

Factors affecting golden-crowned sifaka (*Propithecus tattersalli*) densities and strategies for their conservation

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ABSTRACT

Habitat degradation and hunting pose the most proximate threats to many primate species, while climate change is expected to exacerbate these threats (habitat and climate change combined henceforth as “global change”) and present new challenges. Madagascar’s lemurs are earth’s most endangered primates, placing added urgency to their conservation in the face of global change. My dissertation focused on the critically endangered golden-crowned sifaka (*Propithecus tattersalli*; hereafter, “sifaka”) which is endemic to fragmented forests across a gradient of dry, moderate, and wet forest types in northeastern Madagascar. I surveyed sifakas across their global range and investigated factors affecting their densities. I explored sifaka diets across different forest types and evaluated if nutritional factors influenced sifaka densities. Lastly, I investigated sifaka range-wide genetic diversity and conducted a connectivity analysis to prioritize corridor-restoration and other potential conservation efforts. Sifaka densities varied widely across forest fragments (6.8 (SE = 2.0-22.8) to 78.1 (SE = 53.1-114.8) sifakas/km²) and populations have declined by as much as 30-43% in 10 years, from ~18,000 to 10,222-12,631 individuals (95% CI: 8,230-15,966). Tree cutting, normalized difference vegetation index (NDVI) during the wet season, and Simpson’s diversity index (1-D) predicted sifaka densities range-wide. Sifakas consumed over 101 plant species and spent 27.1% of their active time feeding on buds, flowers, fruits, seeds, and young and mature leaves. Feeding effort and plant part consumption varied by season, forest type, and sex. Minerals in sifaka food items (Mg ($\beta = 0.62$, SE = 0.19) and K ($\beta = 0.58$, SE = 0.20)) and wet season NDVI ($\beta = 0.43$, SE = 0.20)

predicted sifaka densities. Genetic measures across forest fragments indicated that sifaka populations are becoming more isolated (moderate F_{IS} values: mean = 0.27, range = 0.11-0.60; high M -ratios: mean = 0.59, range = 0.49-0.82; low overall effective population size: $N_e = 139.8$ -144 sifakas). F_{ST} comparisons between fragments (mean = 0.12, range = 0.01-0.30) supported previous findings that sifakas still moved across the fragmented landscape. Further validation of these genetic results is needed. I identified critical corridors that conservation managers could protect and/or expand via active reforestation to ensure the continued existence of this critically-endangered lemur.

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GENERAL AUDIENCE ABSTRACT

Worldwide, many species of primates are threatened with extinction due to habitat degradation, hunting, and climate change (habitat and climate combined threats, henceforth, “global change”). These threats work at different time scales, with hunting being the most immediate and climate change likely to have its fullest impact experienced from the present to a longer time frame. Lemurs are a type of primate found only on Madagascar, an island experiencing rapid global change, which puts lemurs at a heightened risk of extinction. My dissertation research focused on the critically endangered golden-crowned sifaka (*Propithecus tattersalli*; hereafter, “sifaka”), a species of lemur found only in a few isolated forests across a dry to wet gradient in northeastern Madagascar. To better understand their extinction risk, I conducted surveys to estimate the number of sifakas remaining and investigated several factors that might determine how many sifakas can live in one place. I then explored how sifaka diets varied depending on the forest type that they inhabit and tested whether nutrients in their food might determine sifaka numbers. Lastly, I calculated sifaka genetic diversity to assess their ability to adapt to new environmental conditions and to determine whether sifakas can move across the landscape to find new mates and to potentially colonize new areas of habitat. Sifaka densities varied widely across their range (6.8-78.1 sifakas/km²). Only 10,222-12,631 sifakas remain, which is 30-43% less than the range of estimates obtained 10 years ago (~18,000 sifakas). Tree cutting, normalized difference vegetation index (NDVI; a measure of plant health or “greenness” obtained from satellite data), and a tree species diversity index were useful measures to predict sifaka densities. Sifakas ate

different plant parts (buds, flowers, fruits, seeds, and leaves) from over 101 plant species. The amount of time they spent eating each day varied by the time of year, forest type, and sex. On average, they spent a quarter of their day eating. Magnesium and potassium concentrations in sifaka food items also were useful nutrition-related measures to predict sifaka densities. Genetic analyses suggested that sifaka populations are becoming more isolated and inbred, meaning sifakas are breeding with other sifakas to which they are closely related. However, it appears that sifakas still can move between forest patches to find new mates and to potentially colonize new areas, if such areas are created. Further validation of these genetic results is needed. I also identified critical areas that will be important to protect and reforest to ensure that movements between populations can continue.

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ATTRIBUTIONS

This section describes the contributions made by coauthors towards each of the chapters included in this dissertation.

Chapter 2. Highly variable densities and a decline in critically endangered golden-crowned sifaka (*Propithecus tattersalli*) population abundance from 2008 - 2018

Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) helped to secure funding, provided support, provided methodological and analytical guidance, and substantially edited the manuscript. Meredith Semel (Department of Biological Sciences, Virginia Tech) helped to secure funding and provided substantial support in the field. Dean Stauffer (Department of Fish and Wildlife Conservation, Virginia Tech) provided methodological and analytical guidance and edited the manuscript. Erwan Quéméré (Ecology and Ecosystems Health, French National Institute for Agriculture, Food and Environment) provided logistical, methodological, and analytical guidance and edited the manuscript. Jeff Walters (Department of Biological Sciences, Virginia Tech) provided substantial edits to the manuscript. Angelo Andrianiaina (Département de Zoologie et Biodiversité Animale, Université d'Antananarivo), Ando Rakotonanahary (Département de Biologie Animale et Ecologie, Faculté des Sciences, Université de Mahajanga), Tamby Ranaivoson (Département Zoologie et Biodiversité Animale, Université d'Antananarivo), Dimbisoa Rasolonirina (Département de Biologie Appliqué à l'Environnement, Faculté des Sciences, Université de Mahajanga), and Faramalala Vololonirina (Mention Anthropobiologie et Développement Durable, Faculté des Sciences, Université d'Antananarivo) provided substantial support in the field and help with logistics.

Chapter 3. Minerals and normalized difference vegetation index (NDVI) predict golden-crowned sifaka (*Propithecus tattersalli*) densities

Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) helped to secure funding, provided support, provided methodological and analytical guidance, and substantially edited the manuscript. Meredith Semel (Department of Biological Sciences, Virginia Tech) helped to secure funding and provided substantial support in the field and lab. Angelo Andrianiaina (Département de Zoologie et Biodiversité Animale, Université d'Antananarivo), Ando Rakotonanahary (Département de Biologie Animale et Ecologie, Faculté des Sciences, Université de Mahajanga), Tamby Ranaivoson (Département Zoologie et Biodiversité Animale, Université d'Antananarivo), Dimbisoa Rasolonirina (Département de Biologie Appliqué à l'Environnement, Faculté des Sciences, Université de Mahajanga), and Faramalala Vololonirina (Mention Anthropobiologie et Développement Durable, Faculté des Sciences, Université d'Antananarivo) provided substantial support in the field and help with logistics. Erwan Quéméré (Ecology and Ecosystems Health, French National Institute for Agriculture, Food and Environment) provided logistical, methodological, and analytical guidance. Jessica Rothman (Department of Anthropology, Hunter College, City University of New York and New York Consortium in Evolutionary Primatology (NYCEP), New York, New York) facilitated plant export permits and helped to conduct and interpret all lab analyses.

Chapter 4. Golden-crowned sifaka (*Propithecus tattersalli*) population genetics and recommendations for corridor restoration to promote connectivity of isolated forest fragments

Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) helped to secure

funding, provided support, provided methodological and analytical guidance, and substantially edited the manuscript. Erwan Quéméré (Ecology and Ecosystems Health, French National Institute for Agriculture, Food and Environment) provided logistical, methodological, and analytical guidance. Meredith Semel (Department of Biological Sciences, Virginia Tech) helped to secure funding and provided support in the field. Angelo Andrianaina (Département de Zoologie et Biodiversité Animale, Université d'Antananarivo), Ando Rakotonanahary (Département de Biologie Animale et Ecologie, Faculté des Sciences, Université de Mahajanga), Tamby Ranaivoson (Département Zoologie et Biodiversité Animale, Université d'Antananarivo), Dimbisoa Rasolonirina (Département de Biologie Appliqué à l'Environnement, Faculté des Sciences, Université de Mahajanga), and Faramalala Vololonirina (Mention Anthropobiologie et Développement Durable, Faculté des Sciences, Université d'Antananarivo) provided substantial support in the field and help with logistics. Eric Hallerman (Department of Fish and Wildlife Conservation, Virginia Tech) helped to secure funding, provided support and laboratory space, provided methodological and analytical guidance, and edited the manuscript.

CHAPTER 1: INTRODUCTION

Madagascar's lemurs (Primates: Lemuridae) have been declared Earth's most threatened mammals, with 103 of 107 species currently threatened with extinction (IUCN 2020; Schwitzer et al. 2014). Lemurs are found nowhere else on the planet and represent 15% of all primate taxa (Schwitzer et al. 2013). Madagascar's unique combination of high species endemism and numerous highly threatened species earned the island recognition as one of Earth's highest priority biodiversity hotspots (Myers et al. 2000). Currently, habitat degradation and hunting pose the two greatest near-term threats to lemur survival (Cowlshaw and Dunbar 2000; Schwitzer et al. 2014). However, large-scale anthropogenic change in the form of climate and land cover change (henceforth "global change") present additional long-term threats that, if left unaddressed by conservationists today, may render management efforts ineffective (Brown and Yoder 2015; Morelli et al. 2019; Schwitzer et al. 2013). Only by considering both near- and long-term threats will conservation efforts ultimately prove successful.

Forest degradation, in particular, presents a major near- and long-term challenge to conservation efforts in Madagascar. Between 1953 and 2014, forest cover decreased by 44%, and remaining habitats are increasingly fragmented due to unsustainable land use practices (Harper et al. 2007; Vieilledent et al. 2018). Slash-and-burn agriculture, or *tavy* in the Malagasy language, is a traditional agricultural technique practiced by the Malagasy people to fertilize nutrient-poor soils. However, increased food demands from a growing population now prevent adequate fallow periods, resulting in increased agricultural encroachment into remaining forests (Mittermeier et al. 2010; Schwitzer et al. 2013). Vieilledent et al. (2018) found that 46% of Madagascar's remaining forest is within 100 m of the forest edge. Forest fragmentation limits species' dispersal and increases human access to forest interiors. Increased forest access by people often leads to

accelerated resource extraction (Cowlshaw and Dunbar 2000; Laurance et al. 2009), such as hunting imperiled species (Smith et al. 1997; MacDonald et al. 2012).

Lemur hunting, including of critically endangered species, is now widespread across much of Madagascar. Traditional taboos that once protected many species from hunting pressures are rapidly eroding (Barrett and Ratsimbazafy 2009; Conservation International 2010; Jenkins et al. 2011). As people increasingly leave their homelands in search of new opportunities, they are unlikely to abide by the new taboos that they encounter (Golden and Comaroff 2015). Hunting also is integrally linked to human health and welfare (Borgerson et al. 2016), categories in which Madagascar has received some of the lowest global rankings (Economist Intelligence Unit 2015). Additionally, an increasing urban demand for lemur meat adds a new dimension to illegal hunting in Madagascar (Barrett and Ratsimbazafy 2009).

Unfortunately, the causal factors behind deforestation, habitat fragmentations, and hunting are likely to only worsen during periods of political instability. For example, Madagascar's coup d'état in 2009 further exacerbated lemur habitat degradation and hunting mortality (Barrett and Ratsimbazafy 2009; Schwitzer et al. 2014). National Parks and World Heritage Sites in eastern Madagascar were raided by illegal loggers for prized timber species such as rosewood (*Dalbergia sp.*) and ebony (*Diospyros sp.*; Barrett et al. 2010; Schwitzer et al. 2013, 2014). Critically endangered golden-crowned sifakas (*Propithecus tattersalli*), formerly protected from hunting by taboos, were even sold in restaurants as a luxury bushmeat (Barrett and Ratsimbazafy 2009; Conservation International 2010). Return to a more stable governance following internationally-recognized democratic elections in 2013 highlighted these internal threats and some effort is being made to address them. However, climate change represents a

more far-ranging and less well-defined threat to Madagascar's biodiversity, especially in highly fragmented habitats (Brown and Yoder 2015; Morelli et al. 2019).

Historical climate change has played a significant role in shaping habitats and species extinctions across Madagascar due to wide fluctuations in multi-year wet and dry periods (Burney 1987; Wells 2003). Climate-induced environmental change is particularly challenging for species in discontinuous habitats if they lack viable movement corridors to seek more favorable conditions (Ingram and Dawson 2005; Brown and Yoder 2015). For example, recent genetic studies revealed that northern grassland expansion during a prolonged Holocene drought may have triggered a population bottleneck of golden-crowned sifakas inhabiting a dynamic forest and grassland mosaic (Quéméré et al. 2012; Salmona et al. 2017). Current climate models suggest that Madagascar will again face significant climate shifts, with some parts of the island expected to experience increased rainfall during wet periods and other parts to experience reduced rainfall during dry periods (Ingram and Dawson 2005). In response to climate change, species face three options. They may 1) shift their range to spatially track their ecological niche, 2) behaviorally or genetically adapt at the population- or species-level to new conditions, or 3) be extirpated. As noted above, forest corridors between large forested areas that enable species to shift their range to more suitable locations are limited by forest loss and degradation in Madagascar (Harper et al. 2007; Brown and Yoder 2015). Additionally, reduced population sizes, due to hunting and habitat loss and degradation, tend to decrease behavioral and genetic variability (Cowlshaw and Dunbar 2000; Frankham et al. 2010). Together, these facts paint a grim picture of the long-term outlook for Malagasy fauna.

In March 2019, the Malagasy government announced a plan to reforest at least 40,000 hectares across the island between 2020 and 2025 (Vyawahare 2019). The scale of the effort

recognizes the need of the island's growing population to meet ever increasing resource needs (CIA 2020), to stabilize soil runoff on this already nutrient-poor tropical island (Aubréville 2015; Gade 1996), and to halt and hopefully reverse the loss of its unique biota (Harper et al. 2007; Vieilledent et al. 2018). This reforestation plan also presents an opportunity to strategically assist in the restoration of gene flow and to facilitate species movement in response to climate changes across the island (Schüßler et al. 2020). Determining which plant species will best support imperiled wildlife and where corridors will be most effective is crucial to effective corridor planning and preserve design.

Research is needed to assess current populations of endangered Malagasy species, imminent anthropogenic threats, and habitat connectivity. The better we understand the extent of any behavioral and genetic variation within existing populations, the better we will be able to predict the likelihood that Madagascar's threatened fauna will be able to adapt and persist in the face of global change. This is only possible when we study species over a gradient of habitats. The goal of my dissertation research was to assess these needs and to identify practical steps that could be implemented by conservation biologists concerned with the long-term survival of the critically endangered golden-crowned sifaka (IUCN 2019). Compared to other sifaka species, the golden-crowned sifaka remains poorly studied. This species also has one of the most restricted distributions of all lemur species, making it particularly vulnerable to the threats described above (Vargas et al. 2002).

In Chapter 2, "Highly variable densities and a decline in critically endangered golden-crowned sifaka (*Propithecus tattersalli*) population abundance from 2008-2018," I discuss survey results of golden-crowned sifakas in forest fragments and mixed-cover areas across their entire global range. Those surveys were critical in providing an update to the population estimate

for the species from 10 years prior. I also conducted extensive vegetation and human disturbance surveys to characterize the forests in which extant populations were found. I then combined these datasets to determine factors that affected sifaka densities using a model selection approach.

In Chapter 3, “Minerals and normalized difference vegetation index (NDVI) predict golden-crowned sifaka (*Propithecus tattersalli*) densities,” I collected feeding data on sifaka groups in three different forest types (dry, moderate, and wet) to capture the full gradient of sifaka feeding and dietary diversity. I conducted nutritional analyses on the predominant food items consumed by sifakas from each of these forest types during both the wet and dry seasons. Using density data from Chapter 2, I then used model selection to evaluate whether any nutritional variables provided by these food items were useful for predicting sifaka densities.

Finally, in Chapter 4, “Golden-crowned sifaka (*Propithecus tattersalli*) population genetics and recommendations for corridor restoration to promote connectivity of isolated forest fragments,” I collected fecal samples from sifakas across their range for genetic analyses. I evaluated population structure, inbreeding, effective population sizes, and potential migrants within and across fragments throughout the species’ known range. Using the program Circuitscape (Shah and McRae 2008), I developed likely movement corridors between forest fragments based on my findings in this dissertation. Combining genetic data and corridor modelling results offered an adaptive resource management approach and clear guidance for conservation managers on how to implement increased monitoring, protection, and reforestation efforts to ensure the long-term population viability of this critically endangered species amidst ongoing global change.

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Chapter 2

Highly variable densities and a decline in critically endangered golden-crowned sifaka (*Propithecus tattersalli*) population abundance from 2008 – 2018

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**Highly variable densities and a decline in critically endangered golden-crowned sifaka
(*Propithecus tattersalli*) population abundance from 2008 - 2018**

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Abstract

Animal abundance is determined by a number of ecological factors, including vegetation structure, food availability and quality, human activities, predation risk, and disease. While the latter two can often be difficult to assess, vegetation structure, food availability, and human activity are often used to guide major conservation efforts, such as protected area zoning and reforestation, especially for primates. We sought to determine whether critically endangered golden-crowned sifaka (*Propithecus tattersalli*) densities could be predicted at both local and landscape scales across a heterogeneous landscape as a function of vegetation structure, food availability, and human activity. Walking transect surveys were conducted across the sifakas' entire global range in the Loky-Manambato Protected Area of Madagascar from 2016–2018, expanding upon a smaller-scale study conducted in 2006/2008. Potential predictors of sifaka density included metrics of vegetation structure (*e.g.*, tree density, forest fragment area, forest type), food availability (*e.g.*, Simpson's index of diversity and Hill evenness indices of food tree species, food tree basal area, and normalized difference vegetation index (NDVI)), and human activity (*e.g.*, tree cutting, livestock grazing). The best predictors of sifaka densities were tree cutting and wet season NDVI value, which both positively related to sifaka densities. From 2008 to 2018, populations declined by 30-43%, from ~18 000 animals to 10 222-12 631 individuals (95% CI: 8 230-15 966). Sifaka densities within forest fragments across their restricted range (880 km²) were highly variable (6.8 (SE = 2.0-22.8) to 78.1 (SE = 53.1-114.8) sifakas/km²), emphasizing the importance of large-scale and randomized study designs for assessing species abundance, regardless of the species' area of occupancy.

Keywords: abundance, Madagascar, primate, NDVI, lemur, golden-crowned sifaka

1. Introduction

Understanding which ecological and anthropogenic factors affect animal abundance is important to long-term conservation planning (Mills, 2012). Previous studies have demonstrated that animal densities, even for species with limited global ranges, may vary widely in response to vegetation structure and landscape composition (Anderson et al., 2003; Bakker et al., 2002; Flather and Sauer, 1996; Pardini et al., 2005). Variation in population density presents a challenge to conservationists, who often use density estimates to extrapolate species abundance estimates both within patches and across the species' range (Caughley, 1994). Overestimates could lead to inadequate protection efforts, while underestimates could lead to improper resource allocation and erosion of public trust.

For primates, several factors have been suggested to affect population abundance including food availability (Herrera et al., 2018; Stevenson, 2001) and nutrition (Chapman et al., 2002; Hanya and Chapman, 2013; Milton, 1979), forest structure (Anzures-Dadda and Manson, 2007; Linder and Lawler, 2012; Mborra and Meikle, 2004; Phoonjampa et al., 2011; Rovero and Struhsaker, 2007), predation (Lwanga et al., 2011), and disease (Nunn and Altizer, 2006; Strindberg et al., 2018). Additionally, human activities may limit abundance directly (*e.g.*, via habitat destruction or hunting) or be the underlying cause of changes in any of these factors (Murphy et al., 2016; Ray et al., 2015; Sharma et al., 2013).

Madagascar's lemurs were recently declared Earth's most threatened mammals, with 103 of 107 extant species listed as critically endangered (IUCN, 2020; Schwitzer et al., 2014). Lemurs are found nowhere else on the planet and represent 15% of all primate taxa (Schwitzer et al., 2013). Currently, less than 15% of Madagascar's primary forest cover is thought to remain, and forests continue to be lost at a precipitous rate, with deleterious consequences for lemurs,

which rely on forest cover (Vieilledent et al., 2018). While some species have evolved to become habitat specialists with highly restricted ranges (*e.g.*, *Hapalemur alaotrensis*; Mittermeier et al., 2010), other species have adapted to a variety of habitats, but have been restricted to a small geographic area due to physical barriers (*e.g.*, *Eulemur* spp.; Markolf and Kappeler, 2013) or habitat change and fragmentation (*e.g.*, *Lepilemur septentrionalis*; Mittermeier et al., 2010).

Determining the factors that drive variation in lemur population densities is critical for conservation planning and management activities for these imperiled taxa. However, lemur density, distribution, and response to these factors all vary markedly among lemur species depending on habitat heterogeneity and species ecology. Frugivorous species tend to require areas dominated by mature forests, while more folivorous and insectivorous species tend to be more tolerant of, or even to prefer, areas with some level of disturbance (Lehman et al., 2006; Murphy et al., 2016). Herrera et al. (2018) found that species distribution models of lemur food trees strongly predicted densities of several lemur species in eastern Madagascar, even more strongly than climate variables. Taken together, these findings suggest that food resource availability is a good predictor of lemur density.

One challenge to this food availability hypothesis has been that many lemur taxa exhibit higher densities in drier than wetter forest when found in both, and wetter areas generally are assumed to be more resource abundant. Lehman and Fleagle (2006) suggested that significant nutrient leaching in high rainfall areas may explain reduced lemur densities in wet forests. Similarly, the seasonal flush of new leaves that often are lower in toxins while still high in nutrients in dry forests (van Schaik et al., 2005), or the reduced photosynthetic production of specific proteins in wet forests due to dense cloud cover provide additional nutrition-based explanations for higher densities in dry as opposed to wet forests (Ganzhorn, 1992; Irwin, 2006).

Non-food-related hypotheses also have been proposed, such as that differences in densities may be due to higher lemur species diversity in evergreen versus dry forests (Setash et al., 2017).

Critically endangered golden-crowned sifakas (*Propithecus tattersalli*; hereafter ‘sifakas’) are endemic to the Loky-Manambato Protected Area in northeastern Madagascar. They exhibit wide density variation across their limited range (880 km²) and have a tolerance for edge habitats (Quéméré et al., 2010a; Vargas et al., 2002). The species’ geographic range once was far more extensive and less fragmented, but it remains unclear to what extent droughts during the Holocene or human-induced changes restricted their current range and the size of the forest fragments between the Loky and Manambato Rivers (Quéméré et al., 2012, Salmona et al., 2017; Douglass et al., 2019). Population assessments for this species have been few and their results varied, with one study estimating a global population between 6 100 and 10 000 individuals (Vargas et al., 2002), while a subsequent study conducted in 2006 and 2008 (henceforth, “2006/2008”) estimated a total population of roughly 18 000 animals (Quéméré et al., 2010a). This latter study documented significant variation in population densities among forest fragments (34.0 – 85.8 individuals/km²). While Quéméré et al. (2010a) did not directly test for factors driving density variation, they did suggest habitat variation and resource availability as potential influencing factors. Meyers (1993) found that young leaves and flowers are their preferred foods, though this has been questioned, as most sifaka species appear to be frugivore-folivores (Irwin, 2006). Unripe fruits and seeds make up the bulk of the sifakas’ diet; buds, bark, mature leaves, ripe fruits, and leaf petioles also are consumed (Meyers, 1993).

The objectives of this study were to: (1) estimate sifaka densities in forest fragments across their entire global range, (2) establish accurate forest cover loss estimates for the region, (3) determine whether vegetation structure, food availability, human activity and/or forest type

could be used to predict sifaka density, and (4) update the global population abundance estimate for this species. We expected to see a decrease in forest cover within the golden-crowned sifaka range over the past 10 years, as has been documented for forest habitat across Madagascar in general (Vieilledent et al., 2018). We expected that sifaka densities in available forest would remain relatively consistent since the last survey in 2006/2008 (10 years prior) due to local taboos against hunting. We hypothesized that sifaka abundance would be driven by food availability. More specifically, we expected to find that food tree basal area would be the best predictor of sifaka densities, as food tree basal area has been shown to be highly correlated with food availability for frugivorous species (Chapman et al., 1992). We also expected that densities would be higher in dry forests due to the seasonal flushes of nutrient-rich vegetation (Ganzhorn, 1992; van Schaik et al., 2005). Overall, we predicted a decline in range-wide abundance in the past 10 years due to forest cover loss.

2. Materials and methods

2.1 Study area and survey design

Golden-crowned sifakas are endemic to northeastern Madagascar and are confined between the Loky and Manambato Rivers (49°56'E, 13°31'S), though a few groups have been found in an isolated forest block on the west side of the Loky River near the town of Maromokotra (Fig. 1). Sifakas are found from low-elevation (10 m) dry deciduous forest and scrubland to moderate-elevation (1 000 m) wet evergreen forest across their range. Forests are highly fragmented and comprise dry sclerophyllous, deciduous to dense, humid forests (Meyers,

1993; Nusbaumer et al., 2010; Quéméré et al., 2010a). A mix of cattle pasture, agricultural areas, and scattered forest patches and riverine forest corridors separate large contiguous forested areas that are largely restricted to higher elevations (Quéméré et al., 2013). All of the forest fragments surveyed are part of the 250 000 ha Loky-Manambato Protected Area (PA), which is managed by the NGO Fanamby (Gardner et al., 2013).

We conducted lemur and vegetation surveys May-July 2016 (cool, early dry season), August-December 2017 (cool, late dry season), and September-December 2018 (cool, late dry season). We did not conduct any surveys during the wet season due to logistical constraints. Transect start points were randomly selected along the forest edge and either continued into the interior or followed some forested corridor along a streambed if a straight line could not be followed (*e.g.*, steep embankment or large rocks). Transects were spaced at least 600 m apart to avoid double-counting groups (*i.e.*, 1.5x the radius of the largest observed home range (25 ha); M. Semel, unpublished data).

We established 28, 1-3 km line transects in 11 of the largest forest fragments within the golden-crowned sifaka global range (Fig. 1; Supplemental Table 1). Previous studies did not divide the Bekaraoka forest fragment in two; therefore, for all direct comparisons between our study and previous studies, we also combined and analyzed Bekaraoka Avaratra and Bekaraoka South as a single fragment. Vargas et al. (2002) conducted point count surveys in three of these fragments (Antsahabe, Binara, Bekaraoka (surveying only Bekaraoka South but projecting values to the whole fragment)) in 2001 and Quéméré et al. (2010a) surveyed five fragments (Ambohitsintondroina, Antsaharaingy, Bekaraoka (Avaratra and South), Benanofy, and Tsarahitsaka = Solaniampilana) in 2006/2008. We also established seven “mixed-cover” area transects to assess the sifakas’ use of the mixed pasture, grassland, agricultural, and

riparian/patchy forest areas between the large forest fragments. Previous studies included forest patches in these areas as part of their total forest cover estimate, but assumed that such areas had the same average density as the surveyed contiguous forest fragments. If any transect did not yield any lemur sightings over the course of five days of survey effort, it was replaced by a transect in a different location the following year. We included transects that did not yield any lemur sightings in the analyses. Henceforth, the 11 forest fragments and the mixed-cover area will be collectively referred to as “study units” ($N = 12$).

Two-member teams walked each transect every morning (0600-0830hr) and afternoon (1500-1730hr) for 4-10 days (mean = 6.7 days) in each study unit during each year that the study unit was sampled (Supplemental Table 1). One member rotated daily to avoid observational bias and to ensure transect familiarity (Buckland et al., 2010). Perpendicular distance to the first animal seen was measured using a range finder, a measuring tape, or visual estimation when direct measurements were not feasible due to vegetation or terrain (Buckland et al., 2010; Whitesides et al., 1988). Group location and group size were recorded. Animals found within 100 m of one another were considered part of the same group unless they were moving in opposite directions or displayed signs of group aggression (*e.g.*, group “sifak” vocalizations, tossing head back, agitated vigilance in the direction of other individuals; Fichtel and Kappeler, 2002).

2.2 Forest Cover

Vargas et al. (2002) and Quéméré et al. (2010a) conducted surveys in 2001 and 2006/2008 and estimated sifaka abundance based on forest area estimates from LANDSAT™

1994 and 2002 imagery (30-m² resolution), respectively. We created land cover maps in ENVI 5.3 (Harris Geospatial Solutions, Broomfield, Colorado, USA) using composite LANDSAT 7 and 8 satellite imagery (30-m² resolution) from 2002 and 2017-2019 to determine forest area changes over the course of all three studies. Clouds and cloud shadows were removed from images using the program MFMask, which uses digital elevation models to improve pixel selection for removal (Qiu et al., 2017). Nine broad land cover types (water, evergreen forest, semi-deciduous forest, deciduous forest, scrub, grass, bare ground, sand, and flooded sand) were determined using the IsoData unsupervised classification method (Tou and Gonzalez, 1974). An accuracy assessment for the 2017-2019 map was conducted based on high-resolution imagery (Google Earth, 7 May 2013 - 23 April 2017) and personal visits to the sites. Ten points (30-m² pixels) were assessed for each cover type using the Google Earth imagery. Grass, bare ground, and flooded sand were condensed into one land-cover type (bare ground) following this assessment. The 11 forest fragments were delineated using the boundaries of contiguous tracts of all combined forest classes (evergreen forest, semi-deciduous forest, deciduous forest, and scrub). All remaining forest class areas were considered part of the mixed-cover area. We recalculated abundances for the previous studies based on their density estimates and our more precise forest area estimates. This provided not only more accurate, but also more fully comparable estimates of both abundance and forest cover loss.

2.3 Predictors of sifaka abundance

Vegetation structure and human activity surveys were conducted along each walking transect in all 12 study units by assessing a list of predictors (*italicized below and listed in*

Supplemental Table 2). A sub-sample average was calculated for each walking transect, and walking transect averages were computed so that each study unit was a sampling unit for subsequent analyses. All analyses were conducted in the program R (R Core Team, 2019).

2.3.1 Vegetation structure

Every 200 m along each walking transect, one 50-m vegetation transect was established perpendicular to the walking transect.

We measured *vegetation stratification*, *canopy height*, and *tree canopy cover* at 10-m intervals along the vegetation transect for a total of six samples per vegetation transect, which were then averaged. To evaluate vegetation stratification, a 2-m pole was held perpendicular to the ground and the presence or absence of vegetation that would touch the imagined vertical extension of the pole from 2-5 m above ground level was recorded (Davis et al., 2011). Canopy percent cover was determined using ocular estimates of vegetation cover through a cylinder at 2 m height. These values were then averaged from two separate observers.

Tree density, *total basal area* for all trees, and average *basal area per tree* for all trees were assessed using the point-centered quarter method (PCQ; Pollard, 1971) at 25 m and 50 m on the vegetation transect. Tree species (Malagasy vernacular names), diameter at breast height (DBH), and distance to nearest tree with a DBH ≥ 5 cm in each point-quarter were recorded and a correction factor was applied to account for quarters without trees (Warde and Petranka, 1981).

Tree crown volume was calculated using the formula for an ellipsoid for each tree within the PCQ:

$$V = \frac{4}{3}\pi \left(\frac{CH}{2}\right) \left(\frac{CD1}{2}\right) \left(\frac{CD2}{2}\right)$$

where CH represents crown height and CD1 and CD2 are perpendicular crown diameters based on vertical and horizontal reference poles (2-5 m long). For the purpose of this analysis, snags were not identified to the species level.

Tree species diversity was determined using *Shannon's index* and *Simpson's index of diversity (1-D)* based on tree species recorded within PCQ plots. Tree species evenness was determined using *Hill* and *Pi evenness* scores using the R package, “vegan” (Oksanen et al., 2019).

2.3.2 Food availability

We documented tree species used by sifakas for feeding in nine forest fragments (Ambohitsintondroina, Ampondrabe, Antsahabe, Antsaharaingy, Bekaraoka (South and Avaratra), Benanofy, Binara, and Solaniampilana) in the dry season (August – December in 2017 and 2018) and also from three of these fragments (Bekaraoka South, Binara, and Solaniampilana) in the wet season (February – April 2018) using Malagasy vernacular names. We identified food trees using 15-minute scan samples from sunrise to sunset of two groups of sifaka groups at each forest fragment for a maximum of 10 days per sifaka group (Altmann, 1974). Because preferred food trees varied by site due to availability and phenology (Quéméré et al., 2013), we assumed that any tree species used for feeding in one fragment was used in all other fragments. We then determined *food tree basal area*, *food tree basal area per tree*, *food tree density*, *food tree crown volume*, *food tree Shannon's index*, *food tree Simpson's index of diversity (1-D)*, and *food tree Hill and Pi evenness* scores as described in the “Vegetation structure” section above using only data from food trees.

Average normalized difference vegetation index (NDVI) values have been used widely in ecology as a metric of food availability to successfully predict herbivore abundance and distribution (Pettorelli et al., 2011). NDVI is an index ranging from -1.0 to 1.0 and can predict the abundance of vegetation. Based on the fact that chlorophyll strongly absorbs visible light for use in photosynthesis, while in contrast the cell structure of the leaves strongly reflects near-infrared light, the more leaves a plant has, the more these wavelengths of light are affected, respectively. If there is more reflected radiation in near-infrared wavelengths than visible wavelengths, then the vegetation is likely to be dense. More negative NDVI values thus indicate standing water or areas barren of vegetation while values closer to 1.0 indicate increasingly chlorophyll-rich, thick vegetation indicative of temperate or tropical forests (Pettorelli et al., 2011). We calculated both *NDVI dry* and *NDVI wet* season values for each study unit.

2.3.3 Human activity

We recorded signs of human activity within a 10-m radius of the center point for each point-quarter plot at 25 m and 50 m perpendicular to the walking transect. Each of the following was measured on a five-point scale indicative of the degree of activity (1 = lowest intensity, 5 = highest intensity): *tree cutting* (the number of cut trees/limbs), *fire*, *mining* (*i.e.*, soil disturbance), and *livestock grazing* (henceforth, “grazing;” mostly by zebu/cows; Supplemental Table 3). Other incidental observations were recorded as well, such as evidence of hunting lemurs, but these were not measured on a scale (*i.e.*, traps, camp sites).

2.3.4 Forest types

We sought to quantify differences among forest types in our model in a manner similar to previously identified forest types based on extensive remote sensing and on-the-ground vegetation surveys by Chatelain et al. (2006) to use as a predictor in our models. We performed a detrended correspondence analysis (DCA) using tree species from the PCQ plots for each fragment (Hill and Gauch., 1980). Forest fragments were grouped into different forest types by performing a cluster analysis on the *DCA1* values (Folega et al., 2012) using the Euclidean distance method and hierarchical clustering in the R package, “vegan” (Oksanen et al., 2019). Raw *DCA1* and *DCA2* values also were considered as individual density predictors. Mixed-cover areas were set aside as their own type *a priori* since by their definition they did not represent a forest type.

2.4 Sifaka density and abundance estimation

We estimated population densities using the multiple covariates distance sampling engine (MCDS) in the program Distance v. 7.3 (Thomas et al., 2010). To ensure adequate sample size for density estimation (40 group sightings; Peres, 1999), transects were grouped by study unit ($N = 12$). Prior to analyses, we truncated the farthest 10% of observations and adjusted distance binning to ensure acceptable goodness-of-fit ($p > 0.05$; Buckland et al., 2010; Thomas et al., 2010). Group size was included as a covariate to account for imperfect group detection (Clement et al., 2017). All covariates that we suspected might have an impact on detection were scaled (normalized to 0 and 1) and included as covariates on the detection function (Supplemental Table

4). The effect of these variables on the detection function is independent of the effect of these variables on animal densities (Buckland et al., 2010; Thomas et al., 2010).

We modeled all key function (*i.e.*, half-normal or hazard rate) and adjustment expansion (*i.e.*, cosine, polynomial, or hermite polynomial) combinations. We stratified observations by study unit to obtain a density estimate for each individual study unit. Using each study unit as a sampling unit, we examined how densities varied by vegetation structure, food availability, human activity, and forest type variables (see Section 2.5 below). To obtain a global density estimate for the stratified model, we weighted the density estimate of each study unit by its area (Thomas et al., 2010). We ranked resulting models using AICc (AIC corrected for small sample size), and models whose $\Delta AICc < 4.0$ were considered competing (Arnold, 2010).

To determine the total forest likely to support sifaka populations for abundance estimates, we removed the following from the land cover maps: 1) forested areas outside of the species' known range (Jiménez and Vargas, 2000; Quéméré et al., 2010b; Vargas et al., 2002), 2) single, isolated forest pixels (30 m^2 , $<0.01 \text{ km}^2$), and 3) forested areas too small to satisfy minimum home range requirements ($<0.09 \text{ km}^2$) that were beyond the maximum inferred sifaka dispersal distance of a “large” forest fragment ($>1.5 \text{ km}$; Quéméré et al., 2010b). We subtracted the large contiguous forest fragments from the total forest area to obtain an area for mixed-cover areas. We compared the resulting total forest area estimates against those determined by Vargas et al. (2002) and Quéméré et al. (2010a) to evaluate any resulting change in overall abundance estimates.

2.5 Relationship between sifaka density and vegetation structure, food availability, human activity, and forest type predictors

We first evaluated correlations between predictors. If two variables were highly correlated ($|r| > 0.70$), we kept the most easily measured variable and removed the other from the analysis (*e.g.*, readily obtained remote sensing variables were preferred over difficult-to-obtain field measures). We used negative binomial models to evaluate which non-correlated predictor variables best-predicted sifaka abundance in the R package, “MASS” (Supplemental Table 2; Venables and Ripley, 2002). Because these models use count data, sifaka abundance values were used as model response values, not density values. To account for study unit area, models were offset by the log value of contiguous forest area for each fragment (O’Hara and Kotze, 2010). These models responded better to overdispersion tests than models with a Poisson distribution as confirmed in the R package, “DHARMA” (Hartig, 2020). We ranked the resulting models using AICc values, and models whose $\Delta\text{AICc} < 4.0$ were considered competing (Arnold, 2010). We were unable to include multiple variables in a single model due to small sample size. Prediction plots were produced in R using the package “ggplot2” (Wickham, 2016).

This research complied with protocols approved by the Virginia Tech Institutional Animal Care and Use Committee (IACUC # 15-223) and adhered to the legal requirements for research conducted in Madagascar (Permit No. 117/16/MEEF/SG/DGF/DAPT/SCBT).

3. Results

3.1 Forest cover

Agreement between classification of land cover classes from 2017-2019 Landsat imagery and visual inspections based on high-resolution satellite data and personal visits to sites was 92.0% (Supplemental Table 5). Total forest within the study area in 2002 was 537.3 km² compared to 475.3 km² in 2017-2019, representing an 11.5% loss in forest cover area in less than 20 years (0.58% loss/year; Fig. 1). Our revised estimate of 537.3 km² of forest in 2002 was 22.1% greater than the previously published estimate of 440 km² of total forest area in that same year (Vargas et al. 2002, Quéméré et al., 2010a).

3.2 Vegetation structure, food availability, human activity, forest types

We estimated understory cover, vegetation stratification, canopy height, and canopy cover along 651, 50-m vegetation transects in 12 study units (11 forest fragments and mixed-cover areas; mean = 54.25 (SE = 11.44) vegetation transects per study unit). A total of 1 338 PCQ plots (mean = 111.48 (SE = 22.12) PCQ plots per study unit) contained 375 tree species representing at least 66 families and 220 genera. Over half of tree species encountered (282/512) while conducting plant and animal surveys that were identified to unique Malagasy vernacular names could not be identified to the family or genus level – we assumed that these were unique species. Overall, species diversity in all study units was high (Simpson's index of diversity (1-D): mean = 0.95, SE = 0.01), while tree density varied greatly across study units (range in forest fragments: 554.2 – 2 306.9 trees/ha; 254.4 trees/ha in the mixed-cover areas, Table 1).

Food trees were determined based on ~3 200 hours of observations of 18 groups of sifakas in nine fragments (two groups per fragment). Sifakas consumed plant parts (*e.g.*, ripe/unripe fruits, young/mature leaves, seeds, flowers) from at least 101 plant species, with 28 species constituting > 80% of the diet overall (Supplemental Table 6). We followed several sifaka groups from the forest edge out into mixed-cover areas, but we were unable to locate sifaka groups that lived exclusively in mixed-cover areas.

We conducted a total of 1 239 samples from our human activity surveys. Tree cutting was the most intense activity (1 = lowest intensity, 5 = highest intensity) across all study units, with an average score of 1.74 (range 1.03 – 1.89; Table 1). Tree cutting was also the most pervasive activity across all study units, with 42.7% of plots having a score >1 (median = 1; range 1-5). Fire was the next most pervasive, with 25.1% of plots having a score >1. Across all study units, grazing was most prevalent in mixed-cover areas (mean = 2.51, SE = 0.48). The highest grazing index in any of the 11 forest fragments was in Bekaraoka Avaratra (mean = 1.77, SE = 0.77).

The DCA plot aligned forest fragments by tree species similarity based on 375 tree species (Fig. 2). *DCA1* accounted for 54.4% of the variation and *DCA2* accounted for an additional 27.0% based on eigenvalues. Cluster analysis of *DCA1* generated four clusters that each contained roughly the same number of forest fragments. Based on previous vegetation mapping efforts by Chatelain et al. (2006), we chose to describe these sites as dry (mean *DCA1* = -1.05, SE = 0.16), moderate/dry (mean *DCA1* = -0.41, SE = 0.09), moderate/wet (mean *DCA1* = 0.40, SE = 0.04), and wet (mean *DCA1* = 1.29, SE = 0.12; Fig. 3).

3.3 Sifaka density and abundance estimation

We observed 465 sifaka groups (1 490 individual sifakas) across 35 total transects in 12 study units (Table 1). Observations were conducted over 1 514 km of sampling effort over the full study period. Mean group size was 3.1 individuals (SE = 0.1, range 1 – 8). Only one transect (a mixed-cover area transect on the northwest side of Antsaharaingy) failed to yield any sifaka observations after five days of sampling (Supplemental Table 1). We did not remove this transect from the analyses, as we expected other similar areas within the study area to be void of sifakas. The top detection model used a hazard rate key function and cosine series expansion with *vegetation stratification* as a covariate (Table 2). The second-ranked model (Δ AIC within 2.22) had *vegetation stratification* as the primary predictor of detection with stratification and a lower density estimate, but also a slightly lower coefficient of variation (0.11 vs. 0.12, Table 2). All other models yielded density estimates similar to the top model (Supplemental Table 4). Density estimates from the strata-specific models were lower than all of the other models, likely because the strata-specific model took study unit areas into account, and the mixed-cover area represented the largest area and one of the smallest density estimates. Because of this, we chose to evaluate results from the stratified model as well as the competing top model.

