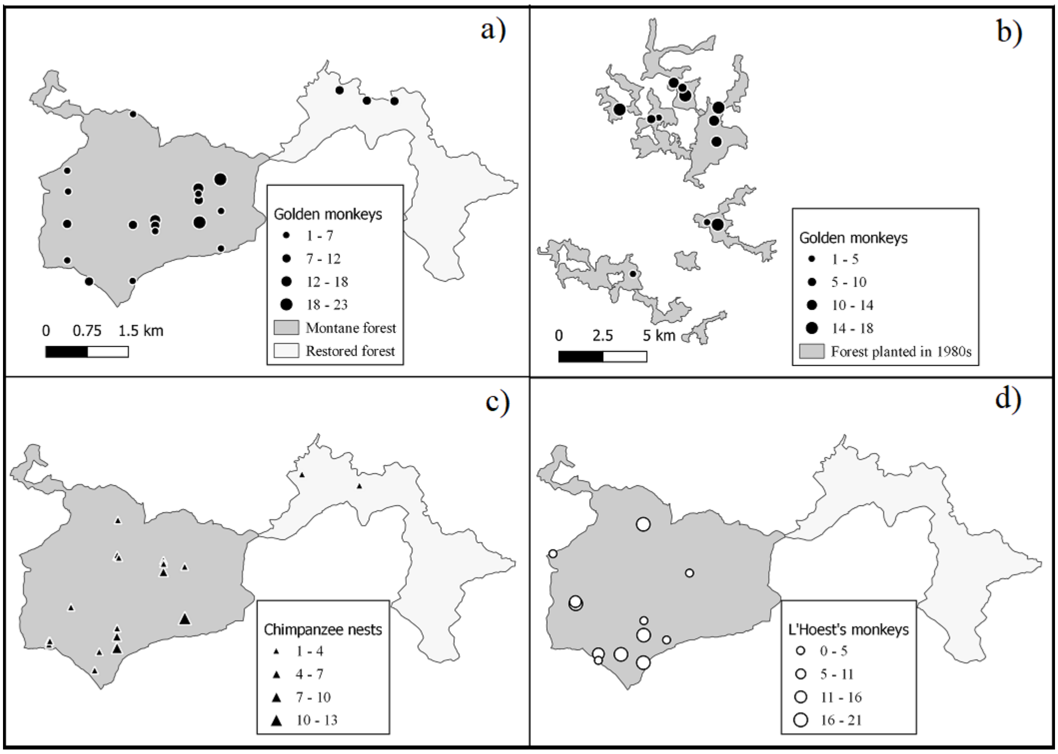

Figure 5. 3. Location of direct observations of golden monkeys (a), the distribution of golden monkey sightings in planted forests (b), and (c) chimpanzee nests in the remnant tropical montane forest and the restored forest in Gishwati-Mukura landscape, Rwanda. Panel (d) direct observations of L'Hoest's monkeys.

Golden monkey and chimpanzee encounter rates were higher in the remnant tropical montane forest than in the restored forest (Table 5.1). The unweighted Cramer-von Mises test indicated that the half-normal detection function with forest type as a covariate fitted best chimpanzee nest data (test statistic = 0.05, p=0.9). The associated average individual detection probability was 0.359 (0.48 in montane forest and 0.1 in restored forest; Figure 5.4). The individual nest density in the montane forest overlapped with individual nest density in restored forest (see Table 5.1). In forests planted in mid-1980s, we observed 15 golden monkey groups (range: 4-18 individuals) at an encounter rate of 0.26 per km; mean group size was 11.5 (4-18) individuals.

Table 5. 1. Summary of the results of primate (chimpanzee, golden monkey, L'Hoest's monkey) transect surveys conducted in the tropical montane and restored forests of Gishwati, part of Gishwati-Mukura National Park, Rwanda between June and August 2019.

	Golden monkey	**L'Hoest's monkey**	**Chimpanzee nests**
Montane forest			
# Observations	19	12	70 (19 clusters)
Encounter rate (no. groups per km)	0.3	0.19	1.1
Group size range	2-23	4-21	2-13
Mean group size (95%CI)	11.8 (2-23)	13.4 (4-21)	4.2 (2-13)
Individual nest density (95%CI)	NA	NA	0.54 (0.21-1.39)
Restored forest			
# Observations	3	0	8 (3 clusters)
Encounter rate (no. groups per km)	0.12		0.32
Group size range	8-11	0	2-4
Mean group size (95%CI)	9.7 (8-11)	0	2.7 (2-4)
Individual nest density (95%CI)	NA	NA	0.77 (0.17-3.52)

*NA: Not Applicable (due to few data points)

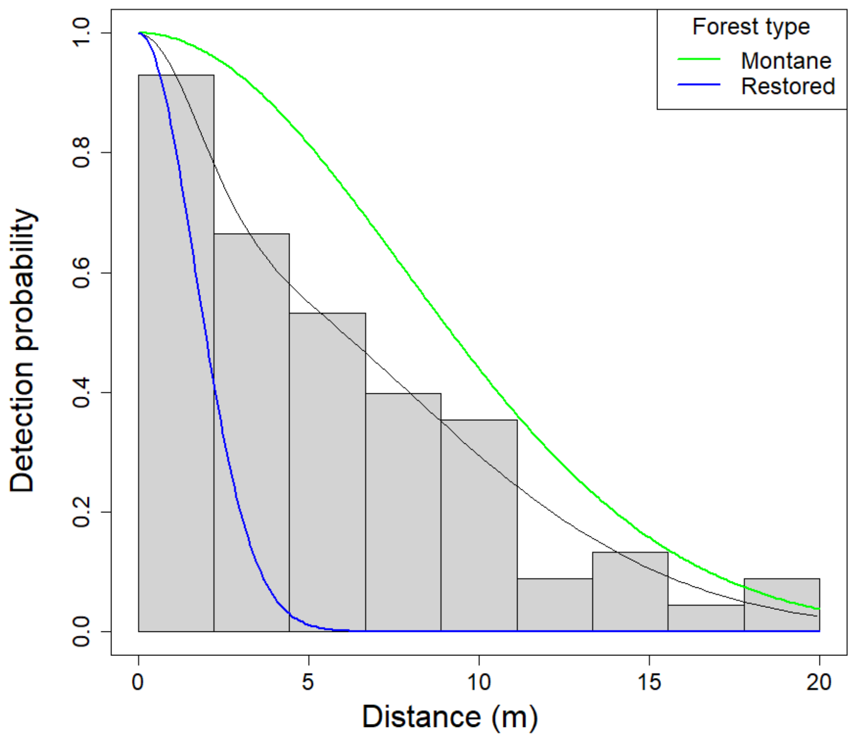

Figure 5. 4. Detection probability of chimpanzee nests in the montane and restored forests, between June and August 2019 in Gishwati-Mukura National Park, Rwanda. Black lines denote mean detection probability. Blue line denotes detection probability in restored forest, while green line denotes detection probability in restored forest, while green line denotes detection probability in montane forest.

Crop foraging incidences

We interviewed 97 farmers (55 females and 42 males) around the tropical montane forest and restored forest fragments. Between July 2017 and June 2018, 72% of the farmers reported that primates had foraged on their crops in the previous 12 months. This percentage declined to 43% between July 2018 and June 2019 (χ^2=4.41, p=0.03). Crops grown within 200 m of the tropical montane forest and restored forest included corn (*Zea mays*) also known as maize, potatoes (*Solanum tuberosum*), beans (*Phaseolus vulgaris*), peas (*Pisum sativum*), and sweet potatoes (*Ipomoea batatas*). The proportion of farmers that identified corn-foraging was the largest (64% of farmers mentioned this crop) followed by potatoes (20%) and peas (11%). All respondents reported having lost crops to L'Hoest monkeys, golden monkeys, and chimpanzees in previous years, mainly between July 2015 and June 2017 and between July 2017 and June 2018. Respondents perceived a decline in crop foraging incidences by primate species, especially by chimpanzees and golden monkeys. All the reported incidents due to chimpanzees and golden monkeys occurred before July 2018. After that date, all the incidents were due to L'Hoest's monkeys, and less than 10% of the interviewed farmers reported having observed chimpanzees and golden monkeys at the edge of the forest, and never on people's farmland (Figure 5.5). To deter crop foraging, 89% of the farmers claimed that they protected their crops by guarding them during the day.

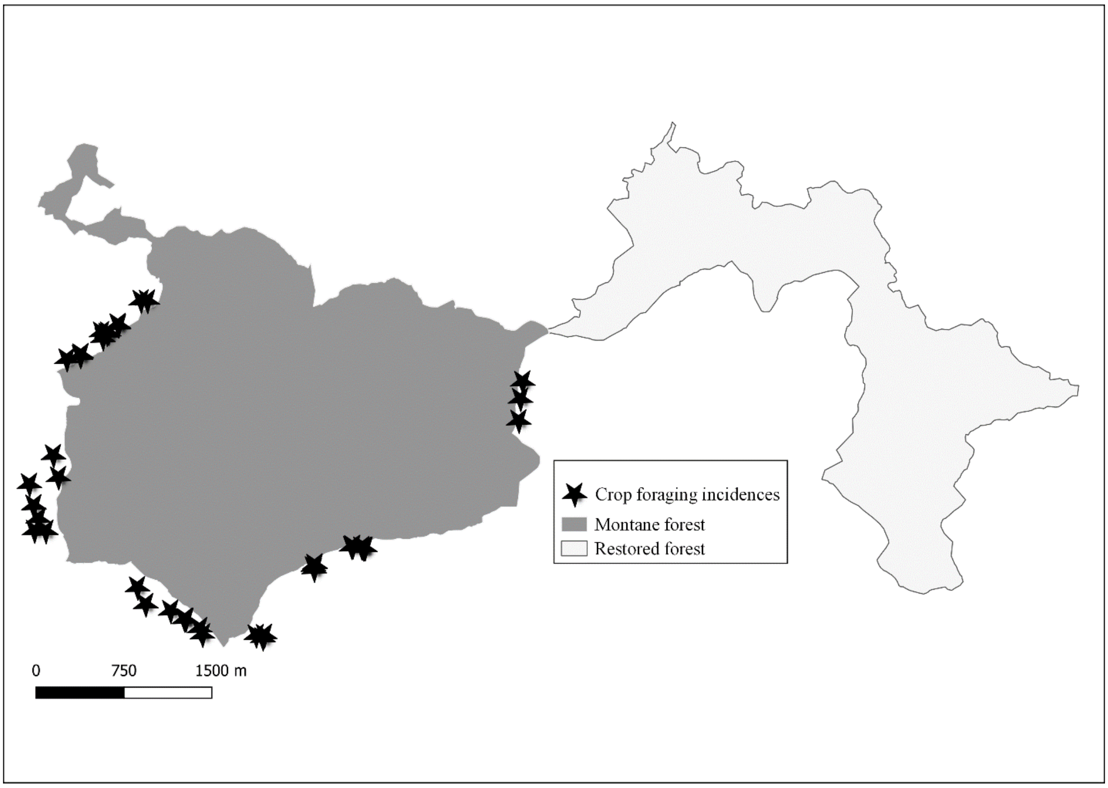

Figure 5. 5. Distribution of crop foraging incidences by primates around the remnant montane forest fragment and the restored forest fragment of the Gishwati-Mukura landscape between July 2018 and August 2019. All these incidents were due to L'Hoest's monkeys, which only occurred in the montane forest fragment.

DISCUSSION

The primate populations in the remnant tropical montane forest fragment, newly gazetted as part of the Gishwati-Mukura National Park, appear to be relatively stable or possibly increasing. The density of chimpanzee nests estimated in this remnant montane forest fragment is similar to previous estimates in Gishwati Forest (range: 1.01 and 2.15/km^2) (Barakabuye et al. 2007). In the montane forest, the golden monkey encounter rate (0.3 sightings/km) was greater than (0.16 sightings/km) previously reported from a study conducted between 2017 and 2018 (Tuyisingize et al. 2022), but this difference might be related to small sample size. Furthermore, encounter rates for L'Hoest's monkeys were high compared to estimates from the nearby Nyungwe National Park (0.01-0.14 sightings/km), while encounter rate for chimpanzees nests in the Gishwati Forest overlaps (0.14-1.57 sightings/km) with the encounter rate of chimpanzee nests in Nyungwe National Park (Easton et al. 2011; Kaplin 2014).

In comparison with previous surveys in the study area (Barakabuye et al. 2007; Chancellor et al. 2012; Tuyisingize et al. 2022), our findings show that primates are expanding their range from the remnant montane forest to the restored forest fragment in the Gishwati-Mukura landscape. Field staff reported seeing a few chimpanzees (~3 individuals) and a small group of golden monkeys (~9 individuals) crossing to the restored forest fragment from the montane forest fragment after 2016, and researchers observed a few chimpanzee nests in the restored forest fragment after 2018 (Chancellor pers. com. 2021). We observed golden monkeys, L'Hoest's monkeys, and chimpanzees in the remnant tropical montane forest, but we also observed golden monkeys and chimpanzees in the restored forest fragment, while golden monkeys only used the exotic planted forest patches initiated in the mid-1980s. Furthermore, chimpanzee nest density did not differ significantly between the montane forest and the restored forest fragment. Most of chimpanzee nests were found in *Macaranga kilimandscharica* and *Symphonia globulifera* (D. T. pers. obs. 2018-2019). Further studies on seasonality and availability of key food are needed to understand the capacity of the restored forest fragment to sustain primates. We also recommend additional studies with a larger sampling effort in both the montane and restored forest fragments to generate accurate density estimates of all Gishwati primate species and to monitor trends over time.

The remnant tropical montane forest fragment is less disturbed and contains a greater diversity of native food plants than the restored forest fragment (Arakwiye 2020; Bizuru et al. 2015; Chancellor et al. 2012). The undergrowth vegetation is dominated by native perennial herbs and vines (e.g., ferns, *Sericostachys scandens*) in montane forest fragments and by ruderal plants (mostly Asteraceae family) in restored fragments (D.T. pers. obs. 2019). In the montane forest fragment, chimpanzees and golden monkeys relied on fruiting trees and fed on fallback foods (leaves) during the low-fruit period (Chancellor et al. 2012; Tuyisingize et al. 2021), while they are suspected to feed mainly on fallback food in the restored forest fragment. The golden monkey population living in the planted forests mainly feed on *Pinus* spp. and *Acacia* spp. trees, and a few other plant species available in these forests (Ngabikwiye 2019).

Current and previous primate species distribution patterns suggest that the remnant tropical montane forest served as refuge site for primates during the periods of forest destruction in this Gishwati-Mukura landscape from the 1980s to 1990s, and our findings show that primates have dispersed to other forest patches in this landscape as it has been protected and restored. Golden monkeys occupied the forest planted in mid-1980s during the 1990s forest conversion period (local community pers. com). As observed in golden monkeys in Mgahinga National Park, Uganda (Twinomugisha et al. 2007), and chimpanzees in the Taï National Park, Ivory Coast, and Gombe National Park, Tanzania (Goodall 2015; Marchesi et al. 1995), the restored forest fragment may represent new habitat for primates in the Gishwati-Mukura landscape, benefiting from the new protection afforded by the recent gazettement of national park status. There was no evidence that L'Hoest's monkeys were present in the restored forest fragment. This species feeds on a larger proportion of terrestrial herbaceous vegetation typical of tropical montane forest than conspecific *Cercopithecus* monkeys (Kaplin and Moermond 2000), which may have kept them in the remnant tropical montane forest rather than expanding to restored forest where the availability of terrestrial herbaceous vegetation may be limited.

This study provides evidence of the presence of Endangered golden monkeys in the pine-dominated planted forest fragments, composed mainly of exotic tree species, within the Gishwati-Mukura landscape. Individuals living in the vicinity of the forest fragments said that golden monkeys may have colonized the planted forest fragments bordering the remnant tropical montane forest fragment during forest conversion to farmland in the 1990s (personal communication, 24 July 2019). The remnant tropical montane forest declined from 280 km^2 to less than 10 km^2 between 1995 and 2000 (Nyandwi and Mukashema 2011). We did not find signs of chimpanzees or L'Hoest's monkeys in planted forests. Compared to these other sympatric primate species (chimpanzees and L'Hoest's monkeys), golden monkeys may have greater ability and flexibility to adapt to new habitats (Chancellor et al. 2012; Chapman et al. 2002; Kaplin 2001; Tuyisingize et al. 2021), which enabled them to include exotic plant species in their diet. The restoration of the Gishwati-Mukura landscape may provide protection and connectivity for the primates that range between the fragments comprising this landscape, and further studies are needed to document movements and use of the different fragments over time. Studies are also needed to understand factors limiting the chimpanzees and L'Hoest's monkeys from colonizing planted forests, and to determine the demography and health of the golden monkey populations using forests planted with exotic species.