Average sifaka densities were 26.6 individuals/km² (95% CI: 21.0 – 33.6) across all study units. Average sifaka densities where study unit densities were weighted by study unit area were 21.5 individuals/km² (95% CI: 17.3 – 26.7). Sifaka densities were highly variable across forest fragments, ranging from just 6.8 sifakas/km² (95% CI: 2.0 – 22.8) in Antsahabe to 78.1 sifakas/km² (95% CI: 53.1 – 114.8) in Bekaraoka South (Table 1, Fig. 4). Sifaka density for the Bekaraoka fragment as a whole (Bekaraoka Avaratra and Bekaraoka South combined) was 59.4

sifakas/km² (95% CI: 38.3 – 92.1). Mean sifaka density in the mixed-cover areas was 10.0 sifakas/km² (95% CI: 4.4 – 22.7).

Our abundance estimate for sifaka abundance from our top model was 12 631 (95% CI: 9 993 – 15 966) sifakas. The abundance estimate for sifaka abundance from the stratified model was 10 222 (95% CI: 8 230 – 12 697) sifakas likely represents a more accurate estimate. These abundance estimates are 30-43% less than the estimate obtained by Quéméré et al. (2010a; 18 000 sifakas) but slightly higher than the range estimated by Vargas et al. (2002; 6 100 to 10 000 sifakas). However, based on forest area estimates from this study and the densities calculated by Vargas et al. (2002; 17 - 28 sifakas per km²), populations in 2002 may have been as high as 9 133 to 15 043 sifakas. Likewise, our elevated forest cover estimate also would increase the estimates obtained by Quéméré et al. (2010a) to a minimum of ~13 432 and a maximum of ~31 749, with a new “best” estimate of 21 980 sifakas. Using these estimates, sifaka populations may have declined by as much as 53% in the last decade (2008-2018) or remained roughly the same in the last 20 years (2001-2018; Fig. 5). A sifaka abundance comparison between the same four forest fragments surveyed in this study and in Quéméré et al. (2010a; Antsaharaingy, Bekaraoka, Benanofy, and Solaniampilana/Tsarahitsaka) suggested that sifaka populations declined by 39.1%.

3.4 Relationship between sifaka density and predictors

Of the 28 predictors, nine non-correlated variables ($|r| < 0.70$) plus forest type were selected to use as predictors in models (Supplemental Table 2). Because several predictors correlated with one another, the selection of one variable in a class (*i.e.*, vegetation structure,

food availability, human activity) of predictors while another was discarded (*e.g.*, grazing selected as a human activity, while fire was discarded) does not mean that a variable was selected to best represent its class (*e.g.*, fire also correlated with tree density, which is based on highly consistent DBH measures; Chapman et al., 1992). We chose to maintain both NDVI dry and NDVI wet to better inform discussion regarding previous sifaka studies. Tree cutting, NDVI during the wet season, forest fragment area, and Simpson's diversity (1-D) were the best predictors of sifaka density (Table 3). Forest type was not supported as a predictor of sifaka densities based on model selection. Sifaka densities increased with evidence of tree cutting ($\beta = 0.54$, 95% CI: 0.20 – 0.88, $p < 0.01$; Fig. 6 & 7), wet-season NDVI values ($\beta = 0.39$, 95% CI: -0.01 – 0.78, $p = 0.05$), and Simpson's diversity (1-D; $\beta = 0.37$, 95% CI: -0.05 – 0.80, $p > 0.05$). Densities decreased with forest fragment area ($\beta = -0.03$, 95% CI: -0.06 – 0.00, $p > 0.05$).

Discussion

Species with highly variable population densities present unique challenges to conservation and highlight the importance of conducting surveys across a species' full range and all available habitats. For example, Braithwaite et al. (1983) found that just 9% of eucalyptus forests in southeastern Australia contained 63% of arboreal folivores. Even well-designed surveys could have easily missed or misrepresented these important subsets of otherwise seemingly similar habitats. This may have been the case in the Quéméré et al. (2010a) study. Time and funding constraints may drive survey efforts toward areas with higher densities. At such sites, minimum sample sizes (40 independent samples; Peres, 1999) with high confidence intervals around estimates can be more readily achieved, but may only be applicable to a small

area. In contrast, including lower-density areas surveyed using the same amount of effort would provide estimates with a wider range of uncertainty, but this wider range of uncertainty would be more likely to include the true overall density estimate for extrapolation across a wider area.

As expected, sifaka densities varied greatly over study units. Encouragingly, estimates for the Benanofy forest fragment were similar between Quéméré et al. (2010a) and this study (55.4 sifakas/km² vs. 49.9 sifakas/km², respectively), though the small number of sifaka groups observed in the current study ($N = 25$) suggests that this population estimate should be viewed with caution. However, these closely aligned estimates add confidence to the comparability of results between these two studies at the forest fragment level. While our estimate for Bekaraoka South in 2016-2018 (78.1 sifakas/km²) was similar to estimates obtained by Quéméré et al. (2010a) for the whole Bekaraoka fragment in 2006 (78.1 sifakas/km²) and 2008 (85.5 sifakas/km²), when we look at the Bekaraoka fragment as a whole (Bekaraoka Avaratra and Bekaraoka South combined) the 2016-2018 densities drop to 59.4 sifakas/km². While we expected that sifaka densities around the mining area in Bekaraoka South might have declined due to an influx of mining immigrants who might not adhere to the same taboos against sifaka hunting, this did not appear to be the case.

Sifaka density estimates derived from this study for Solaniampilana were much lower than those of Quéméré et al. (2010a) for the same area (26.7 sifakas/km² this study vs. Tsarahitsaka = Solaniampilana; 90.2 sifakas/km²). Estimates from this study also were lower at Antsaharaingy than those obtained by Quéméré et al. (2010a). While this may be a matter of small sample size in the data at Antsaharaingy (samples sizes for both studies were below the desired 40 group observations (Peres, 1999), though only marginally in 2016-2018 ($N = 37$)), sample size was not an issue at Solaniampilana ($N > 40$ for both studies). It also is unlikely that

seasonal influence impacted differing estimates between studies, as surveys were conducted during roughly the same time of year (dry season, May to November). While most local people denied targeting sifakas for bushmeat at Solaniampilana, two people said that they had consumed sifakas, and several people admitted to hunting other lemur species in the area using traps and poisoned water holes (*e.g.*, *Eulemur coronatus* and *Lepilemur milanoii*; M. Semel, unpublished data). A direct comparison of abundance loss from fragments surveyed in both this study and Quéméré et al. (2010a) yields a 39.1% decline in sifakas, within our estimated range of decline (30-43%).

Discerning which ecological variables drive variation in density are important to inform effective conservation activities. For example, while we predicted that golden-crowned sifaka densities would be higher in dry forests than in wet forests, our data did not support this trend. Rather, average tree cutting index and NDVI values during the wet season were both positive, significant predictors of sifaka densities. Both of these metrics are likely related to food availability.

Tree cutting positively predicting primate abundance, although at first counterintuitive, is not unprecedented. Several studies have found that some primate species have higher densities in selectively logged and secondary forests, or in areas with canopy gaps (often due to tree falls), likely due to the new growth that such areas promote (Chapman et al., 2000; Thomas, 1991). Meyers (1993) suggested that young leaves and flowers were preferred sifaka foods, which are expected to be more abundant following low-level disturbance. Quéméré et al. (2010a) found that sifakas were not encountered more frequently near the forest edge, which would be expected if sifakas were targeting more open areas, but food availability was not assessed. Regardless, it is likely that there is a point at which selective tree cutting effectively becomes clearcutting, with

obvious negative consequences for forest-dependent sifakas. The median tree cutting score for all of our plots was 1 (no tree cutting) and < 8% of all plots had a tree cutting score ≥ 4 (>25% of trees cut), making it challenging to determine where this transition might occur within our data, but clearly demonstrating that the positive relationship that we saw occurs only at very low levels of tree cutting.

Our study adds to a growing body of research that finds direct relationships between NDVI and animal densities (Pettorelli et al., 2011). However, few studies have explored the relationships between primate densities and NDVI, and they have been largely restricted to regional or global scales (Marshall and Wich, 2013). Zinner et al. (2002) found that grivet monkeys (*Cercopithecus a. aethiops*) secured home ranges within areas of higher NDVI values than predicted based on average values for the surrounding areas, while Willems et al. (2009) found that vervet monkeys (*C. aethiops*) preferred areas with higher productivity and reduced seasonality based on fine-scale NDVI data (232-m² pixel size). As imagery resolution improves with the advent of improved satellite technology and use of unmanned aerial vehicle (UAV) mounted cameras, we expect finer-scale NDVI to become regarded as an important predictor of plant quality and primate population density.

Our finding that average NDVI during the wet season was a strong predictor of sifaka densities suggests that greater plant productivity during the wet season has a positive effect on sifaka densities. Irwin et al. (2015) found that related diademed sifakas (*P. diadema*) in both disturbed and undisturbed forests converged on similar diets during the dry (“lean”) season, but groups in undisturbed areas experienced large wet (“abundant”) season nutritional improvements. While mortality may peak during the dry season, they suggested that this was due to a lack of adequate fat and tissue accumulation during the wet (“abundant”) season. For

golden-crowned sifakas, the degree to which the wet season “green-up” occurs as quantified by NDVI may be a suitable proxy for the availability of higher-nutrient wet (“abundant”) season foods. Alternatively, Milne-Edwards’ sifaka (*P. edwardsi*) infant survival was linked to elevated rainfall during the dry season lactation period (King et al., 2005). NDVI in the dry season was not a strong predictor in our analysis. Assessment of relations between long-term sifaka density and NDVI measures would be required to validate either of these predictions, but they do provide insight into the role that plant productivity, as indicated by NDVI, may play in explaining sifaka densities in the Loky-Manambato Protected Area. Future studies also should more broadly investigate the nutritional quality of golden-crowned sifaka food items and links between NDVI, food quality and sifaka demographic parameters.

Contrary to our findings, previous work has shown that sifaka species inhabiting Madagascar’s western, dry forests tend to have much higher densities than those inhabiting eastern rainforests (Irwin, 2006). Similar patterns have been noted for other lemur species as well (Setash et al., 2017). Recent hunting pressures and limited dispersal between areas with different hunting intensity due to habitat fragmentation may explain this discrepancy. Alternatively, NDVI wet season values may be a better predictor of densities for all sifaka species than broad forest type classifications, though this has yet to be tested.

Neither NDVI values nor density alone should be used as an indicator of habitat quality in the absence of sifaka demographic data. The assumed positive relationship between a species’ population density and habitat quality may break down as a result of: 1) seasonal resource use and availability, 2) multi-annual variability in food resource, predator populations, or abiotic factors, or 3) social interactions that limit the use of high-quality habitat by subdominant animals

(van Horne, 1983). Future studies should collect long-term demographic data to further explore these relationships.

Golden-crowned sifakas are found almost exclusively within the Loky-Manambato Protected Area and are further protected by a local taboo against their consumption. Despite these protections and assuming that the 2006/2008 estimates are accurate (Quéméré et al., 2010a), the total golden-crowned sifaka population size decreased by 30-43% over the past 10 years. This apparent major decline may be due to a variety of factors. First, this study presents the most extensive survey of golden-crowned sifaka populations to date. Both previous studies sampled a much smaller subset of the species' global range, but importantly noted the wide variation in sifaka densities across different forest fragments (Quéméré et al., 2010a; Vargas et al., 2002). Results from this study suggest that most of the forest fragments that Quéméré et al. (2010a) did not survey had lower sifaka densities than those that were included in their study (Antsahabe, Bobankora, Ambohitsintondroina, and Ambilondamba). In contrast, Vargas et al. (2002) conducted most of their surveys in fragments with lower overall densities (Antsahabe, Binara, and a small fragment near Bobankora). Additionally, Vargas et al. (2002) conducted point-count surveys rather than line transects, which alone might explain their lower estimates, as tree leaf cover may have obscured many groups or individuals (even in the dry season) and sifakas do not regularly vocalize. This suggests that the overall abundance estimate by Quéméré et al. (2010a) may have been higher, while estimates by Vargas et al. (2002) were lower than the actual number of sifakas present at those times. This casts some uncertainty over the true percent change in the population over the past 10-20 years.

Second, as discussed above, in all fragments surveyed in both 2006/2008 and 2016-2018, sifaka densities were lower in the current study than in 2006/2008 (Quéméré et al., 2010a).

Drought conditions, hunting, or other factors (*e.g.*, disease) all may have contributed to this decline. Unfortunately, we know very little about sifaka disease ecology or the impacts of predators on this species. Hunting is on the rise across Madagascar, both for subsistence (Borgerson et al., 2016), and increasingly for commercial purposes (Schwitzer et al., 2014). Sifaka hunting was reported across the region in and after the coup d'état in 2009 (Barrett and Ratsimbazafy 2009; Conservation International 2010), and presents the most likely explanation for the sifaka decline. This challenges the notion that local taboos provide a strong umbrella of protection to this species. Lastly, forest loss certainly played a role in the overall decline in abundance, as 11.5% of the forest present in 2002 was lost by 2018, and sifakas rely on forest cover for their persistence (Meyers, 1993). Assuming that forest cover directly limits sifaka populations, this percent of forest loss puts a lower bound on the percent loss of sifakas in the past two decades.

Between 1953 and 2014, Madagascar lost 44% of its forest cover (Vieilledent et al., 2018), and protected areas have not been immune to forest loss (Gardner et al., 2018). Furthermore, recent analyses of forest habitats for ruffed lemurs (*Varecia spp.*) in Madagascar's eastern rainforest suggest a potential 29 – 59% decrease in suitable forest habitat due to deforestation alone by 2070 (Morelli et al., 2019). When climate change models are included, ruffed lemur habitat is expected to decline by 62%, optimistically assuming that protected areas avoid further deforestation, and to decline by 81% should current rates of deforestation continue. This species-specific study supports a broad-scale analysis of lemur species habitat responses to climate change, which found that 60% of the 57 lemur species analyzed would experience considerable range reductions by 2080 due to climate change alone (Brown and Yoder, 2015).

Other, less direct threats also may have an impact on sifaka populations. Non-commercial gold mining is expanding and intensifying within the golden-crowned sifaka range, as it is across much of Madagascar. Not only does this lead to increased forest loss, but the influx of human migrants from across the country may erode the local taboos that currently protect the sifakas from hunting (Golden and Comaroff, 2015). Additionally, long-rumored improvements to the national road that bisects the sifaka's range are currently underway thanks to major investments by foreign interests (A. Bensouleimany, Daraina guide association, pers comm). While this development may improve local livelihoods and improve access for ecotourism, it threatens to exacerbate forest loss, mining, and human migration across the region; its effects should be watched closely in the years to come. Encouragingly, Fanamby has recently reported seeing sifakas in the Andrafiarana Andavokoera Protected Area, which is located approximately 15 km west of the area surveyed in this study (T. Andriamanana, Fanamby, pers. comm.). With so many threats facing this species, applied research and implementation of protection strategies that will lead to population expansion rather than further contraction are needed.

Author Contributions

Brandon P. Semel: Conceptualization, Funding Acquisition, Methodology, Formal analysis, Writing; **Sarah M. Karpanty:** Supervision, Conceptualization, Funding Acquisition Writing – review & editing; **Meredith A. Semel:** Investigation, Project Administration; Writing – review & editing; **Dean Stauffer:** Conceptualization, Methodology, Writing – review & editing; **Erwan Quéméré:** Conceptualization, Methodology, Writing – review & editing; **Jeffrey R. Walters:** Writing – review & editing; **Angelo F. Andrianiaina:** Investigation, Project Administration;

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Table 1: Descriptive statistics of covariates used in golden-crowned sifaka (*Propithecus tattersalli*) density modelling for the 12 study units (11 forest fragments and mixed-cover area) surveyed for sifaka in the Loky-Manambato Protected Area in northeastern Madagascar 2016-2018. Variables shown had a correlation $< |0.7|$ except for NDVI wet and NDVI dry (see text for justification). Values in parentheses are standard error (SE) or 95% confidence interval (95% CI) as noted. No SE is provided for NDVI wet/dry values as they were determined from the whole fragment area and therefore do not represent a sample. Study units are grouped by wet, moderate/wet, moderate/dry, and dry forest types and the mixed-cover area.

Forest Fragment (Year Surveyed; total transect length (km))	Forest Area (km ²) ^a	Sifaka Groups Observed	Sifaka Density (sifakas/km ² ; 95% CI) ^b	Sifaka Abundance (95% CI) ^b	No. of Veg. Plots ^c	Tree Density (trees/ha; SE) ^d	Simpson Diversity (1-D) (SE) ^d	Hill Even (SE) ^d	NDVI Wet (SE) ^e	NDVI Dry (SE) ^e	Grazing (SE) ^f	Tree Cutting (SE) ^f
Wet												
Binara (2016 – 2018; 6 000 km)	43.61	64	20.7 (11.2-38.0)	902 (490-1 659)	182	936.0 (35.9)	0.97 (0.01)	0.48 (0.03)	0.77 (-)	0.71 (-)	1.18 (0.09)	1.89 (0.44)
Antsahabe (2017 & 2018; 5 988 km)	43.69	11	6.8 (2.0-22.8)	297 (89-997)	132	1 437.5 (65.3)	0.97 (0.01)	0.53 (0.06)	0.77 (-)	0.63 (-)	1.00 (0.00)	1.03 (0.02)

Forest Fragment (Year Surveyed; total transect length (km))	Forest Area (km ²) ^a	Sifaka Groups Observed	Sifaka Density (sifakas/km ² ; 95% CI) ^b	Sifaka Abundance (95% CI) ^b	No. of Veg. Plots ^c	Tree Density (trees/ha; SE) ^d	Simpson Diversity (1-D) (SE) ^d	Hill Even (SE) ^d	NDVI Wet (SE) ^e	NDVI Dry (SE) ^e	Grazing (SE) ^f	Tree Cutting (SE) ^f
Moderate/Wet												
Ampondrabe (2017; 4 450 km)	19.78	29	69.5 (37.1-130.3)	1 375 (733-2 578)	48	2 306.9 (173.4)	0.96 (0.01)	0.58 (0.03)	0.80 (-)	0.54 (-)	1.11 (0.11)	1.82 (0.37)
Bekaraoka South (2016 – 2018; 4 000 km)	26.15	126	78.1 (53.1-114.8)	2 042 (1 389- 3 001)	136	1 606.8 (70.1)	0.96 (0.00)	0.31 (0.02)	0.80 (-)	0.50 (-)	1.05 (0.03)	1.87 (0.08)
Bobankora (2016; 4 500 km)	21.34	11	13.6 (5.3-34.6)	290 (114-739)	24	1 800.0 (133.8)	0.95 (0.01)	0.66 (0.04)	0.80 (-)	0.58 (-)	1.00 (0.00)	1.29 (0.08)
Moderate/Dry												
Ambohitsintondroina (2018; 7 450 km)	46.33	10	9.1 (3.8-21.9)	420 (174-1 012)	66	554.2 (38.6)	0.90 (0.04)	0.48 (0.08)	0.78 (-)	0.47 (-)	1.76 (0.71)	1.87 (0.61)
Bekaraoka Avaratra (2017; 5 000 km)	42.94	16	15.1 (9.4-24.2)	648 (404-1 039)	54	767.2 (56.3)	0.95 (0.02)	0.58 (0.03)	0.80 (-)	0.52 (-)	1.77 (0.77)	1.69 (0.46)
Benanofy (2017; 4 000 km)	33.92	25	49.9 (25.1-99.3)	1 693 (852-3 366)	44	762.6 (62.7)	0.95 (0.02)	0.63 (0.07)	0.78 (-)	0.44 (-)	1.54 (0.41)	1.67 (0.08)

Forest Fragment (Year Surveyed; total transect length (km))	Forest Area (km ²) ^a	Sifaka Groups Observed	Sifaka Density (sifakas/km ² ; 95% CI) ^b	Sifaka Abundance (95% CI) ^b	No. of Veg. Plots ^c	Tree Density (trees/ha; SE) ^d	Simpson Diversity (1-D) (SE) ^d	Hill Even (SE) ^d	NDVI Wet (SE) ^e	NDVI Dry (SE) ^e	Grazing (SE) ^f	Tree Cutting (SE) ^f
Dry												
Ambilondamba (2016; 3 560 km)	13.34	18	19.6 (6.6-58.0)	262 (89-774)	36	610.8 (44.9)	0.94 (0.00)	0.53 (0.00)	0.79 (-)	0.46 (-)	1.22 (0.22)	1.64 (0.19)
Antsaharaingy (2016 – 2018; 4 900 km)	11.58	37	27.4 (13.3-56.2)	317 (154-650)	146	2 012.8 (83.1)	0.96 (0.04)	0.45 (0.12)	0.78 (-)	0.49 (-)	1.16 (0.03)	1.61 (0.03)
Solaniampilana (2017 – 2018; 6 510 km)	14.72	61	26.7 (16.2-44.1)	393 (239-648)	138	1 282.5 (56.7)	0.96 (0.01)	0.48 (0.02)	0.81 (-)	0.43 (-)	1.17 (0.05)	1.74 (0.26)
Mixed-Cover Area												
(2016 – 2018; 19 070 km)	157.92	57	10.0 (4.4-22.7)	1 583 (700-3 581)	296	254.4 (10.2)	0.93 (0.03)	0.51 (0.06)	0.65 (-)	0.37 (-)	2.51 (0.48)	1.74 (0.22)

^a Forest area estimates are based on contiguous forest cover areas except for mixed-cover areas, which is based on all non-contiguous forest area within the species' range.

^b Sifaka density and abundance results are based on results from the top model in Distance and the forest areas presented.

^c Vegetation plots is the number of point-center quarter (PCQ) plots conducted for each fragment.

^d Based on trees in the PCQ plots.

^e NDVI values are the average for all pixels within each forest fragment during the wet and dry seasons.

^f Based on 10 m radius disturbance plots centered around PCQ plots.

Table 2: Top two detection models and density estimates from program Distance for golden-crowned sifakas (*Propithecus tattersalli*) in the Loky-Manambato Protected Area, Madagascar (2016-2018). The furthest 10% of observations were truncated and distance binning was adjusted to ensure acceptable goodness of fit ($p > 0.05$). We stratified observations by fragment to examine how densities varied by vegetation, human activity, and land cover variables. See Supplemental Table 4 for full model list.

Model Name	No. of Parameters	Δ AIC	AIC	ESW ^a	Density (95% CI) ^b	CV ^c
HR cos vegstrat ^{d, e}	3	0	1 355.20	15.99	26.6 (21.0 – 33.6)	0.12
Strata-specific HR cos vegstrat ^{d-f}	24	2.22	1 257.43	-	21.5 (17.3 – 26.7)	0.11
HR cos graze ^g	3	3.71	1358.91	15.91	26.5 (21.0 – 33.5)	0.12

^a ESW = estimated sampling width (m).

^b CI = confidence interval.

^c CV = coefficient of variation.

^d HR = hazard rate key function; cos = cosine series expansion.

^e vegstrat = vegetation stratification based on presence/absence of vegetation at various height intervals.

^f To obtain a global density estimate for the stratified model, we weighted the density estimate of each fragment by its area. No estimated sampling width (ESW) was determined for this model.

^g graze = livestock grazing index determined within a 10m radius of each vegetation plot.

Table 3: Negative binomial model results estimating golden crowned sifaka (*Propithecus tattersalli*) density as a function of vegetation structure, food availability, and human activity predictors in 12 study units in the Loky-Manambato Protected Area in northeastern Madagascar 2016-2018.

Model	K	β Estimates	SE of β	AICc	Δ AICc	Weight	
Tree Cutting ^a	3	0.52	0.18	187.96	0.00	0.29	
Null	2	-	-	189.27	1.31	0.15	
NDVI Wet ^b	3	0.40	0.20	189.64	1.69	0.13	
Simpson's Diversity (1-D) ^c	3	0.43	0.20	190.03	2.08	0.1	
Fragment Area ^d	3	-0.01	0.01	190.07	2.11	0.1	
Grazing ^a	3	-0.40	0.20	190.19	2.23	0.1	
Corrected Tree Density ^d	3	0.23	0.21	191.89	3.94	0.04	
Hill Evenness ^d	3	-0.15	0.22	192.2	4.24	0.04	
NDVI Dry ^b	3	-0.12	0.22	192.74	4.78	0.03	
DCA2 ^e	3	0.06	0.22	192.88	4.92	0.03	
Forest Type	dry	6	-	-	204.69	16.73	0
	dry/mod		0.01	0.45			
	mod/wet		0.78	0.45			
	wet		-0.58	0.50			
	mixed-cover area		-0.89	0.63			

^a Index of disturbance intensity determined within a 10m radius of each vegetation plot.

^b NDVI values are the average for all pixels within each forest fragment.

^c Determined from point-center-quarter (PCQ) plots.

^d Total contiguous forest from 2017-2019 satellite imagery.

^e DCA2 = axis two from the Detrended Correspondence Analysis based on identified tree species from PCQ plots.

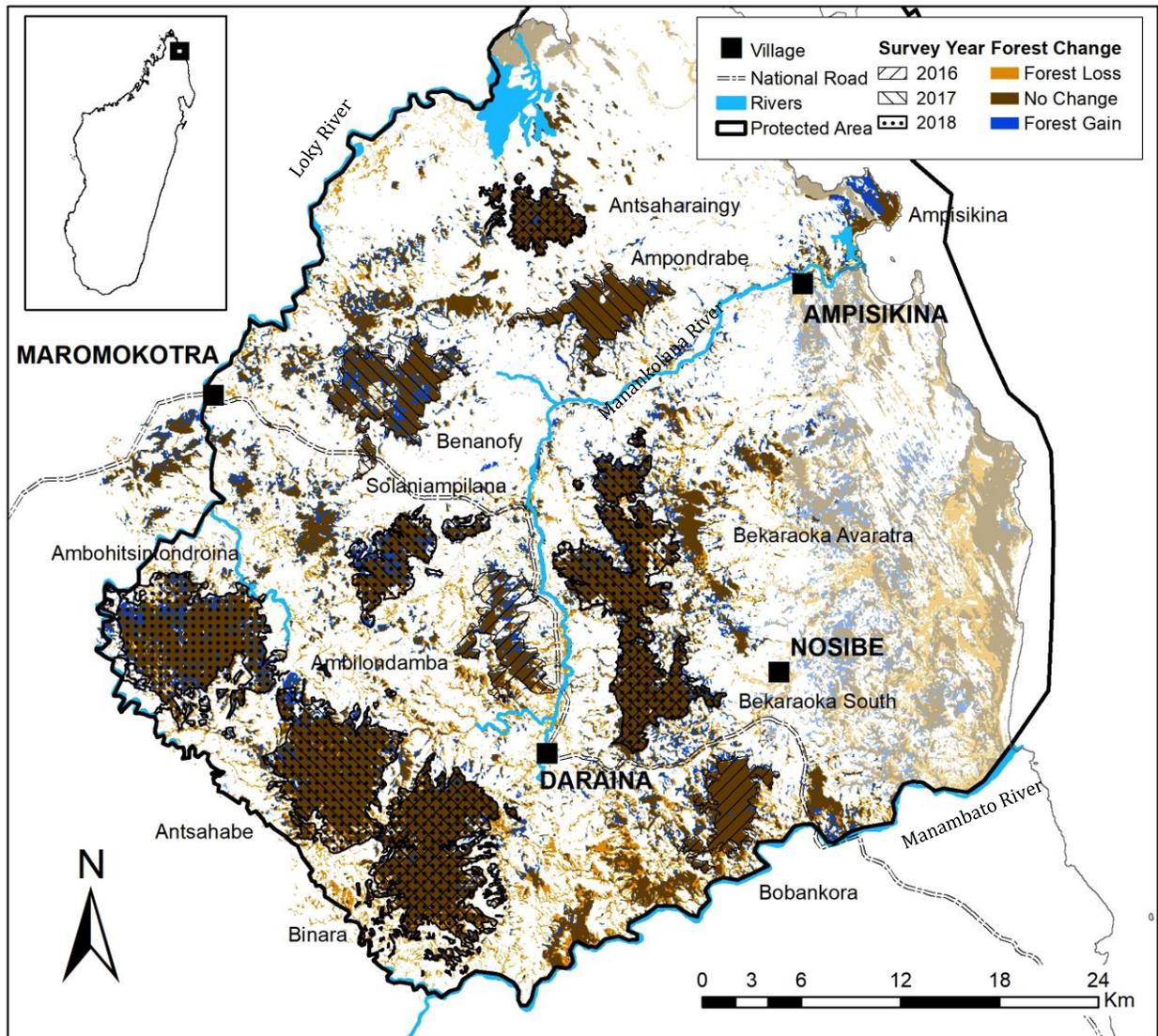


Fig. 1. Map of the golden-crowned sifaka (*Propithecus tattersalli*) range within the Loky-Manambato Protected Area in northeastern Madagascar, as indicated in the box on the inset of Madagascar. Bold colors indicate forested areas suspected to have sifakas (forested areas within the species' known range, $>0.01 \text{ km}^2$, and $>0.09 \text{ km}^2$ if not within 1.5 km of a "large" forest fragment; see methods) and/or confirmed to have sifakas (Jiménez and Vargas, 2000; Quéméré et al., 2010b; Vargas et al., 2002) whereas faded colors indicate forested areas not suspected to

have sifakas. Hashing or dots indicate years that each labeled fragment was surveyed (May - July 2016, August - December 2017, August - December 2018). Orange coloration indicates forest cover lost from 2002 – 2017/2019, dark brown coloration indicates no change in forest cover 2002 – 2017/2019, and blue coloration indicates forest gained in 2002 – 2017/2019. Forested areas outside of the protected area were included only if sifaka presence was confirmed or suspected in those area.

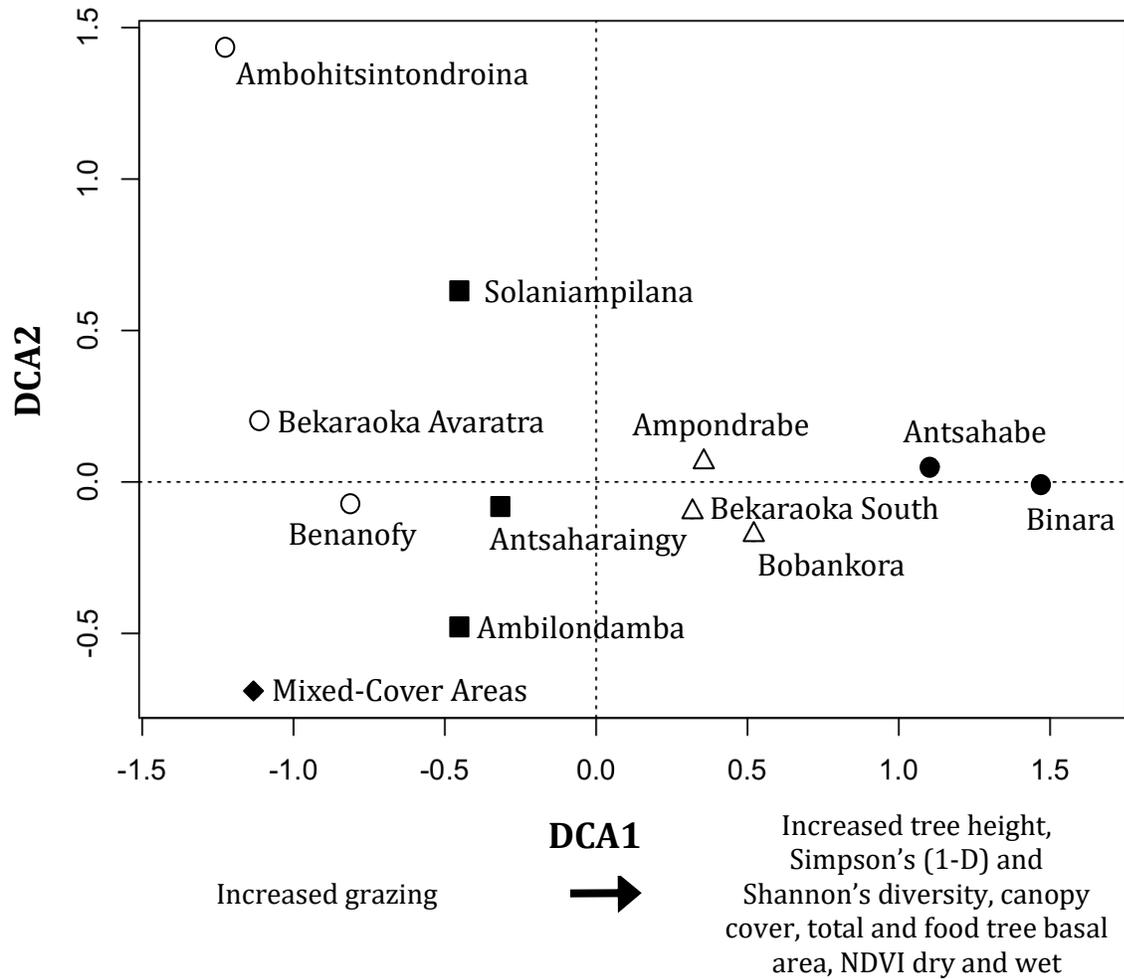


Fig. 2. Results from the detrended correspondence analysis (DCA) arranged study units by their tree species similarity for 11 forest fragments and the mixed-cover areas in the Loky-Manambato Protected Area in northeastern Madagascar. Tree species data were collected along the same transects walked to estimate golden-crowned sifaka (*Propithecus tattersalli*) densities from 2016-2018. Values from DCA2 were used as a predictor in sifaka population density prediction models. The relationship between DCA1 and other predictor variables with $r > |0.70|$ is indicated on the x -axis. DCA2 was not strongly correlated ($r > |0.70|$) with any predictor variables making it more difficult to interpret. It was somewhat positively related to fire and negatively related to tree height and food tree basal area ($r \sim |0.50|$; see Supplemental Table 2 for r values). Different

symbols indicate the four forest types based on cluster analysis: dry forest (open circles), moderate/dry forest (closed squares), moderate/wet forest (open triangles), and wet forest (closed circles). Mixed-cover areas are noted with a closed diamond.

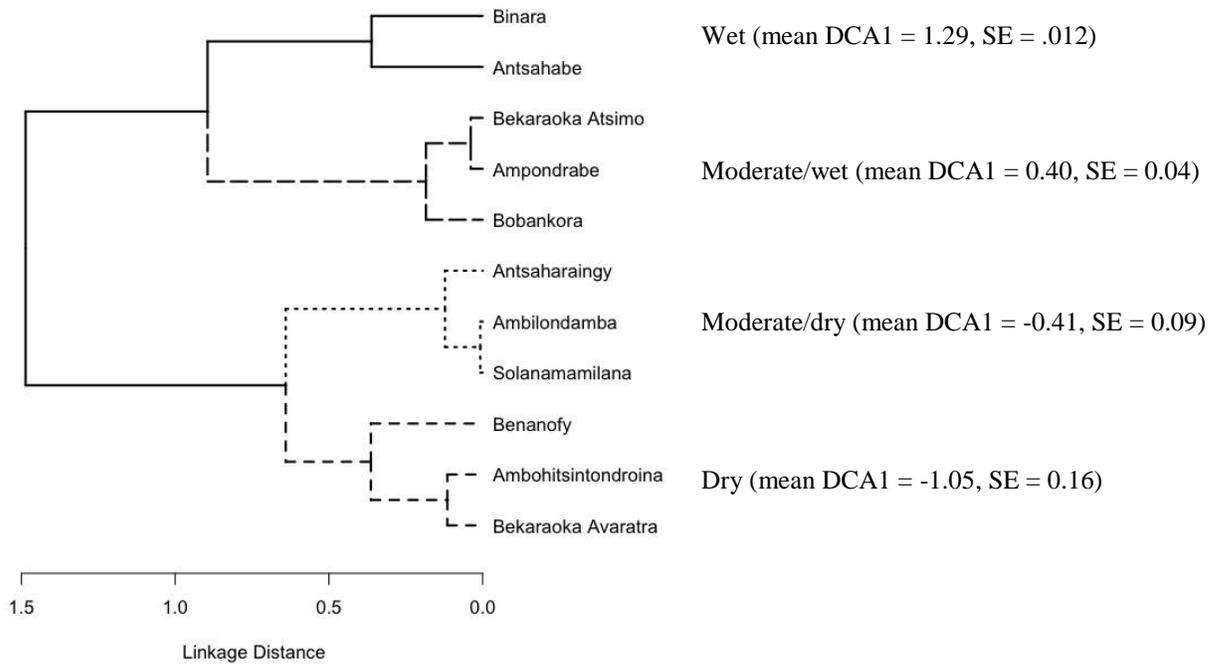


Fig. 3. Results of the cluster analysis for 11 forest fragments in the Loky-Manambato Protected Area in northeastern Madagascar. Forest fragments were grouped into four clusters (dry, moderate/dry, moderate/wet, and wet) by similar tree species composition (DCA1) and site-wide average plant health values (normalized difference vegetation index; NDVI). Tree species data were collected along the same transects walked to estimate golden-crowned sifaka (*Propithecus tattersalli*) densities from 2016-2018. Dashed lines indicate the four forest types based on cluster analysis (top to bottom): wet forest (solid line), moderate/wet forest (long dashes), moderate/dry forest (dots), and dry forest (moderate dashes). Mixed-cover areas were not included in the analysis.

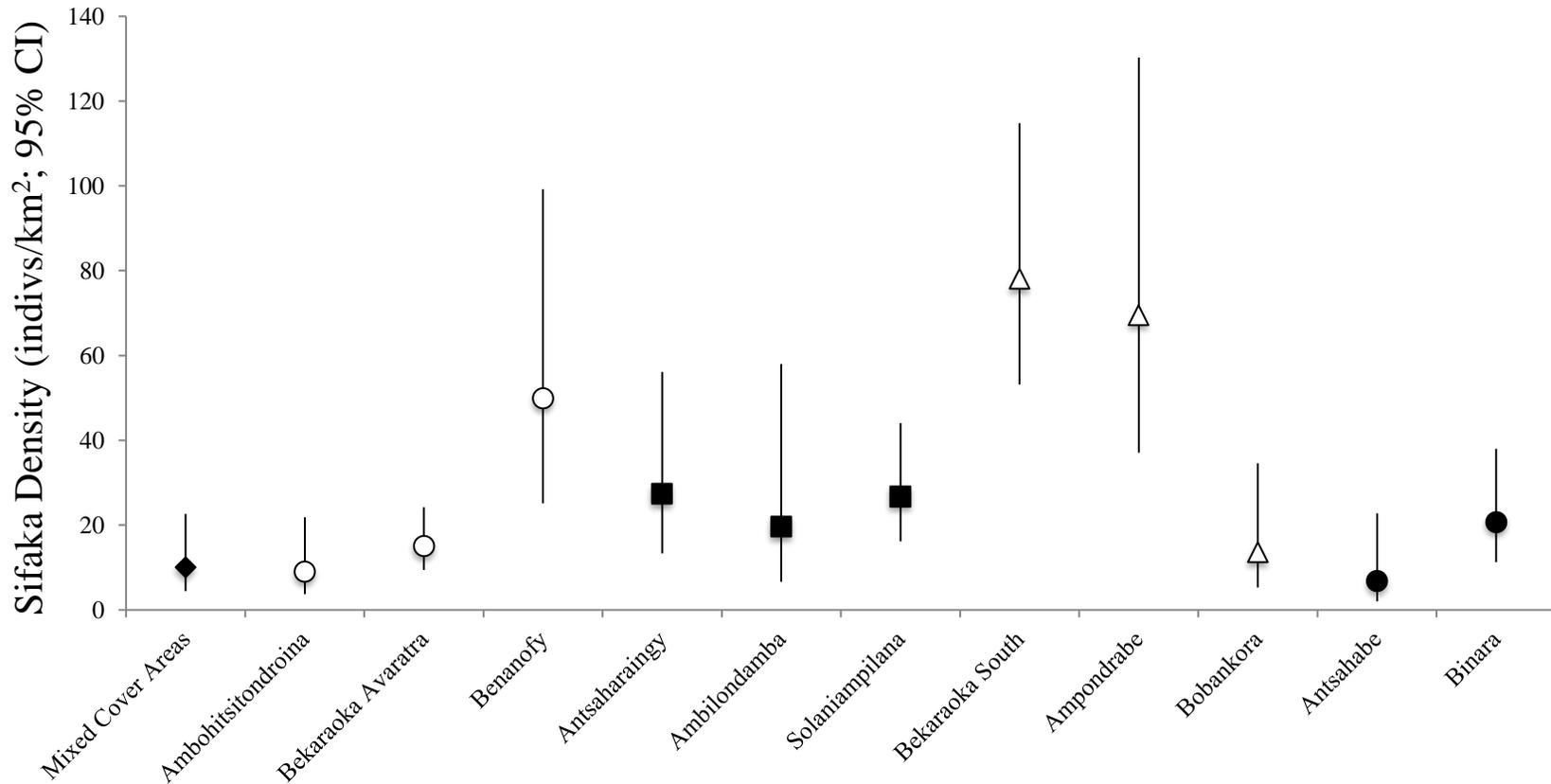


Fig. 4. Golden-crowned sifaka (*Propithecus tattersalli*) densities (individuals/km²) for 11 forest fragments and the mixed cover areas in the Loky-Manambato Protected Area in northeastern Madagascar based on transect surveys conducted from 2016-2018. Different symbols indicate the four forest types based on cluster analysis: dry forest (open circles), moderate/dry forest (closed squares), moderate/wet forest (open triangles), and wet forest (closed circles). Mixed-cover areas are noted with a closed diamond. There was no significant difference in sifaka densities among forest types (see Table 3 for model results).