Farmers reported that crop-foraging had reduced, potentially owing to the ongoing efforts to protect and restore the Gishwati Forest, as suggested by some farmers. Previous studies reported both chimpanzees and monkeys (golden monkeys and L'Hoest monkeys) as crop foragers (McGuinness and Taylor 2014; Rundus et al. 2022) but according to our results, this study found L'Hoest's monkeys being the only crop foraging primate species. The recent landscape restoration initiatives, including the forest restoration, and the establishment of the

Gishwati-Mukura National Park may have increased habitat availability for the primates, including fruiting trees and bamboo shoots preferred by the primates in this study, which may have reduced conflicts between primates and people. Given that the tropical forest remnant is very small, the incidence of crop foraging should be closely monitored as primate populations may grow due to improved protection, which may result in increasing crop foraging incidences. Climate change could also change or reduce food resource availability for the primates inside the park and force primates to adapt to and rely more on alternative food resources in the surrounding farmlands (Estrada et al. 2017; Graham et al. 2016). Crop-foragers are influenced by proximity of fields to their habitats or by the types of crops grown around the forest (Hill 1997). It may thus be advantageous to encourage local farmers to plant alternative crops (non-palatable plants for primates) or vegetation barriers (see e.g. Wallace and Hill 2016, for crop foraging mitigation strategies in western Uganda), and to promote pasture lands near the forest and move palatable crops away from the park boundary to mitigate existing and future conflicts between agricultural crop production and the Gishwati primates (Rundus et al. 2022).

Conclusion and recommendations

This study highlights the importance of forest landscape restoration to increase available habitat for primates and reduce human-wildlife conflicts. We found uneven distribution of primate species in the Gishwati-Mukura landscape most likely related to their species-specific adaptability to different habitats and food resources. Given that we found golden monkeys using the planted forests dominated by exotic tree species, further studies are needed to ascertain whether the planted forest fragments represent ecological 'traps' or 'sinks' for the primates in this landscape (Dias 1996; Robertson and Hutto 2006). Future studies are needed to investigate and compare birth rates and mortality, diet, activity budget, and energetic balance of primates inhabiting the different forest types to understand habitat effects on fitness, health, and survival. Given that L'Hoest's monkeys are semi-terrestrial forest-adapted monkeys (Kaplin and Moermond 2000), a better understanding of their ecological niche and adaptive capacity in the remnant tropical montane forest is needed to understand why they are not using the restored forest in this landscape.

We show that forest landscape restoration efforts may contribute to the conservation of primates, particularly golden monkeys and chimpanzees. We propose that such forest restoration may also benefit those golden monkeys which currently range in pine-dominated planted forests owned by communities (Oldekop et al. 2016). For example, owners of planted forests could be encouraged to plant native tree species which can provide food resources for golden monkeys (see Tuyisingize et al. 2021, for a list of food plants in the Gishwati forest), and all planted forest fragments could be connected to the Gishwati-Mukura National Park. Because the Gishwati primates, as frugivorous species, need relatively large ranges with adequate supplies of fruiting species and fallback foods (Chancellor et al. 2017; Tuyisingize et al. 2021), it is important to continue the forest restoration actions using plants that are known primate foods, and consider future forest extension strategies that include adjacent peoples' rights and development needs (Nelson 2010), and planting of appropriate montane tropical forest species.

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CHAPTER SIX

REGIONAL GOLDEN MONKEY CONSERVATION ACTION PLAN 2022-2027

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INTRODUCTION

Taxonomy

The golden monkey or golden guenon (*Cercopithecus mitis* spp. *kandti*) is currently recognized as a subspecies *Cercopithecus mitis* spp. *kandti by* the International Union for Conservation of Nature (IUCN) (Butynski & de Jong, 2020a). This classification is used in this Action Plan, although some authors consider it a separate species, *Cercopithecus kandti*. Matschie (1905) described the golden monkey as *Cercopithecus kandti* under Taxonomic Serial No: 944227, a classification also adopted by Groves (2006), Myers *et al.* (2019), and the Convention on International Trade in Endangered Species (CITES) under taxon identification number 9726 (taxon_id: 9726).

Distribution and ecology

The golden monkey today is found in just two small populations in the central part of the Albertine Rift region (Aveling, 1984; Butynski & de Jong, 2020a; Groves, 2006; Myers et al., 2019). These remaining populations are mainly restricted to two forest fragments of different habitat types, the Virunga massif and the Gishwati forest (Figure 6.1). The Virunga massif spans three neighboring countries and consists of the Volcanoes National Park (VNP) in Rwanda, the Mgahinga Gorilla National Park (MGNP) in Uganda, and the Park National des Virunga (PNVi) in the Democratic Republic of the Congo (DRC), mostly in bamboo zone. The other population of golden monkeys is found in the Gishwati forest portion of the Gishwati-Mukura National Park (GMNP), Rwanda, which is tropical montane forest dominated by fruit-producing trees and is located approximately 26 km from the southernmost border of the VNP (Butynski & de Jong, 2020a). Golden monkeys were quoted as being present in Nyungwe forest, but no confirmed golden monkey sightings have been made over the last 25 years of systematic surveys by the Wildlife Conservation Society (WCS) teams and general biodiversity surveys (Plumptre *et al.* 2002; B. A. Kaplin pers. obs.).

Today, the golden monkey is restricted to a narrow elevational distribution from 2100 m to 3550 m, mostly within the bamboo (*Yushania alpina*) zone in the Virunga massif and the Afromontane forest in Gishwati (Aveling, 1984; Groves, 2006; Tuyisingize, 2016; Twinomugisha et al., 2003). In addition, there is a small population living in part of the cleared forest that has been planted with a pine-dominated forest in Gishwati in the 1980s (Tuyisingize *et al.* in revision).

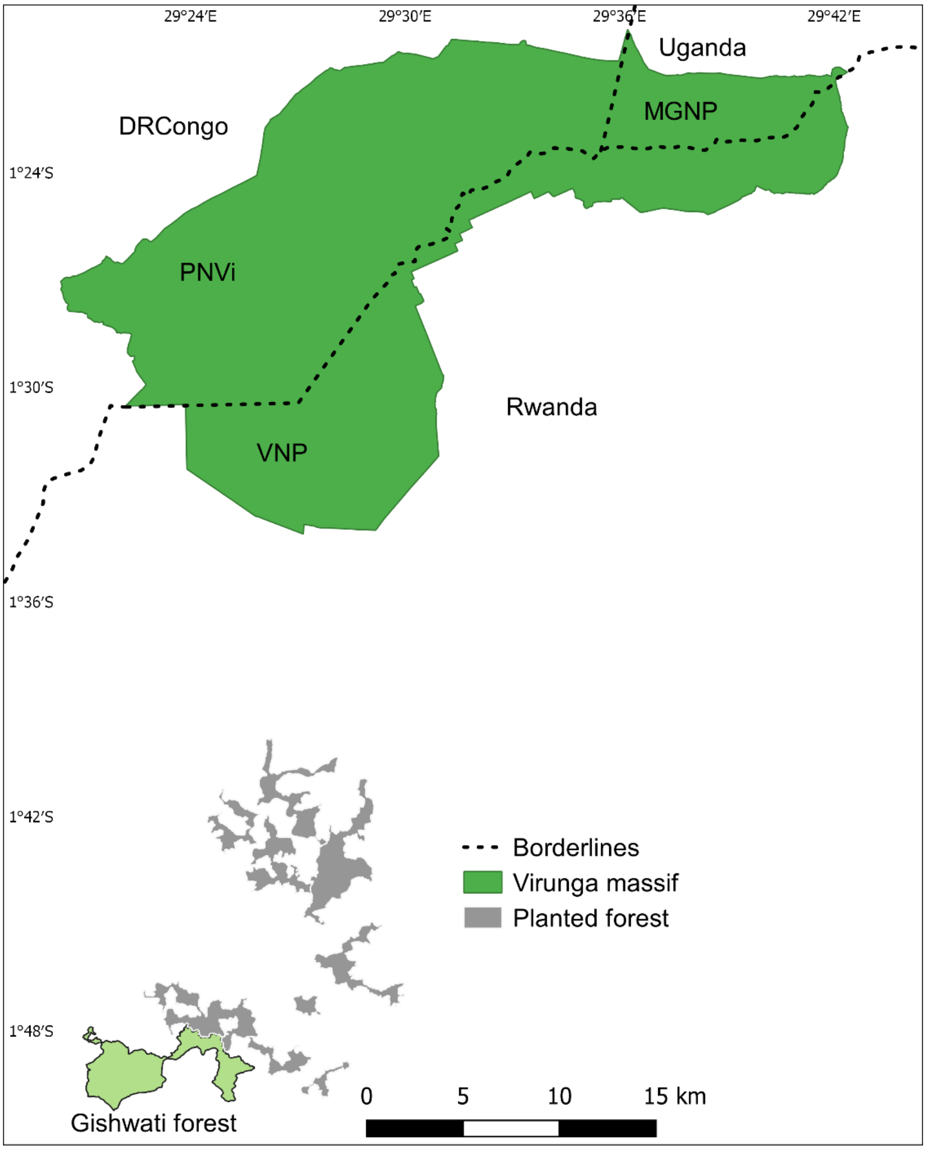

Figure 6. 1. Golden monkey habitats as of 2018: Virunga massif (VNP, MGNP, PNVi), Gishwati forest part of Gishwati-Mukura National Park, and planted forest.

Golden monkeys are mostly arboreal and exhibit a high degree of dietary flexibility, reflecting adaptations to different habitat types and differences in food availability in the respective locations, which is typical in the *Cercopithecus* genus (Butynski, 1990; Takahashi et al., 2019). More than 100 different food plant species have been recorded in their diet across habitats (Tuyisingize et al., 2021; Twinomugisha et al., 2007). Bamboo is the key habitat and the most consumed food plant species for the population in the Virunga massif, while the Gishwati population relies on fruit, leaves and insects (Tuyisingize et al., 2021).

Population trends

Following habitat loss and degradation, the golden monkey population declined by approximately 59% in MGNP (Uganda) between 1998 and 2003, leaving the subpopulation with less than 1,000 individuals (Twinomugisha & Chapman, 2006). This decline is attributed largely to intensive bamboo harvesting and habitat loss (Twinomugisha & Chapman, 2006).

In VNP (Rwanda), however, surveys conducted in 2007, 2011 and between 2017 and 2018 suggest that this golden monkey subpopulation is stable, with 4,626 (range: 4,165 to 5,088) individuals estimated in the most recent survey (Tuyisingize et al., 2021). This stability might be linked to the long-term protected status since 1925 and protection measures that have intensified since the 1980s (Table 6.1). However, golden monkeys seemed to avoid areas with illegal activities (Tuyisingize et al., 2021).

Table 6. 1. Golden monkey population estimates in the Virunga massif (VNP, Rwanda and MGNP, Uganda) and the Gishwati-Mukura National Park (GMNP), Rwanda.

Sites	Population estimates	Year	References
VNP	4,331 (2,723-5,938)	2007	Tuyisingize *et al.* (2021)
VNP	4,487 (2,903-6,071)	2011	Tuyisingize *et al*. (2021)
VNP	4,626 (4,165-5,088)	2017-2018	Tuyisingize *et al*. (2021)
GMNP	172 (154-190)	2017-2018	Tuyisingize *et al.* (2021)
MGNP	2438 (975-3,901)	1998	Twinomugisha *et al.* 2006
MGNP	989 (467-1511)	2003	Twinomugisha *et al.* 2006

No golden monkey survey data are available for the Parc National des Virunga (PNVi) in DRC. Given that many illegal human activities are still observed in the PNVi (Hickey et al., 2019), and golden monkey are hunted for bushmeat, we expect that this golden monkey subpopulation is declining. Regular golden monkey surveys in the PNVi are, therefore a critical step to improve conservation and management. Previous field studies pointed out possible habitat overlap between Stuhlmann's blue monkey, *Cercopithecus mitis stuhlmanni*, near the corridor connecting Mikeno and Nyamuragira sectors of the PNVi (Hickey et al., 2019), and future research would be helpful to determine if hybridization occurs there.

The most recent golden monkey survey in the Gishwati forest estimated a total of 172 individuals (range 154 to 190) in 2018 (Tuyisingize et al., 2021). The abundance of golden monkeys in Gishwati certainly declined from 1995 to 2000 during the deforestation that left only 2% of the Gishwati forest remaining (Nyandwi & Mukashema, 2011; Plumptre et al., 2001). The size of the population living in the planted forests is likely small, and their conservation prospects are of concern given they have limited formal protection.

Threats

Although today the golden monkey populations are predominantly found in protected areas, they are still facing a number of human-related threats and challenges (Ayebare et al., 2018; Hickey et al., 2019; Ndayishimiye, 2018). The main illegal human activities that threaten the golden monkeys across their habitats include bamboo and tree cutting, feral dogs, stoning and chasing by humans following the monkey's crop foraging in cultivated fields, forest fire, snares and the collection of grass in the parks (McGuinness & Taylor, 2014; Ndayishimiye, 2018). In the Virunga massif, most of the illegal activities were found in zones dominated by bamboo (Hickey et al., 2019), the main habitat for golden monkeys in this population (Tuyisingize, 2016; Twinomugisha & Chapman, 2006). There are also illegal human activities reported that are specific to the different national parks, and possible poaching and potential disease transmission (Butynski & de Jong, 2020a).

In the PNVi (DRC), there are some records of golden monkeys being hunted for bushmeat (PNVi staff, pers. comm.). This information is further supported by the presence of hunting camps in the PNVi, detected during the 2015-2016 gorilla survey in the Virunga massif (Table 6.2). In Uganda, the harvest of bamboo shoots as a food source used by the local communities has been observed in MGNP (Twinomugisha & Chapman, 2006). This practice is thought to have been imported from communities around Mt. Elgon, where bamboo shoots are commonly consumed by local people (Karanja, 2017).

Table 6. 2. Summary of common threats to golden monkeys in the Virunga massif and Gishwati-Mukura National Park, Rwanda. X = present; NR = not recorded.

Threats per sites	MGNP	VNP	PNVi	GMNP
Bamboo cutting	X	X	X	X
Forest fire	X	X	X	X
Snaring	X	X	X	X
Wood collection	X	X	X	X

Feral dogs	X	X	X	X
Disease	X	X	X	X
Stoning and chasing	X	X	X	X
Grazing	X	X	X	X
Grass cutting	X	X	X	X
Hunting	NR	NR	X	NR
Water collection	NR	X	NR	NR

A survey involving farmers affected by golden monkey crop foraging and a number of observations by staff of the Gorilla Doctors confirmed the death of several golden monkeys by stoning by local people following crop foraging instances around VNP (Ndayishimiye, 2018). Further potential threats include disease transmission between golden monkeys and human communities as well as between golden monkeys and livestock surrounding VNP (Muhayimana, 2018). In addition, VNP is surrounded by villages with little access to water, and local communities tend to fetch water from the forest especially during the dry seasons. This illegal use of the park may elevate the potential risk of zoonotic disease transmission and illegal activities opportunistically conducted while fetching water. The Gishwati forest part of GMNP and the planted forests in this landscape are surrounded by mining concessions and illegal mining activities, which directly affect the golden monkey habitat. Furthermore, the illegal grazing, wood collection, and grass collection were mainly recorded in the Gishwati forest in the GMNP, which can be a risk of zoonotic disease transmission and further habitat loss.

Conservation status

Since the 1950s, the habitat of the golden monkey has been dramatically reduced and degraded throughout its historical range as a result of intensive human activities (Nyandwi & Mukashema, 2011; Plumptre et al., 2001; Spinage, 1972; Twinomugisha et al., 2003). The two golden monkey populations were once connected but were separated by road construction between the two largest towns (Musanze and Rubavu) in the north-west of Rwanda and agriculture-related activities in the surrounding landscape (Spinage, 1972). VNP was reduced by 50% from 328 km^2 to 160 km^2 between 1958 and 1973 (Plumptre et al., 2001; Spinage, 1972), and the area surrounding VNP is one of the most densely populated areas in Africa with up to 1,000 people/km^2 (NISR, 2012). Such forest clearance and land use change has resulted in the loss of most of the lower elevation forests such as the Afromontane mixed forest zone (similar forest type to the Gishwati forest), which was the only vegetation zone containing fruit-producing trees in VNP (Spinage, 1972).