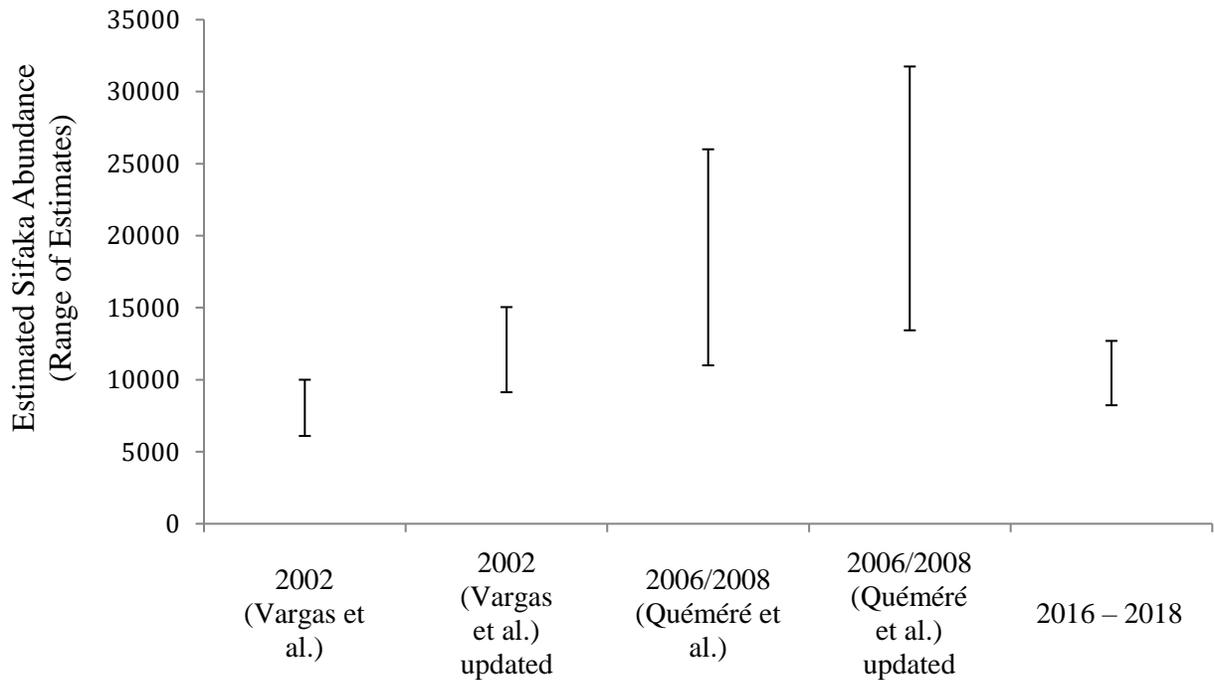


Fig. 5. Three studies have estimated golden-crowned sifaka (*Propithecus tattersalli*) abundance in the Loky-Manambato Protected Area in northeastern Madagascar. Vargas et al. (2002) conducted point counts in 2001 in three large, contiguous forest fragments to estimate minimum and maximum density estimates and determined total forest area using Landsat data from 1994 that was below 700 m ASL. Bars indicate the provided range of their estimates. Quéméré et al. (2010) used these total forest area estimates as well as expanded area estimates based on observations of sifakas at higher elevations and updated 2002 satellite imagery to calculate abundance values from surveys of five large, contiguous forest fragments. Bars indicate the provided range of their estimates. This study recalculated total forest area based on 2002 LANDSAT 7 data and estimated a higher updated abundance based on the same density estimates from Vargas et al. (2002). Quéméré et al. (2010) conducted line transect surveys in 2006/2008. Their updated estimates were based on a 22.1% change in total forest cover. This

study estimated sifaka densities in 2016-2018 and used total forest area from 2017-2019 LANDSAT 7 and 8 data. Our estimates were based on surveys in 11 large, contiguous forest fragments as well as surveys in the mixed-cover areas between these fragments. While previous studies included these areas in their overall forest area estimates, they were not surveyed independently of the large, contiguous fragments. Bars on this study indicate 95% confidence intervals from the stratified model that weighted the global density estimate by forest cover area for each study unit.

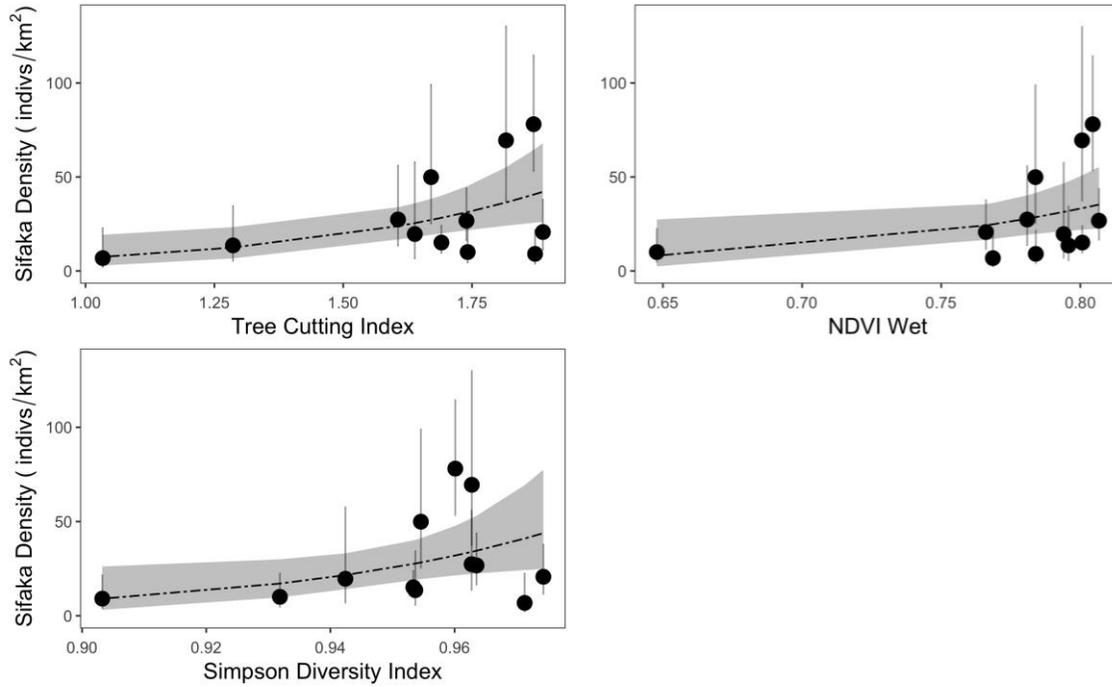


Fig. 6. Golden-crowned sifaka (*Propithecus tattersalli*) densities in 12 study units in the Loky-Manambato Protected Area in northeastern Madagascar from 2016-2018 (black dots with 95% CI) plotted against the fitted values from the best predictors of sifaka density (hashed line with shaded 95% CI). The outlier in all plots is the mixed-cover areas. All trends and significance levels were maintained when analyses were run without this variable.

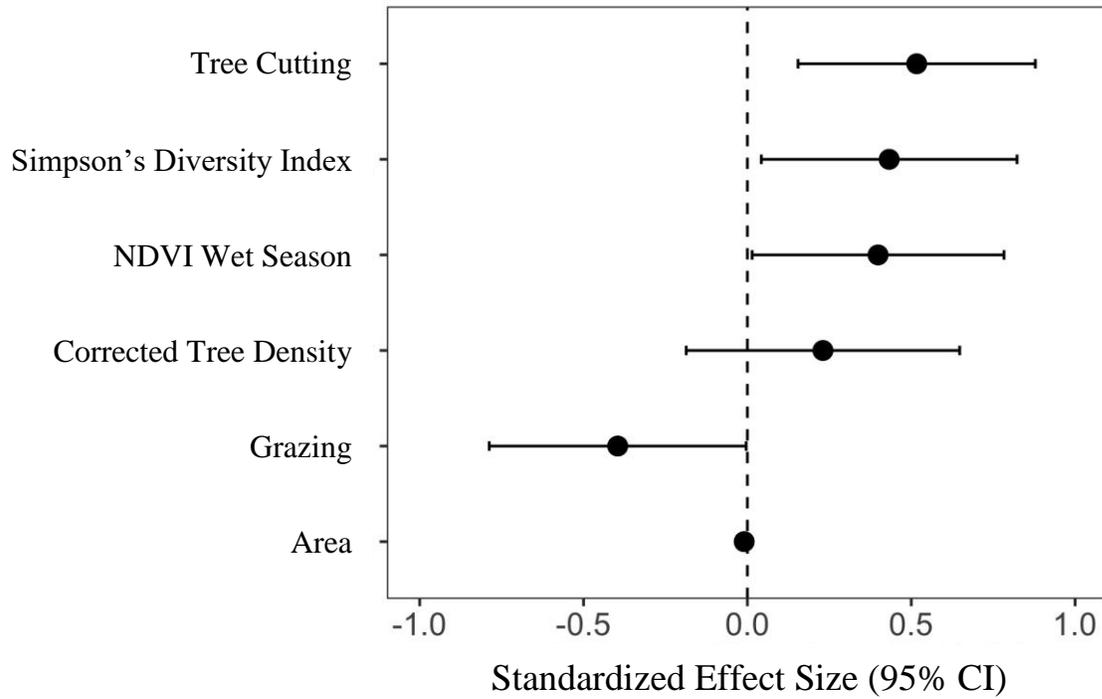


Fig. 7. Plot of standardized beta coefficient estimates with 95% confidence intervals from the top negative binomial model predictors ($\Delta AICc < 4.0$) of golden crowned sifaka (*Propithecus tattersalli*) densities in 12 study units from 2016-2018 in the Loky-Manambato Protected Area in northeast Madagascar. Confidence intervals that overlap zero (dashed line) indicate a non-significant predictor.

Supplemental Table 1: Twenty-eight, 1-3 km long line transects were established between 2016 and 2018 in 11 forest fragments and seven 1-3 km long transects were established in mixed-cover areas in the Loky-Manambato Protected Area in northeastern Madagascar. Some transects that were constructed during the 2016 pilot season were extended the following survey period. One transect (*) was abandoned after the first year due to a lack of sifaka observations. All points use UTM UPS position format with WGS 84. Survey effort (m) was defined as the total length of surveys completed in a fragment across the whole study period.

Forest Fragment	Transect	Location on Transect	Latitude	Longitude	Elevation (m)	Survey Effort (m)
Ambilondamba	1	Start	-13.116791	49.630195	178	
		End	-13.121912	49.643436	237	20 640
	2	Start	-13.115349	49.655885	87	
		End	-13.109918	49.640585	175	16 560
	3	Start	-13.138855	49.639498	125	
		End	-13.146528	49.633096	310	11 700
Ambohitsintondroina	1	Start	-13.118029	49.456546	204	
		End	-13.119931	49.444544	132	20 000
	2	Start	-13.121537	49.46347	135	
		End	-13.135742	49.456339	294	20 000
	3	Start	-13.115479	49.466554	79	
		End	-13.103397	49.47309	59	20 000
Ampondrabe	1	Start	-12.973995	49.70236	93	

Forest Fragment	Transect	Location on Transect	Latitude	Longitude	Elevation (m)	Survey Effort (m)
Ampondrabe	1	End	-12.955921	49.698168	555	29 400
	2	Start	-12.97443	49.700106	141	
		End	-12.983014	49.686435	96	24 000
Antsahabe	1	Start	-13.210359	49.556931	576	
		End	-13.22279	49.548408	1 069	48 000
	2	Start	-13.210151	49.558837	536	
		End	-13.198655	49.554769	930	48 000
Antsaharaingy	3	Start	-13.209891	49.556415	584	
		End	-13.20957	49.542099	934	43 856
	1	Start	-12.903583	49.659017	64	
		End-2016	-12.91013	49.650684	55	24 000
		End	-12.918308	49.674054	86	64 800
Bekaraoka Avaratra	2	Start	-12.896968	49.649081	47	
		End	-12.915116	49.652652	117	91 040
	1	Start	-13.106336	49.705832	125	
		End	-13.122398	49.709691	242	34 200
Bekaraoka South	2	Start	-13.1045	49.69626	131	
		End	-13.090495	49.681605	86	36 000
Bekaraoka South	1	Start	-13.170772	49.717183	283	
		End-2016	-13.166008	49.711157	98	23 040

Forest Fragment	Transect	Location on Transect	Latitude	Longitude	Elevation (m)	Survey Effort (m)
Bekaraoka South	1	End	-13.159696	49.701744	98	68 800
		Start	-13.176355	49.702861	137	
	2	End-2016	-13.182489	49.708396	224	13 780
		End	-13.188307	49.71443	243	55 640
Benanofy	1	Start	-13.020973	49.563757	220	
		End	-13.021271	49.550246	88	24 000
	2	Start	-13.026154	49.571838	174	
		End	-13.026946	49.5836	112	24 000
Binara	1	Start	-13.240701	49.630458	186	
		End	-13.229005	49.622765	483	82 000
	2	Start	-13.254165	49.619294	272	
		End	-13.263192	49.606337	674	79 520
	3	Start	-13.277871	49.614406	425	
		End	-13.287527	49.60131	852	68 000
Bobankora	1	Start	-13.229	49.769083	435	
		End	-13.218284	49.773734	348	8 800
	2	Start	-13.231965	49.767222	438	
		End	-13.231558	49.776317	118	11 200
	3	Start	-13.231972	49.759972	166	
		End	-13.24825	49.763718	460	16 000

Forest Fragment	Transect	Location on			Survey Effort (m)	
		Transect	Latitude	Longitude		Elevation (m)
Solaniampilana	1	Start	-13.083005	49.582075	109	
		End	-13.086584	49.571934	105	59 800
	2	Start	-13.089804	49.587938	239	
		End	-13.094649	49.572978	208	57 640
	3	Start	-13.099608	49.583296	164	
		End	-13.110804	49.571095	323	62 000
Mixed-Cover Areas	1	Start	-12.962959	49.707182	195	
		End	-12.983294	49.723335	35	36 000
	2*	Start	-12.898849	49.639953	49	
		End	-12.911949	49.632567	77	19 200
	3	Start	-12.895767	49.664517	32	
		End	-12.869236	49.669668	21	78 000
	4	Start	-13.165608	49.696527	117	
		End-2016	-13.150701	49.68729	81	32 000
		End	-13.14668	49.683869	84	76 000
	5	Start	-13.102004	49.704415	103	
		End	-13.083929	49.68803	81	24 000
	6	Start	-13.030563	49.564226	125	
		End	-13.051193	49.557216	99	30 500
	7	Start	-13.223867	49.749249	143	

Forest Fragment	Transect	Location on Transect	Latitude	Longitude	Elevation (m)	Survey Effort (m)
Mixed-Cover Areas	7	End	-13.239059	49.753047	216	14 000

Supplemental Table 2: Correlation matrix for predictors in negative binomial models of sifaka density from vegetation structure, food availability, and human activity data collected for each forest fragment ($N = 11$) from 2016 - 2018 in the Loky-Manambato Protected Area in Northeastern Madagascar. Highly correlated variables ($|r| > 0.70$) were removed such that the most readily measured variable remained (e.g., remotely sensed NDVI values kept over basal area measures). Variables kept for use in models are in bold.

	Sifaka densities*	Area	Vegetation stratification	Tree height	Canopy cover	Tree density	Total basal area	Basal area per tree	Tree crown volume	Shannon diversity**	Simpson diversity (1-D)**	Hill evenness**	Pi evenness**	Food tree basal area	Food tree basal area/tree	Food tree dens	Food tree crown volume	NDVI dry	NDVI wet	Tree cutting	Fire	Mining	Grazing	DCA1	DCA2
Sifaka densities*	1.00	-0.32	0.52	0.13	0.04	0.17	-0.10	-0.36	-0.14	0.26	0.26	-0.31	-0.12	-0.13	-0.39	0.18	-0.13	-0.25	0.44	0.47	-0.33	0.64	-0.24	-0.11	-0.01
Area	-0.32	1.00	-0.70	0.12	0.26	-0.18	0.04	0.46	0.46	-0.06	-0.21	0.06	-0.04	0.04	0.55	-0.34	0.46	0.45	-0.51	-0.02	0.36	-0.10	0.51	0.11	0.07
Vegetation stratification	0.52	-0.70	1.00	0.40	0.36	0.69	0.41	-0.32	-0.26	0.53	0.67	0.02	0.33	0.36	-0.46	0.75	-0.28	0.01	0.27	-0.31	-0.83	0.23	-0.78	-0.54	-0.24
Tree height	0.13	0.12	0.40	1.00	0.93	0.46	0.90	0.65	0.64	0.66	0.65	0.08	0.43	0.88	0.53	0.37	0.61	0.76	-0.22	-0.27	-0.64	0.16	-0.66	-0.82	-0.52
Canopy cover	0.04	0.26	0.36	0.93	1.00	0.48	0.87	0.60	0.61	0.65	0.63	0.12	0.43	0.85	0.50	0.39	0.58	0.85	-0.46	-0.44	-0.62	0.10	-0.61	-0.83	-0.44
Tree density	0.17	-0.18	0.69	0.46	0.48	1.00	0.60	-0.09	-0.17	0.45	0.52	0.06	0.26	0.53	-0.15	0.98	-0.19	0.34	0.08	-0.48	-0.84	0.07	-0.52	-0.46	-0.38
Total basal area	-0.10	0.04	0.41	0.90	0.87	0.60	1.00	0.64	0.45	0.43	0.49	0.29	0.53	0.99	0.52	0.55	0.42	0.76	-0.18	-0.49	-0.67	-0.06	-0.64	-0.75	-0.49
Basal area per tree	-0.36	0.46	-0.32	0.65	0.60	-0.09	0.64	1.00	0.87	0.21	0.15	0.16	0.27	0.69	0.98	-0.16	0.87	0.80	-0.38	0.02	-0.05	-0.17	-0.10	-0.44	-0.48
Tree crown volume	-0.14	0.46	-0.26	0.64	0.61	-0.17	0.45	0.87	1.00	0.50	0.35	-0.10	0.15	0.48	0.86	-0.28	1.00	0.80	-0.54	0.19	-0.04	-0.04	-0.17	-0.57	-0.43
Shannon diversity**	0.26	-0.06	0.53	0.66	0.65	0.45	0.43	0.21	0.50	1.00	0.92	-0.33	0.19	0.38	0.13	0.38	0.48	0.55	-0.27	-0.12	-0.70	0.27	-0.65	-0.79	-0.46
Simpson diversity (1-D)**	0.26	-0.21	0.67	0.65	0.63	0.52	0.49	0.15	0.35	0.92	1.00	-0.01	0.50	0.45	0.01	0.48	0.33	0.47	-0.13	-0.27	-0.80	0.11	-0.65	-0.73	-0.44
Hill evenness**	-0.31	0.06	0.02	0.08	0.12	0.06	0.29	0.16	-0.10	-0.33	-0.01	1.00	0.84	0.29	0.07	0.09	-0.12	0.08	-0.06	-0.43	0.02	-0.73	0.16	0.14	0.08
Pi evenness**	-0.12	-0.04	0.33	0.43	0.43	0.26	0.53	0.27	0.15	0.19	0.50	0.84	1.00	0.51	0.13	0.25	0.13	0.36	-0.09	-0.49	-0.37	-0.54	-0.24	-0.32	-0.05
Food tree basal area	-0.13	0.04	0.36	0.88	0.85	0.53	0.99	0.69	0.48	0.38	0.45	0.29	0.51	1.00	0.58	0.50	0.46	0.77	-0.18	-0.46	-0.63	-0.05	-0.62	-0.73	-0.50
Food tree basal area/tree	-0.39	0.55	-0.46	0.53	0.50	-0.15	0.52	0.98	0.86	0.13	0.01	0.07	0.13	0.58	1.00	-0.24	0.87	0.77	-0.41	0.11	0.07	-0.16	0.03	-0.34	-0.43

	Sifaka densities*	Area	Vegetation stratification	Tree height	Canopy cover	Tree density	Total basal area	Basal area per tree	Tree crown volume	Shannon diversity**	Simpson diversity (1-D)**	Hill evenness**	Pi evenness**	Food tree basal area	Food tree basal area/tree	Food tree dens	Food tree crown volume	NDVI dry	NDVI wet	Tree cutting	Fire	Mining	Grazing	DCA1	DCA2
Food tree dens	0.18	-0.34	0.75	0.37	0.39	0.98	0.55	-0.16	-0.28	0.38	0.48	0.09	0.25	0.50	-0.24	1.00	-0.29	0.22	0.17	-0.46	-0.85	0.06	-0.53	-0.39	-0.42
Food tree crown volume	-0.13	0.46	-0.28	0.61	0.58	-0.19	0.42	0.87	1.00	0.48	0.33	-0.12	0.13	0.46	0.87	-0.29	1.00	0.79	-0.52	0.24	-0.02	-0.03	-0.14	-0.55	-0.42
NDVI dry	-0.25	0.45	0.01	0.76	0.85	0.34	0.76	0.80	0.80	0.55	0.47	0.08	0.36	0.77	0.77	0.22	0.79	1.00	-0.61	-0.28	-0.38	-0.13	-0.38	-0.75	-0.44
NDVI wet	0.44	-0.51	0.27	-0.22	-0.46	0.08	-0.18	-0.38	-0.54	-0.27	-0.13	-0.06	-0.09	-0.18	-0.41	0.17	-0.52	-0.61	1.00	0.30	-0.19	0.40	0.04	0.38	0.08
Tree cutting	0.47	-0.02	-0.31	-0.27	-0.44	-0.48	-0.49	0.02	0.19	-0.12	-0.27	-0.43	-0.49	-0.46	0.11	-0.46	0.24	-0.28	0.30	1.00	0.37	0.29	0.39	0.33	-0.13
Fire	-0.33	0.36	-0.83	-0.64	-0.62	-0.84	-0.67	-0.05	-0.04	-0.70	-0.80	0.02	-0.37	-0.63	0.07	-0.85	-0.02	-0.38	-0.19	0.37	1.00	-0.28	0.72	0.65	0.51
Mining	0.64	-0.10	0.23	0.16	0.10	0.07	-0.06	-0.17	-0.04	0.27	0.11	-0.73	-0.54	-0.05	-0.16	0.06	-0.03	-0.13	0.40	0.29	-0.28	1.00	-0.27	-0.16	-0.01
Grazing	-0.24	0.51	-0.78	-0.66	-0.61	-0.52	-0.64	-0.10	-0.17	-0.65	-0.65	0.16	-0.24	-0.62	0.03	-0.53	-0.14	-0.38	0.04	0.39	0.72	-0.27	1.00	0.88	0.21
DCA1	-0.11	0.11	-0.54	-0.82	-0.83	-0.46	-0.75	-0.44	-0.57	-0.79	-0.73	0.14	-0.32	-0.73	-0.34	-0.39	-0.55	-0.75	0.38	0.33	0.65	-0.16	0.88	1.00	0.33
DCA2	-0.01	0.07	-0.24	-0.52	-0.44	-0.38	-0.49	-0.48	-0.43	-0.46	-0.44	0.08	-0.05	-0.50	-0.43	-0.42	-0.42	-0.44	0.08	-0.13	0.51	-0.01	0.21	0.33	1.00

*Sifaka densities = density of sifakas; Area = contiguous forest area from remote sensing; Vegetation stratification = presence or absence of vegetation along an imagined line stretching vertically from 2 to 5 m above the ground; Tree height = tree heights from PCQ trees; Canopy cover = estimated canopy cover from points along perpendicular vegetation transects; Tree density = corrected tree densities from PCQ plots; Total basal area = total tree basal area/ha from PCQ plots; Basal area per tree = basal area per ha/tree density for all trees based on PCQ plots; Tree crown volume = estimate of tree crown volume from trees within PCQ plots; Shannon diversity = index for tree species diversity from PCQ plots; Simpson diversity (1-D) = index for tree species diversity from PCQ plots; Hill evenness = index for tree species evenness from PCQ plots; Pi evenness = index for tree species evenness from PCQ plots; Food

tree basal area = total food tree basal area/ha from PCQ plots; Food tree basal area/tree = basal area per ha/food tree density based on PCQ plots; Food tree density = corrected densities of food tree species from PCQ plots; Food tree crown volume = estimate of tree crown volume from food trees within PCQ plots; NDVI dry = normalized difference vegetation index from remote sensing during the dry season (May-November); NDVI wet = normalized difference vegetation index from remote sensing during the wet season (December-April); Tree cutting = evidence of tree removal from disturbance plots; Fire = evidence of fire or past burning from disturbance plots; Mining = evidence of mining from disturbance plots; Grazing = evidence of browsing/grazing by domestic animals from disturbance plots; DCA1 = decorana values along the first axis of the detrended correspondence analysis of tree species; DCA2 = decorana values along the second axis of the detrended correspondence analysis of tree species

** Food tree Shannon's index, food tree Simpson's index of diversity ($1-D$), and food tree Hill and Pi evenness values also were run, but were highly correlated with the non-food tree equivalent ($r > 0.90$) and are not shown in this matrix to conserve space.

Supplemental Table 3: Human activity variables were collected every 200 m along 35 forest transects at two points 25 m and 50 m perpendicular to the transect from 2016 - 2018 in the Loky-Manambato Protected Area in Northeastern Madagascar. These were indexed within a 10 m radius of point-centered quarter plots using five different activity metrics. Low index values indicate no visible activity and high values indicate high levels of activity.

Disturbance	1	2	3	4	5
Tree Cutting	None	1-2 trees cut	<25% of trees cut	25-50% of trees cut	>50% of trees cut
Fire	None	1-2 scarred trunks, old	Charred logs or trunks present	Charred logs/ trunks, no dead grass/leaves	Fire or smoke visible
Mining	None	1-2 small holes, >75% understory present	Multiple pits, 75-25% of understory present	Many large pits, <25% of under-story intact	Landscape completely altered
Livestock Grazing	None	<25% of stems consumed	25-75% of stems consumed	75-90% of stems consumed	No greenery below browse line

Supplemental Table 4: Detection models and density estimates from program Distance for golden-crowned sifakas in the Loky-Manambato Protected Area, Madagascar (2016-2018). The furthest 10% of observations were truncated and distance binning was adjusted to ensure acceptable goodness of fit ($p > 0.05$). Detection models included hazard rate (HR) and half normal (HN) key functions with cosine (cos) and simple polynomial (sp) expansions. We stratified observations by fragment (Strata-specific) to examine how densities varied by vegetation, human activity, and land cover variables. To obtain a global density estimate for the stratified models, we weighted the density estimate of each fragment by its area. No estimated sampling width (ESW) was determined for these models. CI = confidence interval; CV = coefficient of variation; NoFactor = the covariate was not listed as a factor variable in the detection function

Model Name	No. of Parameters	Δ AIC	AIC	ESW ^a	Density (95% CI) ^b	CV ^c
HR cos VegStratification nofactor ^{d,e}	3	0.00	1355.20	15.99	26.6 (21.0-33.6)	0.12
Strata-specific HR cos	24	2.22	1357.43	-	21.5 (17.3-26.7)	0.11
HR cos graze nofactor ^f	3	3.71	1358.91	15.9	26.5 (21.0-33.5)	0.12
HR cos VegStratification ^{d,e}	13	4.58	1359.78	15.8	26.6 (21.0-33.7)	0.12
HR cos NDVIwet ^g	13	4.60	1359.80	16.0	26.4 (20.8-33.4)	0.12
HR cos NDVIdry ^g	13	5.09	1360.29	16.2	26.1 (20.6-33.0)	0.12

Model Name	No. of Parameters	Δ AIC	AIC	ESW ^a	Density (95% CI) ^b	CV ^c
HR cos TreeDensity nofactor ^e	3	5.31	1360.51	15.2	27.3 (21.6-34.5)	0.12
HR cos TreeCutting nofactor ^f	3	10.16	1365.37	16.4	25.5 (20.2-32.3)	0.12
HR cos cluster nofactor bootstrap ^h	3	10.77	1365.98	16.3	25.2 (na)	na
HR cos cluster nofactor ^h	3	10.77	1365.98	16.3	25.2 (na)	na
HR cos	2	11.61	1366.81	15.4	26.4 (20.3-34.2)	0.13
HR sp	2	11.61	1366.81	15.4	26.4 (20.3-34.2)	0.13
HR cos NDVIwet nofactor ^g	3	12.86	1368.07	15.8	26.4 (20.9-33.3)	0.12
HR cos treeheight nofactor ^e	3	15.29	1370.50	15.6	26.5 (21.0-33.5)	0.12
HR cos CanopyCover nofactor ^{e,i}	3	15.78	1370.98	15.6	26.4 (20.9-33.4)	0.12
HR cos PiEvenness nofactor ^e	3	16.92	1372.12	16.5	24.9 (19.7-31.4)	0.12
HR cos ShannonDiversity nofactor ^e	3	17.79	1372.99	16.5	25.4 (20.1-32.0)	0.12
HR cos HillEvenness nofactor ^e	3	17.89	1373.10	15.3	26.9 (21.3-33.9)	0.12
HR cos fire nofactor ^f	3	18.28	1373.48	15.2	27.2 (21.5-34.3)	0.12
HR cos year nofactor ^j	3	18.57	1373.77	16.4	25.4 (20.1-32.0)	0.12
HR cos BasalArea nofactor ^e	3	18.60	1373.80	15.6	26.5 (21.0-33.4)	0.12

Model Name	No. of Parameters	Δ AIC	AIC	ESW ^a	Density (95% CI) ^b	CV ^c
HR cos CrownVolume nofactor ^{e,k}	3	18.72	1373.92	16.5	25.3 (20.1-32.0)	0.12
HR cos SimpsonDiversity nofactor ^e	3	18.94	1374.15	15.8	26.3 (20.9-33.3)	0.12
HR cos NDVI _{dry} nofactor ^g	3	18.95	1374.15	15.6	26.5 (21.0-33.5)	0.12
HR cos mining nofactor ^f	3	19.11	1374.32	15.3	26.9 (21.3-34.0)	0.12
HN cos	1	29.37	1384.58	17.4	23.6 (18.6-29.8)	0.12
HN sp	1	29.37	1384.58	17.4	23.6 (18.6-29.8)	0.12

^a ESW = estimated sampling width

^b CI = confidence interval

^c CV = coefficient of variation

^d Based on presence/absence of vegetation at various height intervals.

^e Determined from point-center-quarter (PCQ) plots.

^f Index of disturbance intensity determined within a 10m radius of each vegetation plot.

^g NDVI values are the average for all pixels within each forest fragment for the wet or dry season.

^h “Cluster” or animal group size with or without bootstrap adjustment.

ⁱ Average estimated canopy cover along vegetation transects.

^j Year when data were collected.

^k Determined from trees in PCQ plots based on the max estimated crown width, length, and height.

Supplemental Table 5: Land cover class accuracy assessment for imagery classified using the IsoData unsupervised classification method in ENVI 5.3 (Harris Geospatial Solutions, Broomfield, Colorado, USA) from the Loky-Manambato Protected Area in northeastern Madagascar. Classified cover types from Landsat 7 and 8 imagery (30 m² resolution, 2017-2019) are given on the left, while cover types determined from visual interpretation of 10 points (30 m² resolution) per cover type from high resolution satellite data (Google Earth, imagery dates 7 May 2013 - 23 April 2017) and personal visits (May – July 2016, August – December 2017, and September – December 2018) to sites are listed as column headers. Commission error (percent of sites belonging to a class in the classified map that visual inspection indicated should belong to a different class) and omission error (percent of sites that visual inspection indicated should belong to as class, but was classified as a different class) accuracies are calculated for rows and columns, respectively. Overall accuracy is indicated with an asterisk (*).

		Visual Interpretation								
	Land Cover Class	Water	Ever-green	Semi-deciduous	Deciduous	Bare Ground	Scrub	Sand	Row Total	Commission Error
Classification	Water	10	-	-	-	-	-	-	10	0.0%
	Evergreen	-	10	1	-	-	1	-	12	17.0%

Visual Interpretation										
	Land Cover Class	Water	Ever-green	Semi-deciduous	Deciduous	Bare Ground	Scrub	Sand	Row Total	Commission Error
	Semi-deciduous	-	-	9	-	-	1	-	10	10.0%
	Deciduous	-	-	-	10	-	-	-	10	0.0%
	Bare Ground	-	-	-	-	27	1	1	29	17.0%
Classification	Scrub	-	-	-	1	1	8	-	10	20.0%
	Sand	-	-	-	-	-	-	9	9	0.0%
	Column Total	10	10	10	11	28	11	10	90	
	Omission Error	0.0%	0.0%	10.0%	9.0%	4.0%	27.0%	10.0%		92.0%*

Supplemental Table 6: Malagasy vernacular names of tree species consumed by golden-crowned sifakas (*Propithecus tattersalli*)

between 2016 and 2018 in the Loky-Manambato Protected Area in northeastern Madagascar in 12 study units. Genus-level identification was made from vernacular names using Schatz (2001). For some species, a vernacular name may refer to multiple tree species in different genera. Genus-level identification could not be made from all vernacular species names. Species that combined represented >80% of sifaka diet (based on the percentage of total feeding scans in which that food plant was consumed) are in bold. Codes for plant parts consumed: BD = buds; FL = flowers; ML = mature leaves; PT = petioles; RF = ripe fruits; SD = seeds; URF = unripe fruits; YL = young leaves

Food Plant	Genus	Plant Part Consumed	Percent of Diet (%)
Aboringa	<i>Hildegardia</i>	FL	0.11
Aboringa mavo	-		0.02
Ambavy	<i>Erythroxylum</i>	BD, FL, SD, YL	1.08
Amontana	<i>Garcinia</i>	BD, FL, SD, URF, YL	2.17
Anamorongo ravina	-	YL	0.02
Antsimay	-	SD	0.05
Antsimonina	-	BD, SD, YL	0.15
Antsimonina mena	-	BD, PT, YL	0.11
Antsiniragna	-	YL	0.06
Aviavy	<i>Ficus/Hibiscus</i>	BD, URF	0.71
Bankarana	-	ML	0.03
Barabanja	<i>Mascarenhasia</i>	BD, ML, PT, YL	0.48
Beandy	-	YL	0.02

Food Plant	Genus	Plant Part Consumed	Percent of Diet (%)
Bonara	<i>Albizia</i>	BD, FL, SD, YL	0.84
Fagnito	-	BD, YL	0.06
Famehy fary	-	YL	0.02
Famoha	-	YL	0.15
Famoha ala	-	YL	0.08
Fanamponga	<i>Albizia/Entada</i>	BD	0.48
Fanazava	<i>Blotia/Petalodiscus/Rhopalocarpus/Stadmania</i>	BD	0.08
Fotsy avadika	<i>Croton</i>	ML	0.02
Hazomafana	<i>Anisophyllea/Dicoryphe/Diospyros/Micronychia/ Paropsia/Turraea</i>	Bark, BD, ML, SD	0.25
Hazomalany	<i>Cassipourea/Crateva/Hernandia/Macarisia/ Melanophylla/Molinaea/Moringa/Paropsia/ Pittosporum/Viguieranthus</i>	BD, FL	0.09
Hazomena	<i>Homalium</i>	SD, YL	0.51
Hidiny	<i>Schrebera</i>	YL	0.11
Hodiboay	-	ML	0.08
Jobiapototra	<i>Brexia</i>	ML, RF, URF, YL	0.85
Jobiapototra mavo	-	ML, YL	0.25
Kafeala	<i>Chapelieria</i>	ML	0.02
Katrafay	<i>Cedrelopsis</i>	BD	0.08
Kimbimba	<i>Olex</i>	ML, YL	0.77
Kolohoto	<i>Neoapaloxylon/Obetia/Trilepisium</i>	ML, YL	0.28
Konikony	<i>Annona</i>	RF, URF	0.08
Koropetaka	<i>Annona</i>	URF	0.05
Lalongo	-	Bark, ML, SD, YL	0.26
Lamonty	<i>Ziziphus</i>	BD, ML	0.15
Lonjo	-	ML, RF	0.06
Mabibo ala	-	BD, ML, PT, YL	0.94
Madiovozona	<i>Dypsis</i>	BD, ML	0.05
Madiro	<i>Tamarindus</i>	BD, FL, ML, YL	1.08

Food Plant	Genus	Plant Part Consumed	Percent of Diet (%)
Madirokarana	<i>Pithecellobium</i>	BD	0.09
Magonga	<i>Erythrina/Ziziphus</i>	YL	0.02
Makarana	-		0.05
Malazavoavy	<i>Homalium</i>	FL	0.03
Mampay	<i>Cynometra</i>	BD, ML, SD, URF, YL	18.36
Manary	<i>Albizia/Chadsia/Dalbergia/Pongamiopsis</i>	BD, ML, PT, YL	0.54
Manary boraka	<i>Albizia</i>	BD, SD	0.57
Manary mavo	<i>Dalbergia</i>	ML	0.06
Manary mena	-	PT	0.03
Mango	<i>Mangifera</i>	BD, FL, PT, RF, SD, URF, YL	2.99
Mankarana	<i>Mantalania</i>	BD, YL	0.25
Mantaly	<i>Terminalia</i>	BD, ML, RF, URF, YL	0.34
Mantsikariva	<i>Phyllanthus</i>	BD, FL, YL	0.28
Mapingo	<i>Pyrostria</i>	ML, YL	0.11
Marohefaka		BD	0.02
Matambelo	<i>Commiphora/Sakoanala</i>	BD	0.14
Matambelona	<i>Polycardia/Polyscias</i>	Bark, SD, URF	0.09
Matifoditra ala/ Matifihoditra ala	<i>Crossonephelis/Majidea</i>	Bark, BD, FL, ML, SD	2.10
Mendivoatanana	<i>Diospyros</i>	BD, YL	0.60
Merana	<i>Androstachys/Asteropeia/Brachylaena</i>	SD, URF	3.56
Meridina	<i>Afrosavia</i>	ML	0.02
Moramena	<i>Acridocarpus/Brackenridgea</i>	YL	0.08
Morango	<i>Senna/Xylopia</i>	BD, FL, YL	0.36
Morasira	<i>Blotia/Grangeria</i>	YL	0.02
Nanto	<i>Capurodendron</i>	BD, ML, SD, URF, YL	1.66
Nonosay	-	YL	0.17
Ontrombengy	<i>Bauhinia</i>	FL	0.31
Ramy	<i>Canarium/Schefflera</i>	URF, YL	0.09

Food Plant	Genus	Plant Part Consumed	Percent of Diet (%)
Rasaonjo	<i>Physena</i>	FL, ML, YL	0.90
Rotro	<i>Syzygium</i>	BD, FL, PT, URF, YL	1.30
Rotro ala	-	BD	0.11
Rotro mena	-	YL	0.02
Sakoadia	<i>Poupartia</i>	RF	0.45
Sakoambanditra	<i>Poupartia</i>	BD, FL	0.06
Sakoana	<i>Poupartia</i>	BD, YL	0.82
Sakoanala	<i>Commiphora/Poupartia/Sakoanala/Xanthocercis</i>	SD	0.03
Sambalahiravina	<i>Bussea/Caesalpinia/Chadsia/Dalbergia</i>	FL, ML	0.03
Sambalahy	<i>Albizia</i>	BD, FL, SD, YL	2.35
Sambalaravina	-		0.11
Santibonane	-	Bark, BD, SD, YL	0.54
Saribaro	-	BD, FL	0.03
Sarinanto	<i>Ochna/Rhus</i>	YL	0.15
Sarobarabanja	-	BD	0.06
Selimavo	<i>Cf. linearifolia</i>	BD, ML	0.43
Selivato	<i>Brandzeia/Dombeya/Grewia/Helmiopsiella/Helmiopsis/Rhopalocarpus</i>	BD, URF	0.05
Sely	<i>Grewia</i>	SD, YL	0.20
Sohihy	<i>Abrahamia/Breonadia/Sapindaceae/Viguiерanthus</i>	BD, PT, YL	0.09
Somatsohihy	-	YL	0.03
Somotrorana	<i>Stadmania</i>	SD, YL	0.09
Sondrindrinala	-	URF	0.05
Soritry	<i>Filicum</i>	BD, ML, PT, SD, YL	2.07
Sosorimalandy	-	ML	0.14
Taimbarika	<i>Abrahamia/Allantospermum/Cleistanthus/Leptolaena/Macarisia/Malleastrum</i>	BD, ML, YL	0.79
Taindrabosy	<i>Viguiерanthus</i>	BD, YL	0.43
Taintsafitry	-	FL	0.06

Food Plant	Genus	Plant Part Consumed	Percent of Diet (%)
Taintsindambo	<i>Pongamiopsis</i>	BD, FL, SD, YL	2.06
Taipapango	<i>Dryptes</i>	BD, FL, RF, URF, YL	6.39
Tapiaka	<i>Ormocarpopsis/Syzygium</i>	BD, ML	0.15
Tovonia	-	BD, ML	0.14
Tsarafanahy	<i>Bourreria</i>	ML, PT, RF, URF	8.41
Tsiaramiaramy	-	YL	0.03
Tsibabena	-	ML	0.02
Tsifo	<i>Tarenna</i>	ML	0.06
Tsilaity	<i>Erythroxylum</i>	BD, RF	0.29
Tsimatimanota	<i>Garcinia</i>	URF, YL	0.08
Unknown*	<i>Chrysophyllum/Mammea/Memeclylon/Olax/Plagioxyphus/Pongamiopsis/Vytex (among others)</i>	BD, FL, ML, RF, SD, URF, YL	10.94
Vaheny	<i>Landolphia</i>	RF, URF, YL	0.28
Vaho	-	PT, URF	0.36
Vahonda	<i>Dupuya</i>	BD, FL, SD, YL	0.87
Vahy*	<i>Combretum/Etanda/Talinella (among others)</i>	BD, FL, ML, PT, RF, SD, URF, YL	4.49
Vahy joby	-	UR, FYL	0.06
Vahy laoka	-	RF, URF	0.09
Vahy loaka	-	URF	0.11
Vahy lombiro	-	YL	0.02
Vahy lombirolahy	-	YL	0.02
Vahy maragna	-	URF	0.03
Vahy tsivory	-	YL	0.02
Vahy vy	-	YL	0.08
Valotra	<i>Breonia</i>	URF	0.54
Vapendela	-	BD, ML, URF, YL	0.15
Varona	<i>Antidesma</i>	FL, SD, URF, YL	0.48
Voamora	-	YL	0.02

Food Plant	Genus	Plant Part Consumed	Percent of Diet (%)
Voankazomeloka	<i>Xanthocercis</i>	YL	0.19
Voantsilaka	<i>Xanthocercis</i>	BD	0.06
Voara	<i>Ficus</i>	BD, PT, RF, URF, YL	0.91
Voatsikomoka	-	SD	1.70
Volomborona	<i>Albizia</i>	BD, FL, YL	1.08
Vongo	<i>Garcinia</i>	BD, SD, URF, YL	0.97
Zahana	<i>Leptolaena</i>	BD, FL, ML, YL	1.90
Zanakanivato	<i>Bandouinia</i>	URF	0.02

*These are general terms (“vahy” means vine) and therefore may apply to a number of potential genera. Those that could be confirmed are listed, though others are also likely.

Chapter 3

Minerals and normalized difference vegetation index (NDVI) predict golden-crowned sifaka (*Propithecus tattersalli*) densities

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Minerals and normalized difference vegetation index (NDVI) predict golden-crowned sifaka (*Propithecus tattersalli*) densities

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Abstract

Quantifying the nutritional composition of primate food items has greatly enhanced our understanding of primate adaptations, evolutionary history, and dietary requirements, but there remains no single nutritional measure that can be used to predict primate densities across their range. Here, we explore the nutritional ecology of the golden-crowned sifaka (*Propithecus tattersalli*) across a forest moisture gradient in northeastern Madagascar that encompassed the species' entire known range. We hypothesized that the recently described relationship between sifaka densities and the normalized difference vegetation index (NDVI) may be because NDVI is a good proxy for available nitrogen (*i.e.*, N available for protein synthesis), which is known to limit many animal populations. Sifaka feeding patterns, plant parts consumed, and nutritional profiles of their food items varied seasonally and across three different forest types (dry, moderate, and wet). While we found no relationship between sifaka densities and macronutrients or the protein-to-fiber ratio, several minerals found in sifaka food items were useful for predicting densities (positive relationships with magnesium ($\beta = 0.62$, SE = 0.19), potassium ($\beta = 0.58$, SE = 0.20), and sodium ($\beta = 0.43$, SE = 0.23); negative relationship with manganese ($\beta = -0.41$, SE = 0.22)). NDVI also was a positive predictor of sifaka densities ($\beta = 0.43$, SE = 0.20). Our findings highlight the importance of minerals and wet season NDVI, likely a proxy for available nitrogen, as influences upon sifaka densities. Conservationists seeking to better understand or to predict current and future densities of this critically endangered primate may thereby find substantial benefits from remotely sensed data, allowing greater geographic coverage while spending significantly less time and effort on diet sampling or other on-the-ground evaluations.

Introduction

Ecologists have long sought to better understand factors influencing animal population heterogeneity across landscapes. Frequently cited explanations include resource availability and quality (Doncaster and Woodroffe 1993; Herrera et al. 2018; McNamara and Houston 1987), disease (Newey et al. 2007), habitat area and quality (Crozier and Niemi 2003), predators (McNamara and Houston 1987; Wayne et al. 2006), and nutrition (Bishop et al. 2009; McNaughton 1988). Increasingly, anthropogenic factors such as habitat fragmentation due to urbanization and resource consumption and extraction (*e.g.*, mining, agriculture, hunting) are imposing large and rapid impacts on species density and abundance as well, either indirectly, through habitat loss and fragmentation or directly by human-caused mortality (Afriyie and Asare 2020; Harrisson et al. 2013; Kataev 2017). Researchers commonly use environmental variables to predict species density and abundances across landscapes that have been or may be impacted by these factors, allowing for more accurate mapping of species abundance at a variety of spatial scales (Elith and Leathwick 2009).

Primatologists have evaluated the use of different nutritional variables as predictors of primate densities across landscapes. Two non-mutually exclusive hypotheses have been proposed. First, certain key minerals may limit primate populations (Behie and Pavelka 2012; Rode et al. 2006), especially in mineral-poor evergreen, tropical forests (Medina 1984). Indeed, minerals like magnesium, sodium, and phosphorous are known to limit some herbivore populations (Freeland et al. 1985; McNaughton 1988). This mineral-related hypothesis has not been widely tested in the primate literature. Second, like many animals, primate populations are expected to be limited by available nitrogen, a key building block of protein (Ganzhorn et al. 2017; Tamm 1991; Vitousek and Howarth 1991). Primates also must compensate for plant

defense compounds, which may directly or indirectly limit available nitrogen, when seeking to meet nutritional targets (Feeny 1992; Iason 2005; Murdoch 1966; Pimm et al. 1991). Plant defenses, like indigestible fiber, may act to discourage herbivory when consumed in bulk. To compensate for these repellent compounds, primates may target plants or plant parts with higher protein-to-fiber ratios (Chapman et al. 2002; Milton 1979; Oates et al. 1990; Waterman et al. 1988; but see Felton et al. 2009; Gogarten et al. 2012; Wallis et al. 2012). Plant defenses may also include toxins that interfere with the consumer's metabolism. Uptake of toxins may be mitigated by diet mixing to reduce the intake of any one toxin at a time (McKey 1978), while some primates have evolved specialized physiology to metabolize toxins in their diet (Lauterbur et al. 2019; Lauterbur et al. 2017) or adapted other behavioral strategies to neutralize consumed toxins (*e.g.*, geophagy; Pebsworth et al. 2019; Semel et al. 2019).

Seasonal food availability further complicates primate nutrient acquisition (Hemingway and Bynum 2005). “Abundant season” foods often are assumed to be highly nutritious and enable primates to build up fat reserves to make it through the resource-poor “lean season,” thereby limiting primate populations. Alternatively, rather than rely on fat stores, primates may be limited by the nutritional quality of “fallback” foods available during the “lean season” (Hanya and Chapman 2013). Understanding seasonal variation in primate nutrition therefore is critical to understanding factors that affect primate densities.

Golden-crowned sifakas (*Propithecus tattersalli*; hereafter, ‘sifakas’) are endemic to highly fragmented forests in northeastern Madagascar. These forests are botanically diverse, with some fragments dominated by deciduous plant species more characteristic of western Madagascar and others dominated by evergreen species more characteristic of the eastern rainforests (Chatelain et al. 2006). Previous studies shed considerable light on golden-crowned

sifaka feeding behavior, diet, and nutrition in different forest types across their range. Sifakas spend 30-47% of their feeding time consuming young and mature leaves, while fruits and seeds represented 40-54% of feeding time, depending on the forest type and season (Meyers 1993). In prior work and this dissertation research, sifakas were found to consume plant parts from at least 101 plant species comprising 80 genera and 49 families (see *Chapter 2*; Meyers 1993; Quéméré et al. 2013). However, previous studies did not capture the full biogeographic range of the species (*e.g.*, Meyers 1993 was unable to sample forests in the driest parts of their range) or were limited to higher taxonomic level identification of food items (Quéméré et al. 2013).

Furthermore, sifaka densities varied widely across their range, from 6.8 sifakas/km² (95% CI: 2.0 – 22.8) to 78.1 sifakas/km² (95% CI: 53.1 – 114.8; see *Chapter 2*). Previous work demonstrated that tree cutting, NDVI during the wet season, and Simpson's diversity index (1-*D*) of plant species were the best predictors of sifaka densities (see *Chapter 2*). Broadly speaking, NDVI often is described as a proxy for plant productivity (Pettorelli et al. 2001). Researchers have begun to explore whether NDVI may effectively be a proxy for some nutritional component in animal diets, highlighting available nitrogen as a likely candidate (*i.e.*, N that is available as a building block of protein; Johnson et al. 2018). Given the relative ease of access and calculation of this remotely-sensed NDVI predictor compared to collecting and analyzing plant parts consumed, we hypothesized that it could be a useful metric for conservation planning for sifakas.

The wide range of forest types exploited by these sifakas over such a small geographic range makes this species a good case study to investigate the role of different plant part nutrients on primate densities. While many studies have simply correlated primate biomass with protein-to-fiber ratios across select sites (Chapman et al. 2002; Ganzhorn 1992; Oates et al. 1990), we explored whether assessment of the nutritional composition of top food items across a highly

variable, yet geographically limited range would clarify the role plant nutrition has in driving primate abundance. Our objectives were to: 1) establish the first complete activity budgets for golden-crowned sifakas across the full range of forest types in which they are found to provide a contextual basis for their feeding habits, 2) establish the first dietary profile (*i.e.*, plant species, plant parts consumed) for golden-crowned sifakas across the full range of forest types in which they are found, 3) establish the first nutritional profile (*i.e.*, macro- and micronutrients) for golden-crowned sifakas across the full range of forest types in which they are found, and 4) evaluate the power of remotely-sensed NDVI values (see *Chapter 2*) relative to more conventional field-collected nutritional variables to predict sifaka densities across their range.

Methods

Study Site and Subjects

Golden-crowned sifakas (*Propithecus tattersalli*) are endemic to northeastern Madagascar and are confined to the area between the Loky and Manambato Rivers (49°56'E, 13°31'S), with the exception of one population that inhabits an isolated forest block on the west side of the Loky River (Fig. 1). Sifakas are found from low elevation (10 m) dry deciduous forest and scrubland to moderate elevation (1000 m) wet evergreen forest over a 40 km long transitional zone. Forests are highly fragmented. Each of the 11 largest, contiguous forest fragments was categorized as dry, dry/moderate, moderate/wet, or wet (see *Chapter 2*). A mixed-cover area of cattle pasture, grassland, small forest patches, and agricultural areas separate large forest fragments that are mostly restricted to higher elevations (Quéméré et al. 2013). Although bushmeat hunting historically has not affected populations due to traditional taboos (*fady*), sifaka hunting was reported across the region in and after the coup d'état in 2009 (Barrett and

Ratsimbazafy 2009; Conservation International 2010). All of the forest fragments studied are part of the 250,000 ha Loky-Manambato Protected Area (PA), which is managed by the non-governmental organization (NGO), Fanamby.

Sifaka Density Estimation

Twenty-two, 1-3 km long line transects were established in nine of the largest forest fragments within the golden-crowned sifaka global range (Ambohitsintondroina, Ampondrabe, Antsahabe, Antsaharaingy, Bekaraoka Avaratra, Bekaraoka South, Benanofy, Binara, and Solaniampilana). Line transect surveys for this study were conducted May-July 2016, August-December 2017, and September-December 2018. Transects were distributed across dry, dry/moderate, moderate/wet, and wet forest types (as described in *Chapter 2*). For this study, we combined dry and dry/moderate forest types into the class “dry.” Sifaka densities were estimated for each individual forest fragment using program Distance (Thomas et al. 2010) and fragments were used as the unit of analysis. A complete description of survey and density estimation methods can be found in *Chapter 2*.

Sifaka Feeding Data and Food Item Collection

Sifaka food trees were determined based on observations of 18 unique sifaka groups within the same nine surveyed forest fragments described above. Two sifaka groups were followed at each of the nine fragments: one group used areas near the forest edge, while the other used areas > 500 m away from the nearest forest edge. Individuals were identified by physical characteristics (*e.g.*, sex, scars, color patterns), and groups were followed to their sleep trees each night to ensure that the same group could be located the following morning before sunrise and

first movements. All group members were photographed to ensure that the same groups (and in most cases the same individuals) were followed in subsequent seasons.

Data for the dry season were collected August - December from 16 sifaka groups in 2017 (two groups each from Ampondrabe, Antsahabe, Antsaharaingy, Bekaraoka Avaratra, Bekaraoka South, Benanofy, Binara, and Solaniampilana), 12 groups in 2018 (two groups each from Ambohitsintondroina, Antsahabe, Antsaharaingy, Bekaraoka South, Binara, and Solaniampilana), and six groups in 2019 (two groups each from Bekaraoka South, Binara, and Solaniampilana). Data for the wet season were collected February – March 2019 from six sifaka groups (two groups each from Bekaraoka South, Binara, and Solaniampilana).

We conducted instantaneous scan samples at 15-minute intervals for each group for a maximum of 10 days per sifaka group per season (Altmann 1974). We recorded the instantaneous behavior of each individual in the group as close to the time interval as possible. The name of each individual was recorded if it could be confidently identified (*i.e.*, clear sight lines on all key features and agreement among observers). We allowed a maximum of one minute to search for individuals that could not be immediately observed before marking lost individuals as out of sight. Hereafter, these instantaneous behavior samples will be referred to as “counts.” Activities recorded were feeding (F), resting (R), travelling (T), or socializing (S). Socializing was defined as grooming, playing, or aggression between two or more individuals as well as scent marking and vocalizing. During a feeding count, we also recorded whether individuals were consuming bark (BARK), buds (BD), flowers (FL), ripe or unripe fruits (RF or URF), seeds (SD), leaf petioles (PT), or young (YL) or mature (ML) leaves. Feeding trees were marked with flagging tape and their GPS coordinates recorded. Data were recorded for adult, sub-adult, and juvenile individuals that were fully weaned during the sampling period.

At the end of each 10-day period for each sifaka group, samples of the top five most-used plant food items during that 10-day sampling window, defined as the five most frequently used plants by number of feeding counts, were collected from the home range of each followed group. Items were obtained from branches as close as possible to where animals were observed feeding within marked feeding trees, as nutritional contents were expected to vary both spatially and temporally in a tree (Chapman et al. 2003). A pole-axe (8 m long) was used to obtain canopy samples as needed. Samples that remained out of reach were collected opportunistically from the forest floor immediately after being dislodged from the trees by foraging animals. Voucher specimens were collected for species identification at the Missouri Botanical Garden in Antananarivo, Madagascar.

Plant samples were brought to a drying tent on the forest edge to facilitate preparation for storage. The tent was erected in direct sunlight to increase temperature inside while keeping the samples out of direct sunlight to prevent the breakdown of tannins. Only the parts of the plant actually consumed by animals (*e.g.*, leaf petiole) were retained for processing. Each part was finely sliced, placed on trays with desiccants (silica gel in mesh bags), and allowed to dry before being placed in Ziploc® bags with desiccants and stored in the dark until they were exported for laboratory analysis (Rothman et al. 2012).

Predictors of Sifaka Density

Nutritional values from plant samples collected from each of the two groups per forest fragment (one near the forest edge, one in areas > 500 m away from the forest edge) were averaged for each forest fragment for use as predictors of sifaka density (*italicized below and*

listed in Supplemental Table 1). All analyses were conducted in the program R (R Core Team 2019).

Laboratory Analyses

Nutritional analyses were conducted at the Primate Ecology Lab at Hunter College (New York, NY) and at Dairy One Nutritional Forage Laboratory (Ithaca, NY) using protocols as detailed in Rothman et al. (2012). Dried samples were milled to a uniform particle size using a Wiley® mill fitted with a 1-mm screen. *Crude protein (CP)* was determined using a Leco FP-528 nitrogen/protein analyzer. Three fiber fractions (*neutral detergent fiber (aNDF)*, *acid detergent fiber (ADF)*, and *acid determined lignin (ADL)*) were measured via sequential digestion in NDF, ADF, and sulfuric acid solutions, respectively, in an ANKOM A200 Digestion Unit. Acid Detergent Insoluble Crude Protein (ADICP), or the protein fraction bound to the fiber, was determined using ADF or NDF residue analyzed using a Leco TruMac N Macro Determinator. *Available protein (AP)* was calculated as: $AP = CP - ADICP$. Protein made unavailable by heating was referenced as adjusted crude protein and was calculated as: $adjusted\ CP = CP - unavailable\ protein + 1\%$. *Protein-to-fiber ratio (P:F ratio)* was determined as: $AP / aNDF$. *Crude fat* was determined via gravimetric analysis of the dried ether extract. *Water-soluble carbohydrates (WSC)* were determined using a Thermo Scientific Genesys 10S Spectrophotometer after samples were soaked in water and underwent acid hydrolysis with sulfuric acid and colorimetric reaction with potassium ferricyanide. *Soluble sugars* were determined using a phenol-sulfuric acid assay and a sucrose standard. Ash was determined by ignition at 600°C for two hours (AOAC Method 942.05). Atomic adsorption spectroscopy was

used to determine the mineral contents of the ashed samples (*Ca, P, Mg, K, Na, Fe, Zn, Cu, Mn,* and *Mo*; Rothman et al. 2012).

Nitrogen (N) availability was measured using the method described by DeGabriel et al. (2008). Dry matter from each sample was prepared for a two-stage in vitro digestion experiment. In the first stage, samples were incubated with pepsin and cellulose to mimic digestion in an animal's gut. In the second stage, the tannin-blocking agent, polyethylene glycol (PEG), was added to neutralize the effect of tannins on protein digestion. *Available N* was calculated as the difference between the protein content measured before and after the digestion experiment using the Leco protein analyzer.

Remote-Sensing

We created land cover maps in ENVI 5.3 (Harris Geospatial Solutions, Broomfield, Colorado, USA) from LANDSAT 8 satellite imagery (30 m² resolution) collected from 2017-2019. We calculated NDVI values for each fragment during the wet and the dry seasons using the standard equation:

$$\frac{(NIR - Red)}{(NIR + Red)} = NDVI$$

See *Chapter 2* for full details of forest cover pixel extraction. We calculated both *NDVI dry* and *NDVI wet* season values for each forest fragment.

Statistical Analyses

For all modeling approaches, our sampling unit was feeding count/individual/day. A feeding count was defined as any feeding behavior observed instantaneously at 15-minute interval scans that occurred throughout each sampling day. Because individuals from the same

group were unlikely to be independent samples, we included Group Identity as a random effect in all models. We conducted linear mixed-effects models in the R package “lme4” to evaluate the effects of season (wet or dry), sex (we included males and females of all age classes simultaneously due to sample size constraints), and forest type (*i.e.*, dry, moderate, or wet) on feeding bout frequency (Bates et al. 2015). To investigate the effects of seasons, sex, and forest type on feeding counts of different food items (*i.e.*, buds/flowers, fruits, mature leaves, seeds, and young leaves), we conducted zero-inflated negative binomial (ZINB) models due to the excess of zeros in our dependent variable (bouts/individual/day; Zuur et al. 2009). ZINB models had the same covariates on both the zero-inflated and count processes.

We performed overdispersion tests to verify the superiority of ZINB models over those with a Poisson distribution in the R package, “DHARMA” (Hartig 2020). We ranked model sets using AICc values, and we considered models whose $\Delta\text{AICc} < 4.0$ to be competing (Arnold 2010). We determined the significance of beta (β) estimates using the Satterthwaite approximation using the R package, “lmerTest” (Kuznetsova et al. 2017; Luke 2017).

We used z -scores to evaluate differences in the percent of time spent consuming different plant parts. We conducted Kruskal-Wallis tests on the nutritional analyses outputs (measured as a percent of total dry matter or parts per million (ppm)) for non-correlated ($r < |0.70|$) predictors to examine any effects of plant part or forest type on plant nutrients. Each plant sample was considered a sampling unit for these analyses. Dunn’s test was conducted *post hoc* to evaluate which ranked means were significantly different from one another (Zar 2010). We set $\alpha = 0.05$ for all analyses.

Before we modeled relationships between sifaka densities and nutritional predictors, we removed predictors that were highly correlated with one another ($|r| > 0.70$). We prioritized the

selection of remote sensing variables over nutritional variables in an effort to promote more easily obtained data. To evaluate which non-correlated nutritional variables best predicted sifaka abundance, we used negative binomial models in the R package “MASS” (Venables and Ripley 2002). Sifaka densities for each forest fragment were converted to abundances for use as the response variable because these models only use count data. To account for study unit area, models were offset by the log of each forest fragment area (O’Hara and Kotze 2010). We performed overdispersion tests to verify the superiority of these models over those with a Poisson distribution in the R package, “DHARMA” (Hartig 2020). We ranked models using AICc values, and we considered models whose $\Delta\text{AICc} < 4.0$ to be competing (Arnold 2010). Multiple variables were not included in single models due to sample size constraints. We produced prediction plots in the R package “ggplot2” (Wickham 2016) and predicted overall abundance using the “predict()” function in R (R Core Team 2019).

This research complied with protocols approved by the Virginia Tech Institutional Animal Care and Use Committee (IACUC # 15-223) and adhered to the legal requirements for research conducted in Madagascar (Permit No. 117/16/MEEF/SG/DGF/DAPT/SCBT).

Results

Sampling Effort and Sifaka Densities

We observed 18 sifaka groups in nine forest fragments for 1,503 hours (1,098 hours in the dry season and 405 hours in the wet season; Fig. 1) over three years of field study. Sifakas consumed plant parts (*e.g.*, buds, flowers, ripe/unripe fruits, young/mature leaves, seeds) from over 101 plant species, and 28 species represented $> 80\%$ of the total diet (Supplemental Table 2). The 114 plant samples collected represented 63 unique species, 49 unique genera, and 30

unique families. Eighty-four samples were collected during the dry season across nine forest fragments, and 30 samples were collected during the wet season across three forest fragments (Table 1). We used a subset of data (979 hours of observation) that contained all observations where individual identity was recorded to evaluate the effects of sex or age class on feeding behavior.

During transect surveys, we counted 379 sifaka groups across nine forest fragments (Fig. 1). Survey observations were conducted over 1,417.2 km from 2016 - 2018. Sifaka densities in fragments were variable: 9.1 sifakas/km² (95% CI: 3.8 – 21.9) in Ambohitsintondroina, 69.5 sifakas/km² (95% CI: 37.1 – 130.3) in Ampondrabe, 6.8 sifakas/km² (95% CI: 2.0 – 22.8) in Antsahabe, 27.4 sifakas/km² (95% CI: 13.3 – 56.2) in Antsaharaingy, 15.1 sifakas/km² (95% CI: 9.4 – 24.2) in Bekaraoka Avaratra, 20.7 sifakas/km² (95% CI: 11.2 – 38.0) in Binara, 78.1 sifakas/km² (95% CI: 53.1 – 114.8) in Bekaraoka South, 49.9 sifakas/km² (95% CI: 25.1 – 99.3) in Benanofy, and 26.7 sifakas/km² (95% CI: 16.2 – 44.1) in Solaniampilana. Complete survey and density results can be found in *Chapter 2*.

Feeding Activity

Based on our subset of data for behavior and feeding analyses, sifakas spent 25.3% of their activity budget feeding during the dry season and 29.5% of their time feeding during the wet season (Supplemental Table 3). Sex and forest type best predicted sifaka feeding counts, but the global model that also included season was in the top set of models ($\Delta\text{AICc} = 1.95$; Table 2). Males had about the same number of feeding counts as females ($\beta = 0.00$, SE = 0.33), and animals in dry forest had about the same number of feeding counts as both those in moderate ($\beta = -1.99$, SE = 3.42) and wet ($\beta = -5.00$, SE = 3.03) forests (Table 3).

Plant Parts Consumed

Plant parts consumed varied widely between seasons (Fig. 2; Supplemental Table 4). Compared to the wet season, sifakas spent a greater percentage of counts consuming buds (23.9% vs. 9.6%; $z = 11.31$, $p < 0.05$, two-tailed) and mature leaves (16.7% vs. 3.0%; $z = 11.31$, $p < 0.05$, two-tailed) in the dry season. Ripe and unripe fruits made up a greater part of the diet in the wet season (49.1%) than in the dry season (18.2%; $z = 19.37$, $p < 0.05$, two-tailed).

Sex and season best explained sifaka bud and flower consumption (Table 4). The probability of a zero count (not consuming buds and flowers) was not significantly different between males and females ($\beta = 0.29$, $SE = 0.23$), but increased in the wet compared to the dry season ($\beta = 0.95$, $SE = 0.25$; Table 5). Males spent roughly the same number of counts consuming buds and flowers as did females ($\beta = -0.10$, $SE = 0.09$). Sifakas spent fewer counts consuming buds and flowers in the wet compared to the dry season ($\beta = -0.49$, $SE = 0.10$).

Fruit consumption was best explained by sex, season, and forest type (Table 4). The probability of a zero count (not consuming fruits) was about the same between males and females ($\beta = 0.02$, $SE = 0.32$; Table 5) and decreased during the wet compared to the dry season ($\beta = -5.12$, $SE = 0.84$; Table 5). The probability of a zero-count was about the same for the moderate compared to the dry forest ($\beta = 1.49$, $SE = 1.01$), and for the wet compared to the dry forest ($\beta = -0.38$, $SE = 0.89$; Table 5). Males spent about the same number of counts consuming fruits as females ($\beta = -0.14$, $SE = 0.08$), but the number of counts sifakas spent consuming fruits was higher in the wet compared to the dry season ($\beta = 0.42$, $SE = 0.12$). Compared to dry forests, sifakas had more feeding counts on fruits in the moderate ($\beta = 0.85$, $SE = 0.32$) and wet ($\beta = 0.68$, $SE = 0.31$) forest types.

Mature leaf consumption was best explained by sex, season and forest type (Table 4). The probability of a zero count (not consuming mature leaves) was lower for males compared to females ($\beta = -1.88$, SE = 0.78), increased during the wet season ($\beta = 6.18$, SE = 1.29), and was higher for wet forests compared to dry forests ($\beta = 9.35$, SE = 4.05), but about the same between moderate and dry forests ($\beta = 2.44$, SE = 3.75; Table 5). Males had fewer counts consuming mature leaves than females ($\beta = -0.46$, SE = 0.23). The number of counts sifakas spent consuming mature leaves was higher in the wet season ($\beta = 2.27$, SE = 0.49) and in moderate forests compared to dry forests ($\beta = 2.50$, SE = 0.65), but about the same between wet and dry forests ($\beta = 0.72$, SE = 1.32).

Most models for counts spent consuming seeds and all models for young leaves failed to converge, likely due to small sample sizes (Supplemental Table 5).

Bark was occasionally consumed by sifakas in moderate forests (0.2% of feeding counts), and by sifakas in wet forests (0.2% of feeding counts; Supplemental Table 4). The only sifakas observed licking moisture off plants occurred in Antsaharaingy (dry forest) on two days during the dry season. Male, female, adult, and sub-adult individuals all engaged in leaf licking on one day in Antsaharaingy, while only an adult male was observed on the second day in the same group and fragment.

Nutritional Analyses

Unfortunately, delays in laboratory analysis due to COVID-19 restrictions in New York, NY precluded the inclusion of any results from the available N analysis. Results are expected in Spring-Summer 2021 pending lab opening and will be included in peer-reviewed publication of this dissertation chapter.

We selected 17 nutritional predictors of sifaka density based on correlations between predictors (Supplemental Table 1). Several macronutrient predictors (*e.g.*, aNDF, crude protein) were highly correlated with other predictors ($|r| > 0.70$), while no micronutrients were correlated with one another. We chose to retain both the protein-to-fiber ratio and available protein despite their correlation ($r = 0.76$) due to the prominence of the former in the historical literature and in current absence of the available N data for reasons described above.

Some plant nutrition variables varied by plant part, while others did not (Table 6, 7). Notably, mature leaves contained significantly more Ca than seeds ($Z = 6.13$, $p\text{-adj.} < 0.001$), buds/flowers contained significantly more Cu than mature leaves ($Z = 5.76$, $p\text{-adj.} < 0.001$), and buds/flowers contained significantly more Zn than mature leaves ($Z = 4.79$, $p\text{-adj.} < 0.001$; Table 7). Three nutritional predictors measured in sifaka foods varied significantly across forest types (Supplemental Table 6). We found significant differences in Fe ($Z = 8.02$, $p < 0.05$), Mn ($Z = 6.90$, $p < 0.05$), and Na ($Z = 7.77$, $p < 0.05$). These minerals were generally higher in drier forest types compared to wetter forest types. The only exceptions to this were not significant (samples from moderate forests trended lower in Mn than those from wet forests ($Z = -1.87$, $p\text{-adj.} > 0.05$) and that samples from dry forests trended lower in Na than those from moderate forests ($Z = -1.69$, $p\text{-adj.} > 0.05$; Supplemental Table 6)).

We found that Mg (%), K (%), NDVI wet, Mn (ppm), and Na (%) all showed some relationships with sifaka densities ($\Delta\text{AICc} < 4.0$; Table 8 and Fig. 3). However, it is important to note that the null model was also present within the set of competing models. Collectively, these top nutritional models are most likely the best models for predicting sifaka densities among all of the variables that we considered (combined AICc weight of non-null, competing models = 0.65; null AICc weight = 0.14). Sifaka densities increased with Mg (%; $\beta = 0.62$, $\text{SE} = 0.19$), K (%; β

= 0.58, SE = 0.20), and NDVI wet ($\beta = 0.43$, SE = 0.20). Densities also decreased with Mn (ppm; $\beta = -0.41$, SE = 0.22) and increased with Na (%; $\beta = 0.43$, SE = 0.23), but confidence intervals on the β estimates for these predictors overlapped zero (*i.e.*, were not significant). Sifaka densities are most reliably predicted (*i.e.*, confidence intervals are the narrowest) when positive predictors of density (Mg, K, NDVI wet, and Na) have lower values and when negative predictors of density (Mn) have higher values (Fig. 3).

Discussion

Factors Impacting Sifaka Feeding Rates

Sifakas in wetter forests spent less time feeding than sifakas in drier forests. Previous work has similarly shown that the percent of time Milne-Edwards' (*Propithecus edwardsi*) and diademed (*P. diadema*) sifakas spent feeding in wetter forests (Arrigo-Nelson 2006; Irwin 2006a) generally is less than that spent by Coquerel's (*P. coquereli*) and Verreaux's (*P. verreauxi*) sifakas in drier forests (McGoogan 2011; Norscia et al. 2006). Sifakas in Madagascar's wet forests also generally are larger than sifakas in western dry forests (Lehman et al. 2005). Larger animals tend to be more energetically efficient in digestion than smaller animals, enabling them to spend less time feeding than smaller animals (Schmidt-Nielson 1997). The resource seasonality hypothesis suggests that highly seasonal (*i.e.*, drier forest) habitats result in selection for smaller adult body size across species (Ravosa et al. 1993; Ravosa et al. 1995); future work should compare golden-crowned sifaka body sizes across a gradient of forest types to explore the body size-feeding rate relationship further (within a species).

Factors Impacting Plants and Plant Parts Consumed

This and previous studies together demonstrate that golden-crowned sifakas consume plant parts from >101 different species with seasonal and spatial differences in both species and plant parts consumed (see *Chapter 2*; Meyers 1993; Quéméré et al. 2013). One species of special note was *Cynometra* sp. (mampay). Sifakas consumed buds, young and mature leaves, unripe fruits, and seeds from this species. Mampay was an important food item in all three of Meyers' (1993) primary study groups and was a top-five food item at three forest fragments in both seasons. Sifakas in wetter forests were less likely to consume mature leaves and consumed more fruits than sifakas in drier forests. The only notable differences in plant part consumption between our study and that of Meyers (1993) was in foliage (young and mature leaves) and flowers. This may be explained by methodological differences. While Meyers (1993) separated leaf and flower buds, we grouped buds into a single category, as it was often difficult to distinguish between the two early in growth stages, especially at a distance.

Not surprisingly, season frequently emerged as a significant predictor of the frequency of food item consumption. Primates are known to face variable nutritional challenges throughout the year and among different forest types (Hemingway and Bynum 2005). Hanya and Chapman (2013) proposed two hypotheses to address resource limitation as it relates to seasonal food availability. These arise from the observation that primates often have high food availability during an “abundant season” until the “ecological crunch” of a “lean season” limits food availability. First, primates may be limited by the quantity of preferred foods during the abundant season that would allow them to build up fat reserves to endure the lean season, when less nutritious fallback foods are more available (Irwin 2008; Irwin et al. 2014). Second, primates may be limited by the availability of fallback foods if the quality of these fallback foods is

enough to satisfy their nutritional requirements (*i.e.*, animals are not also relying on fat reserves to supplement these foods; Marshall and Leighton 2006; Wich et al. 2004). Our study was not sufficiently long to confidently identify specific fallback foods. Differences in the top plant species consumed and plant communities across sites and seasons suggest that fallback foods likely differ across the species' range. More research will be needed to identify which hypothesis best describes golden-crowned sifakas' diet. However, the relationship between sifaka densities and wet season NDVI supports the hypothesis that abundant season foods drive golden-crowned sifaka densities. This also aligns with previous studies on related sifaka species in similarly seasonal environments that highlight the importance of abundant season foods (Irwin 2008; Irwin et al. 2014).

Sex also was a predictor for plant part consumption in several models, but it seldom was significant. Males were more likely to consume mature leaves than females, but when both sexes did consume this abundant resource, females spent more counts consuming mature leaves than males. Assuming that golden-crowned sifaka food preferences mirror those of related sifaka species, this may reflect the ability of dominant females to gain access to preferred food items (*e.g.*, fruits, seeds) over less desired items (*e.g.*, mature leaves; Irwin 2006b; Wright 1999). More research is needed on the use versus the availability of these food items, as well as the social interactions (*e.g.*, fighting, submissive behavior) surrounding food selection for this species.

Food Item Nutritional Content

Plant parts varied significantly in their concentrations of key minerals, including Ca, Cu, Na, P, and Zn. This result highlights the importance of a varied diet for these sifakas to meet their nutritional goals. Similar to results of other studies, mature leaves and leaf petioles in our

study were notable for their higher Ca concentrations (Cancelliere et al. 2014; Irwin et al. 2017; Nagy and Milton 1979). The variability of mineral concentrations across the same plant part in our data supports the growing consensus that plant part alone often serves as a poor predictor of nutritional content. Similar to the results of Irwin et al. (2017) for food items of related diademed sifaka (*Propithecus diadema*), we found that concentrations of most of these minerals in food items (with Ca as a notable exception) were below National Research Council recommended guidelines for captive primates (National Research Council 2003). This supports the view that the NRC guidelines are either too conservative (Irwin et al. 2017), or that wild primates face significant nutrient-balancing challenges (Behie and Pavelka 2012), though these explanations are not mutually exclusive possibilities.

Nutritional Predictors of Sifaka Density

Mg, K, and Na in consumed food items all were predictors of sifaka densities, with only Mn showing a negative correlation. Mg, K, and Na ions are all essential for animal osmoregulatory, nervous, and motor system functions (Kaspari 2020). Some of these minerals have complex interactions, complicating simple explanations. For example, animals deficient in Mg show higher uptake of Mn (Sanchez-Morito et al. 1999), while Mn uptake can also be depressed by Mg (Maas et al. 1969). These complex interactions may help to explain the opposite effects of these minerals in our models. Because few plants require and retain it, Na is considered one of the most limiting minerals for herbivores (Kaspari 2020). It is necessary for herbivore growth and reproduction (Batzli 1986; Weeks and Kirkpatrick 1978), improves the digestion of proteins in the presence of tannins (Freeland et al. 1985), may help to maintain the gut microbiome (Kaspari 2020), and has been directly linked to herbivore densities and

distributions (Joern et al. 2012; McNaughton 1988), including those of primates (Harris and Chapman 2007; Rode et al. 2006).

Behie and Pavelka (2012) demonstrated that mineral acquisition drove food selection in black howler monkeys (*Alouatta pigra*) and that the bioavailability of certain minerals was likely much lower than what was found in the plants sampled. While geophagy is often reported among primates as a means for obtaining minerals lacking in the diet (Johns and Duquette 1991; Pebsworth et al. 2019; Semel 2015), it was never observed over the course of this nor the year-long study of sifakas by Meyers (1993). Sifakas in this study did, however, consume bark. Other folivores (Au et al. 2017), including primates (Rothman et al. 2006), are known to consume bark and wood to supplement their diets with Na. Meyers (1993) merely included bark in an “other” category in his long-term study of golden-crowned sifakas, but also noted that bark consumption did occur and mostly in the dry season. The role of mineral acquisition in shaping primate diets remains poorly understood, and studies focusing more closely on nutrient bioavailability are needed.

We suspected that NDVI during the wet season, another top density predictor (see *Chapter 2*), may be a proxy for nitrogen availability (Johnson et al. 2018). Meyers (1993) suggested that golden-crowned sifakas targeted foods with lower fiber content (measured by NDF and NDF-ADF). However, we found that the protein-to-fiber ratio of consumed food items varied neither by forest type nor by plant part, and was not a significant predictor of sifaka densities. While this ratio may have worked well for some highly folivorous colobine species (Chapman et al. 2002; Oates et al. 1990; Waterman et al. 1988), sifakas (and many colobines; Kirkpatrick 1999) tend to prefer fruits, despite their unique adaptations for folivory (*e.g.*, extended cecum, rapid dental development; Irwin 2006b). This added complication may simply

break down the already overburdened protein-to-fiber ratio explanation (Wallis et al. 2012). We expect that measurements of available N will provide improved insights.

Future Directions

In addition to the incomplete available N analysis, our study included a few additional shortcomings that should be addressed in future research. As noted by Meyers (1993), golden-crowned sifaka feeding patterns and nutritional intake vary significantly throughout the year. While our study focused on the two extremes of this spectrum (peak of the wet and peak of the dry seasons, from February to March and August to December, respectively), we were unable to collect diet and nutrition data year-round. Additionally, while our data provided clear nutritional profiles for the plant parts and species that we collected, they did not account for what nutrients were bioavailable to the sifakas (with the exception of available N), nor did they account for what was actually ingested by the sifakas. Future studies should incorporate more *in vitro* methods to account for nutrient bioavailability and collect bite rates to approximate nutrients consumed.

Conservation Implications

Wet season NDVI remained a top predictor of sifaka densities (see *Chapter 2*). Average normalized difference vegetation index (NDVI) values have been used widely in ecology as a metric of food availability and quality to successfully predict herbivore abundance and distribution (Pettorelli et al., 2011). NDVI indicates plant health on a scale ranging from -1.0 to +1.0, where high values indicate a greater amount of chlorophyll and water in leaves that can absorb near-infrared (NIR) and red light. Small or negative NDVI values indicate areas barren of

vegetation. In *Chapter 2* of this dissertation we hypothesized that higher wet season NDVI values may reflect increased food availability. While we were unable to confirm a nutritional link between wet season NDVI sifaka population densities (*i.e.*, nitrogen availability; Johnson et al. 2018), it raises important conservation implications. Recent climate vulnerability maps based on down-scaled climate model projections suggest that northeastern Madagascar is vulnerable to prolonged drought periods (Busby et al. 2014). As the climate becomes warmer and more arid, wet season NDVI values are likely to decrease across the sifaka range, likely resulting in lower sifaka density and abundance and making forests more vulnerable to destruction by fire. These restrictions would likely outweigh any benefits from small sifaka range expansion that may result from sifakas being able to live in higher elevations within their range.

Changing climate variables (*e.g.*, CO₂, temperatures) may reduce forage quality by increasing fiber and tannin concentrations and decreasing protein availability, which in turn may reduce sifaka abundance even if their range remains stable (Coley et al. 2002; Robinson et al. 2012; Rothman et al. 2015). Climate change also is expected to change plant phenology (Cleland et al. 2007; Richardson et al. 2013). While sifakas exhibit dietary flexibility throughout the year, their reproductive cycles are seasonally synced so that weaning occurs during the season most likely to have abundant resources (Wright 1999), meaning changes in rainfall and subsequent plant phenology will have important fitness consequences (King et al. 2005). Though shifts in growing season patterns are evident in the northern hemisphere (Linderholm 2006), high growing season variation in the southern hemisphere makes similar predictions more challenging (Dubovyk et al. 2015).

Reducing the impacts of climate change plays an important role in the overall conservation strategy for this species. However, a recent study in Madagascar found that climate

change impacts may be outpaced by the rate of forest loss for some species (Morelli et al. 2019). Reforestation efforts aimed at improving or reconnecting sifaka habitat should concentrate on augmenting the abundance of food items highlighted in this study (*e.g.*, mampay), with attention paid to local environmental conditions. Forested corridors should be planned in such a way to facilitate the movement of sifakas to forests that may become more suitable as plant communities change with the climate (see *Chapter 4*; Brown and Yoder 2015; Gibson et al. 2013).

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Table 1. Number of plant samples of golden-crowned sifaka (*Propithecus tattersalli*) food items collected from nine unique forest fragments (six only in dry season, three in both wet and dry seasons) in the Loky-Manambato Protected Area in northeastern Madagascar. Dry season samples were collected August – December in 2017 – 2019. Wet season samples were collected February – March 2019.

Site	Forest Type	Dry Season Samples	Wet Season Samples
Ambohitsintondroina	Moderate	5	0
Ampondrabe	Moderate	4	0
Antsahabe	Wet	9	0
Antsaharaingy	Dry	11	0
Bekaraoka South	Moderate	17	9
Bekaraoka Avaratra	Moderate	5	0
Benanofy	Moderate	2	0
Binara	Wet	19	10
Solaniampilana	Dry	12	11

Table 2. Linear mixed-effects models to predict golden-crowned sifakas' (*Propithecus tattersalli*) feeding counts per individual sifaka per day in the Loky Manambato Protected Area ($N = 544$). Data were collected from males and females in 18 total groups during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons in nine unique forest fragments (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet). All models contained “Group ID” as a random effect.

Model	K^a	AICc ^b	Δ AICc ^c	w_i^d
Sex ^e + Forest Type ^f	6	2914.57	0.00	0.70
Sex + Season ^g + Forest Type	7	2916.52	1.95	0.27
Sex	4	2921.38	6.81	0.02
Sex + Season	5	2923.33	8.76	0.01
Forest Type	5	2985.26	70.69	0.00
Season + Forest Type	6	2987.23	72.65	0.00
Null	3	2992.05	77.47	0.00
Season	4	2994.01	79.44	0.00

^a K = number of model parameters

^b AICc = Akaike's Information Criterion corrected for sample size

^c Δ AICc = difference between a model's AIC and that of the best-fitting model

^d w_i = Akaike model weight

^e Sex = male or female

^f Forest Type = dry, moderate, or wet forest type

^g Season = wet season (February – March) or dry season (August – December)

Table 3. Parameter estimates (β) from the most parsimonious linear mixed-effects model (sex and forest type) to predict golden-crowned sifaka (*Propithecus tattersalli*) feeding counts per individual sifaka per day in the Loky Manambato Protected Area ($N = 544$). Data were collected from males and females in 18 total groups during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons in nine unique forest fragments (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet). “Group ID” was included as a random effect.

Predictors	β^a	SE ^b	t value	Pr(> t) ^c
Intercept	8.35	1.99	4.19	0.01
Male	0.00	0.33	0.01	0.99
Moderate Forest	-1.99	3.42	-0.58	0.58
Wet Forest	-5.00	3.03	-1.65	0.15

^a β = beta estimate

^b SE = standard error of the β estimate

^c Pr(>| t) = probability that the absolute value of the t value is > the t critical value computed via the Satterthwaite approximation (Kuznetsova et al. 2017)

Table 4. Zero inflated negative binomial (ZINB) mixed-effects models to predict the probability of golden-crowned sifakas (*Propithecus tattersalli*) feeding on a specific plant (zero-inflated process) and the number of feeding counts on that plant part ('conditional' count process) in the Loky Manambato Protected Area. Sample units were measured as the number of feeding counts per individual sifaka per day ($N = 544$). Data were collected from males and females in 18 total groups during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons in nine unique forest fragments (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet). All models had the same covariates on both the zero-inflated and count processes and contained "Group ID" as a random effect.

Plant Part	Model	K^a	AICc ^b	Δ AICc ^c	w_i^d	LL ^e
Buds and flowers	Sex ^f + Season ^g	9	2270.74	0.00	0.69	-1126.20
	Sex + Season + Forest Type ^h	13	2272.31	1.57	0.31	-1122.81
	Season	7	2283.95	13.21	0.00	-1134.87
	Season + Forest Type	11	2286.07	15.32	0.00	-1131.79
	Sex + Forest Type	11	2309.48	38.74	0.00	-1143.49
	Sex	7	2309.87	39.13	0.00	-1147.83
	Null	5	2324.95	54.20	0.00	-1157.42
	Forest Type	9	2325.38	54.64	0.00	-1153.52
Fruits	Sex ^f + Season ^g + Forest Type ^h	13	2123.79	0.00	0.51	-1048.55
	Sex + Season	9	2123.91	0.13	0.48	-1052.79

Plant Part	Model	K^a	AICc ^b	Δ AICc ^c	w_i^d	LL ^e
Fruits	Season + Forest Type	11	2131.83	8.05	0.01	-1054.67
	Season	7	2132.02	8.24	0.01	-1058.91
	Sex + Forest Type	11	2385.37	261.58	0.00	-1181.44
	Sex	7	2385.47	261.69	0.00	-1185.63
	Null	5	2393.55	269.76	0.00	-1191.72
	Forest Type	9	2394.46	270.67	0.00	-1188.06
Mature leaves	Sex ^f + Season ^g + Forest Type ^h	13	996.05	0.00	0.86	-484.68
	Sex + Season	9	999.77	3.73	0.13	-490.72
	Season	7	1008.32	12.27	0.00	-497.06
	Sex + Forest Type	11	1096.76	100.72	0.00	-537.13
	Sex	7	1105.46	109.42	0.00	-545.63
	Forest Type	9	1108.61	112.56	0.00	-545.14
	Null	5	1119.83	123.79	0.00	-554.86

^a K = number of model parameters

^b AICc = Akaike's Information Criterion corrected for sample size

^c Δ AICc = difference between a model's AIC and that of the best fitting model

^d w_i = Akaike model weight

^e LL = log-likelihood

^f Sex = male or female

^g Season = wet season (February – March) or dry season (August – December)

^h Forest Type = dry, moderate, or wet forest type

Table 5. Parameter estimates (β) from the most parsimonious zero-inflated negative binomial (ZINB) mixed-effects regression models to predict if golden-crowned sifakas (*Propithecus tattersalli*) fed on a specific plant part (zero-inflated process) and the number of feeding counts on that plant part ('conditional' count process) in the Loky Manambato Protected Area. Sample units were measured as the number of feeding counts per individual sifaka per day ($N = 544$). Data were collected from males and females in 18 total groups during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons in nine unique forest fragments (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet). All models contained “Group ID” as a random effect.