The Ugandan side of the Virunga massif was gazetted in 1930 as the Mgahinga forest reserve with 33.7 km^2. Since then, it has experienced several bouts of habitat loss and degradation, including human settlement that removed 10.4 km^2 of the forest, which was regained in 1993 when the forest was declared a national park (MGNP) (Twinomugisha et al., 2003). Similarly, for DRC, the PNVi-Mikeno sector (240 km^2) experienced habitat loss and degradation though its size remained the same. It was first invaded by cattle herders in the late 1950s (Dart, 1960), and then degraded by forest clearing (about 16 km^2) by refugees, between 1994 and 1996 (Plumptre et al., 2001).

The Gishwati forest has particularly suffered significant habitat loss due to a World Bank project that clear-cut forest for cattle pasture and pine plantations in the 1980s, and further habitat degradation and loss for human settlements after 1995 (Nyandwi & Mukashema, 2011; Plumptre et al., 2001). These activities reduced the Gishwati forest cover from 280 km^2 in the 1980s to less than 10 km^2 in the 2000s (Nyandwi & Mukashema, 2011). A part of Gishwati (5.6 km^2) was restored in 2015 through efforts from the Government of Rwanda and conservation partners. Approximately 15 km^2 was restored, which prompted the gazettement of the Gishwati forest together with another isolated forest patch, the Mukura forest, to form the Gishwati-Mukura National Park (34 km^2) in the same period (Table 6.3).

Further imminent threats to the habitat of the golden monkey across its range include potential effects of climate change on the bamboo habitat (van der Hoek et al., 2019). A decline in bamboo regeneration has already been observed in VNP and MGNP (Sheil et al., 2012; van der Hoek et al., 2019), with an anticipated impact on golden monkey food availability and distribution (Ayebare et al., 2018).

Table 6. 3. Summary of conservation status of the golden monkey habitats

Conservation status of golden monkey habitat	VNP Rwanda	MGNP Uganda	PNVi DRC	GMNP Rwanda
Size of the park (km^2)	160	33.7	240	34
Establishment year	1925	1993	1925	2016
Management	Park authority	Park authority	Park authority	Park authority
Human density (# people/ km^2) around the park	Up to 1,000	Up to 500	Up to 110	up to 300
Golden monkey population size (recent)	4,626 (4,165-5,088) in 2018	989 (467-1,511) in 2003	NS	172 (154-190) in 2018

Main crops grown around park boundary	Potatoes and *Pyrethrum*	Potatoes and maize	Potatoes and maize	Potatoes and maize
Type of buffer zone	None	None	None	*Alnus sp*
Width of the buffer zone	None	None	None	10-20m

*NS: Not surveyed

Current management strategies

The conservation of golden monkeys benefits greatly from conservation efforts within their habitats, which are mainly within national parks. Additionally, the presence within their range of charismatic and endangered species such as mountain gorillas and eastern chimpanzees (*Pan troglodytes schweinfurthii*), has led to increased conservation funding from donor support and tourism revenues.

However, during the last 16 years golden monkey trekking has increasingly contributed to tourism revenue generation in the VNP and MGNP, making golden monkeys second in income generation after mountain gorilla tourism. Existing tourism plans recommend golden monkey habituation for both research and tourism in both Rwanda and Uganda. Today, golden monkey tourism, research and health monitoring are conducted in Rwanda and Uganda, but not in DRC. Tourism activities are contributing to economic development and job creation in Rwanda and Uganda. Golden monkeys must, therefore, also be recognized for their contribution to tourism revenue generation (*e.g.* in the VNP and MGNP) and the potential to generate additional tourism revenue in Gishwati and the PNVi in the near future (Mehta & Katee, 2005).

We believe that this value can change people's attitude towards a species and thus may also mitigate human-wildlife conflict between local people and golden monkeys (Sabuhoro et al., 2017). Specific and targeted management strategies especially concerning wood collection and the use of bamboo in these areas are needed to reduce the serious threats to the golden monkey's habitats.

GOLDEN MONKEY CONSERVATION ACTION PLAN

Preparation and process

Two workshops were convened, in 2018 and 2019, which brought together 43 people, including conservation biologists, conservation practitioners, park authorities, researchers, and local community members (representatives of cooperatives of ex-illegal park users, and leaders of community conservation groups), from Uganda, Rwanda, and DRC (see Annex 1 and 2). The first workshop focused on developing the plan's vision and goals, and the development of a problem tree that helps to find solutions of cause and effect of threats (problems) around the golden monkeys and their habitat, while the second workshop focused on the design of possible interventions (actions) needed to minimize threats to golden monkeys and their habitat. *Guidelines for Species Conservation Planning* (IUCN, 2017) and the *Conservation Action Planning Handbook* (TNC, 2007) were the main references used to guide participants through the process.

The first workshop with 20 participants was held in Musanze, Rwanda, on 5 October 2018. Participants shared and reviewed existing information on the status of golden monkeys, such as published articles, reports, and data on distribution, ecology, population size, conflicts with local communities, illegal human activities, as well as conservation opportunities in their respective habitats within VNP, MGNP, PNVi and GMNP. After reviewing the available information, the participants jointly identified known and perceived threats to the golden monkeys to be used for threat analyses at each site. The second workshop was held in Musanze, Rwanda, on 18 February 2019, and attended by 23 participants. Participants shared results from the threat-listing for each site to guide the identification of actions to reverse the threats. Based on the Action Plan's vision, the participants were grouped by golden monkey habitat (one of the four national parks) and asked to create a table showing budgets for proposed key activities to be implemented during a five-year plan.

Vision and goals

Through a participatory process during the first workshop, the following vision was articulated: To secure that viable golden monkey populations thrive across their range by 2027. A set of shared goals for all the habitats (VNP, MGNP, PNVi and GMNP) based on the agreed vision were identified:

1. To stabilize the golden monkey population, including building resilience within local communities.
2. To halt the loss and degradation of the habitats and restore those previously degraded.
3. To develop sustainable golden monkey-centered tourism to reduce pressure on existing groups while increasing the contribution of golden monkey tourism to revenue sharing mechanisms.

Threat analysis and problem tree

During the first workshop, participants were given guidance on how to conduct a threat analysis to be used in building a problem tree indicating the main threat that was identified as the "small, fragmented and declining golden monkey populations". The threat analysis allowed participants to identify direct threats (any factor that causes a detrimental impact on population abundance), drivers of threats (the root causes of a direct threat), and constraints (major factors that have an impact on a population) to the golden monkeys and their habitats (IUCN, 2017).

In order to gather more specific and detailed information on the most important threats (which the conservation strategy and plan later prioritized) to the golden monkeys and their habitats, park staff and researchers with the most on-the-ground experience ranked (by considering the degree to which each threat affects affect golden monkeys) each of the threats to the golden monkey on a Likert scale from one to four (1 = low; 2 = medium; 3 = high; 4 = very high), following guidelines of The Nature Conservancy (TNC) and the World Wildlife Fund (WWF) (TNC, 2007; WWF, 2007). All information on the identified threats - including drivers and constraints - were used to build the problem tree (a visualization technique which links threats with their drivers and constraints to addressing the threats) (Figure 6.2).