Plant Part	Process	Model	β^a	SE ^b	z-value	Pr(> z) ^c
Buds and flowers	Zero-inflation	Intercept	-1.10	0.52	-2.10	0.04
		Male	0.29	0.23	1.25	0.21
		Wet Season	0.95	0.25	3.83	<0.01
	Conditional	Intercept	1.90	0.22	8.54	<0.01
		Male	-0.10	0.09	-1.17	0.244
		Wet Season	-0.49	0.10	-4.70	<0.01
Fruits	Zero-inflation	Intercept	0.53	0.62	0.86	0.39

Plant Part	Process	Model	β^a	SE ^b	Z value	Pr(> z) ^c
Fruits		Male	0.02	0.32	0.06	0.95
	Zero-inflation	Wet Season	-5.12	0.84	-6.12	<0.01
		Moderate Forest	1.49	1.01	1.48	0.14
		Wet Forest	-0.38	0.89	-0.43	0.67
	Conditional	Intercept	0.90	0.22	4.13	<0.01
		Male	-0.14	0.08	-1.61	0.11
		Wet Season	0.42	0.12	3.38	<0.01
		Moderate Forest	0.85	0.32	2.65	0.01
		Wet Forest	0.68	0.31	2.20	0.03
Mature leaves	Zero-inflation	Intercept	-4.21	2.59	-1.63	0.10
		Male	-1.88	0.78	-2.41	0.02
		Wet Season	6.18	1.29	4.81	<0.01
		Moderate Forest	2.44	3.75	0.65	0.52
		Wet Forest	9.35	4.05	2.31	0.02
	Conditional	Intercept	-0.78	0.52	-1.50	0.13

Plant Part	Process	Model	β^a	SE ^b	Z value	Pr(> z) ^c
Mature leaves		Male	-0.46	0.23	-1.97	0.05
	Conditional	Wet Season	2.27	0.49	4.64	<0.01
		Moderate Forest	2.50	0.65	3.83	<0.01
		Wet Forest	0.72	1.32	0.55	0.58

^a β = beta estimate

^b SE = standard error of the β estimate

^c Pr(>|z|) = significance level

Table 6. Plant part sample sizes and average nutrition values measured as a percent of total dry matter or in parts per million (ppm) with standard errors (SE) for plant parts consumed by golden-crowned sifakas (*Propithecus tattersalli*) from August – December 2017 – 2019 and February – April 2019 in the Loky-Manambato Protected Area. Nutritional data were obtained from 114 plant samples representing the top five food items (based on scan sampling of males and females) consumed by 18 sifaka groups in nine unique forest fragments (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet).

Plant Part	N	Avail. Protein (%) ^a	P:F Ratio ^b	ADF (%) ^c	WSC (%) ^d	Crude Fat (%) ^e	Sol. Sugar (%) ^f	Ca (%) ^g	K (%) ^h	Mg (%) ⁱ	Na (%) ^j	P (%) ^k	Cu (ppm) ^l	Fe (ppm) ^m	Mn (ppm) ⁿ	Mo (ppm) ^o	Zn (ppm) ^p
BD/FL ^q	27	12.91 (1.27)	0.64 (0.06)	20.71 (1.12)	11.74 (2.47)	4.98 (1.07)	5.32 (0.50)	0.56 (0.10)	1.59 (0.09)	0.23 (0.02)	0.03 (0.01)	0.29 (0.03)	11.65 (1.01)	146.44 (23.27)	89.43 (20.29)	0.69 (0.16)	28.48 (2.22)
FR ^r	24	4.22 (0.56)	0.26 (0.04)	22.92 (2.05)	9.38 (1.60)	6.08 (1.79)	13.53 (2.35)	0.38 (0.05)	1.89 (0.19)	0.20 (0.02)	0.04 (0.01)	0.16 (0.02)	9.83 (1.07)	145.23 (33.93)	36.38 (7.20)	0.39 (0.07)	18.08 (3.18)
ML ^s	19	8.01 (0.79)	0.38 (0.05)	25.07 (1.61)	9.32 (2.01)	8.50 (2.49)	8.18 (1.22)	1.42 (0.17)	1.12 (0.12)	0.30 (0.02)	0.06 (0.01)	0.11 (0.01)	4.24 (0.32)	88.39 (14.94)	85.21 (29.20)	0.44 (0.07)	14.05 (2.45)
PT ^t	2	*	*	24.40 (2.20)	*	5.55 (1.85)	5.98 (2.44)	2.58 (0.81)	1.04 (0.15)	0.36 (0.03)	0.00 (0.00)	0.13 (0.01)	7.00 (1.00)	80.50 (23.5)	123.00 (106.00)	0.60 (0.20)	23.00 (0.00)

Plant Part	N	Avail.	P:F	ADF	WSC	Crude	Sol.	Ca	K	Mg	Na	P (%) ^k	Cu	Fe	Mn	Mo	Zn
		Protein (%) ^a	Ratio ^b	(%) ^c	(%) ^d	Fat (%) ^e	Sugar (%) ^f	(%) ^g	(%) ^h	(%) ⁱ	(%) ^j		(ppm) ^l	(ppm) ^m	(ppm) ⁿ	(ppm) ^o	(ppm) ^p
SD ^u	26	10.03	0.86	16.18	15.55	10.77	9.10	0.29	1.33	0.22	0.02	0.28	9.69	125.04	41.08	1.00	24.85
		(2.08)	(0.17)	(2.04)	(3.07)	(2.37)	(0.84)	(0.06)	(0.12)	(0.02)	(0.01)	(0.03)	(1.12)	(32.65)	(10.05)	(0.23)	(2.26)
YL ^v	16	8.98	0.58	19.75	9.47	2.24	4.73	0.56	1.55	0.24	0.04	0.24	8.09	76.41	59.41	0.48	18.88
		(2.04)	(0.12)	(2.38)	(1.44)	(0.43)	(0.49)	(0.13)	(0.15)	(0.03)	(0.01)	(0.04)	(0.92)	(7.73)	(21.58)	(0.06)	(1.99)

* Not enough material could be obtained to run all analyses.

^a Avail. Protein (%) = available protein as a percent of total dry matter

^b P:F Ratio = protein-to-fiber ratio, the available protein (%) divided by acid detergent fiber (ADF; %)

^c ADF (%) = acid detergent fiber as a percent of total dry matter

^d WSC (%) = water soluble carbohydrates as a percent of total dry matter

^e Crude Fat (%) = crude fat as a percent of total dry matter

^f Sol. Sugar (%) = soluble sugars as a percent of total dry matter

^g Ca (%) = calcium as a percent of total dry matter

^h K (%) = potassium as a percent of total dry matter

ⁱ Mg (%) = magnesium as a percent of total dry matter

^j Na (%) = sodium as a percent of total dry matter

^k P (%) = phosphorous as a percent of total dry matter

^l Cu (ppm) = copper content in parts per million

^m Fe (ppm) = iron content in parts per million

ⁿ Mn (ppm) = manganese content in parts per million

^o Mo (ppm) = molybdenum content in parts per million

^p Zn (ppm) = zinc content in parts per million

^q BD/FL = buds/flowers

^r FR = fruits

^s ML = mature leaves

^t PT = petioles

^u SD = seeds

^v YL = young leaves

Table 7. Comparisons for nutritional analysis outputs (measured as a percent of total dry matter or in parts per million (ppm)) and plant parts consumed by golden-crowned sifakas (*Propithecus tattersalli*) in the Loky Manambato Protected Area using Kruskal-Wallis tests. Nutritional data were obtained from 114 plant samples representing the top five food items consumed by 18 total groups during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons in nine unique forest fragments (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet). Dunn’s *post hoc* tests were conducted for significant comparisons and their significance was evaluated using unadjusted and adjusted *p*-values. Plant parts consumed: BD/FL = buds/flowers; FR = fruits; ML = mature leaves; PT = petioles; SD = seeds; YL = young leaves

Nutrient	<i>N</i>	χ^2	df	<i>p</i> -value	Dunn's Test				
					Comparison		<i>Z</i>	<i>p</i> -unadjusted	<i>p</i> -adjusted ^a
ADF (%) ^b	114	14.7	5	0.012	BD/FL	SD	2.05	0.040	0.151
					FR	SD	2.64	0.008	0.063
					ML	SD	3.45	0.001	0.008
					ML	YL	2.06	0.039	0.196
Available Protein (%) ^c	56	13.0	4	0.011	BD/FL	FR	3.36	0.001	0.008
					BD/FL	YL	2.07	0.039	0.194

Nutrient	N	χ^2	df	p-value	Dunn's Test		Z	p-unadjusted	p-adjusted ^a
					Comparison				
Available Protein (% ^c , cont'd) ^c					BD/FL	FR	3.36	0.001	0.008
Ca (%) ^d	114	45.1	5	<0.001	BD/FL	ML	-3.23	0.001	0.005
					FR	ML	-4.47	<0.001	<0.001
					FR	PT	-2.50	0.012	0.026
					BD/FL	SD	3.21	0.001	0.004
					ML	SD	6.13	<0.001	<0.001
					PT	SD	3.16	0.002	0.004
					ML	YL	3.63	<0.001	0.001
					PT	YL	2.27	0.023	0.044
Crude Fat (%) ^e	109	14.5	5	0.013	ML	YL	2.92	0.003	0.026
					SD	YL	3.38	0.001	0.011
Cu (ppm) ^f	114	35.9	5	<0.001	BD/FL	ML	5.76	<0.001	<0.001
					FR	ML	4.43	<0.001	<0.001
					ML	SD	-4.27	<0.001	<0.001

Nutrient	N	χ^2	df	p-value	Dunn's Test		Z	p-unadjusted	p-adjusted ^a
					Comparison				
Cu (ppm, cont'd) ^f					ML	YL	-3.12	0.002	0.007
Fe (ppm) ^g	114	10.2	5	0.069	n.s.				
K (%) ^h	114	15.6	5	0.008	BD/FL	ML	2.79	0.005	0.040
					FR	ML	3.30	0.001	0.014
					FR	SD	2.34	0.019	0.097
					ML	YL	-2.22	0.027	0.100
Mg (%) ⁱ	114	14.0	5	0.016	BD/FL	ML	-2.26	0.024	0.118
					FR	ML	-3.10	0.002	0.029
					FR	PT	-2.19	0.029	0.107
					ML	SD	2.59	0.009	0.071
					PT	SD	1.97	0.049	0.148
Mn (ppm) ^j	114	12.0	5	0.035	BD/FL	FR	2.56	0.010	0.077
					FR	ML	-2.06	0.040	0.149
					BD/FL	SD	2.71	0.007	0.100

Nutrient	N	χ^2	df	p-value	Dunn's Test		Z	p-unadjusted	p-adjusted ^a
					Comparison				
Mn (ppm, cont'd) ^j					ML	SD	2.18	0.029	0.147
Mo (ppm) ^k	95	10.6	5	0.061	n.s.				
Na (%) ^l	114	19.8	5	0.001	ML	SD	3.91	<0.001	0.001
					SD	YL	-2.77	0.006	0.042
P (%) ^m	114	32.4	5	<0.001	BD/FL	FR	3.06	0.002	0.011
					BD/FL	ML	4.77	<0.001	<0.001
					FR	SD	-2.89	0.004	0.011
					ML	SD	-4.60	<0.001	<0.001
					ML	YL	-3.02	0.003	0.010
P:F Ratio ⁿ	55	8.0	4	0.092	n.s.				
Soluble Sugars (%) ^o	93	22.7	5	<0.001	BD/FL	FR	-3.54	<0.001	0.003
					BD/FL	SD	-2.87	0.004	0.015
					FR	YL	3.74	<0.001	0.003
					SD	YL	3.10	0.002	0.010

Nutrient	N	χ^2	df	p-value	Dunn's Test		Z	p-unadjusted	p-adjusted ^a
					Comparison				
Water Soluble Carbohydrates (WSC; %) ^f	55	2.2	4	0.702	n.s.				
Zn (ppm) ^g	114	32.7	5	<0.001	BD/FL	FR	4.10	<0.001	<0.001
					BD/FL	ML	4.79	<0.001	<0.001
					FR	SD	-3.01	0.003	0.010
					ML	SD	-3.76	<0.001	0.001
					BD/FL	YL	2.49	0.013	0.038

^a P-values adjusted with the Benjamini-Hochberg method

^b ADF (%) = acid detergent fiber as a percent of total dry matter

^c Avail Protein (%) = available protein as a percent of total dry matter

^d Ca (%) = calcium as a percent of total dry matter

^e Crude Fat (%) = crude fat as a percent of total dry matter

^f Cu (ppm) = copper content in parts per million

^g Fe (ppm) = iron content in parts per million

^h K (%) = potassium as a percent of total dry matter

ⁱ Mg (%) = magnesium as a percent of total dry matter

^j Mn (ppm) = manganese content in parts per million

^k Mo (ppm) = molybdenum content in parts per million

^l Na (%) = sodium as a percent of total dry matter

^m P (%) = phosphorous as a percent of total dry matter

ⁿ P:F Ratio = protein-to-fiber ratio, the available protein (%) divided by acid detergent fiber (ADF; %)

^o Soluble Sugars (%) = soluble sugars as a percent of total dry matter

^p WSC (%) = water soluble carbohydrates as a percent of total dry matter

^q Zn (ppm) = zinc content in parts per million

Table 8. Negative binomial model results estimating golden crowned sifaka (*Propithecus tattersalli*) density as a function of plant nutrient predictors in the Loky-Manambato Protected Area in northeastern Madagascar ($N = 9$). Sifaka density data were collected in 2016 (May – July) and in 2017 and 2018 (August – December for both years). Nutritional data were obtained from 114 plant samples representing the top five food items consumed by 18 total groups during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons in nine unique forest fragments (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet). Beta values, standard errors, beta value confidence intervals, Z values, and Z-score probabilities are for the predictor in the specified model.

Model	K^a	β^b	SE ^c	LCI ^d	UCI ^e	z-value	Pr(> z) ^f	AICc ^g	Δ AICc ^h	w_i^i
Mg (%) ^j	3	0.62	0.19	0.24	1.00	3.23	<0.01	144.27	0.00	0.29
K (%) ^k	3	0.58	0.20	0.18	0.98	2.85	<0.01	145.40	1.13	0.17
Null	2	3.52	0.25	3.03	4.00	14.24	<0.01	145.80	1.53	0.14
NDVI Wet ^l	3	0.43	0.20	0.04	0.83	2.15	0.03	147.11	2.84	0.07
Mn (ppm) ^m	3	-0.41	0.22	-0.85	0.03	-1.82	0.07	147.34	3.07	0.06
Na (%) ⁿ	3	0.43	0.23	-0.01	0.88	1.90	0.06	147.64	3.37	0.05
Mo (ppm) ^o	3	-0.33	0.24	-0.81	0.14	-1.37	0.17	148.99	4.72	0.03

Model	K^a	β^b	SE ^c	LCI ^d	UCI ^e	z -value	Pr(> z) ^f	AICc ^g	Δ AICc ^h	w_i^i
Cu (ppm) ^p	3	0.32	0.24	-0.16	0.79	1.29	0.20	149.09	4.82	0.03
P (%) ^q	3	0.31	0.25	-0.17	0.79	1.26	0.21	149.27	5.00	0.02
NDVI Dry ^r	3	-0.25	0.24	-0.72	0.21	-1.08	0.28	149.72	5.45	0.02
Crude fat (%) ^s	3	-0.29	0.25	-0.79	0.21	-1.14	0.25	150.00	5.74	0.02
Fe (ppm) ^t	3	0.24	0.26	-0.26	0.74	0.93	0.35	150.10	5.83	0.02
Avail protein (%) ^u	3	-0.14	0.26	-0.64	0.37	-0.53	0.60	150.20	5.93	0.01
P:F Ratio ^v	3	-0.11	0.26	-0.61	0.40	-0.41	0.68	150.35	6.08	0.01
Zn (ppm) ^w	3	0.09	0.26	-0.42	0.60	0.33	0.74	150.47	6.20	0.01
Ca (%) ^x	3	0.09	0.26	-0.42	0.60	0.33	0.74	150.50	6.23	0.01
Soluble Sugars (%) ^y	3	-0.08	0.26	-0.59	0.43	-0.30	0.76	150.52	6.25	0.01
Water Soluble										
Carbohydrates										
(WSC; %) ^z										
ADF (%) ^{aa}	3	0.03	0.26	-0.49	0.54	0.10	0.92	150.58	6.31	0.01

^a K = number of model parameters

^b β = beta estimate

^c SE = standard error of β estimate

^d LCI = lower 95% confidence interval

^e UCI = upper 95% confidence interval

^f $\Pr(>|z|)$ = significance level

^g AICc = Akaike's Information Criterion corrected for sample size

^h Δ AICc = difference between a model's AIC and that of the best fitting model

ⁱ w_i = Akaike model weight

^j Mg (%) = magnesium as a percent of total dry matter

^k K (%) = potassium as a percent of total dry matter

^l NDVI Wet = fragment-wide average normalized difference vegetation index (NDVI) during the wet season

^m Mn (ppm) = manganese content in parts per million

ⁿ Na (%) = sodium as a percent of total dry matter

^o Mo (ppm) = molybdenum content in parts per million

^p Cu (ppm) = copper content in parts per million

^q P (%) = phosphorous as a percent of total dry matter

^r NDVI Dry = fragment-wide average normalized difference vegetation index (NDVI) during the dry season

^s Crude Fat (%) = crude fat as a percent of total dry matter

^t Fe (ppm) = iron content in parts per million

^u Avail Protein (%) = available protein as a percent of total dry matter

^v P:F Ratio = protein-to-fiber ratio, the available protein (%) divided by acid detergent fiber (ADF; %)

^w Zn (ppm) = zinc content in parts per million

^x Ca (%) = calcium as a percent of total dry matter

^y Soluble Sugars (%) = soluble sugars as a percent of total dry matter

^z WSC (%) = water soluble carbohydrates as a percent of total dry matter

^{aa} ADF (%) = acid detergent fiber as a percent of total dry matter

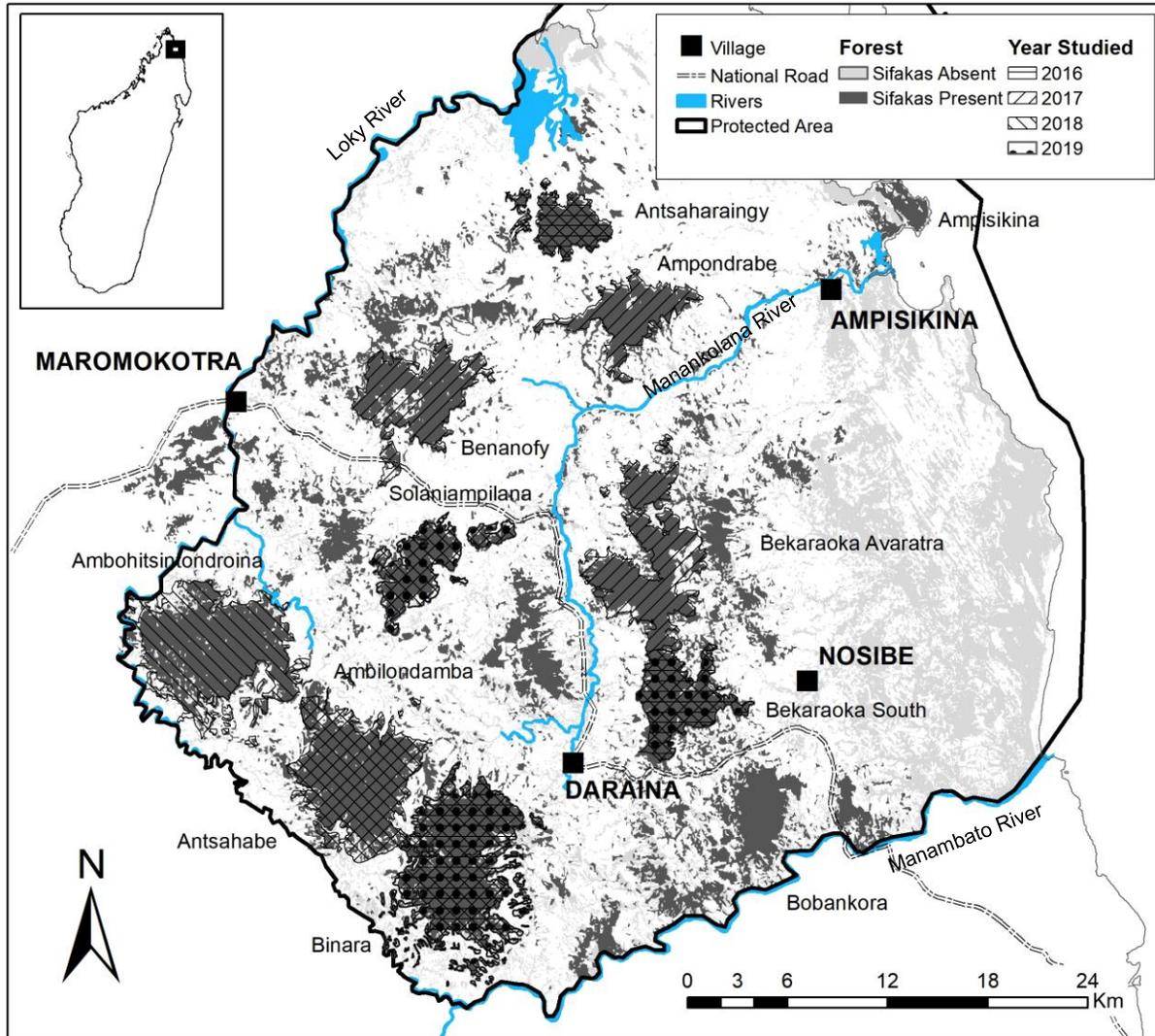


Fig. 1. Map of forest fragments within the Loky Manambato Protected Area in northeastern Madagascar. Golden-crowned sifaka (*Propithecus tattersalli*) density estimates were obtained for each of these fragments during surveys conducted in 2016 (May – July) and in 2017 and 2018 (August – December for both years). Behavioral and feeding data were collected from 18 sifaka groups (two per forest fragment) from nine forest fragments (Ambohitsintondroina, Ampondrabe, Antsahabe, Antsaharaingy, Bekaraoka Avaratra, Bekaraoka South, Benanofy, Binara, and Solaniampilana) during the dry (August – December in 2017 – 2019) and wet

(February – March 2019) seasons (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet).

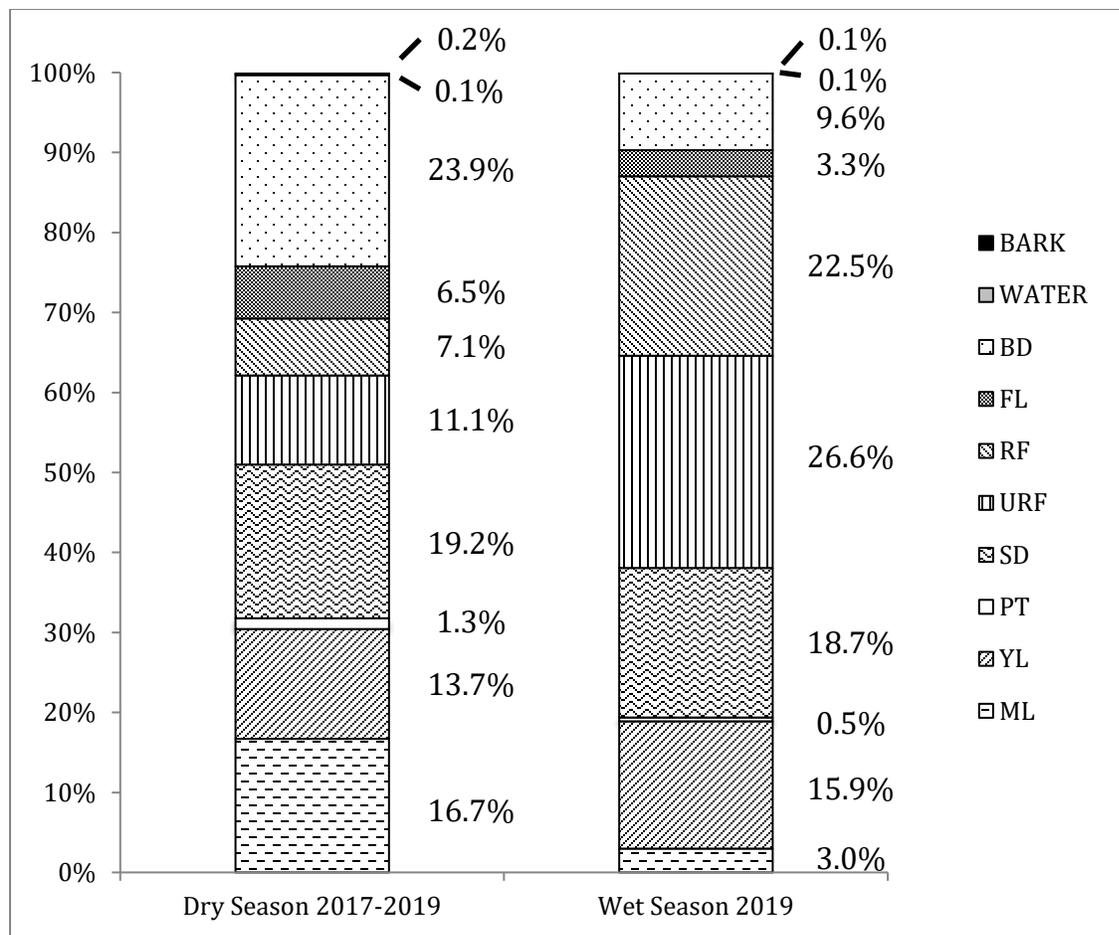


Fig. 2. Percent of total feeding time spent consuming different plant parts by golden-crowned sifakas (*Propithecus tattersalli*) inhabiting nine forest fragments (two groups per fragment) in the Loky-Manambato Protected Area in northeastern Madagascar during the dry (August – December 2017 – 2019) and wet (February – March 2019) seasons. Male and female sifakas were followed in three different forest types: dry, moderate, and wet. Adults, sub-adults, and juveniles were assessed based on physical features or on knowledge from the previous sample period (*i.e.*, known infants in 2017 would be juveniles in 2018). Percentage of time spent consuming each plant part was based on the total number of feeding counts (one count collected every 15 minutes per weaned individual; $N = 3566$). Sections may not add up to 100% as a result of animals being out of sight or rounding. BARK = tree bark, WATER = licking moisture from

plant parts, BD = buds, FL = flowers, RF = ripe fruits, URF = unripe fruits, SD = seeds, PT =
leaf petioles, YL = young leaves, ML = mature leaves

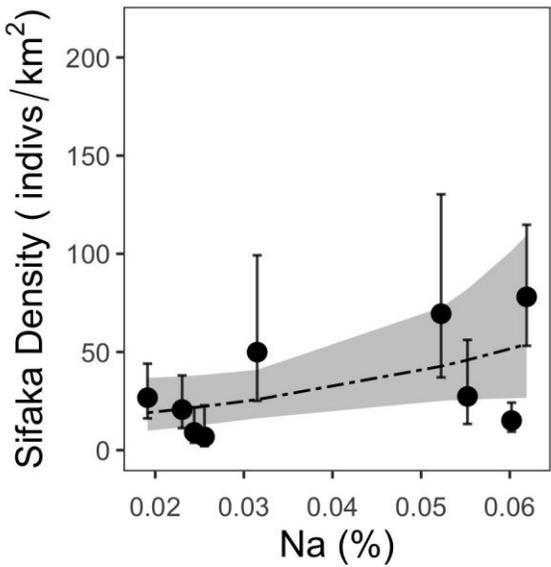
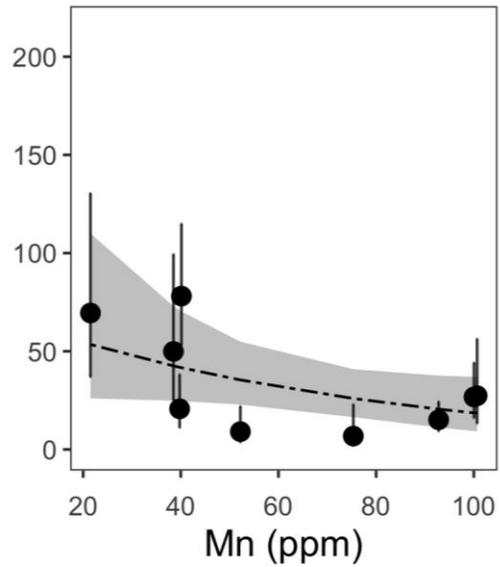
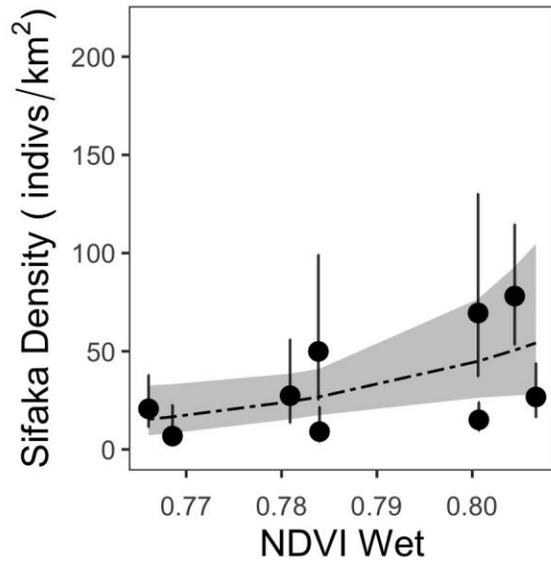
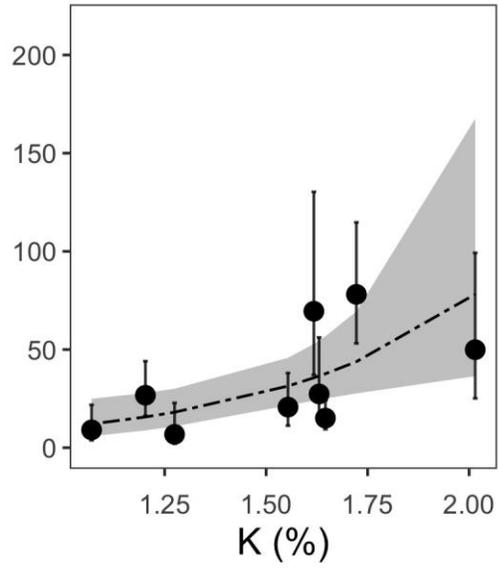
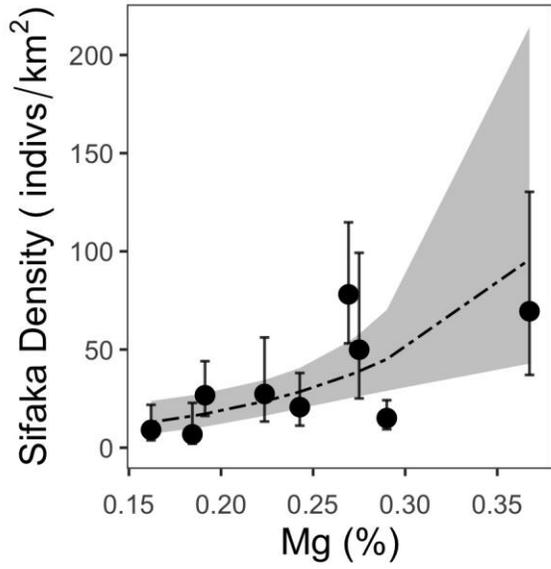


Fig. 3. Prediction plots for the competing models ($\Delta AICc < 4.0$) used to predict golden-crowned sifaka (*Propithecus tattersalli*) densities in the Loky-Manambato Protected Area in northeastern Madagascar. Sifaka density estimates were obtained for nine forest fragments during surveys conducted in 2016 (May – July) and in 2017 and 2018 (August – December for both years) using the program Distance. Whiskers show 95% confidence intervals on density estimates. Nutritional analysis predictors (measured as a percent of total dry matter or in parts per million (ppm)) were obtained from 114 plant samples representing the top five foods consumed by each of two groups of sifakas in each of the nine unique forest fragments during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons. Shaded areas represent the 95% confidence intervals from predicted sifaka densities (dashed line) based on each of the five nutritional predictor variables. NDVI Wet = fragment-wide average normalized difference vegetation index (NDVI) during the wet season

Supplemental Table 1. Correlation matrix of food nutrient predictors and golden-crowned sifaka (*Propithecus tattersalli*) densities in each of nine forest fragments in the Loky-Manambato Protected Area in northeastern Madagascar. Density data were collected in 2016 (May – July) and in 2017 and 2018 (August – December). Nutritional data were obtained from 114 plant samples representing the top five food items consumed by 18 sifaka groups (two per forest fragment) from nine forest fragments (Ambohitsintondroina, Ampondrabe, Antsahabe, Antsaharaingy, Bekaraoka Avaratra, Bekaraoka South, Benanofy, Binara, and Solaniampilana) during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons (six fragments only in the dry season, three in the wet and dry seasons) from three different forest types (dry, moderate, and wet). Highly correlated variables ($|r| > 0.70$) were removed such that the most readily measured variable remained (*e.g.*, remotely sensed NDVI values kept over basal area measures). Variables kept for use in models are in bold.

	Crude Protein (%)	Available Protein (%)	ADF (%)	Lignin (%)	aNDF (%)	P:F Ratio	WSC (%)	Crude Fat (%)	Soluble Sugars (%)	Ca (%)	P (%)	Mg (%)	K (%)	Na (%)	Fe (ppm)	Zn (ppm)	Cu (ppm)	Mn (ppm)	Mo (ppm)	NDVI Dry	NDVI Wet	Densities
Crude Protein (%) ^a	1	0.97	-0.11	0.02	-0.12	0.37	-0.08	0.10	-0.19	-0.13	0.74	0.15	0.23	-0.17	0.11	0.59	0.27	0.04	0.53	0.14	-0.16	-0.14
Avail Protein (%) ^b	0.97	1	-0.03	0.13	-0.02	0.76	-0.01	0.17	-0.20	-0.14	0.65	0.05	0.38	-0.25	0.12	0.61	0.14	0.10	0.35	0.04	-0.12	-0.20

	Crude Protein (%)	Available Protein (%)	ADF (%)	Lignin (%)	aNDF (%)	P:F Ratio	WSC (%)	Crude Fat (%)	Soluble Sugars (%)	Ca (%)	P (%)	Mg (%)	K (%)	Na (%)	Fe (ppm)	Zn (ppm)	Cu (ppm)	Mn (ppm)	Mo (ppm)	NDVI Dry	NDVI Wet	Densities
ADF (%) ^c	-0.11	-0.03	1	0.76	0.95	-0.29	-0.12	-0.12	-0.14	0.25	-0.20	0.12	-0.03	0.04	-0.20	-0.16	-0.08	0.02	-0.16	-0.08	0.15	0.18
Lignin (%) ^d	0.02	0.13	0.76	1	0.69	-0.06	-0.19	-0.01	-0.07	0.2	-0.08	0.16	0.13	0.02	-0.20	-0.03	-0.10	0.02	-0.17	-0.04	0.07	0.16
aNDF (%) ^e	-0.12	-0.02	0.95	0.69	1	-0.24	0.02	-0.09	-0.10	0.21	-0.20	0.08	-0.05	0.07	-0.17	-0.13	-0.09	0.03	-0.16	-0.14	0.23	0.22
P:F Ratio ^f	0.37	0.76	-0.29	-0.06	-0.24	1	0.12	0.03	-0.11	-0.08	0.15	0.02	0.04	-0.03	-0.08	0.14	-0.14	0.08	-0.01	0.03	-0.19	-0.19
WSC (%) ^g	-0.08	-0.01	-0.12	-0.19	0.02	0.12	1	-0.18	-0.04	-0.07	-0.07	0.04	0.03	0.07	-0.01	-0.09	0.04	-0.05	0.16	-0.16	0.33	0.14
Crude Fat (%) ^h	0.10	0.17	-0.12	-0.01	-0.09	0.03	-0.18	1	0.13	-0.04	-0.03	-0.17	-0.22	-0.05	0.09	-0.01	-0.24	-0.07	0.06	-0.03	0.04	-0.09
Soluble Sugars (%) ⁱ	-0.19	-0.20	-0.14	-0.07	-0.10	-0.11	-0.04	0.13	1	-0.13	-0.17	-0.22	0.19	0.08	0.26	-0.12	0.03	-0.17	-0.03	0.00	-0.04	0.02
Ca (%) ^j	-0.13	-0.14	0.25	0.20	0.21	-0.08	-0.07	-0.04	-0.13	1	-0.3	0.54	-0.32	0.22	-0.12	-0.18	-0.21	0.18	-0.14	0.13	-0.06	0.01
P (%) ^k	0.74	0.65	-0.20	-0.08	-0.20	0.15	-0.07	-0.03	-0.17	-0.3	1	0.21	0.39	-0.23	0.12	0.60	0.50	-0.13	0.42	0.10	-0.09	0.05
Mg (%) ^l	0.15	0.05	0.12	0.16	0.08	0.02	0.04	-0.17	-0.22	0.54	0.21	1	0.14	0.15	-0.17	-0.03	0.06	0.03	0.05	0.08	0.06	0.29
K (%) ^m	0.23	0.38	-0.03	0.13	-0.05	0.04	0.03	-0.22	0.19	-0.32	0.39	0.14	1	-0.05	0.11	0.10	0.35	-0.13	-0.03	0.07	-0.01	0.2
Na (%) ⁿ	-0.17	-0.25	0.04	0.02	0.07	-0.03	0.07	-0.05	0.08	0.22	-0.23	0.15	-0.05	1	0.06	-0.05	0.00	0.03	-0.14	-0.10	0.14	0.26
Fe (ppm) ^o	0.11	0.12	-0.20	-0.20	-0.17	-0.08	-0.01	0.09	0.26	-0.12	0.12	-0.17	0.11	0.06	1	0.23	0.31	0.14	0.11	-0.18	0.17	0.10
Zn (ppm) ^p	0.59	0.61	-0.16	-0.03	-0.13	0.14	-0.09	-0.01	-0.12	-0.18	0.60	-0.03	0.10	-0.05	0.23	1	0.50	0.12	0.48	0.06	-0.07	-0.04
Cu (ppm) ^q	0.27	0.14	-0.08	-0.10	-0.09	-0.14	0.04	-0.24	0.03	-0.21	0.50	0.06	0.35	0.00	0.31	0.50	1	0.11	0.20	-0.14	0.17	0.22
Mn (ppm) ^r	0.04	0.10	0.02	0.02	0.03	0.08	-0.05	-0.07	-0.17	0.18	-0.13	0.03	-0.13	0.03	0.14	0.12	0.11	1	-0.03	-0.18	0.09	-0.15

	Crude Protein (%)	Available Protein (%)	ADF (%)	Lignin (%)	aNDF (%)	P:F Ratio	WSC (%)	Crude Fat (%)	Soluble Sugars (%)	Ca (%)	P (%)	Mg (%)	K (%)	Na (%)	Fe (ppm)	Zn (ppm)	Cu (ppm)	Mn (ppm)	Mo (ppm)	NDVI Dry	NDVI Wet	Densities
Mo (ppm) ^s	0.53	0.35	-0.16	-0.17	-0.16	-0.01	0.16	0.06	-0.03	-0.14	0.42	0.05	-0.03	-0.14	0.11	0.48	0.20	-0.03	1	0.26	-0.22	-0.09
NDVI Dry ^t	0.14	0.04	-0.08	-0.04	-0.14	0.03	-0.16	-0.03	0.00	0.13	0.10	0.08	0.07	-0.10	-0.18	0.06	-0.14	-0.18	0.26	1	-0.87	-0.35
NDVI Wet ^u	-0.16	-0.12	0.15	0.07	0.23	-0.19	0.33	0.04	-0.04	-0.06	-0.09	0.06	-0.01	0.14	0.17	-0.07	0.17	0.09	-0.22	-0.87	1	0.60
Densities ^v	-0.14	-0.20	0.18	0.16	0.22	-0.19	0.14	-0.09	0.02	0.01	0.05	0.29	0.20	0.26	0.10	-0.04	0.22	-0.15	-0.09	-0.35	0.60	1

^a Crude Protein (%) = crude protein as a percent of total dry matter

^b Avail Protein (%) = available protein as a percent of total dry matter

^c ADF (%) = acid detergent fiber as a percent of total dry matter

^d Lignin (%) = lignin as a percent of total dry matter

^e aNDF (%) = neutral detergent fiber (with amylase) as a percent of total dry matter

^f P:F Ratio = protein-to-fiber ratio, the available protein (%) divided by acid detergent fiber (ADF; %)

^g WSC (%) = water soluble carbohydrates as a percent of total dry matter

^h Crude Fat (%) = crude fat as a percent of total dry matter

ⁱ Soluble Sugars (%) = soluble sugars as a percent of total dry matter

^j Ca (%) = calcium as a percent of total dry matter

^k P (%) = phosphorous as a percent of total dry matter

^l Mg (%) = magnesium as a percent of total dry matter

^m K (%) = potassium as a percent of total dry matter

ⁿ Na (%) = sodium as a percent of total dry matter

^o Fe (ppm) = iron content in parts per million

^p Zn (ppm) = zinc content in parts per million

^q Cu (ppm) = copper content in parts per million

^r Mn (ppm) = manganese content in parts per million

^s Mo (ppm) = molybdenum content in parts per million

^t NDVI Dry = fragment-wide average normalized difference vegetation index (NDVI) during the dry season

^u NDVI Wet = fragment-wide average normalized difference vegetation index (NDVI) during the wet season

^v Densities = sifaka densities (sifakas/km²)