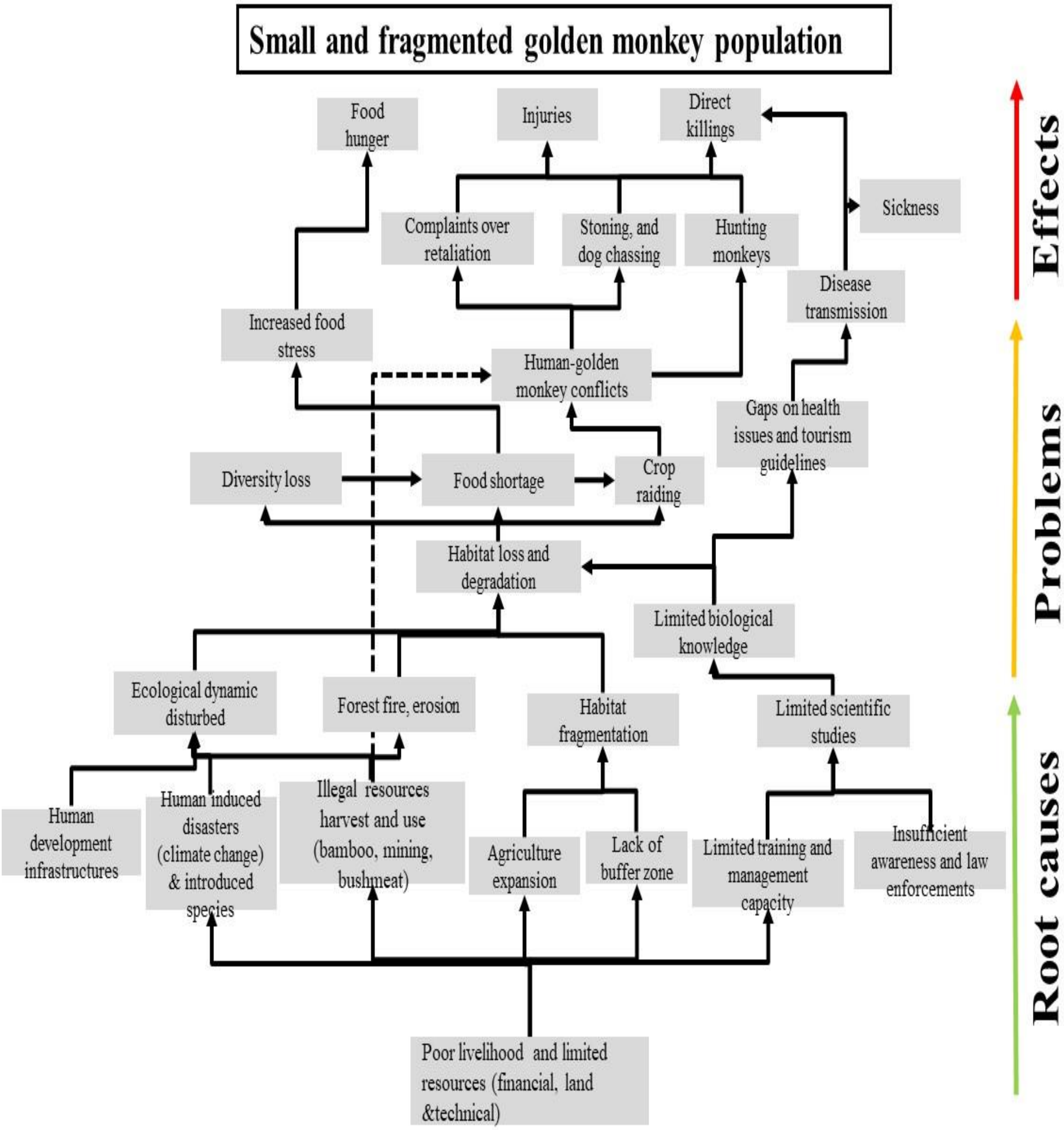

Figure 6. 2. Problem tree depicting the analysis of threats to the golden monkey, their drivers, and constraints (based on workshop discussions

Proposed objectives and actions

Most of golden monkey habitats are protected areas that have been through different phases of habitat loss and land use change policies, therefore, threats to these habitats have different magnitudes at each of the habitats, such that there are common objectives (habitats overlapping) and site-specific objectives (Table 6.4).

Site overlapping objectives

Participants with expertise from the four protected areas where golden monkeys are found identified common objectives for conservation of this species:

a) Reinforce the protection and monitoring of the golden monkey population and its habitats.
b) Carry out more research on the ecology, population dynamics, and population trends of the golden monkeys and their habitats.
c) Reinforce existing and planned golden monkey tourism opportunities and visitor guidelines.
d) Initiate and reinforce programs that create alternative livelihood opportunities (e.g., bamboo harvesting opportunities outside protected areas) with low impact on the golden monkey habitat.

Site-specific objectives

Table 6. 4. The site-specific objectives for Golden Monkey Conservation

Sites	Specific objectives
VNP, Rwanda	Document rates and impact of golden monkey crop-foraging and retaliation incidences and reinforce measures to mitigate the conflict between local people and crop-foraging golden monkeys.
MGNP, Uganda	Remove invasive and alien species from the park and establish fire prevention measures.
PNVi, DRC	Initiate golden monkey tourism opportunities, initiate research on the ecology, population dynamics, and population trends of golden monkeys and their habitats.
GMNP, Rwanda	Assist in rehabilitating the degraded areas; initiate tourism experiences focused on golden monkeys.

Actions to achieve each of objectives

During the second workshop, participants identified and recommended activities to be implemented to achieve goals for each of the protected areas with golden monkey populations. A total of US$1,047,000 (one million and forty-seven thousand dollars) was estimated as the amount needed to carry out the activities recommended in VNP (Table 6.5), in MGNP (Table 6.6), in PNVi (Table 6.7), and in GMNP (Table 6.8).

Table 6. 5. Summary of budget of recommended activities needed in VNP, Rwanda.

Recommended actions	**Potential Partners**	**Time frame**	**Estimated Funding needed US$**
Improve golden monkey protection	RDB, conservation partners, local communities	5 years	70,000
Improve knowledge on golden monkey disease	RDB, conservation partners, local communities	5 years	20,000
Golden monkey population survey	RDB, conservation partners, local communities	5 years	15,000
Reduce habitat degradation	RDB, conservation partners, local communities	5 years	85,000
Improve sustainable golden monkey ecotourism	RDB, conservation partners, local communities	5 years	20,000

Table 6. 6. Summary of budget of recommended activities needed in MGNP, Uganda.

Recommended actions	**Potential Partners**	**Time frame**	**Estimated Funding needed US$**
Reduce illegal bamboo harvesting	UWA, conservation partners, local communities	5 years	22,000
Establish a sustainable bamboo harvesting program benefitting local communities	UWA, conservation partners, local communities	5 years	65,000
Improve knowledge on golden monkey ecology, behavior and population dynamics and trends	UWA, conservation partners, local government	5 years	50,000
Preserve golden monkey habitat from habitat loss and invasive species	UWA, conservation partners, local government	5 years	24,000

Reduce the impact of fire on MGNP	UWA, conservation partners, local government	5 years	20,000
Establish sustainable golden monkey ecotourism	UWA, conservation partners, local government	5 years	8,000
Increase local community awareness and support golden monkey tourism	UWA, conservation partners, local government	5 years	12,000

Table 6. 7. Summary of budget of recommended activities needed in PNVi, DRC.

Recommended actions	**Potential Partners**	**Time frame**	**Estimated Funding needed US$**
Improve protection of the golden monkey population	ICCN, conservation partners, local community	5 years	33,000
Improve knowledge on the conservation ecology of the golden monkeys, and possible disease transmission	ICCN, conservation partners, local community	5 years	58,000
Preserve golden monkey habitat from the loss	ICCN, conservation partners, local community	5 years	115,000
Establish and initiate a golden monkey tourism and tourism regulation	ICCN, conservation partners, local community	5 years	33,000
Initiate local community awareness and sensitization	ICCN, conservation partners, local community	5 years	75,000

Table 6. 8. Summary of budget of recommended activities needed in GMNP, Rwanda.

Recommended actions	Potential Partners	Time frame	Estimated Funding needed US$
Improve knowledge on golden monkey ecology, behavior, population dynamics and trends	RDB, conservation partners, local communities	5 years	35,000
Improve knowledge on golden monkey disease	RDB, conservation partners, local communities	5 years	20,000
Assist in restoration of degraded habitat	RDB, conservation partners, local communities	5 years	49,000
Reduce threats leading to habitat degradation	RDB, conservation partners, local communities	5 years	108,000
Develop and implement the program of ecotourism based on golden monkeys	RDB, conservation partners, local communities	5 years	40,000
Reinforce programs that address alternative local people's livelihoods	RDB, conservation partners, local communities	5 years	70,000

IMPLEMENTATION OF THE ACTION PLAN

The implementation of this Regional Golden Monkey Conservation Action Plan should begin as soon as possible. The accomplishment will be measured by levels of achievements (e.g., habitat protected, reduced threats to golden monkeys, increased income for communities, reduced poverty) the time it takes to achieve the objectives through the implementation of the site-specific activities, focusing on the golden monkey and its habitats, as well as the communities living around them. To coordinate the activities, we grouped all activities into five categories:

a) Community engagement and development
b) Community sensitization
c) Tourism
d) Research
e) Protection and law enforcement

Community engagement and development

Most illegal human activities around the Virunga massif are induced by poverty (Munanura et al., 2018; Sabuhoro et al., 2017); the proposed golden monkey CAP activities must therefore, take into consideration poverty alleviation in the communities surrounding the golden monkey habitats. This can be possible by building on existing governmental and conservation partner initiatives, as well as through the development and support for community-based conservation, such as improving security and access to electricity in the DRC, and support to public infrastructure (e.g., health clinics, clean water) and individual households in Uganda and Rwanda. Support to individuals can include housing, livestock, capacity building of off-farm income-generating activities such as mushroom farming and wool production, and training cooperatives to grow and transform bamboo outside of parks.