Supplemental Table 2. Top plant species and parts consumed by golden-crowned sifakas (*Propithecus tattersalli*) and collected for nutritional analyses from nine forest fragments in the Loky-Manambato Protected Area in northeastern Madagascar. Dry season samples were collected August - December based on feeding data from 16 sifaka groups in 2017 (two groups each from Ampondrabe, Antsahabe, Antsaharaingy, Bekaraoka Avaratra, Bekaraoka South, Benanofy, Binara, and Solaniampilana), 12 groups in 2018 (two groups each from Ambohitsintondroina, Antsahabe, Antsaharaingy, Bekaraoka South, Binara, and Solaniampilana), and three groups in 2019 (two groups each from Bekaraoka South, Binara, and Solaniampilana). Wet season samples were collected February – March 2019 based on feeding data from six sifaka groups (two groups each from Bekaraoka South, Binara, and Solaniampilana). All plant species were identified by the Missouri Botanical Garden in Antananarivo, Madagascar. Plant parts consumed: BD = buds, FL = flowers, ML = mature leaves, PT = petioles, RF = ripe fruits, RFSD = ripe fruits and seeds, SD = seeds, URF = unripe fruits, UFSD = unripe fruits and seeds, YL = young leaves

Forest Fragment	Year	Season	Vernacular	Family	Genus	Species	Plant Part
Ambohitsintondroina	2018	Dry	Taintsindambo	FABACEAE	<i>Pongamiopsis</i>	<i>pervilleana</i>	FL
Ambohitsintondroina	2018	Dry	Soritry	SAPINDACEAE	<i>Filicum</i>	<i>longifolium</i>	YL
Ambohitsintondroina	2018	Dry	Nanto	SAPOTACEAE	<i>Capurodendron</i>	<i>sp.</i>	SD
Ambohitsintondroina	2018	Dry	Rotro	MYRTACEAE(?)	<i>Syzygium(?)</i>	-	URF
Ambohitsintondroina	2018	Dry	Manary	-	-	-	YL

Forest Fragment	Year	Season	Vernacular	Family	Genus	Species	Plant Part
Ampondrabe	2017	Dry	Sakoana	ANACARDIACEAE	<i>Poupartia</i>	<i>sp.</i>	BD, YL
Ampondrabe	2017	Dry	Voankazomeloka	FABACEAE	<i>Xanthocercis</i>	<i>madagascariensis Baill.</i>	SD
Ampondrabe	2017	Dry	Matifioditra ala	SAPINDACEAE	<i>Crossonephelis</i>	<i>sp.</i>	ML
Antsahabe	2017	Dry	Vongo	CLUSIACEAE	<i>Garcinia</i>	<i>orthoclada Baker</i>	BD
Antsahabe	2017, 2018	Dry	Sambalahy	FABACEAE	<i>Albizia</i>	<i>gummifera (J.F. Gmel.) C.A. Sm.</i>	FL, SD
Antsahabe	2018	Dry	Mampay	FABACEAE	<i>Cynometra</i>	<i>aurita</i>	YL
Antsahabe	2017	Dry	Arika	FABACEAE	<i>Dupuya</i>	<i>haraka (Capuron) J.H. Kirkbr.</i>	FL
Antsahabe	2018	Dry	Hazomena	SALICACEAE	<i>Homalium</i>	<i>albiflorum (Boivin ex Tul.) O. Hoffm.</i>	RFSD
Antsahabe	2017	Dry	Tavolo	SAPOTACEAE	<i>Manilkara</i>	<i>perrieri Aubrév</i>	ML
Antsahabe	2018	Dry	Voatsikomoka	-	-	-	SD
Antsahabe	2018	Dry	Vahy sp	-	-	-	BD/FL
Antsaharaingy	2017	Dry	Mango	ANACARDIACEAE	<i>Mangifera</i>	<i>indica L.</i>	URF
Antsaharaingy	2017	Dry	Sakoana	ANACARDIACEAE	<i>Poupartia</i>	<i>sp.</i>	BD, YL
Antsaharaingy	2018	Dry	Barabanja	APOCYNACEAE	<i>Mascarenhasia</i>	<i>arborescens A. DC.</i>	ML, YL
Antsaharaingy	2017	Dry	Satrabe	ARECACEAE	<i>Bismarckia</i>	<i>nobilis</i>	RF
Antsaharaingy	2018	Dry	Amontana	CLUSIACEAE	<i>Garcinia</i>	<i>commersonii</i>	BD
Antsaharaingy	2017	Dry	Bonara	FABACEAE	<i>Albizia</i>	<i>lebbeck (L.) Benth.</i>	YL
Antsaharaingy	2018	Dry	Valomborona	FABACEAE(?)	<i>Albizia(?)</i>	-	BD, FL

Forest Fragment	Year	Season	Vernacular	Family	Genus	Species	Plant Part
Antsaharaingy	2018	Dry	Merana	-	-	-	SD
Bekaraoka South	2019	Wet	Tsarafanahy	BARRAGINACEAE	<i>Bourreria</i>	<i>labatii</i>	URF
Bekaraoka South	2019	Wet	Mendivoatanana	EBENACEAE	<i>Diospyros</i>	<i>sp.</i>	BD
Bekaraoka South	2019	Wet	Tsilaity	ERYTHROXYLACEAE	<i>Erythroxylum</i>	<i>rignyanm</i>	RF
Bekaraoka South	2019	Wet	Ambavy	ERYTHROXYLACEAE	<i>Erythroxylum</i>	<i>sp.</i>	BD
Bekaraoka South	2018, 2019	Dry, Wet	Mampay	FABACEAE	<i>Cynometra</i>	<i>aurita</i>	ML, YL
Bekaraoka South	2019	Dry	Madiro	FABACEAE	<i>Tamarindus</i>	<i>indica</i>	SD
Bekaraoka South	2017	Dry	Voankazomeloka	FABACEAE	<i>Xanthocercis</i>	<i>madagascariensis Baill.</i>	SD
Bekaraoka South	2019	Dry	Sely	MALVACEAE	<i>Grewia</i>	<i>saligna</i>	URFSD
Bekaraoka South	2019	Dry	Afomena	MALVACEAE	<i>Helmiopsis</i>	<i>pseudopopulus</i>	SD
Bekaraoka South	2018, 2019	Dry	Kimbimba	OLACACEAE	<i>Olax</i>	<i>andronensis</i>	ML, YL
Bekaraoka South	2017	Dry	Rasaonjo	PHYSENACEAE	<i>Physena</i>	<i>sessiliflora Tul.</i>	ML
Bekaraoka South	2019	Dry	Lamonty	RHAMNACEAE	<i>Ziziphus</i>	<i>mauritiana</i>	URF
Bekaraoka South	2019	Dry	Valotra	RUBIACEAE	<i>Breonia</i>	<i>perrieri</i>	URF
Bekaraoka South	2019	Dry	Kafeala	RUBIACEAE	<i>Chapelieria</i>	<i>sp.</i>	URFSD
Bekaraoka South	2018	Dry	Matifoditra ala	SAPINDACEAE	<i>Crossonephelis</i>	<i>sp.</i>	ML
Bekaraoka South	2019	Wet	Matifihoditra ala	SAPINDACEAE	<i>Majidea</i>	<i>zanguebarica</i>	SD
Bekaraoka South	2019	Wet	Unknown 2	SAPINDACEAE	<i>Plagioxyphus</i>	<i>louvelii</i>	SD

Forest Fragment	Year	Season	Vernacular	Family	Genus	Species	Plant Part
Bekaraoka South	2019	Dry	Nanto	SAPOTACEAE	<i>Capurodendron</i>	<i>aff. ludiifolium</i>	ML
Bekaraoka South	2019	Dry	Nanto	SAPOTACEAE	<i>Capurodendron</i>	<i>sp.</i>	ML
Bekaraoka South	2017	Dry	Manambomalaka	SPHAEROSEPALACEAE	<i>Rhopalocarpus</i>	<i>undulatus Capuron</i>	SD
Bekaraoka South	2019	Wet	Vahy	TALINACEAE	<i>Talinella</i>	<i>boiviriana</i>	URF
Bekaraoka South	2019	Wet	Unknown 1	VERBENACEAE	<i>Vytex</i>	<i>sp.</i>	URF
Bekaraoka South	2018	Dry	Aviavy	-	-	-	BD, RF
Bekaraoka South	2018	Dry	Taimbarika	-	-	-	YL
Bekaraoka Avaratra	2017	Dry	Manga	ANACARDIACEAE	<i>Mangifera</i>	<i>indica L.</i>	FL
Bekaraoka Avaratra	2017	Dry	Madirokarana	FABACEAE	<i>Pithecellobium</i>	<i>dulce (Roxb.) Benth.</i>	FL
Bekaraoka Avaratra	2017	Dry	Madiro	FABACEAE	<i>Tamarindus</i>	<i>indica L.</i>	FL
Bekaraoka Avaratra	2017	Dry	Voara	MORACEAE	<i>Ficus</i>	<i>sp.</i>	ML
Bekaraoka Avaratra	2017	Dry	Hazondrano	SALICACEAE	<i>Homalium</i>	<i>albiflorum (Boivin ex Tul.) O. Hoffm.</i>	YL
Benanofy	2017	Dry	Sarinanto	ANACARDIACEAE	<i>Rhus</i>	<i>perrieri (Courchet) H. Perrier</i>	SD
Benanofy	2017	Dry	Taindrabosy	FABACEAE	<i>Viguieranthus</i>	<i>sp.</i>	BD
Benanofy	2017	Dry	Taindrabosy	FABACEAE	<i>Viguieranthus</i>	<i>sp.</i>	BD
Binara	2019	Dry, Wet	Manga	ANACARDIACEAE	<i>Mangifera</i>	<i>indica</i>	BD, PT, RF, SD
Binara	2019	Wet	Sakoadia	ANACARDIACEAE	<i>Poupartia</i>	<i>birrea sbsp caffra</i>	RF

Forest Fragment	Year	Season	Vernacular	Family	Genus	Species	Plant Part
Binara	2019	Dry	Konikony	ANNONACEAE	<i>Annona</i>	<i>sp.</i>	URFSD
Binara	2019	Dry	Unknown 1	CALOPHYLLACEAE	<i>Mammea</i>	<i>punctata</i>	PT
Binara	2019	Wet	Vongo	CLUSIACEAE	<i>Garcinia</i>	<i>pervillei</i>	SD
Binara	2018, 2019	Dry	Vongo	CLUSIACEAE	<i>Garcinia</i>	<i>sp.</i>	SD, ML
Binara	2017	Dry	Vongo	CLUSIACEAE	<i>Garcinia</i>	<i>verrucosa</i> Jum. & H. Perrier	ML
Binara	2019	Wet	Sambalahy	FABACEAE	<i>Albizia</i>	<i>adianthifolia</i>	FL
Binara	2019	Wet	Bonara	FABACEAE	<i>Albizia</i>	<i>aurisparsa</i>	BD
Binara	2019	Dry	Bonara	FABACEAE	<i>Albizia</i>	<i>lebbeck</i>	BD
Binara	2017, 2018, 2019	Dry	Mampay	FABACEAE	<i>Cynometra</i>	<i>aurita</i>	ML, SD, YL
Binara	2019	Dry	Vahintsikidy	FABACEAE	<i>Etanda</i>	<i>chrysostachys</i>	SD
Binara	2017	Dry	Madiro	FABACEAE	<i>Tamarindus</i>	<i>indica</i> L.	ML
Binara	2017	Dry	Voantsilaka	FABACEAE	<i>Xanthocercis</i>	<i>madagascariensis</i> Baill.	SD
Binara	2019	Dry	Sarinanto	OCHNACEAE	<i>Ochna</i>	<i>sp.</i>	ML
Binara	2019	Wet	Unknown 7	OLACACEAE	<i>Olox</i>	<i>dissitiflora</i>	BD, YL
Binara	2019	Wet	Taipapango	PUTRANJIVACEAE	<i>Dryptes</i>	<i>perrieri</i>	RF
Binara	2017, 2019	Dry	Soritry	SAPINDACEAE	<i>Filicum</i>	<i>longifolium</i>	ML, YL
Binara	2019	Wet	Unknown 2	SAPINDACEAE	<i>Plagioxyphus</i>	<i>louvelii</i>	SD

Forest Fragment	Year	Season	Vernacular	Family	Genus	Species	Plant Part
Binara	2017	Dry	Unknown 4	SAPOTACEAE	<i>Chrysophyllum</i>	<i>guerelianum</i> (Aubrév.) G.E. Schatz & <i>L. Gaut.</i>	ML
Binara	2018	Dry	Hidiny	OLEACEA(?)	<i>Schrebera</i> (?)	-	ML
Solaniampilana	2019	Dry	Vaheny	APOCYNACEAE	<i>Landolphia</i>	<i>myrtifolia</i>	URFSD
Solaniampilana	2019	Dry, Wet	Amontana	CLUSIACEAE	<i>Garcinia</i>	<i>commersonii</i>	BD, SD
Solaniampilana	2019	Dry	Pistasiala	COMBRETACEAE	<i>Combretum</i>	<i>sp.</i>	SD
Solaniampilana	2019	Wet	Vahy 1	COMBRETACEAE	<i>Combretum</i>	<i>sp.</i>	ML, URF
Solaniampilana	2019	Wet	Manary boraka	FABACEAE	<i>Albizia</i>	<i>boivinii</i>	SD
Solaniampilana	2019	Dry	Zanakanivato	FABACEAE	<i>Bandouinia</i>	<i>fluggeiformis</i>	URF
Solaniampilana	2019	Wet	Vahonda	FABACEAE	<i>Dupuya</i>	<i>madagascariensis</i>	SD
Solaniampilana	2019	Wet	Unknown 3	FABACEAE	<i>Pongamiopsis</i>	<i>amygdalina</i>	SD
Solaniampilana	2019	Wet	Taintsindambo	FABACEAE	<i>Pongamiopsis</i>	<i>pervilleana</i>	SD
Solaniampilana	2019	Dry	Selimavo	MALVACEAE	<i>Cf. linearifolia</i>	-	SD
Solaniampilana	2019	Dry	Unknown 1	MELASTOMATACEAE	<i>Memeclylon</i>	<i>delphinense</i>	URF
Solaniampilana	2019	Wet	Valotra	RUBIACEAE	<i>Breonia</i>	<i>perrieri</i>	URF
Solaniampilana	2018, 2019	Dry, Wet	Soritry	SAPINDACEAE	<i>Filicum</i>	<i>longifolium</i>	SD, YL
Solaniampilana	2019	Dry	Nanto	SAPOTACEAE	<i>Capurodendron</i>	<i>sp.</i>	ML

Forest Fragment	Year	Season	Vernacular	Family	Genus	Species	Plant Part
Solaniampilana	2019	Dry, Wet	Zahana	SARCOLAENACEAE	<i>Leptolaena</i>	<i>villosa</i>	BD, FL, RFSD
Solaniampilana	2018	Dry	Unknown 1	-	-	-	FL
Solaniampilana	2018	Dry	Taindrabosy	FABACEA(?)	<i>Viguieranthus(?)</i>	-	YL
Solaniampilana	2018	Dry	Fagnamponga	-	-	-	BD

(?) indicates a possible identifier based on the vernacular names provided in Schatz (2001).

Supplemental Table 3. Activity budgets for golden-crowned sifakas (*Propithecus tattersalli*) inhabiting nine forest fragments (two groups per fragment) in the Loky-Manambato Protected Area in northeastern Madagascar as a percentage of total counts (one count collected every 15 minutes per weaned individual) spent engaged in each activity ($N = 11,533$). Male and female sifakas were followed in the dry (August – December in 2017 – 2019) and wet seasons (February – March 2019) in three different forest types: dry, moderate, and wet. Adults, sub-adults, and juveniles were assessed based on physical features or on knowledge from the previous sample period (*i.e.*, known infants in 2017 would be juveniles in 2018). Sections may not add up to 100% as a result of animals being out of sight or rounding. F = feeding, R = resting, S = socializing, T = travelling

Forest Types Combined												
	Dry Season				Wet Season				Both Seasons			
	F	R	S	T	F	R	S	T	F	R	S	T
Total	25.3%	53.3%	8.8%	12.6%	29.5%	48.3%	8.4%	13.8%	27.1%	51.1%	8.6%	13.2%
Females	24.4%	54.8%	8.2%	12.7%	28.8%	50.0%	8.1%	13.1%	26.2%	52.7%	8.2%	12.9%
Males	26.2%	51.7%	9.4%	12.6%	23.7%	36.6%	6.9%	11.4%	27.9%	49.5%	9.1%	13.4%

Forest Types Combined

	Dry Season				Wet Season				Both Seasons			
	F	R	S	T	F	R	S	T	F	R	S	T
<i>Adults</i>	24.4%	54.7%	8.3%	12.6%	27.9%	50.4%	8.2%	13.5%	25.7%	53.1%	8.3%	12.9%
Females	24.4%	55.9%	7.7%	12.1%	27.7%	51.8%	8.0%	12.5%	25.7%	54.3%	7.8%	12.2%
Males	24.3%	53.0%	9.3%	13.4%	28.2%	48.5%	8.4%	14.8%	25.8%	51.3%	9.0%	13.9%
<i>Sub-Adults</i>	27.6%	49.9%	10.1%	12.4%	31.9%	45.6%	8.8%	13.7%	29.3%	48.2%	9.6%	12.9%
Females	24.2%	49.6%	10.6%	15.6%	25.0%	53.4%	6.3%	15.2%	24.5%	50.9%	9.1%	15.5%
Males	29.3%	50.0%	9.7%	10.9%	34.6%	42.5%	9.8%	13.1%	31.5%	46.9%	9.7%	11.8%
<i>Juveniles</i>	24.9%	51.4%	9.6%	14.1%	31.2%	44.9%	8.9%	15.0%	30.4%	45.8%	9.0%	14.9%
Females	-	-	-	-	35.0%	41.2%	9.9%	13.9%	35.0%	41.2%	9.9%	13.9%
Males	27.0%	48.0%	9.9%	15.1%	27.8%	48.3%	8.0%	16.0%	27.6%	48.2%	8.4%	15.8%

Dry Forest

	Dry Season				Wet Season				Both Seasons			
	F	R	S	T	F	R	S	T	F	R	S	T
Total	29.8%	53.0%	5.0%	12.2%	31.0%	48.6%	7.0%	13.4%	30.2%	51.3%	5.8%	12.6%
Females	27.3%	56.9%	4.4%	11.4%	32.4%	45.6%	8.1%	13.9%	29.3%	52.6%	5.8%	12.3%
Males	31.4%	50.5%	5.4%	12.7%	17.4%	29.3%	3.7%	7.6%	30.9%	50.5%	5.7%	12.8%
<i>Adults</i>	27.9%	55.8%	4.7%	11.6%	29.5%	49.5%	7.7%	13.3%	28.5%	53.4%	5.8%	12.3%
Females	26.6%	58.4%	4.0%	11.0%	30.6%	48.3%	8.2%	12.9%	28.0%	54.8%	5.5%	11.7%
Males	29.2%	53.2%	5.4%	12.3%	28.5%	50.5%	7.3%	13.6%	28.9%	52.1%	6.2%	12.8%
<i>Sub-Adults</i>	-	-	-	-	36.3%	44.4%	5.7%	13.6%	36.3%	44.4%	5.7%	13.6%
Females	-	-	-	-	37.8%	37.8%	7.8%	16.7%	37.8%	37.8%	7.8%	16.7%
Males	-	-	-	-	34.9%	50.8%	3.7%	10.6%	34.9%	50.8%	3.7%	10.6%
<i>Juveniles</i>	33.2%	47.9%	5.6%	13.1%	29.9%	50.8%	5.6%	13.6%	32.8%	48.3%	5.6%	13.2%
Females	30.5%	49.7%	6.6%	13.2%	-	-	-	-	30.5%	49.7%	6.6%	13.2%
Males	33.9%	47.5%	5.4%	13.1%	29.9%	50.8%	5.6%	13.6%	33.2%	48.1%	5.5%	13.2%

Moderate Forest

	Dry Season				Wet Season				Both Seasons			
	F	R	S	T	F	R	S	T	F	R	S	T
Total	29.5%	51.5%	8.5%	10.5%	31.6%	45.7%	10.5%	12.2%	30.8%	48.0%	9.7%	11.6%
Females	28.5%	52.6%	7.9%	11.0%	31.5%	48.3%	9.9%	10.4%	30.2%	50.1%	9.1%	10.6%
Males	31.6%	50.1%	8.8%	9.5%	31.7%	43.1%	11.1%	14.1%	31.7%	45.6%	10.2%	12.4%
<i>Adults</i>	29.2%	52.0%	8.9%	9.9%	28.2%	50.6%	10.3%	10.9%	28.7%	51.3%	9.6%	10.4%
Females	28.4%	52.4%	8.6%	10.6%	28.7%	52.3%	9.6%	9.4%	28.5%	52.4%	9.1%	10.0%
Males	31.0%	51.2%	9.6%	8.3%	27.3%	46.8%	11.8%	14.1%	29.3%	49.1%	10.6%	11.0%
<i>Sub-Adults</i>	27.0%	48.0%	9.9%	15.1%	30.4%	44.0%	10.9%	14.7%	29.7%	44.9%	10.7%	14.8%
Females	-	-	-	-	33.6%	42.9%	10.9%	12.6%	33.6%	42.9%	10.9%	12.6%
Males	27.0%	48.0%	9.9%	15.1%	23.7%	46.2%	11.0%	19.1%	25.2%	47.1%	10.5%	17.2%
<i>Juveniles</i>	33.9%	51.2%	5.3%	9.6%	36.4%	40.8%	10.4%	12.4%	35.8%	43.4%	9.1%	11.7%
Females	29.2%	54.0%	3.5%	13.3%	39.3%	42.3%	8.6%	9.8%	35.1%	47.1%	6.5%	11.2%
Males	36.7%	49.5%	6.4%	7.4%	35.8%	40.5%	10.8%	13.0%	36.0%	42.3%	9.9%	11.8%

Wet Forest												
	Dry Season				Wet Season				Both Seasons			
	F	R	S	T	F	R	S	T	F	R	S	T
Total	18.3%	54.7%	12.8%	14.3%	24.1%	52.2%	6.6%	17.1%	20.2%	53.9%	10.7%	15.2%
Females	20.4%	54.5%	10.7%	14.5%	21.9%	55.9%	5.6%	16.5%	20.9%	55.0%	9.0%	15.1%
Males	15.0%	54.7%	15.9%	14.3%	27.2%	47.0%	8.1%	17.8%	19.2%	52.0%	13.2%	15.5%
Adults	19.0%	55.1%	11.0%	14.8%	25.9%	51.3%	6.5%	16.3%	21.2%	53.9%	9.6%	15.3%
Females	20.6%	56.1%	9.6%	13.6%	24.5%	53.9%	6.0%	15.6%	21.9%	55.4%	8.4%	14.3%
Males	16.5%	53.6%	13.1%	16.7%	28.5%	46.5%	7.3%	17.7%	20.0%	51.5%	11.4%	17.0%
Sub-Adults	12.0%	72.0%	8.0%	8.0%	25.1%	47.7%	9.2%	18.0%	23.9%	50.0%	9.1%	17.0%
Females	-	-	-	-	-	-	-	-	-	-	-	-
Males	-	-	-	-	25.1%	47.7%	9.2%	18.0%	25.1%	47.7%	9.2%	18.0%
Juveniles	16.0%	52.3%	19.2%	12.5%	12.4%	63.2%	4.3%	20.0%	15.2%	54.7%	15.9%	14.2%
Females	19.4%	48.2%	14.8%	17.5%	12.4%	63.2%	4.3%	20.0%	17.1%	53.2%	11.3%	18.3%
Males	10.3%	58.1%	25.0%	6.6%	-	-	-	-	10.3%	58.1%	25.0%	6.6%

Supplemental Table 4. Percent of feeding counts spent consuming different plant parts by golden-crowned sifakas (*Propithecus tattersalli*) inhabiting nine forest fragments (two groups per fragment) in the Loky-Manambato Protected Area in northeastern Madagascar during the dry (August – December 2017 – 2019) and wet (February – March 2019) seasons. Weaned male and female sifakas were followed in three different forest types: dry, moderate, and wet. Counts were collected based on 15-minute instantaneous scan sampling of a sifaka group ($N = 3,566$). Sections may not add up to 100% as a result of animals being out of sight or rounding. Licking water from substrates was removed but represented <1.5% of feeding counts observed by individuals in dry forests during the dry season. BARK = bark, BD = buds, FL = flowers, FR = fruits, ML = mature leaves, PT = petioles, SD = seeds, YL = young leaves

Forest Types Combined								
	BARK	BD	FL	FR	ML	PT	SD	YL
Total	0.1%	19.1%	8.8%	24.4%	6.7%	0.5%	22.0%	18.0%
Female	0.1%	18.1%	8.5%	24.4%	6.6%	0.6%	21.0%	20.6%
Male	0.2%	20.1%	9.0%	24.4%	6.9%	0.4%	23.0%	15.6%

Dry Forest								
	BARK	BD	FL	FR	ML	PT	SD	YL
Total	0.0%	25.4%	17.9%	8.9%	5.3%	0.2%	31.8%	9.8%
Female	0.0%	24.7%	20.5%	8.5%	4.4%	0.2%	30.5%	10.8%
Male	0.0%	25.8%	16.2%	9.1%	5.8%	0.2%	32.7%	9.2%

Moderate Forest

	BARK	BD	FL	FR	ML	PT	SD	YL
Total	0.2%	20.3%	2.1%	32.5%	12.8%	0.1%	5.2%	26.8%
Female	0.2%	20.8%	2.1%	29.6%	13.7%	0.2%	4.8%	28.7%
Male	0.3%	19.8%	2.1%	35.7%	11.8%	0.0%	5.6%	24.7%

Wet Forest

	BARK	BD	FL	FR	ML	PT	SD	YL
Total	0.2%	7.6%	4.2%	37.0%	0.2%	1.5%	31.1%	18.2%
Female	0.2%	8.3%	4.6%	33.8%	0.2%	1.5%	31.3%	20.2%
Male	0.3%	6.5%	3.5%	42.1%	0.3%	1.5%	30.9%	15.0%

Supplemental Table 5. Sample sizes for activity budget and feeding count data of golden-crowned sifakas (*Propithecus tattersalli*) in the Loky-Manambato Protected Area. Data were collected from males and females in 18 total groups during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons in nine unique forest fragments (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet). For each fragment, one group was selected because it was found along the forest edge (matrix) and one group was selected because it was found >500 m away from the forest edge (contiguous). Individual golden-crowned sifakas were identified, photographed, and named based on readily distinguishable physical characteristics (*e.g.*, sex, scars, color patterns) and groups were followed to their sleep trees each night to ensure that the same group could be located the following morning. F = female, M = male

			Dry			Dry Total	Wet		Wet Total	Grand Total
Forest										
Type	Group ID	Individual	F	M	Unknown		F	M		
Dry	Antsaharaingy-contiguous	Andy	-	9	-	9	-	-	-	9
		Carina	9	-	-	9	-	-	-	9
		Domenic	-	9	-	9	-	-	-	9
		Marco	-	8	-	8	-	-	-	8
Dry	Solaniampilana-contiguous	Chloe	5	-	-	5	-	-	-	5

			Dry			Dry Total	Wet		Wet Total	Grand Total
Forest										
Type	Group ID	Individual	F	M	Unknown		F	M		
Dry	Solaniampilana-contiguous	Clara	5	-	-	5	-	-	-	5
		Gila	-	-	-	-	-	6	6	6
		Jamel	-	5	-	5	-	-	-	5
		Koly	-	-	-	-	6	-	6	6
		Kombo	-	-	-	-	-	6	6	6
		Liv	-	5	-	5	-	-	-	5
		Sonia	-	-	-	-	6	-	6	6
	Solaniampilana-matrix	Vola	-	-	-	-	6	-	6	6
		Bera	-	-	-	-	-	6	6	6
		Karl	-	5	-	5	-	-	-	5
		Kelly	5	-	-	5	-	-	-	5
		Leoni	-	-	-	-	-	6	6	6
		Lynn	-	-	-	-	6	-	6	6
		Nala	5	-	-	5	-	-	-	5
Simba	-	5	-	5	-	-	-	5		

			Dry			Dry Total	Wet		Wet Total	Grand Total	
Forest											
Type	Group ID	Individual	F	M	Unknown		F	M			
Dry	Solaniampilana-matrix	Theo	-	-	-	-	-	6		6	6
		Toky	-	-	-	-	-	6		6	6
Dry Forest Total			29	46	0	75	24	36	60	135	
Moderate	Ambohitsintondroina-contiguous	Jane	5	-	-	5	-	-	-	5	
		Lova	-	5	-	5	-	-	-	5	
		Max	-	-	4	4	-	-	-	4	
		Naina	-	5	-	5	-	-	-	5	
		Ranja	-	5	-	5	-	-	-	5	
			Sandler	5	-	-	5	-	-	-	5
		Bekaraoka-contiguous	Borisofina	-	6	-	6	-	-	-	6
			Bota	-	-	-	-	-	8	8	8
			Hery	-	-	-	-	-	8	8	8
			Jess	-	-	-	-	8	-	8	8

			Dry			Dry Total	Wet		Wet Total	Grand Total	
Forest											
Type	Group ID	Individual	F	M	Unknown		F	M			
Moderate	Bekaraoka-contiguous	Joby	-	-	-	-	-	8		8	8
		Manja	-	6	-	6	-	-		-	6
		Meva	5	-	-	5	8	-		8	13
		Nify	-	6	-	6	-	-		-	6
		Ratsy	-	5	-	5	-	-		-	5
		Reny Be	6	-	-	6	2	-		2	8
		Soa	6	-	-	6	8	-		8	14
	Teboka	4	-	-	4	-	-		-	4	
	Bekaraoka-matrix	Dorian	-	-	-	-	-	7		7	7
		Eric	-	-	-	-	-	7		7	7
		Kanto	-	4	-	4	-	-		-	4
		Kate	-	-	-	-	7	-		7	7
		Keira	-	-	-	-	7	-		7	7
		Lisy	4	-	-	4	-	-		-	4
Mena		-	-	-	-	-	7		7	7	

			Dry			Dry Total	Wet		Wet Total	Grand Total
Forest										
Type	Group ID	Individual	F	M	Unknown		F	M		
Moderate	Bekaraoka-matrix	Rambo	4	-	-	4	7	-	7	11
		Reny C	4	-	-	4	-	-	-	4
		Rija	-	4	-	4	-	-	-	4
		Sofina	4	-	-	4	7	-	7	11
		Tohira	-	-	-	-	-	7	7	7
Moderate	Bekaraoka-matrix	Traka	4	-	-	4	-	-	-	4
		Voretra	-	4	-	4	-	-	-	4
		Zaza	-	4	-	4	-	-	-	4
Moderate Forest Total			51	54	4	109	54	52	106	215
Wet	Antsahabe-contiguous	Banga	-	-	6	6	-	-	-	6
		Mainty	5	-	-	5	-	-	-	5
		Reny Kely	7	-	-	7	-	-	-	7
		Ringitra	-	7	-	7	-	-	-	7
		Sola	-	-	6	6	-	-	-	6

			Dry			Dry Total	Wet		Wet Total	Grand Total
Forest										
Type	Group ID	Individual	F	M	Unknown		F	M		
Wet	Binara-contiguous	Barb	7	-	-	7	1	-	1	8
		Brido	-	-	-	-	-	8	8	8
		Everett	-	7	-	7	-	7	7	14
		George	-	7	-	7	-	7	7	14
		Molly	-	-	-	-	6	-	6	6
		Norma	7	-	-	7	1	-	1	8
		Sandra	-	-	-	-	5	-	5	5
		Sandy	7	-	-	7	8	-	8	15
		Thomas	-	7	-	7	-	8	8	15
	Binara-matrix	Arwen	7	-	-	7	-	-	-	7
		Eragorn	7	-	-	7	-	-	-	7
		Frodo	-	7	-	7	-	-	-	7
		Galadriel	7	-	-	7	-	-	-	7
		Melo	-	-	-	-	7	-	7	7
		Mony	-	-	-	-	7	-	7	7

			Dry			Dry Total	Wet		Wet Total	Grand Total
Forest										
Type	Group ID	Individual	F	M	Unknown		F	M		
Wet	Binara-matrix	Sanga	-	-	-	-	7	-	7	7
		Sam	-	7	-	7	-	-	-	7
		Smeagol	-	-	-	-	-	7	7	7
		Steve	-	-	-	-	-	7	7	7
Wet Total		54	42	12	108	42	44	86	194	
							12	13		
Grand Total			134	142	16	292	0	2	252	544

Supplemental Table 6. Kruskal-Wallis comparisons for nutritional analysis outputs (measured as a percent of total dry matter or in parts per million (ppm)) by forest type (dry, moderate, wet) of foods consumed by golden-crowned sifakas (*Propithecus tattersalli*) in the Loky Manambato Protected Area. Nutritional data were obtained from 114 plant samples representing the top five food items consumed by 18 sifaka groups (two per forest fragment) from nine forest fragments (Ambohitsintondroina, Ampondrabe, Antsahabe, Antsaharaingy, Bekaraoka Avaratra, Bekaraoka South, Benanofy, Binara, and Solaniampilana) during the dry (August – December in 2017 – 2019) and wet (February – March 2019) seasons (six fragments only in the dry season, three in both wet and dry seasons) from three different forest types (dry, moderate, and wet).

Nutrient	N	χ^2	df	p-value	Dunn's Test		Z	p-unadjusted	p-adjusted ^a
					Comparison				
ADF (%) ^a	114	4.43	2	0.11					
Available Protein (%) ^b	56	2.46	2	0.29					
Ca (%) ^c	114	0.65	2	0.72					
Crude Fat (%) ^d	109	1.08	2	0.58					
Cu (ppm) ^e	114	4.65	2	0.10					
Fe (ppm) ^f	114	8.02	2	0.02	Dry	Wet	2.59	0.009	0.028

Nutrient	N	χ^2	df	p-value	Dunn's Test		Z	p-unadjusted	p-adjusted ^a
					Comparison				
Fe (ppm, cont'd) ^f					Moderate	Wet	2.26	0.024	0.035
K (%) ^g	114	2.80	2	0.25					
Mg (%) ^h	114	3.37	2	0.19					
Mn (ppm) ⁱ	114	6.90	2	0.03	Dry	Moderate	2.59	0.010	0.029
					Moderate	Wet	-1.87	0.061	0.091
Mo (ppm) ^j	95	4.93	2	0.09					
Na (%) ^k	114	7.77	2	0.02	Dry	Moderate	-1.69	0.091	0.137
					Moderate	Wet	2.79	0.005	0.016
P (%) ^l	114	1.00	2	0.61					
P:F Ratio ^m	55	3.37	2	0.19					
Soluble Sugars (%) ⁿ	93	1.74	2	0.42					
Water Soluble Carbohydrates (WSC; %) ^o	55	1.32	2	0.52					
Zn (ppm) ^p	114	1.80	2	0.41					

- ^a *P*-values adjusted with the Benjamini-Hochberg method
- ^b ADF (%) = acid detergent fiber as a percent of total dry matter
- ^c Avail Protein (%) = available protein as a percent of total dry matter
- ^d Ca (%) = calcium as a percent of total dry matter
- ^e Crude Fat (%) = crude fat as a percent of total dry matter
- ^f Cu (ppm) = copper content in parts per million
- ^g Fe (ppm) = iron content in parts per million
- ^h K (%) = potassium as a percent of total dry matter
- ⁱ Mg (%) = magnesium as a percent of total dry matter
- ^j Mn (ppm) = manganese content in parts per million
- ^k Mo (ppm) = molybdenum content in parts per million
- ^l Na (%) = sodium as a percent of total dry matter
- ^m P (%) = phosphorous as a percent of total dry matter
- ⁿ P:F Ratio = protein-to-fiber ratio, the available protein (%) divided by acid detergent fiber (ADF; %)
- ^o Soluble Sugars (%) = soluble sugars as a percent of total dry matter
- ^p WSC (%) = water soluble carbohydrates as a percent of total dry matter
- ^q Zn (ppm) = zinc content in parts per million

Chapter 4

Golden-crowned sifaka (*Propithecus tattersalli*) population genetics and recommendations for corridor restoration to promote connectivity of isolated forest fragments

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Golden-crowned sifaka (*Propithecus tattersalli*) population genetics and recommendations for corridor restoration to promote connectivity of isolated forest fragments

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Abstract

Small, isolated populations are expected to be at greater risk of extinction due to genetic and demographic constraints. Non-invasive genetic sampling and new advances in connectivity modeling can help conservation managers identify populations that are at the highest risk of these threats and inform intervention strategies, such as reforestation of corridors to allow animal movement between sub-populations. We investigated inbreeding and connectivity across the global range of the golden-crowned sifaka (*Propithecus tattersalli*), a critically endangered lemur endemic to northern Madagascar. We quantified variation at nine microsatellite loci from 175 sifakas sampled from nine forest fragments. Sifakas' high F_{IS} values (mean = 0.27, range = 0.11 – 0.60), high M -ratios (mean = 0.59, range = 0.49 – 0.82), and low overall effective population size ($N_e = 139.8 - 144$ sifakas) suggested that populations may be declining and becoming more isolated across the landscape. F_{ST} comparisons between fragments and genetic identification of migrants supported previous findings that sifakas are still able to disperse across this fragmented landscape. Homozygote excess requires that these results be taken with caution until further validation can be completed. Circuitscape analysis highlighted likely movement corridors between populations and identified three priority areas for reforestation. Reforesting and protecting these key areas will help to maintain connectivity between several large sub-populations and help to alleviate the likely negative impacts of a newly paved national road across their range.

Introduction

Conservationists have long been concerned about the small-population paradigm, which details the consequences of a species being rare across a landscape or having a small population size (Caughley 1994). When populations decline to a certain size, inbreeding depression (Keller 2002), demographic stochasticity (Melbourne and Hastings 2008), and genetic drift (Gilroy et al. 2017; Ochoa et al. 2020) drive an “extinction vortex” that can quickly render small populations less viable over the short term and less adaptable over the long term (Gilpin and Soulé 1986). Hence, maintenance of genetic diversity and gene flow are important to promoting long-term population sustainability (Frankham et al. 2017).

While natural processes (*i.e.*, genetic drift) may rapidly drive species down the extinction vortex, human activities may accelerate the decline even further (Frankham et al. 2010). Deforestation and habitat fragmentation may directly result in the loss of individuals while also isolating breeding units and limiting migrations among such subpopulations (Barnett et al. 2020; Latorre-Cardenas 2020; Nehemia et al. 2017). For example, the genetic structure of Pfrimer’s parakeets (*Pyrrhura pfrimeri*), a relatively short-lived bird (average lifespan = eight years) inhabiting highly fragmented dry forests in Brazil, showed no association between genetic and current geographic distances, least-cost paths, or circuit theory-based resistances (Miller et al. 2013). Instead, genetic structure was best associated with a forest connectivity measure based on fragmentation that had occurred 35 years prior. The impacts of habitat fragmentation on even highly mobile avian species (Barr et al. 2015; Miller et al. 2013) highlight the potentially significant impact of habitat fragmentation on the genetic structure of threatened and endangered terrestrial species of lesser mobility (Gallego-Garcia et al. 2018; Lange et al. 2010; Larison et al. 2021).

New tools are emerging to help managers plan to counteract the worst impacts of forest loss and fragmentation. Tools like Circuitscape (Shah and McRae 2008), now freely available online, apply concepts from the field of circuit theory to address these issues. Circuitscape uses layers in a GIS to map likely animal movement patterns in the face of various “resistors” on a landscape, such as cover types or landscape features such as mountains or water bodies that might limit animal movements. Mapping areas of resistance may help to predict viable movement corridors promoting genetically effective migration that could limit the effects of genetic drift and inbreeding. Circuitscape and similar methods have been used extensively to map migration corridors for animals worldwide (Harrisson et al. 2013; Koen et al. 2012), but recommendations based upon using these tools have only recently appeared in the primate literature (Baden et al. 2019; Blair and Melnick 2012; Bonnin et al. 2020; Luo et al. 2016).

In Madagascar, forest habitat loss and fragmentation are widespread. Between 1953 and 2014, Madagascar lost 44% of its natural forest cover (Vieilledent et al. 2018). The rate of loss continues to increase (currently around 1.1% loss/year). In 1953, only 5% of points in Madagascar’s forests were within 100 m of the forest edge, now 46% of points are located less than 100 m from a forest edge, highlighting the extent of forest fragmentation. Moist and dry forests experienced the highest rates of annual loss from 2010-2013 (1.2% and 1.1%, respectively) compared to mangrove and spiny forests (0.0% and 0.3%, respectively). At this rate, Madagascar’s eastern rainforests are expected to disappear by 2080 under “relaxed” protected area scenarios (Morelli et al. 2019).

Golden-crowned sifakas (*Propithecus tattersalli*; hereafter, “sifakas”) are a species of lemur currently restricted to highly fragmented forests in a small, 880-km² region in northeastern Madagascar (Vargas et al. 2002). Historically, the species’ range extended another 40 km west to

the Ankarana massif, double its current range. Analysis of population genetic data, however, suggests that a population bottleneck occurred between 300 and 1,500 years before present (Quéméré et al. 2012; Salmona et al. 2017). The combined effects of severe droughts at the end of the Holocene and the arrival of humans (the exact date of human arrival remains contested, but likely occurred at least 2,000 years before present; Douglass et al. 2019) provides the most likely cause for decline of genetic diversity (Salmona et al. 2017). A recent population assessment across the species' range suggested a population decline of 30-43% over the past 10 years (see *Chapter 2*). Hunting of this species for bushmeat has long been considered taboo (Meyers 1996), though hunting may have had a major impact on this species in 2009 when law and order were disrupted due to a coup d'état (Barrett and Ratsimbazafy 2009; Conservation International 2010).

Genetic analyses from 2006/2008 (Quéméré, Crouau-Roy, et al. 2010) found that the sifakas had reasonably high genetic diversity (mean $H_e = 0.66$, H_e range across sites = 0.57-0.73), significant differentiation between populations inhabiting most forest fragments (mean $F_{ST} = 0.12$, F_{ST} range across site comparisons = 0.01-0.30), and low inbreeding (mean $F_{IS} = -0.03$, F_{IS} range across sites = -0.18 and 0.01). Additionally, causal modeling by Quéméré, Crouau-Roy, et al. (2010) demonstrated that isolation-by-distance and the dispersal barrier of the Manankolana River were the main population-structuring factors for the species across the entire landscape, suggesting significant genetically effective migration among forest patches on the same side of the river. However, isolation by lack of canopy cover received the highest model support and appeared to be the most important factor structuring the population when the effect of the river barrier was removed from the analysis. Those results imply that limited habitat connectivity may be affecting population structure at a local scale (Quéméré, Crouau-Roy, et al. 2010). Long

generation times (>15 years based on closely related Verreaux's sifakas (*P. verreauxi*); Lawler et al. 2009) and limited dispersal capability well beyond the forest edge (~2 km; Jimenez and Vargas 2000; Quéméré, Crouau-Roy, et al. 2010) may be masking the effects of fragmentation on sifaka genetics. The continued listing of this species as critically endangered by the IUCN (IUCN 2019), as well as increasing mining activities and the potential threat of hunting (Barrett and Ratsimbazafy 2009; Conservation International 2010), make it critical that specific actions be taken to ensure the long-term conservation of this species.