Governments have put in place tourism revenue-sharing mechanisms to benefit communities adjacent to national parks. Current tourism revenue-sharing strategies seem to be complex and need restructuring to satisfy stakeholders while ensuring conservation goals. For example, current revenue sharing is criticized for not reaching its potential conservation impacts (Munanura et al., 2016; Tolbert et al., 2019). The existing revenue-sharing programs could evaluate whether individual households, instead of the larger community, should be targeted to improve behaviors towards golden monkey conservation (Cook & Berrenberg, 1981; Sabuhoro et al., 2017).

In the Virunga massif, local communities harvest bamboo heavily as a source of fuelwood, weaving material, and poles for beans, while the bamboo is also the key food species and key habitat for the golden monkeys in the Virunga massif (Sheil et al., 2012; Tuyisingize, 2016, 2017; Twinomugisha & Chapman, 2006). Alternative, sustainable, and accessible sources of poles, weaving materials, and fuelwood sourced from outside golden monkey habitats need to be identified and established to solve this issue. For example the Rwanda Development Board and the Uganda Wildlife Authority and their conservation partners have started planting small indigenous bamboo woodlots along water catchments for stream stabilization in riparian zones and to provide alternative bamboo resources, as it is one of the fastest growing plants and adaptable to any type of soil in the tropical region (Buckingham et al., 2014).

Poor people living around the golden monkey habitats usually use the traditional cooking system on three stones, which wastes much of the energy that would be used for cooking (Manibog, 1984). Providing improved, more energy-efficient cooking stoves to local communities would help to mitigate this conservation issue. It is important to work with communities in the selection of energy-efficient cooking stoves in order to ensure adoption.

Community sensitization

Education programs are needed to build and improve the relationship between local communities and conservation. During the last two decades, the park authorities, together with conservation partners, have been providing conservation education programs to local communities on the importance of the parks. However, illegal human activities persist even though the majority of people report that they benefit from living near parks in the Virunga massif (Tolbert et al., 2019).

There are limited education opportunities for many communities living near the four protected areas that are home to golden monkeys, as well as a lack of off-farm employment opportunities. For example, education programs for school children and community training around the VNP, MGNP, and GMNP are limited to only a few schools and villages (https://www.mcdou.org/ceep-project, https://gorillafund.org/, http://www.fharwanda.org/). Conservation education efforts in communities and schools surrounding golden monkey habitats need to be reinforced and initiated where absent to ensure long-lasting conservation success of the proposed CAP. Park authorities and conservation partners with special skills in conservation education, and conservation donors should be encouraged to organize awareness-raising and funding to support local conservation education.

Given that some local communities still rely on the forests (Munanura et al., 2018), future conservation education training involving students and local community members should focus on building knowledge about and skills for the identification of alternative fuelwood sources (e.g., tree and bamboo planting outside the parks), and on establishing alternative income sources, such as beehive cooperatives. To deliver conservation messages to schools, park authorities and conservation partners have been using environmental and nature clubs, conservation debates, and conservation courses, as well as citizen science programs, which, however, reach a limited number of trainees. These education programs and the teaching content and calendars should be revised and diversified to reach both the students and their parents.

Existing community sensitization programs currently use conservation movies (shown in the evenings) and community cooperatives (https://gorillafund.org/). Although these initiatives reach a large number of people, e.g., 20,000 a year through movies delivered around VNP (https://gorillafund.org/), this number could be increased, and conservation messages could be disseminated throughout the day. For example, conservation messages could be communicated during public community works (using radio drama, local journals in local languages, and in local churches). In addition, the importance of golden monkey conservation and the conservation of biodiversity in general should also be integrated into the national curriculum to ensure that students and teachers around the parks and the wider region are knowledgeable of this unique primate and its conservation status, and the importance of biodiversity. Action-based education programs are powerful tools in conservation and can facilitate links to the need to promote and facilitate park visits by local students and communities (Jacobson, 2010). Furthermore, building upon the success of the gorilla naming ceremony in Rwanda (https://www.rdb.rw/kwitizina/, 2019), park authorities and conservation partners could strengthen existing community sensitization by creating a golden monkey naming ceremony to raise conservation awareness and funding, and to promote positive attitudes.

While education has an important role to play, it is important to combine educational activities with tangible, direct household benefits. The conservation education programs need to support the development of projects that generate revenues for local communities. Participating in golden monkey conservation-centered activities and encouraging local communities to be more active in protecting the golden monkey in its habitats are critical steps for conservation. These activities should ensure the benefits of living near the parks, such as promoting agricultural practices that are friendly to conservation practices (such as mushroom farming) that provide food-rich protein that can substitute bushmeat) and mitigate crop-foraging incidences by golden monkeys (such as cultivating crops that do not attract golden monkeys and other wildlife). Such projects, if developed in a participatory manner with the target communities, can demonstrate the value of conservation in more tangible ways, by improving household revenues, improving nutrition, assuring food security, and providing alternatives to natural resource access outside the parks.

Tourism

As of 2019, two groups of golden monkeys in the VNP and one group in the MGNP are habituated and being visited by tourists (for example, as of 2021 up to 16 tourists visit a golden monkey group per day in the VNP), and the governments share the tourism revenues (10% of revenue in Rwanda, and 5% in Uganda and DRC) with the local communities (Adams & Infield, 1999; Munanura et al., 2016; Sabuhoro et al., 2017). This revenue goes directly to public infrastructure (e.g., schools, clinics, and roads), maintenance of stone walls and trenches at park boundaries to limit wildlife from exiting the parks, cooperatives which then channel the support to households and to support for activities to reduce illegal human activities in the above-mentioned national parks (Adams & Infield, 1999; Munanura et al., 2016; Sabuhoro et al., 2017).

The current tourism revenue sharing strategy needs to be revised to ensure more funds are made available to address urgent community needs. For example, marketing of golden monkey tourism should be intensified, and the number of habituated golden monkey groups should be increased in the VNP and MGNP. The latter would reduce the number of tourists per group visit in the parks and at the same time increase the number of golden monkey tourists resulting in an increased revenue to be shared with local communities. In addition, golden monkey tourism activities should be initiated in the GMNP and PNVi along with the design and implementation of a revenue sharing policy for local development around these golden monkey habitats. Feasibility studies should investigate the maximum number of groups to be habituated as well as the associated risks.

There is no comprehensive study at present on the number of tourists and distances between golden monkeys and visitors that ensure sustainable tourism practices where golden monkey tourism operates. Current regulations need to be revised and harmonized (such as number of tourists per group). A study is needed to provide information to develop guidelines for golden monkey tracking that ensures the sustainability of golden monkey tourism and guarantees conservation benefits for the species. Such guidelines should include instructions that help tourist guides to navigate through golden monkey groups (e.g., splitting tourists into smaller visitor groups while being with the monkeys as opposed to keeping all tourists together in one visitor group during a visit) and rules to be respected while visiting the golden monkey (e.g., minimum allowable distance to the golden monkeys, avoidance of noise, keeping the forest clean, and establish precautionary measures against disease transmission). Extreme conservation measures have the potential to lead to population growth in habituated primates as has been the case for the mountain gorillas (Robbins et al., 2011). The benefits of habituating more groups should be explored, such as ensuring their protection from poaching, avoiding conflicts with humans, and making provisions for regular health monitoring to more golden monkey groups.

Research

Despite their conservation status, little research has been conducted and published on golden monkeys. Using standard methods such as distance sampling, further studies need to document golden monkey population trends, and monitor changes in their distribution, abundance, and effects of illegal activities on golden monkey survival. Studies are needed to investigate whether the isolated forest patches where monkey's inhabitant are population sinks. In addition to surveys, there is a need for long-term ecological research (e.g., impact of climate change on their habitats) in all golden monkey habitats. Studies to resolve taxonomic uncertainties in this species are also of interest. Disease transmission is a critical threat to the golden monkey population of VNP, and studies are needed, therefore, to greatly improve our understanding of golden monkey diseases and their transmission pathways. Such long-term golden monkey research and monitoring projects can offer local employment and capacity building for students.