Our goals were to evaluate inbreeding and genetic metrics of connectivity of golden-crowned sifaka populations a decade after these metrics were first assessed over their global range (Quéméré, Crouau-Roy, et al. 2010). Second, we aimed to clarify the relatedness of a previously unknown population of sifakas in the far eastern portion of their range. Third, we sought to provide fragment-level effective population size estimates across the species' range. Lastly, we created a Circuitscape model based on knowledge of genetic connectivity, dispersal capability, and habitat requirements of this species to provide recommendations on where new forest corridors would be most beneficial to promote long-term gene flow for this species.

Methods

Golden-crowned sifakas (*P. tattersalli*) inhabit fragmented forests in northeastern Madagascar between the Loky and Manambato rivers (49°56'E, 13°31'S; Fig. 1). Sifakas inhabit a range of forest types from dry, sclerophyllous to dense, humid forests at elevations of 10-1000 m (Meyers 1993). Forest fragments mostly persist in more mountainous areas and are separated by cattle pastures, grasslands, and agricultural areas (Quéméré et al. 2013). Most of the sifaka's range lays within the 250,000-ha Loky-Manambato Protected Area (PA), which has been

managed by the NGO Fanamby since it was officially created in 2015 (Goodman et al. 2018). We also investigated a previously unreported sifaka population in littoral forests near the town of Ampisikina, over 11 km from the nearest large fragment (Ampondrabe; Fig. 1) that people living in the town had reported to leaders at Fanamby.

Sample Collection

Fecal samples were collected for genetic analyses from sifaka groups observed along line transects as well as opportunistically (Fig. 1). Line transects were established in 11 large forest fragments, or sub-populations, (Ambilondamba, Ambohitsintondroina, Ampondrabe, Antsahabe, Antsaharaingy, Bekaraoka Avaratra, Bekaraoka South, Benanofy, Binara, Bobankora, and Solaniampilana) as part of a comprehensive population survey effort. Sample collection took place May-July 2016, August-December 2017, and September-December 2018 across dry, moderate, and wet forest types. A full description of survey methods can be found in *Chapter 2*. All fecal samples from the Ampisikina fragment were collected opportunistically over a four-day period in October 2017 for a total of 12 sampling locations.

Once a sifaka group was located along a transect, we determined the number of individuals in the group, their ages, and sex if possible. Males were identified by external genitalia as well as a sternal scent gland that leads to darkening of the chest. If the group was in a location at which we had not previously collected fecal samples, we attempted to follow it until a defecation event occurred. Most groups allowed us to wait under their sleep trees or follow them at a distance for an hour or two in the morning until defecation occurred. We collected fecal samples every time animals were observed to defecate. Repeat samples from the same individual were removed from the data set after genotyping. Three to four fecal pellets were collected

immediately after defecation events to avoid collecting multiple samples from the same individual and to minimize environmental contamination and DNA degradation. Pellets were stored in 2-mL screw-top tubes filled with dimethyl sulfoxide saline solution (DET's buffer [20% dimethyl sulfoxide, 0.25M ethylenediaminetetraacetic acid, 100mM Tris, pH 7.5, and NaCl to saturation]), which has been recommended for the storage of herbivore feces prior to DNA extraction (Seutin et al. 1991; Wultsch et al. 2015). The feces-to-solution volumetric ratio was approximately 1:4. Each vial was marked with the GPS location, collection time, and name of the sample collector.

DNA Extraction and Amplification

Genetic material was extracted using QIAamp DNA Stool kits (Qiagen, Germantown, MD). We used a μ Lite PC analyzer (BioDrop, Cambridge, UK) to determine sample DNA concentrations. Samples with DNA concentrations <10 ng/ μ L were evaporated in an incubator (70°C) in 10-minute increments until the desired concentration range was reached.

Sixteen microsatellite loci were chosen for amplification (Table 1). Eight loci were selected from the 20 polymorphic dinucleotide microsatellite loci isolated for *P. tattersalli* (Razafindrakoto et al. 2008). Eight additional loci were obtained from among those originally described for *P. coquereli* (Rakotoarisoa et al. 2006), the most closely related sifaka species (Mayor et al. 2004).

Polymerase chain reaction (PCR) was conducted in eight multiplex suites, whereby two or more loci were amplified in a single reaction (Table 1). Master mixes included 0.9 μ L 0.2 mM dNTP, 1.1 μ L 10x PCR reaction buffer, 0.1 U/ μ L Platinum *Taq* polymerase (Invitrogen, Carlsbad, CA), 0.4 μ L of 1 mg/mL bovine serum albumin (BSA), 1.5 μ L 50 mM MgCl_2 , 0.7 μ L

of both forward and reverse primers (both 10 mg/mL) for each target locus, and 3 μ L of the genetic sample. Deionized water was added to bring the solution to 14 μ L. Forward primers were fluorescently labeled using PET, 6FAM, NED, HEX, or VIC dyes. We used the following cycling parameters: initial denaturation at 95°C for 15 min; and 40 cycles of denaturation at 95°C for 30 s, annealing at 54-62°C for 90 s, extension at 72°C for 60 s; and a final extension for 30 min at 72°C (Table 1; Quéméré, Louis, et al. 2010). We checked for the presence of amplification products by electrophoresis through an agarose gel and visualization of ethidium bromide-stained bands using a UV transilluminator. We sent all PCR products to the Cornell University Biotechnology Resource Center (Ithaca, NY) for amplification fragment-size analysis on an ABI3730 Genetic Analyzer.

We scored microsatellite fragment sizes by hand using GeneMarker (SoftGenetics, College Park, PA, USA). Genotypes were scored at least twice to reduce error. All inconsistent results were reviewed a third time and were flagged for possible removal from the data set.

Statistical Analyses

Artifacts of PCR amplification such as segregation of null alleles, large-allele dropout, and scoring error, were assessed using MicroChecker (van Oosterhout et al. 2004). Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium were assessed using Arlequin v 3.5.2.2 (Excoffier and Lischer 2010). We also computed observed (H_o) and expected (H_e) heterozygosities to evaluate genetic diversity and M -ratios (ratio of the number of alleles observed at a locus to the number of possible alleles between the largest and smallest alleles (Garza and Williamson 2001), where values < 0.68 indicate a recent population size reduction) to assess recent population size reductions using Arlequin. iNEST 2.2 (Chybicki et al. 2011) was

used to test simultaneously for null allele segregation, genotyping failures, and inbreeding within a dataset, for both the complete dataset and after the removal of data posing concern. Each analysis in iNest was conducted using 200,000 MCMC iterations with a burn-in of 20,000 and a thinning factor of 2,000. We also conducted forest fragment-level analyses on the refined dataset. We ran preliminary analyses iteratively, first by including all samples and loci with null alleles, then after removing samples with >5 loci with null alleles and indication of linkage disequilibrium among genotypes, and last with all loci removed that had null allele frequencies above 0.15.

We used two methods to cluster individuals by genetic similarity. The first method was discriminant analysis of principal components (DAPC; Jombart et al. 2010), which does not assume conformance with HWE. We used the package “adegenet” (Jombart 2008, Jombart and Ahmed 2011) within R (R Core Team 2019) to run this analysis. We retained axes for both the principal components and discriminant analysis steps based on best separation of sub-populations. The second method used a Bayesian algorithm that maximizes conformance to HWE within clusters and contrast among clusters using the program STRUCTURE (Pritchard et al. 2000). STRUCTURE runs had a burn-in period of 100,000 and 100,000 MCMC replications both with and without the option locprior. We visualized results in Structure Harvester (Earl and vonHoldt 2012) to determine the best-supported number of clusters using the criteria established by Evanno et al. (2005).

Using the five clusters of sub-populations (*i.e.*, samples grouped by forest fragment) identified from the DAPC and STRUCTURE results, we performed analysis of molecular variance (AMOVA). We estimated the proportion of genetic variability existing within individuals relative to the total population (F_{IT}), among sub-populations (F_{IS}), among sub-

populations within clusters (F_{SC}), and among clusters (F_{CT}) in Arlequin (Excoffier and Lischer 2010). These F -statistics indicate the degree of departure from HWE, the latter three due to processes occurring among groupings of samples, and range from 0 (completely outbred) to 1 (completely inbred). We used the linkage disequilibrium approach in NeEstimator v 2.1 (Do et al. 2014) to estimate effective population size (N_e) for the species as a whole and at the forest fragment level using the linkage disequilibrium and heterozygote excess methods. We also estimated N_e using the sibship assignment method (Wang 2009) in Colony 2.0.6.5 (Jones and Wang 2010).

Inbreeding was assessed using two approaches. First, Wright's F_{IS} metric was calculated in Arlequin (Excoffier and Lischer 2010) based on the degree of deviation from HWE within populations. Values range from -1 to 1 on a scale from completely outbred (more heterozygotes than expected) to completely inbred (fewer heterozygotes than expected). Second, inbreeding was determined using a Bayesian approach that simultaneously tested for the segregation of null alleles and genotyping failures (Chybicki et al. 2011). Model selection was performed based on the Deviance Information Criterion (DIC) and the iNest model parameters described above.

Individual assignment tests were done in GENECLASS v. 2.0 (Piry et al. 2004) in an attempt to directly identify migrants among demes. We used a Bayesian method (Rannala and Mountain 1997) with 10,000 iterations and a Type I error rate of 0.0001 to assign individuals to their forest fragment of origin. We then used the Paetkau et al. (2004) Monte Carlo resampling method to detect first-generation migrants based on likelihood ratios (L_{home} = likelihood that where the sample was taken is its home sub-population; L_{home}/L_{max} = likelihood that where the sample was taken is its home sub-population divided by the highest likelihood score of the sub-population to which the sample was assigned; and $L_{home}/L_{max \text{ not home}}$ = likelihood that where the

sample was taken is its home population divided by the highest likelihood score of the sub-population to which the sample was not assigned) and 10,000 simulated individuals with a threshold (p -value) of 0.001. We also inspected STRUCTURE output visually to detect migrants.

For all statistical tests, $\alpha = 0.05$.

Circuitscape Analysis

We implemented Circuitscape's Linkage Pathways Tool (Shah and McRae 2008) in ArcMap 10.6 (Esri, Redlands, CA, USA) to evaluate potential sifaka movement corridors. Based on previous work (see *Chapter 2*; Quéméré, Crouau-Roy, et al. 2010) and interpretation of genetic results from this study, we provided the highest resistance values to rivers and the lowest resistance values to forest and scrub pixels (based on the normalized difference vegetation index (NDVI), a measure of plant productivity, and map classification; see *Chapter 2*). We first used forest fragments $>0.1 \text{ km}^2$ as core areas to be connected (*i.e.*, average group home range size; Meyers 1993), but we had to increase minimum core forest areas to be connected to those $> 0.5 \text{ km}^2$ because of limited computational ability in processing so many connections between such a large number of fragments. We placed 2.5 km limits on our bounding circles and maximum Euclidean corridor distance based on proposed sifaka dispersal distances of $\sim 2 \text{ km}$ by previous studies (Jimenez and Vargas 2000; Quéméré, Crouau-Roy, et al. 2010).

This research complied with protocols approved by the Virginia Tech Institutional Animal Care and Use Committee (IACUC # 15-223) and adhered to the legal requirements for research conducted in Madagascar (Permit No. 117/16/MEEF/SG/DGF/DAPT/SCBT).

Results

We collected 275 fecal samples; sample sizes were not even across forest fragments and ranged from 8-49 samples (Table 2, Fig. 1). We removed data for all samples from which we were not able to amplify >10 loci, reducing our total number of samples to 175 and representing ~100 groups (groups may have been resampled in different years). We were not able to amplify any samples from the Bobankora fragment, reducing our forest fragment sample size to 10.

Of the sixteen microsatellite loci screened (Table 1), fifteen were polymorphic across sub-populations (only *93HDZ240* was not), though one locus, *93HDZ257*, was not polymorphic at Ampondrabe and Benanofy. Within sub-populations, all loci showed some evidence of linkage disequilibrium (LD). This was most pronounced among loci *88HDZ9*, *88HDZ81*, *88HDZ127*, *93HDZ179*, and *93HDZ257*. No such linkage disequilibrium was apparent across sub-populations. In general, H_o values were lower than H_e values, suggesting departures from Hardy-Weinberg Equilibrium (HWE) across several loci. Using MicroChecker, null alleles also were inferred to be segregating at all loci, at frequencies above 0.15 for loci *93HDZ5*, *88HDZ81*, *88HDZ127*, *93HDZ240*, and *93HDZ257* (van Oosterhout et al. 2004). iNest results prior to locus removal suggested that null alleles, genotyping failures, and inbreeding were all factors in our data set, with a mean $F_{IS} = 0.15$. Results obtained after loci removal also indicated that all factors remained in our dataset with a mean $F_{IS} = 0.13$ (Table 3). Data for loci *93HDZ5*, *88HDZ9*, *88HDZ81*, *88HDZ127*, *93HDZ240*, and *93HDZ257* were subsequently removed from subsequent analyses, and data for nine loci were retained (Table 1).

Assessment of Population Structure and Inbreeding

We found clustering of genetic samples within the same forest fragments (Fig. 2), with some overlap between forest fragments located geographically near one another (Figs. 1, 2). Based on this grouping of sub-populations and small sample sizes from Ambilondamba ($N = 3$), we chose to combine samples from Ambilondamba with Solaniampilana into one sub-population for subsequent analyses (henceforth, “Ambilondamba/Solaniampilana”). We also chose to combine Bekaraoka Avaratra and Bekaraoka South (henceforth, “Bekaraoka”), as the two forests supporting these sub-populations are connected and the samples from the two sub-populations largely overlapped in the DAPC analysis.

Overall departure of observed genotype frequencies from HWE expectations was $F_{IT} = 0.40$, while localized departure was $F_{IS} = 0.30$. Departure from HWE among sub-populations within clusters was $F_{SC} = 0.03$ and departure between clusters was $F_{CT} = 0.12$. M -ratios were < 0.68 for most sub-populations, suggesting recent demographic bottleneck for those sub-populations (Table 2; Garza and Williamson 2001). The best-supported model from iNest suggested that inbreeding is occurring for the population as a whole, and that our data also contain evidence of segregation of null alleles and genotyping failures (Table 3). F_{IS} values could not be determined for sub-populations within all forest fragments using iNest due to genotyping failures and/or null alleles in the top model for these sub-populations, but high estimates were available from Arlequin results ($F_{IS} = 0.11 - 0.60$; Table 4). Results from Colony also suggested that all sifaka sub-populations are experiencing mild to moderate inbreeding ($F_{IS} = 0.00 - 0.32$; Table 4).

We found the best support for $K = 5$ multi-locus genotypic clusters (Table 5). STRUCTURE results with $K = 5$ suggest that sifaka sub-populations in northern fragments

(Ampisikina, Ampondrabe, Antsaharaingy, and Benanofy) form their own cluster, as do sifaka sub-populations in Bekaraoka and Binara (Fig. 3). Sub-populations in Ambohitsintondroina, Antsahabe, and Ambilondamba/Solaniampilana each represent their own cluster. This structuring largely paralleled DAPC results, with the exception of Benanofy, which was more closely aligned with Ambohitsintondroina and Ambilondamba/Solaniampilana in the DAPC results than in those of STRUCTURE (Fig. 2).

Based on the STRUCTURE and DAPC results, we created five hierarchical groupings (clusters) of sub-populations for analysis of molecular variance (AMOVA). Most variation was within individuals (59.66%), though variation also existed among individuals within sub-populations (25.51%) and among clusters (12.04%; Table 6).

Assessment of Migrants and Population Connectivity

GENECLASS assigned individuals from each sub-population to their sub-population of collection with 48.0% accuracy (Table 7). Half of the sub-populations had over 60% of individuals assigned to the sub-population in the forest fragment where they were collected. For the sub-populations that did not meet this threshold, most of the error came from individuals being assigned to neighboring sub-populations. One notable exception was that 25.0% of samples collected in Antsahabe were suspected to have originated in Benanofy. Few migrants were detected using the L_{home} (3) or $L_{\text{home}}/L_{\text{max}}$ and $L_{\text{home}}/L_{\text{max not home}}$ (1) likelihood ratio approaches. Notably, one individual in Antsahabe was suspected to have moved from Antsaharaingy (minimum Euclidean distance = 29.4 km), while a second individual was suspected to have traveled from Bekaraoka to Antsahabe (minimum Euclidean distance = 12.7 km; see Fig. 1 for map of locations). Both remaining potential migrants moved between

neighboring sub-populations (Ambilondamba/ Solaniampilana to Benanofy, minimum Euclidean distance = 3.2 km). STRUCTURE results (for $K = 5$) suggested a few more migrants (*e.g.*, from northern sub-populations to those in Bekaraoka and Binara (minimum Euclidean distance = 7.8 km), and Antsahabe to Ambilondamba/Solaniampilana (minimum Euclidean distance = 5.3 km)), with some potential long-distance migrants (*e.g.*, Antsahabe to Antsaharaingy (minimum Euclidean distance = 29.4 km)).

Pairwise interpopulation differentiation was highest between sub-populations in Binara and Ambohitsintondroina, $F_{ST} = 0.30$; Table 8). Pairwise differentiation was lowest between sub-populations in Ambilondamba/Solaniampilana and Ampisikina, $F_{ST} = 0.01$) and those in Benanofy and Ampisikina ($F_{ST} = 0.01$).

Estimates of effective population size (N_e) varied widely by method, with the molecular co-ancestry methods providing the lowest values overall ($N_e = 12.7$ sifakas; Table 9) and the linkage disequilibrium ($N_e = 139.8$ sifakas) and sib-ship assignment ($N_e = 144$ sifakas) methods providing much higher overall values. At the sub-population level, N_e was generally low, but varied by method (linkage disequilibrium: median = 30.3, range = 2.2 – 75.6 sifakas; molecular co-ancestry: median = 7.2, range = 4.0 – 43.8 sifakas; sib-ship assignment: median = 46, range = 14 – 68 sifakas; Table 9). Sample sizes for sub-populations in some forest fragments were either too small to estimate N_e at all, or provided unbounded upper confidence intervals.

Five priority areas for monitoring and reforestation were identified using Circuitscape (Fig. 4). First, only two narrow connections exist between the northern sub-population cluster (1) and all of the remaining sub-populations (clusters 2-5; between Benanofy and a fragment west of Solaniampilana; Fig. 4, panel A). A national road that currently is being paved runs between these points. Second, only a single long, narrow riverine corridor connects the sub-population in

the Ampisikina fragment to the rest of the sifaka sub-populations (Fig. 4, panel B). Third, few forest patches provide connectivity throughout the central sifaka sub-populations (*e.g.*, Ambohitsintondroina (2), Ambilondamba/ Solaniampilana (3), and Antsahabe (4); Fig. 4, panel C). Fourth, very few forest patches connect the eastern and western portion of cluster 5 (Bekaraoka and Binara), potentially isolating a large number of sifakas in sub-populations in the Bekaraoka and Bobankora fragments (*see Chapter 2*) from all sifaka sub-populations west of the Manankolana River (Fig. 4, panel D). Last, many potential movement corridors exist between Bekaraoka and Bobankora, but paving the national road may have serious consequences for these connection points, further exacerbating the potential for genetic isolation among sub-populations (Fig. 4, panel E).

Discussion

Sifaka Population Structure and Connectivity

Similar to results of previous population genetics studies of this species, we found that golden-crowned sifaka populations were structured, although sub-populations in several forest fragments remain connected by migrants (Quéméré, Crouau-Roy, et al. 2010; Quéméré, Louis, et al. 2010). Sub-populations in fragments north of the Manankolana River (Ampisikina, Ampondrabe, Antsaharaingy, and Benanofy) formed their own multi-locus genotype cluster with apparent east-west connectivity, and sub-populations in Bekaraoka and Binara formed another cluster. Ambohitsintondroina, Antsahabe, and Ambilondamba formed their own, single-fragment clusters. Genetic variation among these sub-populations was reasonably high, suggesting that these sub-populations are somewhat isolated and should be carefully monitored and measures taken to ensure no future loss of genetic diversity. The differentiation among sub-populations in

forest fragments separated by the Manankolana River supports the results of previous landscape genetics work by Quéméré, Crouau-Roy, et al. (2010). Rivers are well known for isolating primate populations both outside of (Alfaro et al. 2015; Lehman and Fleagle 2006) and within Madagascar (Bachmann et al. 2000; Goodman and Ganzhorn 2004). Citing the year-long study of collared sifakas by Meyers (1993), Quéméré, Crouau-Roy, et al. (2010) also noted that these sifakas tend to disperse during the rainy season when rivers in the region are at their peak, explaining how these barriers to migration are maintained despite most rivers in the region being completely dry for several months out of the year.

Sub-population-level F_{ST} values yielded some unexpected results. Pairwise comparisons between Binara, Antsahabe, and Ambohitsintondroina were higher than expected for sub-populations in forest fragments so close to one another, suggesting that sifakas are not moving readily between these fragments. This differentiation may reflect the low effective population sizes and high elevations at these sites. Golden-crowned sifakas are seldom seen at elevations >1,000 m (B. Semel, unpublished data; Quéméré, Champeau, et al. 2010), and both Antsahabe and Binara have ridgelines bisecting the fragments well above this elevation, which may limit movement to opposite sides of the fragments. Furthermore, there is extensive agricultural activity on the west side of Binara, which may further restrict movement. Sgarlata et al. (2018) found a similar hard boundary between Binara/Antsahabe and Ambohitsintondroina for northern rufous mouse lemurs (*Microcebus tavaratra*). Research on two forest-restricted rodents (*Eliurus spp.*) concluded that a historical elevation shift in forest type coverage within the last 25,000 years explained genetic structuring for these species (Rakotoarisoa et al. 2013). However, the tendency for sifakas to use a range of forest types makes this explanation alone unlikely.

As expected, the sub-population of sifakas in the Ampisikina forest fragment are most genetically similar to those in Ampondrabe and other northern sub-populations, reaffirming the importance of the Manankolana River as a barrier to dispersal. Ampisikina is over 11 linear km from the nearest large forest fragment (Ampondrabe), though a narrow forest corridor does line most of the northern bank of the Manankolana. The body condition of sifakas in this fragment appeared visibly poorer than that of other sifakas in the region (*e.g.*, smaller body size, poor fur quality), lending some anecdotal support to our genetic results that suggest low migration rates (*i.e.*, we did not detect any migrants to Ampisikina using GeneClass2, though our sample size was low for the site). As expected, Ampisikina had relatively high F_{ST} values (suggesting genetic differentiation) when compared to Bekaraoka and Binara. It is unclear as to why F_{ST} values were so low (suggesting genetic similarity) between Ampisikina and the distant Ambilondamba/Solaniampilana fragment (~25 km Euclidean distance; $F_{ST} = 0.01$) compared to between Ampisikina and its closest fragment, Ampondrabe (~11 km Euclidean distance; $F_{ST} = 0.08$). While modest F_{ST} values for comparisons across the study site still suggest movement across the landscape as a whole, there is a lag for equilibrium F_{ST} to be achieved as populations become isolated (Allendorf and Phelps 1981).

Inbreeding appears to be a concern within populations across the sifaka's range. Quéméré, Crouau-Roy, et al. (2010) estimated F_{IS} values between -0.08 and 0.01 for all fragments surveyed except for Antsaharaingy ($F_{IS} = -0.18$). Populations in all forest fragments in this study had F_{IS} values > 0.1 , with a maximum of $F_{IS} = 0.60$. While some of this may be explained by a Wahlund effect (*i.e.*, the reduction of heterozygosity due to subpopulation structure) or sampling error, it is likely that populations are undergoing mild to moderate levels of inbreeding. This inference is supported by our results from iNest, which simultaneously

accounts for inbreeding, segregation of null alleles and genotyping failures. While this may be of concern at the population level, prior research on these sifakas demonstrated that social structure may help to maintain outbreeding within social groups (Parreira et al. 2020). Social group genetic structure was beyond the scope of our current study.

Further investigation into genotyping failures should be pursued as some of the potential migrants we observed (minimum Euclidean distance travelled >10 km) would have moved distances that are much greater than what is typical of long-term studies on marked Verreaux's sifakas (*P. verreauxi*; Richard et al. 1993) or genetically inferred dispersal distances from Quéméré, Crouau-Roy, et al (~1,500 m; 2010). While we do not know if these long-distance dispersers actually bred and can be effectively considered migrants, long-distance dispersal is not unprecedented. This “jumping” behavior helps to explain the well-documented “fat-tailed” distribution of animal dispersal distances (Kesler et al. 2010), and may explain the long dispersal distances inferred from our genetic data. These phenomena are not well-documented within the primate literature. However, the accuracy of GeneClass2 assignments of samples to their fragment of origin was below 50%, calling to question the validity of many of our samples (see *Conclusion* for more on this).

Effective Population Size

Quéméré et al. (2012) estimated that N_e was between 430 and 795 in 2006/2008 (census population estimate ~18,000; Quéméré, Champeau, et al. 2010). An approximate Bayesian computation (ABC) demographic analysis of the same data by Salmona et al. (2017) estimated that the median N_e was around 570. Our estimate based on a combined analysis of all samples was 139.8 (95% CI: 122.1-162.1) sifakas, or at least 267 based on a sum-of-the-parts approach to

estimating overall N_e (census population estimate 10,222 (95% CI: 8,230-12,697; see *Chapter 2*)). Estimates for several fragments have $N_e < 50$ individuals, putting such populations at heightened risk for inbreeding (Harmon and Braude 2010). Populations in these fragments should be monitored closely for any apparent change in fitness and population size, and reforestation of a travel corridor to connect these fragments to nearby forest fragments should be considered.

Overall N_e for this species appears to be below 500 individuals, the general threshold at which genetic drift and the loss of genetic variation is of concern (Harmon and Braude 2010). Based on research on related Milne-Edwards' sifakas (*P. edwardsi*), sifaka groups are likely to contain no more than two breeding males or breeding females at a time (Morelli et al. 2009). This may explain how golden-crowned sifaka groups are able to maintain outbreeding even if inbreeding is occurring at the population level (Parreira et al. 2020). Results from this study suggest a recent population decline and population structure across the species' range. Furthermore, overall population size is low (see *Chapter 2*). All of these factors are known to impact N_e . Further research is needed to determine which factor is having the greatest impact on N_e . It may simply be small population size.

Hunting may also be negatively impacting populations, as hunting was reported across the region during and after the coup d'état in 2009 (Barrett and Ratsimbazafy 2009; Conservation International 2010). The effects of hunting on primate population genetics remains poorly understood (Ferreira da Silva et al. 2014). Ensuring landscape connectivity, increasing potential habitat to grow the overall population size, and limiting the loss of individuals to hunting or road mortality all are appropriate actions that should be undertaken to avert demographic decline.

Connectivity Analysis and Recommendations

Our range-wide connectivity analysis allows us to make several recommendations to managers to ensure ongoing gene flow among populations of this species. Reforestation and increased protection efforts should be practiced between the southeastern fragments (Bekaraoka, Bobankora, and Binara) and between the western fragments (Antsahabe, Ambilondamba/Solaniampilana, and Benanofy) in order to maintain connectivity among these large population clusters. These corridors represent important connection points between major forest fragments with high densities of sifakas (important source populations), while recent or ongoing movement between these fragments is supported by low F_{ST} values. Especially in the central and southern parts of the range (Fig. 4, panels C and D), extensive areas with small forest patches and riverine forest corridors between large forest fragments have been converted to grassland in the last 20 years (see *Chapter 2*), likely as a result of fire being used to expand pastureland (B. Semel, *pers. obs.*). The corridor south of Benanofy is of particular concern, as it represents the only corridor between the northern and southern populations. Special attention should be paid to this location and between Bekaraoka and Bobankora as the national road is currently being paved and may further restrict movement through these corridors.

Reforestation should be carried out with tree species with parts known to be consumed by sifakas (Meyers 1993; Quéméré et al. 2013) and with a strong focus on species that make up significant percentages of the species' diet (see *Chapters 2 and 3*). The Malagasy government made a bold proposal in March 2019 to reforest at least 40,000 hectares across the country between 2020 and 2025 (Vyawahare 2019). This effort reflects the need not only to meet the resource needs of its rapidly growing population (CIA 2020), to stabilize alarming rates of soil

runoff (Aubréville 2015; Gade 1996), and to reverse the direction of habitat loss for its unique biota (Harper et al. 2007; Vieilledent et al. 2018), but also presents an opportunity to strategically restore gene flow between plant and animal populations that have become genetically isolated from one another because of widespread deforestation (Schüßler et al. 2020).

When planning reforestation efforts, the potential impacts of climate change should be at the forefront (Pacifici et al. 2015). It is hard to predict how climate change will impact golden-crowned sifakas. An increasing number of dry days and fewer intense rainfall events are likely to be problematic, as NDVI wet is a good predictor of sifaka densities (see *Chapters 2 and 3*; Chesney and Moran 2016). Related Milne-Edwards' sifaka (*P. edwardsi*) fecundity and infant survival were linked to climate variables (Dunham et al. 2011; King et al. 2005). Drier conditions would also make forested areas more vulnerable to destruction by fire. Golden-crowned sifakas currently inhabit a wide variety of forest types, meaning that they likely will be able to adapt to some degree to changing conditions, and they may even expand their elevational range. Cyclone intensity is expected to increase as a result of climate change, though the frequency of cyclones that make landfall in Madagascar is predicted to decrease and move south, away from the golden-crowned sifaka range (Cattiaux et al. 2020; Muthige et al. 2018). It is unknown to what extent cyclones impact golden-crowned sifakas. Based on studies of related Verreaux's sifakas (*P. verreauxi*; Lewis and Axel 2019; Lewis and Rakotondranaivo 2011) and ruffed lemurs (*Varecia rubra*; Vasey and Borgerson 2009), the impacts may be severe (e.g., reduced body condition, reproductive collapse).

Conclusions

While we did not replicate previous studies, in part due to the difficulty of replicating amplification of all of the same loci using DNA isolated from fecal material (Quéméré et al. 2012; Quéméré, Crouau-Roy, et al. 2010), our results expand on previous findings and offer new insight on population connectivity across the species' range. The Circuitscape analysis provides clear future recommendations for managers.

Some challenges of this study, however, should be noted. Fecal DNA is known for its poor quality, and thus extra assays to re-score and validate the data are required. Furthermore, we stored our samples in a DETs buffer solution for multiple months under field conditions prior to laboratory analysis due to export restrictions on samples stored in ethanol. Amplification success rates for panda fecal samples stored for 6 months in DETs dropped by 24% (Zhu et al. 2017). The biggest challenge with this study was the lack of verified homozygotes and null alleles. To overcome these challenges, loci were selected based on their amplicon size (<300 bp), DNA was extracted as soon as possible in the laboratory, and we used specialized software to evaluate the effects of genotyping errors and null alleles (Chybicki et al. 2011; Taberlet et al. 1999, van Oosterhout et al., 2004). Until we are able to further validate all homozygotes within our sample, results from this study should be viewed with caution. As time and funding allow, samples with homozygotes and null alleles features will be re-analyzed to ensure their validity.

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Table 1. Microsatellite marker loci of golden-crowned sifakas (*Propithecus tattersalli*) within the Loky-Manambato Protected Area in northeastern Madagascar screened for fecal DNA collected May - July 2016, August - December 2017, September - December 2018.

Retained loci are in bold.

Marker Loci Description	Sequence	Annealing Temp. (°C)	Published Size Range (bp)	Size range in <i>P.</i> <i>tattersalli</i> (bp)	Fluor- escent Label ^a	Multiplex Suite ^b
<i>93HDZ5</i>	AGAAGGTTATGGAAGTAGGAAATG	62	129–143	124-150	HEX	1, 6
<i>88HDZ9</i>	CAAATTCAGTCTGGTGCATCA	54	104-114	112-158	PET	2
<i>88HDZ10</i>	GAAAAAAAAAGTAAAACACAGTAGTAAGC	58	192–216	198-222	VIC	2
<i>88HDZ81</i>	AGAACTGTTGTTAGAAAGTGCCA	60	180-206	202-226	NED	3
<i>88HDZ127</i>	CCAAAACAAAAACAAAAACAAAAG	56	196–216	163-229	NED	4, 6
<i>93HDZ164</i>	CGGGGACTACTGGGCAG	62	107–127	112-128	6FAM	1, 3, 5
<i>93HDZ166</i>	TCCCGTTGCCCTCTCC	60	157–169	153-183	6FAM	4, 6
<i>93HDZ169</i>	GAAAATCCTCTATGGTGACGC	52	257–285	255-295	6FAM	2

Marker Loci Description	Sequence	Annealing Temp. (°C)	Published Size Range (bp)	Size range in <i>P.</i> <i>tattersalli</i> (bp)	Fluor- escent Label ^a	Multiplex Suite ^b
93HDZ179	GGCTTGGCAACAGGAAATG	56	151–163	148-186	HEX	3, 7
93HDZ223	CATCACCTCCACCAACCC	60	174–190	162-198	HEX	4, 6
<i>93HDZ240</i>	GGAGGATACTAAATCGGAGTCTTC-30	54	234–266	222-276	PET	3
<i>93HDZ257</i>	GGATGACAGAGTGAGACCCAG	58	187–197	175-205	PET	7
93HDZ261	AAGAAAAAGGAAAAAGAAAAAGAAG	56	121–133	120-138	6FAM	8
93HDZ263	TCGGACTTTCAAATGAGCC	56	111–133	113-147	NED	7
93HDZ265	GATGTGCTTCCTTCCTTTCT	62	166–174	156-176	NED	1, 5, 8

^a Fluorescent Label = enables the length of the microsatellite amplicon to be estimated by the DNA sequencer

^b Multiplex Suite = indicates loci that were co-amplified in a single amplification reaction

Table 2. Microsatellite DNA diversity of golden-crowned sifaka (*Propithecus tattersalli*) within the Loky-Manambato Protected Area in northeastern Madagascar based on fecal DNA collected May - July 2016, August - December 2017, September - December 2018 (Arlequin; Excoffier and Lishcher 2010). Standard deviations (SD) are shown in parentheses. Sub-populations in the Ambilondamba and Solaniampilana forest fragments were combined for analysis (Ambilondamba/Solaniampilana), as were Bekaraoka Avaratra and Bekaraoka South (Bekaraoka). See text for details.

Forest Fragment	Sample Size	Number of Gene Copies ^a	A^b	H_o^c	H_e^d	AR^e	$M\text{-Ratio}^f$
Ambilondamba/ Solaniampilana	23	42.22 (4.06)	7.89 (2.15)	0.52 (0.14)	0.71 (0.15)	11.67 (3.08)	0.65 (0.19)
Ambohitsintondroina	10	18.44 (2.19)	4.44 (1.59)	0.47 (0.18)	0.63 (0.17)	8.11 (3.26)	0.53 (0.23)
Ampisikina	9	17.11 (2.03)	4.11 (1.54)	0.68 (0.22)	0.70 (0.15)	8.67 (5.85)	0.57 (0.31)
Ampondrabe	14	26.22 (2.91)	5.22 (1.86)	0.44 (0.29)	0.63 (0.26)	10.00 (4.80)	0.53 (0.23)
Antsahabe	10	18.89 (1.76)	5.22 (2.28)	0.63 (0.26)	0.69 (0.18)	10.44 (5.41)	0.53 (0.24)
Antsaharaingy	15	27.56 (1.94)	5.89 (1.83)	0.47 (0.21)	0.70 (0.15)	11.56 (3.64)	0.49 (0.14)
Bekaraoka	49	90.00 (8.19)	10.33 (3.00)	0.47 (0.16)	0.69 (0.19)	12.00 (4.69)	0.82 (0.14)

Forest Fragment	Sample Size	Number of Gene Copies ^a	A^b	H_o^c	H_e^d	AR^e	$M\text{-Ratio}^f$
Benanofy	8	15.33 (1.41)	5.11 (1.36)	0.60 (0.22)	0.69 (0.13)	10.00 (4.03)	0.50 (0.17)
Binara	37	68.22 (5.14)	8.44 (2.46)	0.44 (0.18)	0.64 (0.22)	11.67 (4.39)	0.72 (0.24)
Average	19.44	36.00 (3.29)	6.30 (2.01)	0.52 (0.20)	0.68 (0.18)	10.46 (4.35)	0.59 (0.21)

^a Number of gene copies = total number of gene copies found within all samples

^b A = mean number of alleles per locus

^c H_o = mean observed heterozygosity

^d H_e = mean expected heterozygosity

^e AR = mean difference between sizes (*i.e.*, number of base pairs) of the largest and smallest alleles at a particular locus

^f $M\text{-Ratio}$ = ratio of the number of alleles observed at a locus to the number of possible alleles between the largest and smallest alleles

Table 3. iNest (Chybicki et al. 2011) results for nine loci (sample mean inbreeding coefficient = 0.13 (95% posterior densities = 0.04-0.20)) from golden-crowned sifakas (*Propithecus tattersalli*) within the Loky-Manambato Protected Area in northeastern Madagascar based on fecal DNA collected May - July 2016, August - December 2017, September - December 2018. Models evaluated the effects of inbreeding (f), null alleles (n), and genotyping failures (b) using deviance information criterion (*DIC*; lower values have greater model support). Support for the top model suggests that all processes were in play in this system.

Model	Avg(logl(X)) ^a	Var(logl(X)) ^b	logl(Avg(X)) ^c	DBar ^d	Dhat ^e	pD ^f	DIC ^g
nfb	-4,752.61	156.18	-4,684.20	9,505.22	9,368.40	136.82	9,642.04
nb	-4,780.43	63.19	-4,728.02	9,560.86	9,456.03	104.83	9,665.70
fb	-4,762.47	135.11	-4,689.40	9,524.94	9,378.80	146.14	9,671.08
nf	-4,779.67	135.46	-4,716.28	9,559.34	9,432.55	126.79	9,686.12
n	-4,798.31	61.60	-4,748.89	9,596.62	9,497.77	98.85	9,695.47
b	-5,102.05	62.10	-5,051.97	10,204.10	10,103.93	100.17	10,304.28
f*	-	-	-	-	-	-	-
Null*	-	-	-	-	-	-	-

^a Avg(logl(X)) = average of the log-likelihood function across iterations

^b $\text{Var}(\log l(X))$ = variance of the log-likelihood function across iterations

^c $\log l(\text{Avg}(X))$ = the log-likelihood function for the posterior means

^d $D\text{Bar}$ = the mean deviance across iterations

^e $D\text{hat}$ = the deviance estimated for the posterior means

^f pD = the effective number of parameters

^g DIC = the deviance information criterion for the model

*Due to missing genotypes, the model must contain at least one of the components 'b' (failure) or 'n' (null alleles).

Table 4. Inbreeding coefficients (F_{IS}) of golden-crowned sifakas (*Propithecus tattersalli*) within the Loky-Manambato Protected Area in northeastern Madagascar based on fecal DNA collected May - July 2016, August - December 2017, September - December 2018. F_{IS} values equal to +1 indicate completely inbred individuals, while a value of -1 would indicate a completely outbred individual. Values were calculated using three different statistical approaches (see footnotes).

Population	F_{IS}^a	p -value ^b	Mean F^c	Avg. F_i^c	F_{IS} (ML) ^d
Ambilondamba/ Solaniampilana	0.23	<0.01	0.27	0.26	0.26
Ambohitsintondroina	0.34	<0.01	0.12	0.11	0.23
Ampisikina	0.22	0.10	*	*	0.00
Ampondrabe	0.60	<0.01	**	**	0.28
Antsahabe	0.13	0.18	*	*	0.00
Antsaharaingy	0.35	<0.01	0.31	0.32	0.32
Bekaraoka	0.35	<0.01	0.31	0.32	0.32
Benanofy	0.11	0.25	0.11	0.08	0.00
Binara	0.26	<0.01	0.12	0.12	0.29
Overall	0.27	<0.01	0.13	0.13	0.32

^a As calculated in Arlequin (Excoffier and Lishcher 2010)

^b The probability of a random $F_{IS} >$ observed F_{IS} (Arlequin; Excoffier and Lishcher 2010).

^c Estimates based on a Bayesian assessment algorithm that accounts for null allele frequency (iNest; Chybicki et al. 2011).

^d Estimates based on Maximum Likelihood method (Colony; Jones and Wang 2010).

* The best-supported model had genotyping failures (b).

** The best-supported model had genotyping failures (b) and null alleles (n).

Table 5. Assessment of best-supported assignment test-based model of population genetic structure (from admixture model with sampling locations as priors (LOCPRIOR)) using Evanno et al. (2005) metrics for golden-crowned sifakas (*Propithecus tattersalli*) within the Loky-Manambato Protected Area in northeastern Madagascar based on fecal DNA collected May - July 2016, August - December 2017, September - December 2018. The model with the highest ΔK is expected to be closest to the true value for K (shown in bold font).

K^a	Replications ^b	Mean $\text{Ln}P(K)^c$	Stdev	$\text{Ln}'(K)^e$	$ \text{Ln}''(K) ^f$	ΔK^g
			$\text{Ln}P(K)^d$			
2	8	-4,841.55	0.80	—	—	—
3	9	-4,758.42	69.71	83.13	14.99	0.22
4	9	-4,660.30	42.96	98.12	4.97	0.12
5	9	-4,567.14	39.83	93.16	74.52	1.87
6	9	-4,548.51	113.82	18.63	54.22	0.48
7	9	-4,475.66	46.79	72.86	54.82	1.17
8	9	-4,457.62	46.14	18.03	15.79	0.34
9	9	-4,423.80	45.12	33.82	—	—

^a K = number of population clusters

^b Replications = number of times the admixture model was run for K clusters

^c Mean $\text{Ln}P(K)$ = mean of the natural log posterior probability of the data that is conditioned on the number of clusters (K)

^d Stdev $\text{Ln}P(K)$ = standard deviation of the natural log posterior probability of the data that is

conditioned on the number of clusters (K)

^e $\text{Ln}'(K)$ = rate of change of the likelihood function with respect to K

^f $|\text{Ln}''(K)|$ = second order rate of change of the likelihood function with respect to K

^g ΔK = an ad hoc quantity related to the second order rate of change of the log probability of data with respect to the number of clusters (K)

Table 6. Analysis of Molecular Variance (AMOVA) results (Arlequin; Excoffier and Lishcher 2010) to evaluate sources of genetic variation in golden-crowned sifakas (*Propithecus tattersalli*) within the Loky-Manambato Protected Area in northeastern Madagascar. Genetic data were collected from fecal DNA collected May - July 2016, August - December 2017, September - December 2018. The number of groups was equal to best number of K means clusters ($K = 5$) from STRUCTURE. For this analysis, populations correspond with forest fragments (Ambilondamba/Solaniampilana, Ambohitsintondroina, Ampisikina, Ampondrabe, Antsahabe, Antsaharaingy, Bekaraoka, Benanofy, and Binara).

Source of Variation	Df	SS	Variance Components	% of Variation
Among Groups	4	35.56	0.12	12.04
Among Populations	4	8.46	0.03	2.79
Within Groups				
Among Individuals	166	179.52	0.25	25.51
Within Populations				
Within Individuals	175	102.00	0.58	59.66
Total	349	325.53	0.98	100.00

Table 7. Accuracy assessment of Bayesian assignments of golden-crowned sifakas (*Propithecus tattersalli*) to their forest fragment of origin within the Loky-Manambato Protected Area in northeastern Madagascar based on fecal DNA (collected May - July 2016, August - December 2017, September - December 2018) in GENECLASS2 to detect first generation migrants (Piry et al. 2004). The Sampled Population column indicates the forest fragment from which a sample was collected and the Assigned Population is based on genetic similarity. Overall accuracy was fairly low (48.0%), suggesting that several fragments do not represent unique populations.