Protection and law enforcement

Good relationships between parks and the people living around the parks is key for protection and management of biodiversity (Oldekop et al., 2016; Wilkie et al., 2006). Although all golden monkey habitats are regularly patrolled and protected in collaboration with communities (in VNP and MGNP), golden monkeys still face many threats (bamboo cutting, wood collection, and grazing amongst others) related to their habitats and conflicts with local communities. Strengthening the enforcement of the existing protection and laws governing the integrity and management of the existing national parks is, therefore, essential. This can be achieved by reinforcing existing collaboration with local communities, while improving local people's livelihoods and integrating local people in the daily protection of the park. The anti-poaching units should be improved by providing more rangers, while increasing the number of community conservation groups (*animateur de conservation*). This can be supplemented by a campaign of education and law enforcement against illegal activities that aligns with the above section on community sensitization.

Despite some success in arresting poachers and other people that illegally use the park's resources, those arrested people are often released without prosecution due to a lack of evidence or weak environmental laws. To ensure effectiveness of the laws, park authorities should continue working with conservation organizations to influence public institutions (e.g., National Police, the Ministry of Justice, local leaders) in charge of law enforcement.

Ensuring the benefits of living near the parks through reducing human-wildlife conflicts is one of the ways to engender positive attitudes toward conservation (Oldekop et al., 2016). A comprehensive assessment of existing measures and their effectiveness is needed and alternative measures to enforce existing measures should be investigated.

Conclusions

Habitat loss and degradation, human-wildlife conflict, and gaps in biological knowledge are major threats to the golden monkeys. The golden monkey habitat is under human pressure. This five-year (2022–2027) action plan aims to ensure sustained golden monkey populations and to address income generation for local communities that live near golden monkey habitat to reduce threats to the species. The success of this action plan will depend on community engagement and development, community sensitization, tourism, and research, as well as improving protection and law enforcement.

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CHAPTER SEVEN

CONCLUSIONS

The golden monkey (*Cercopithecus mitis kandti*) is an Endangered subspecies of blue monkey (*Cercopithecus mitis*) endemic to the Albertine Rift ecoregion. It is restricted to two isolated forest fragments, the Virunga massif, a landscape comprising three national parks: Volcanoes National Park (VNP) in Rwanda, Mgahinga Gorilla National Park (MGNP) in Uganda, and Virunga National Park (ViNP) in Democratic Republic of the Congo; and the Gishwati-Mukura National Park (GMNP) in Rwanda. This study focused on populations living in VNP and the remnant Gishwati forest fragment, part of GMNP. Both study sites went through different series of habitat fragmentation, degradation, and habitat loss, which resulted in the isolation, reduction, and degradation of the golden monkey habitat in the 1950s, followed by further forest degradation. The VNP has been protected since 1925, while Gishwati forest and Mukura forest fragments were gazetted as the GMNP in 2016. In VNP, golden monkeys mostly live in the bamboo zone where fruiting trees are extremely rare, while in the Gishwati forest, golden monkeys mostly live in the afromontane forest dominated by fruiting trees. My research aimed at understanding how golden monkeys cope with forest fragments of different habitat types. Specifically, I investigated population density, distribution, diet and habitat use, and reproductive patterns in the study areas.

This study confirmed previous research findings on blue monkey diet. Golden monkeys have a very flexible diet. Both study populations (two groups with 60 and 150 individuals in VNP and one group with 30 individuals in Gishwati forest) feed on a diversity of food types, including 111 plant species, and adjust their diets and ranging patterns to local habitat and available food resources. In VNP, they are folivorous and mostly feed on leaves (on average 73-87% of the diet), dominated by bamboo leaves (on average 44-70% of the diet) and on seasonally available bamboo shoots (on average 10-19% of the diet). In contrast, the population inhabiting the Gishwati forest mostly feeds on fruit (on average 17-80% of the diet).

These dietary adjustments to different habitats also determined reproduction patterns in the study populations. Like other guenon species, golden monkeys are seasonal breeders with distinct mating and birthing seasons. Mating was observed year-round but peaked four to six months prior to each group's respective birthing season. Key food availability strongly determines golden monkey birthing seasons, even at a small spatial scale within VNP, likely because of observed fine-scale differences in bamboo phenology. Elevational patterns in the bamboo shoot growing season correlate with the timing of births in the golden monkeys; between September and December, bamboo shoots mainly regenerate in the lower elevation zone, while bamboo shoots in the higher elevation zone mainly regenerate between March and May (van der Hoek et al. 2019). Bamboo shoots are rich in protein, fiber, and minerals, while fruit is rich in carbohydrates and fats which are needed during the most demanding reproductive stages (e.g., lactation, gestation) in mammals (Clutton-Brock 2006; Dufour and Sauther 2002). In the Gishwati population, the birthing season correlates with a high abundance of fruit in the habitat, which occurs between March and August.

Differences in the spatial and temporal distribution of key foods, as well as in previous conservation efforts, may drive differences in golden monkey group sizes and densities between the study sites. Our surveys showed that golden monkey groups in the VNP are larger than groups in the Gishwati forest. Like blue monkey species, the frugivorous Gishwati group had a larger mean monthly home range area (150.07 ha) compared to both folivorous VNP groups (25.24 and 91.3 ha), likely due to the unevenly distributed fruits in Gishwati compared to evenly distribution foliage in VNP. Mean estimates of golden monkey group density in VNP (5.41–7.89 groups/km^2) are closer to the MGNP population in Uganda, and other blue monkey populations living in protected areas (Twinomugisha and Chapman 2006), while the mean density of the Gishwati population (1.27–3.16 groups/km^2) is similar to blue monkeys found in recently logged and fragmented forests in Uganda (Chapman et al. 2000). Recent surveys conducted from 2017–2018, which provide more precise findings based on sufficient field efforts, serve as a baseline to estimate future population trends.

This study also highlights that forest landscape restoration is an important strategy for the recovery of primate species, in the Gishwati-Mukura landscape. We found that golden monkeys and chimpanzees (*Pan troglodytes schweinfurthii*) have expanded their range to the restored forest parts. The restored forest provided additional habitat for primates, and efforts to restore degraded forest appear to have reduced conflicts between local communities and primates. Therefore, it is important to continue forest restoration efforts and park expansion initiatives. Conservation decision-makers need to start exploring future forest extension and planting of appropriate montane tropical forest species to increase suitable habitat for primates in GMNP and in VNP.

Although today the golden monkey populations are predominantly found in protected areas, they are still facing several human-related threats and challenges (habitat loss and degradation, human-wildlife conflict, and gaps in biological knowledge). As part of this thesis, together with key partners acting in golden monkey conservation, we developed the first conservation action plan for this species, and it will be implemented during the next five years (from 2022-2027) across their entire distribution range. This action plan provides guidance for reducing threats and improving the protection of the golden monkey. Actions defined in the plan aim to ensure sustainable golden monkey populations and to address income generation for local communities that live near golden monkey habitat to reduce threats to the species.

Future research and conservation perspectives

This dissertation represents a contribution to understanding the conservation ecology of golden monkeys and their habitats in a changing environment. This study demonstrated how golden monkeys cope with available habitat and resources, but the long-term survival of golden monkey is uncertain. Recent studies found a decline in bamboo shoots and fruit availability in the golden monkey ranges and surrounding tropical forests (Chapman et al. 2005; van der Hoek et al. 2019), and illegal human activities are ongoing throughout the golden monkey range despite ongoing protection efforts. Thus, more conservation efforts and studies are needed to protect golden monkey and better understand its behavioural ecology.

First, it is important to continue exploring the spatial and temporal composition of the golden monkey's diet as well as intraspecific and interspecific food competition in the study areas. It is important to explore changes in key food availability and it affect monkeys' energetic balance, as well as focal studies on females' reproductive events (mating and birthing events). Also, there is a need to understand impact of climate change on the montane tropical ecosystems, and golden monkeys. These studies will help to better understand how food resource availability may affect group size and composition, ranging patterns (e.g., daily travel distances), and golden monkey reproductive patterns (birth rates, infanticides, gestation, and lactation periods) over time. Secondly, given the ongoing forest landscape restoration initiatives especially around VNP and GMNP, more studies are needed to examine habitat use, diet, and distribution of primate species in the restored areas, and how the restored forests help in reducing human-wildlife conflicts. Lastly, we designed a conservation action plan that would help in reducing threats to monkeys. Once this action plan is implemented, we expect reduced threats to golden monkeys and improved golden monkey conservation. We therefore recommend carrying out golden monkey surveys across their distribution range combined with illegal human activities surveys every 5 years. These studies will help to update the golden monkey conservation status at national levels and globally.

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