Sampled Population	Assigned Population								
	Ambilondamba/ Solaniampilana	Ambohitsintondroina	Ampisikina	Ampondrabe	Antsahabe	Antsaharaingy	Bekaraoka	Benanofy	Binara
Ambilondamba/ Solaniampilana	0.609	0.100	-	0.071	-	0.133	0.061	0.125	0.108
Ambohitsintondroina	0.043	0.600	-	-	-	-	-	0.125	-
Ampisikina	0.043	-	0.778	0.143	0.100	-	0.020	-	-
Ampondrabe	0.043	-	0.111	0.214	-	0.267	0.041	0.250	0.027

Sampled Population	Assigned Population								
	Ambilondamba/ Solaniampilana	Ambohitsintondroina	Ampisikina	Ampondrabe	Antsahabe	Antsaharaingy	Bekaraoka	Benanofy	Binara
Antsahabe	-	0.100	-	-	0.700	-	0.102	0.250	-
Antsaharaingy	0.087	-	-	0.286	0.100	0.600	0.020	-	0.027
Bekaraoka	0.043	-	-	-	0.100	-	0.408	-	0.405
Benanofy	0.043	0.200	0.111	0.143	-	-	0.020	0.250	-
Binara	0.087	-	-	0.143	-	-	0.327	-	0.432

Table 8. F_{ST} metrics indicating pairwise genetic differentiation between populations of golden-crowned sifakas (*Propithecus tattersalli*) within the Loky-Manambato Protected Area in northeastern Madagascar based on fecal DNA collected May - July 2016, August - December 2017, September - December 2018. (Arlequin; Excoffier and Lishcher 2010). n.s. = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

	Ambilondamba/ Solaniampilana	Ambohitsintondroina	Ampisikina	Ampondrabe	Antsahabe	Antsaharaingy	Bekaraoka	Benanofy	Binara
Ambilondamba/ Solaniampilana		***	n.s.	***	*	n.s.	***	n.s.	***
Ambohitsintondroina	0.09		**	***	*	***	***	***	***
Ampisikina	0.01	0.13		*	n.s.	n.s.	***	n.s.	***
Ampondrabe	0.13	0.20	0.08		*	*	***	n.s.	***
Antsahabe	0.05	0.11	0.07	0.09		**	n.s.	n.s.	***

	Ambilondamba/ Solaniampilana	Ambohitsintondroina	Ampisikina	Ampondrabe	Antsahabe	Antsaharaingy	Bekaraoka	Benanofy	Binara
Antsaharaingy	0.02	0.13	0.02	0.11	0.11		***	n.s.	***
Bekaraoka	0.15	0.25	0.14	0.13	0.05	0.21		n.s.	n.s.
Benanofy	0.03	0.11	0.01	0.04	0.04	0.03	0.13		***
Binara	0.22	0.30	0.20	0.21	0.12	0.29	0.02	0.22	

Table 9. Estimated N_e for all populations of golden-crowned sifakas (*Propithecus tattersalli*) within the Loky-Manambato Protected Area in northeastern Madagascar based on fecal DNA collected May - July 2016, August - December 2017, August - December 2018. Linkage disequilibrium and molecular co-ancestry models were conducted in Ne Estimator (Do et al. 2014) and the sib-ship assignment method was conducted in Colony (Jones and Wang 2010).

Site	N	Linkage Disequilibrium Method ^a			Molecular Co-Ancestry Method			Sib-ship Assignment Method ^b		
		N_e	95% LCI	95% UCI	N_e	95% LCI	95% UCI	N_e	95% LCI	95% UCI
Ambilondamba/ Solaniampilana	23	32.2	19.4	71.6	4.1	1.9	7.2	53	29	132
Ambohitsintondroina	10	39.7	9.7	Infinite	6.8	0.8	19.0	36	15	Infinite
Ampisikina	9	2.2	1.4	5.4	4.7	2.0	8.6	14	6	53
Ampondrabe	14	28.3	9.6	Infinite	7.6	1.8	17.4	46	22	329
Antsahabe	10	11.9	4.9	50.2	7.2	3.2	12.8	36	15	Infinite
Antsaharaingy	15	13.1	6.9	32.5	4.0	2.8	5.4	47	21	189
Bekaraoka	49	75.6	54.9	115.2	43.8	0.0	219.6	68	46	103
Benanofy	8	Infinite	9.4	Infinite	25.2	0.0	126.4	28	11	Infinite
Binara	37	64.1	39.5	142.2	10.3	2.1	24.7	54	34	90

Site	<i>N</i>	Linkage Disequilibrium Method ^a			Molecular Co-Ancestry Method			Sib-ship Assignment Method ^b		
		<i>N_e</i>	95% LCI	95% UCI	<i>N_e</i>	95% LCI	95% UCI	<i>N_e</i>	95% LCI	95% UCI
All Populations	175	139.8	122.1	162.1	12.7	5.1	23.8	144	111	185

^a Linkage disequilibrium method used the lowest value for lowest allele frequency.

^b Estimates by Colony full likelihood method, assuming random mating ($\alpha = 0.00$).

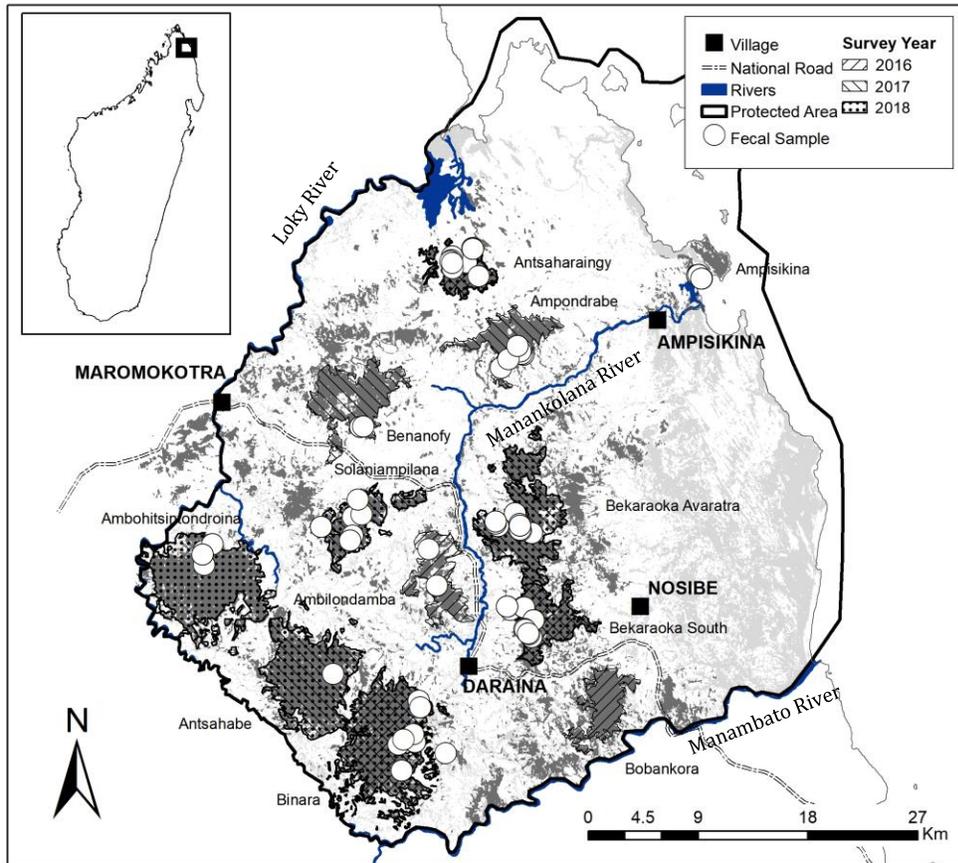


Fig. 1. Map of northeastern Madagascar depicting the Loky-Manambato Protected Area and golden crowned sifakas (*Propithecus tattersalli*) fecal sample collection locations for samples that we were able to amplify ($N = 175$). Hashing indicates the years in which forest fragments were visited and surveyed and samples collected (May - July 2016, August - December 2017, September - December 2018). Gray shading indicates forested areas within the Protected Area, while dark gray shading indicates forests in which sifakas are present.

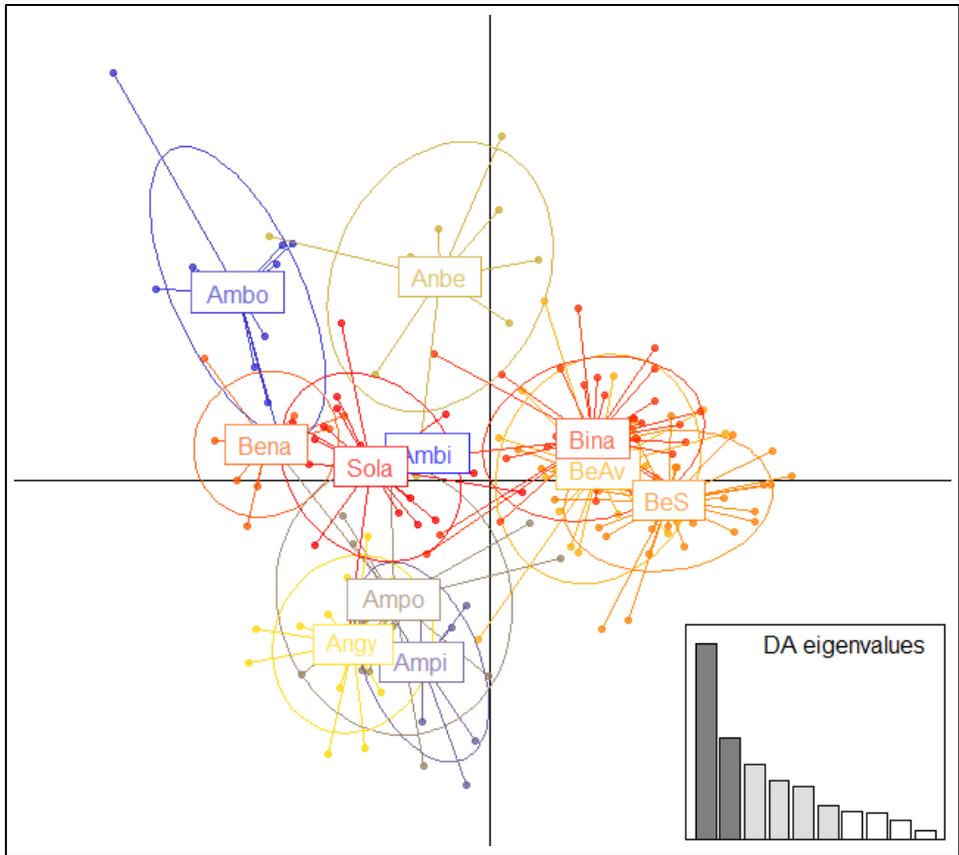
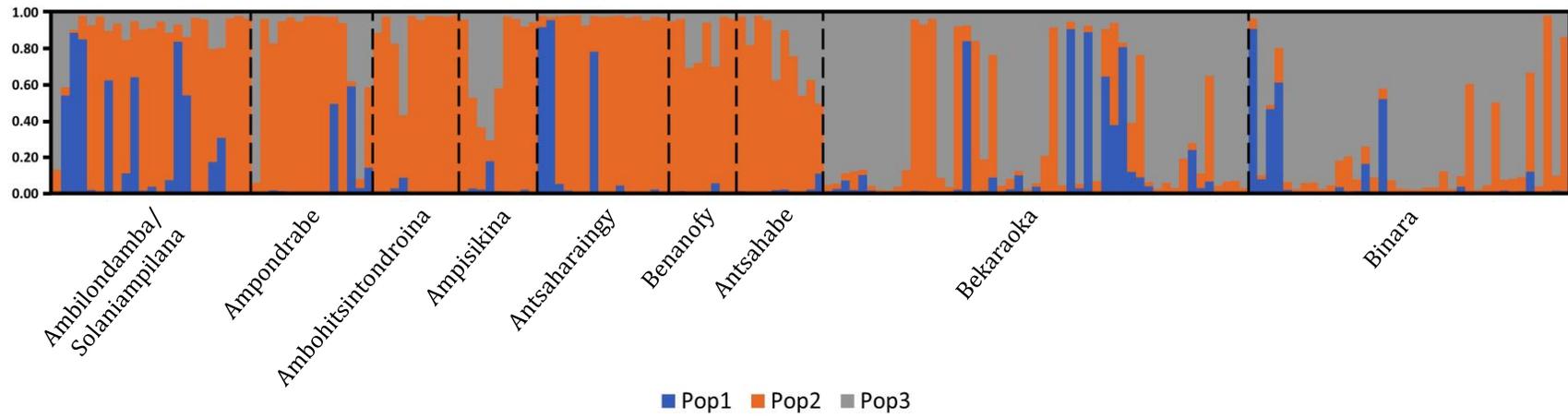
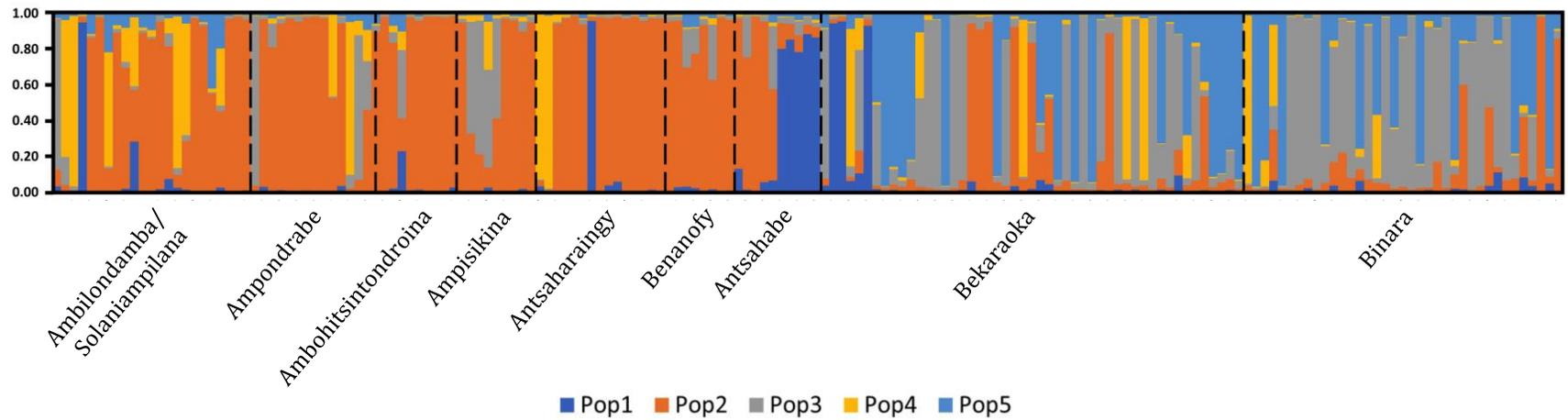


Fig. 2. A multivariate Discriminant Analysis of Principal Components (DAPC) plot depicting golden crowned sifaka (*Propithecus tattersalli*) genetic clusters across 11 forest fragments in the Loky-Manambato Protected Area in northeastern Madagascar. Genetic data were obtained from fecal materials collected from 2016-2018. The analysis included all loci with a subset of samples ($N = 175$). Discriminant analysis (DA) eigenvalues in the plot subset indicate the number of principle components used to capture genetic structure. Forest fragment names have been abbreviated for plot clarity: Ambi = Ambilondamba, Ambo = Ambohitsintondroina, Ampy = Ampisikina, Ampo = Ampondrabe, Anbe = Antsahabe, Angy = Antsaharaingy, BeAv = Bekaraoka Avaratra, BeS = Bekaraoka South, Bena = Benanofy, Bina = Binara, Sola = Solaniampilana.

$K = 3$



$K = 5$



$K = 9$

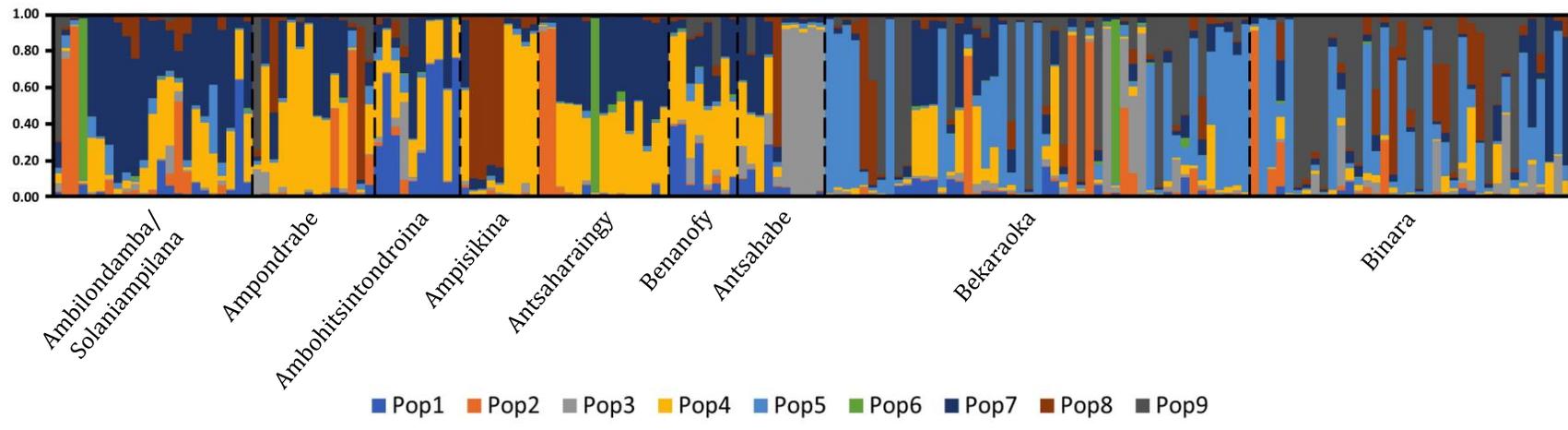


Fig. 3. STRUCTURE plots for different set numbers of K multi-locus genotypic clusters based on fecal DNA from golden crowned sifakas (*Propithecus tattersalli*) collected from the Loky-Manambato Protected Area in northeastern Madagascar from 2016-2018. Vertical lines represent the proportion of genetic similarity to each population cluster (K) for each sampled individual ($N = 175$). Each color represents a different genetic population cluster (K). The forest fragment from which each sample was collected is listed below each plot.

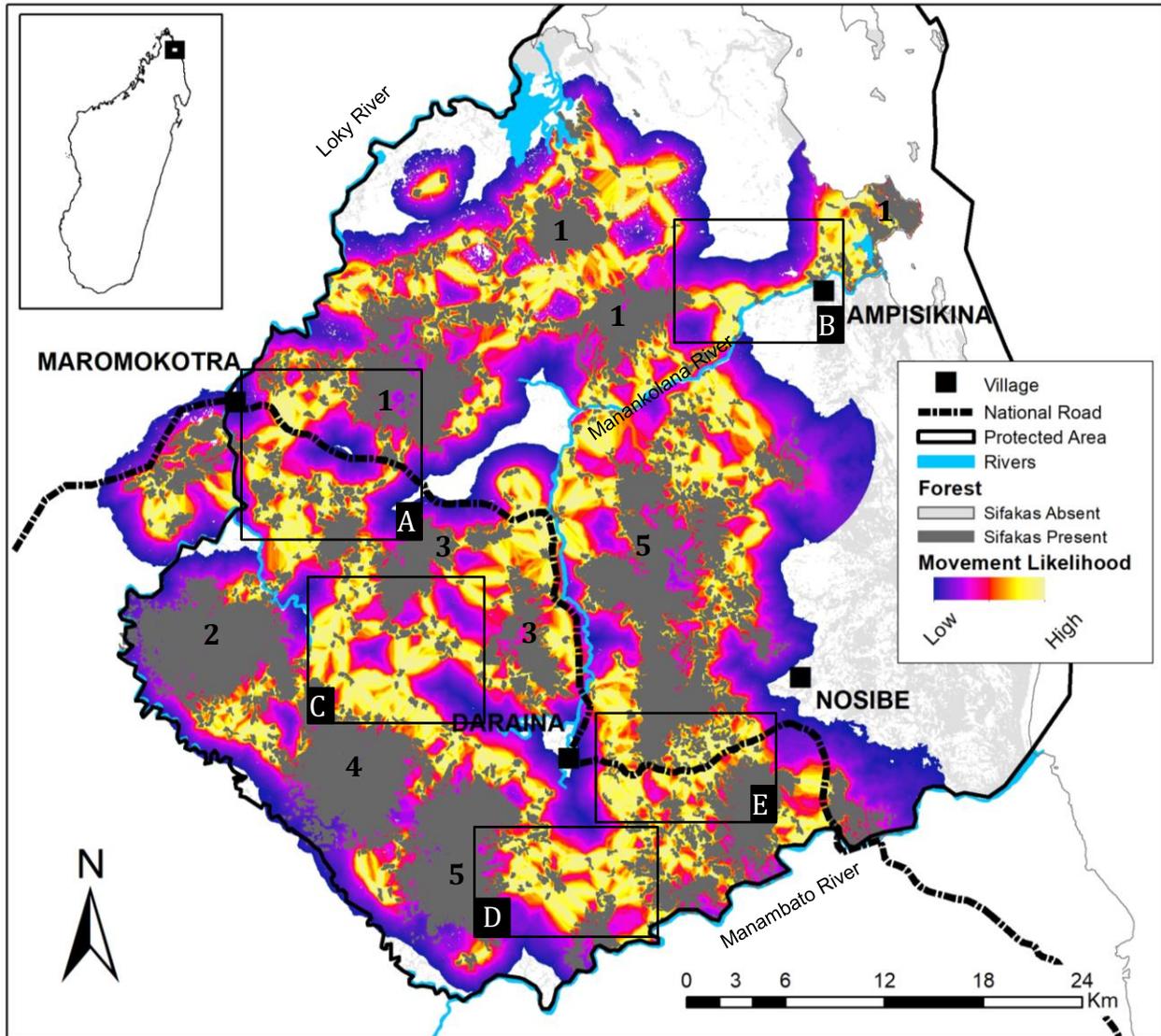


Fig. 4. Map of potential golden-crowned sifaka (*Propithecus tattersalli*) movement corridors between forest fragments within the Loky-Manambato Protected Area in northeastern Madagascar using Circuitscape (Shah and McRae 2008). Dark gray areas indicate large forest fragments ($>0.5 \text{ km}^2$) with known sifaka presence that had to be connected in the Circuitscape analysis. Underlying resistance layers were based on a digital elevation model (DEM), normalized difference vegetation index (NDVI) layer, and land cover types. Areas with high movement potential (yellow) indicate corridors that sifakas likely are using to move across the landscape. Numbers (1-5) indicate population clusters from STRUCTURE (1 = Ampisikina,

Ampondrabe, Antsaharaingy, Benanofy; 2 = Ambohitsintondroina; 3 = Ambilondamba/Solaniampilana; 4 = Antsahabe; 5 = Bekaraoka, Binara). Priority areas for monitoring and reforestation are in boxes A-E: A) only two narrow corridors connect the large northern cluster (1) to all of the southern clusters (2-5), which may be negatively impacted by the paving of the national road, B) only a single long, narrow riverine corridor connects the Ampisikina fragment to the rest of the sifaka populations, C) few forest patches provide connectivity throughout the central sifaka populations (2-4), D) very few forest patches connect the eastern and western portion of cluster 5, potentially isolating a large number of sifakas in the Bekaraoka and Bobankora fragments (see *Chapter 2*) from all sifaka populations west of the Manankolana River, E) many potential movement corridors exist within this area, but paving the national road may have serious consequences for these connection points, further exacerbating the potential problems described in D. Note that no likely corridors cross any rivers, rather sifakas may use forested areas located along the river banks.

CHAPTER 5: CONCLUSION

INTRODUCTION

Golden-crowned sifakas (*Propithecus tattersalli*) are a critically endangered primate endemic to northeastern Madagascar (IUCN 2019). The threats facing this lemur are typical of those facing primates worldwide: habitat loss, degradation, and fragmentation (Anzures-Dadda and Manson 2007; Craul et al. 2009; Gillespie and Chapman 2006; Gray et al. 2010; Irwin et al. 2009; Luo et al. 2016; Marsh and Chapman 2013), hunting (Borgerson et al. 2016; MacDonald et al. 2012; Thoisy et al. 2005), and climate change (Campos et al. 2015; Dunbar 1998; Korstjens and Hillyer 2016; Luo et al. 2015; Morelli et al. 2019). While other primates also are being negatively impacted by the illegal wildlife trade and novel disease (Estrada et al. 2017), golden-crowned sifakas do not appear to be facing those threats at this time.

Conservation biology has been described as a “crisis discipline,” in which managers must often act before all of the facts can be obtained (Soulé 1985). This can make any management decision difficult, and actions not always as effective as hoped. The research presented in my dissertation provides insight into the current conservation status of this species, threats facing it, and actionable steps that can be taken to avert continuing population declines. The three research chapters presented above aimed to determine:

- Chapter 2: Current population size for golden-crowned sifakas across their global range and factors affecting their population size,
- Chapter 3: Sifaka diets across the species’ range and whether nutrient availability from foods in different forest types could be used to predict abundance,

- Chapter 4: Genetic structure, inbreeding, and effective population size across the species' range and where sifakas are most likely to move and disperse between forest fragments to guide reforestation efforts.

In Chapter 2, I summarized survey results from different forest fragments and types (humid, rainforest to dry, deciduous forest) across the sifakas' global range in May – July 2016, August – December 2017, and September – December 2018 to evaluate changes in their population size since last surveyed in 2006/2008 (Quéméré, Champeau, et al. 2010). I also collected field- and remote-sensed vegetation and human disturbance data to evaluate factors affecting sifaka densities.

In Chapter 3, I collected behavior and feeding data from 18 sifaka groups in different forest fragments and types (dry, moderate, and wet) from August – December 2017 – 2019, and February – March 2019. I analyzed the effects of season, forest type, and sex on the percent of time sifakas spent feeding overall and on specific plants and plant parts. Additionally, I collected samples of the top food items for several of these groups for nutritional analyses. Finally, I assessed whether nutritional variables were effective predictors of sifaka population densities.

In Chapter 4, I collected fecal data from sifakas in May – July 2016, August – December 2017, and September – December 2018 for genetic analyses. I evaluated population structure, inbreeding, effective population sizes, and migrant potential within and across populations of sifakas inhabiting different forest fragments throughout their range. I then used the program Circuitscape to develop likely corridors used by sifakas to move between forest fragments and to make reforestation recommendations.

The data and results from my dissertation already have helped to inform the Malagasy conservation community of the level of threat imposed on the sustainability of critically-

endangered golden-crowned sifaka populations in Madagascar (IUCN 2019) and also will help to identify practical steps that managers can take to better conserve this species long-term. The methods presented in my dissertation also may provide a model for prioritizing conservation efforts for other primate species facing global change. Below, I summarize the key research findings, management implications, and future research directions as they relate to the results of this dissertation.

KEY RESEARCH FINDINGS

Chapter 2: “Highly variable densities and a decline in critically endangered golden-crowned sifaka (*Propithecus tattersalli*) population abundance from 2008 - 2018”

- Total forest area within the study area in 2002 was 537.3 km² compared to 475.3 km² in 2017-2019, representing an 11.5% loss in forest cover area in less than 20 years (0.58% loss/year).
- Vegetation structure:
 - Tree species diversity in forest fragments was high (Simpson’s index of diversity (1-D): mean = 0.95, SE = 0.01 for all forest fragments).
 - Tree density varied greatly across fragments (range: 554.2 – 2,306.9 trees/ha; 254.4 trees/ha in mixed-cover areas).
- Food availability:
 - Sifakas consumed plant parts (*e.g.*, ripe/unripe fruits, young/mature leaves, seeds, flowers) from at least 101 plant species, with 28 species constituting > 80% of the overall diet.
- Human disturbance:

- Tree cutting was both the most intense human activity (highest average score of all human activities) and the most pervasive human activity across all fragments (*i.e.*, greatest number of plots with evidence of human activity had some evidence of tree cutting).
- Sifaka density and abundance were lower than estimates in 2006/2008
 - Average sifaka densities were 18.2 individuals/km² (95% CI: 14.8 – 22.4) across all fragments and ranged from 6.8 sifakas/km² (95% CI: 2.0 – 22.8) in Antsahabe to 78.1 sifakas/km² (95% CI: 53.1 – 114.8) in Bekaraoka South.
 - Our estimate for sifaka abundance from our top model was 12 631 sifakas (95% CI: 9 993 – 15 966) and 10,222 (95% CI: 8,230 – 12,697) sifakas from the model that weighted the density estimate of each study unit by its area. This reflected up to a 30-43% population decline in the last 10 years.
- Low intensity tree cutting and normalized difference vegetation index (NDVI) during the wet season were the best predictors of sifaka density. Sifaka densities increased with increasing values of both predictors.

Chapter 3: “Minerals and normalized difference vegetation index (NDVI) predict golden-crowned sifaka (*Propithecus tattersalli*) densities”

- Sifakas spent 25.3% of their activity budget feeding during the dry season and 29.5% of their time feeding during the wet season.
- Sex and forest type best predicted sifaka feeding counts.
 - Sifakas in dry forest had more feeding counts than those in both moderate and wet forests.

- Females were more likely than males to consume fruits; fruit consumption was highest in the wet compared to the dry season, and higher in wetter forests than in drier forests.
- Males were more likely to eat mature leaves; mature leaf consumption was highest in the wet compared to the dry season, and higher in wetter forests than in drier forests.
- Sifaka foods had variable nutrient contents, though mature leaves generally had higher concentrations of Ca, and lower levels of Cu and Zn compared to other plant parts.
- Forest type was a poor predictor of food item nutrient content.
- Mg, K, and NDVI wet were significant, positive predictors of sifaka densities.

Chapter 4: “Golden-crowned sifaka (*Propithecus tattersalli*) population genetics and recommendations for corridor restoration to promote connectivity of isolated forest fragments”

- Heterozygosity was lower than expected, suggesting that sifaka populations are experiencing inbreeding, even after accounting for null alleles and genotyping errors.
- Sifaka populations appear to be clustered into five groups: 1) northern forest fragments (Ampisikina, Ampondrabe, Antsaharaingy, and Benanofy), 2) Bekaraoka and Binara forest fragments, 3) Solaniampilana/Ambilondamba, 4) Ambohitsintondroina, and 5) Antsahabe.
- As expected, sifakas recently found inhabiting forests near Ampisikina are most closely related to those in the Ampondrabe fragment, supporting the Manankolana River as a barrier to dispersal.
- Low *M*-ratios (mean across fragments = 0.59; ratio of the number of alleles observed at a locus to the number of possible alleles between the largest and smallest alleles, values <

0.68 indicate a recent population decline) suggest that populations in most forest fragments have undergone recent population reductions.

- Migrants were rarely encountered across all surveyed fragments.
- Overall effective population size (N_e) was low (overall $N_e = 139.8 - 144$ sifakas) and no forest fragment had an $N_e > 80$ sifakas.
- Forest fragments continue to maintain some degree of genetic connectivity via dispersal between forest fragments based on F_{ST} values ($F_{ST} \leq 0.3$ for all forest fragments).
- Several key areas were identified for needing increased protection or active reforestation efforts to promote gene flow between sifaka populations and population movements in response to climate change.
- Further validation of genetic data is needed. Homozygote samples will be re-analyzed to confirm that they were not the result of a genotyping failure.

MANAGEMENT IMPLICATIONS

My research suggests many direct management actions that should be implemented to ensure the long-term conservation of golden-crowned sifakas.

- Ensure connectivity and the potential for safe sifaka movement between forest fragments via reforestation, increased enforcement patrol efforts, and fire mitigation in key corridor areas. Corridor restoration and active management between forest fragments is critical to maintaining gene flow across the landscape. Reforestation efforts do not need to result in continuous, contiguous forest from one large fragment to the next. It appears that some fragmentation may be the natural result of a late Holocene drought period, though humans certainly increased the degree of habitat fragmentation (Quéméré et al. 2012;

Salmona et al. 2017). Rather, efforts should be made to plant appropriate species of trees in areas in which they are most likely to survive occasional fire and grazing (*e.g.*, along riparian areas) and that provide sifakas large migration stepping stones between large forest fragments (sifakas have been observed crossing more than 200 m of open grassland (Jimenez and Vargas 2000)). The connectivity map in *Chapter 4* (Fig. 4) highlights several priority areas for these activities. The corridors south of Benanofy (Fig. 4, panel A), between Antsahabe and Solaniampilana (Fig. 4 panel C) and between Binara and Bobankora (Fig. 4, panel D) should receive the highest priority, as they represent key migration bottlenecks between large sifaka population clusters that currently have very little forest cover remaining.

- Reforestation activities should concentrate on tree species known to be important sifaka food items. Because drought periods are expected to become longer in this part of Madagascar (Chesney and Moran 2016), trees with a greater tolerance for drought should be preferred, along with those that have some commercial value to local people. Mampay (*Cynometra aurita*) should be included in all plantings as it was frequently consumed by sifakas across their range, as well as tsarafanahy (*Bourreria labatii*) and taipapango (*Dryptes perrieri*). *Chapters 2* and *3* provide lists of additional top sifaka food items that could be used in reforestation efforts.
- Sifaka translocations are not recommended at this time, but may be considered necessary upon more thorough investigation of genetic relatedness to prevent further inbreeding (especially for the isolated Ampisikina fragment).
- Protect and expand existing forested areas throughout the golden-crowned sifaka range. Forest cover across the Loky-Manambato Protected Area has declined by 11.5% in the

last 20 years (537.3 km² to 475.3 km²). While further research is needed to determine the primary driver of forest loss, the most likely explanations for significant loss are slash-and-burn agriculture and cattle pasture expansion. Mining and logging may also play minor, but potentially increasing, roles and should not be ignored. While *Chapter 2* results suggested that sifakas benefit from some tree cutting, this appears to be only in very low intensity (*i.e.*, only 1-2 small trees cut per 300 m²). I discourage use of forest thinning as a management tool without further research; sifakas are critically dependent on forested areas. Forest area expansion via reforestation should take place primarily to increase fragment connectivity (as described above), but may also be prioritized around forest fragments that are likely to support the highest sifaka densities (Bekaraoka South, Ampondrabe; see *Chapter 2*).

- A significant decline (30-43%) in sifaka populations and anecdotal evidence of hunting described in *Chapter 2* provide cause for concern that local taboos protecting sifakas from hunting may no longer be effective. Understanding whether or not sifakas are being hunted and if so, to what extent, is critical. I recommend that (preferably) a local Malagasy person or potentially a foreigner with significant experience in the ethics and best practices for such a sensitive study conduct this research. To achieve the most effective results, they would need to work independently of Fanamby on the ground, as any involvement by the NGO may arouse suspicion or distrust in the people being interviewed. This is in no way a criticism of Fanamby. Their efforts on the ground have clearly conveyed the importance of not hunting lemurs to the local population. However, Fanamby's position on hunting and its powerful position in the region may prevent local people from providing candid responses about the actual prevalence of sifaka hunting.

- While this study did not directly address potential climate change impacts on this species, it provides important information that will help to identify how climate change might impact sifakas. Currently, much uncertainty remains, and changes to the already highly variable predictions in climate impacts on growing season across southern Africa, make fine-scale climate change predictions difficult to make in Madagascar (Dubovyk et al. 2015). As climate models for the region improve, prediction models of NDVI during the wet season may help us to predict future sifaka abundance under different climate change scenarios (see *Chapters 2 and 3*; Chesney and Moran 2016). An increasing number of dry days and less intense rainfall events across the region as a result of climate change would likely be problematic for sifakas. Alternatively, assuming that sifakas seldom spend time at high elevations because the climate is not favorable to them or their preferred food resources, sifakas may be able to expand their elevational range. Additionally, they may benefit from the predicted reduced frequency of, and a southern shift in, cyclones (Cattiaux et al. 2020; Muthige et al. 2018). Research is needed to build upon the data presented in this dissertation to best inform how and where reforestation efforts should be implemented to support sifaka populations as the climate continues to change. For now, my recommendation is to restore and protect corridors between forest fragments to allow sifakas to shift their range in response to changing conditions is critical. Maintaining viable corridors to facilitate genetic exchange and to promote genetic diversity among populations will also increase the chances that sifakas will be able to adapt to their changing environment and is perhaps the most practical step that managers can take at this time.

FUTURE RESEARCH NEEDS

Below I outline several additional research needs directly related to the results and management recommendations presented above. I also identified significant gaps in our knowledge regarding basic questions of life history and ongoing threats to this species. Obtaining better answers to these questions will help managers to ensure this species' survival amidst global change.

Follow-up work to this study:

- Fanamby recently learned of a population of sifakas inhabiting the Andrafiamena Special Reserve just north of the town of Betsiaka and ~8 km west of the nearest known sifaka population. Such a population would extend this species' range well beyond the confines of the Loky and Manambato Rivers, increasing the availability of potentially suitable habitat for the species by as much as 50%. Immediate work is needed to survey these putative populations and to ensure that these sifakas and the forests they inhabit are adequately protected.
- Completion of the available N analysis may add yet another predictive tool to understanding densities. Once this is completed, *Chapter 3* of this dissertation will be revised and submitted for publication.
- Determining parentage of migrants would help to clarify the effective role of migrants, as animals that disperse long distance would make no impact on the population genetics of the species if they fail to breed successfully.
- Further validation of the genetic work completed in *Chapter 4* is needed prior to submitting for publication. Additional screening of homozygotes will take place to

confirm that these samples truly are homozygous and not genotyping failures as a result of poor fecal DNA amplification.

- More research should be conducted on sifaka food trees, to learn which species provide the most use to local people. Trees that can support local needs and sifakas should be prioritized in reforestation efforts as planting and maintaining these trees is more likely to receive local community support.

Basic life history:

Most of what is known about sifaka life history comes from long-term research on Verreaux's sifakas (*P. verreauxi*) in western dry forests (Kappeler and Fichtel 2012; Lawler 2007; Richard et al. 2006) and Milne-Edwards' sifakas (*P. edwardsi*) in eastern rainforests (Hemingway 1995; Wright 1995). Due to their size, habitat preferences, and genetics, golden-crowned sifakas typically are assumed to have life history traits more similar to those of western sifakas (Irwin 2006). Because golden-crowned sifakas live over such a wide gradient of forest types, yet relatively small geographic area, the amount of variation in life history traits across the species' range remains unknown. Future research should focus on the following topics.

- Infant survival and factors influencing reproductive success have never been studied in this species. Low rainfall is known to negatively impact Milne-Edwards' sifaka infant survival (King et al. 2005). Knowing whether golden-crowned populations are similarly impacted is critical to understanding how they will be affected by climate change.
- Nothing is known about inter-birth intervals or fecundity for this species, or the factors that impact them. Without life history data, it is difficult to know how long populations

might take to recover from a significant decline due to disease, natural disaster, or hunting.

- No studies have explored growth or development for this species. Like other sifakas, golden-crowned sifaka reproduction appears synchronized so that weaning occurs during the wet season, when food is most likely to be available. How climate change will affect this synchrony (*e.g.*, extended drought periods, altered tree phenology) and the ability of infants to put on enough weight to survive their first dry season will be an important aspect of future research.
- Very little is known about golden-crowned sifaka dispersal or the reproductive success of migrants. Sex ratios are about equal for dispersing Milne-Edwards' sifakas (Morelli et al. 2009), and while both sexes of Verreaux's sifakas would disperse to form new groups, only males transferred between existing groups (Richard et al. 1993). The range and frequency of dispersal distances for any of these species (by reproductively successful migrants or not) remains unknown, and is important to improving corridor planning.

Ongoing threats to persistence:

- Based on our results from *Chapter 2*, it appears that hunting may have had, or be having, an impact on golden-crowned sifaka populations. Based on informal interviews with local people, many people are comfortable discussing non-lemur bushmeat hunting of some species for subsistence, while they are much more guarded when discussing hunting lemurs, and especially sifakas (*M. Semel, unpublished data*). This makes it difficult to understand the extent and severity of hunting pressures. While conducting this research, our team came across poachers from outside the region harvesting crowned lemurs

(*Eulemur coronatus*) to sell in Sambava, a city nearly 200 km away. Understanding to what extent sifakas are hunted and whether they are being targeted for subsistence or for distant luxury meat markets is critical to addressing this increasing threat that is being recognized across Madagascar. Additionally, increasing numbers of migrants arriving in the region to engage in gold mining may not adhere to the existing local taboos (*fady*) against hunting sifakas (Golden and Comaroff 2015; Quéméré, Champeau, et al. 2010). Whether this is of significant cause for concern needs to be explored further.

- Rates of forest loss in this region appear to be at or below rates experienced elsewhere in Madagascar, but still represent unsustainable rates for these sifakas (see *Chapter 2*; Quéméré et al. 2012; Vieilledent et al. 2018). An influx of immigrants to the region due to mining and the ongoing efforts to pave the national road may lead to increased deforestation rates in the region. More arid conditions and periods of extended drought due to climate change also may increase forest loss due to increased fire frequency and or intensity (Chesney and Moran 2016). More research is needed on the expected intensity of forest cover loss as a result of both increased direct anthropogenic pressures and climate change in the region.
- Apart from potentially increasing hunting and deforestation activities, paving the national road that bisects the sifakas' range also poses a direct threat to the species. While Quéméré, Crouau-Roy, et al. (2010) found that the unpaved road had little impact on sifaka population structure, a paved road presents a much greater risk. Difficult road conditions, especially during the wet season (when sifakas are most likely dispersing long distances across the landscape (Meyers 1993; Quéméré, Crouau-Roy, et al. 2010)), make vehicular travel incredibly slow (typically <20 km/hr) and sifaka mortality by vehicle

collisions highly unlikely. However, a paved road would allow increased vehicle speeds year-round, which could pose a direct mortality threat to sifakas and potentially act to limit forest fragment size even further (*e.g.*, noise buffer, increased development). The long-term impacts of this road improvement on sifakas should be explored and different management actions considered (*i.e.*, speed bumps or animal overpasses at key crossing points as have been implemented in other Malagasy protected areas).

- Gold mining is frequently cited as a potential threat to these sifakas (Quéméré, Champeau, et al. 2010; Vargas et al. 2002). However, studies consistently find that Bekaraoka (more specifically, Bekaraoka South), where the most intensive mining occurs, has among the highest sifaka densities of all of the forest fragments and that the mining area itself has some of the largest group sizes in the region (B. Semel, *pers. obs.*). Future research should investigate whether mining areas provide open forest areas where abundant light creates a food-rich environment to support an abundance of sifakas or if these areas are somehow acting as an ecological trap.

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