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Effects of anthropogenic disturbance and environmental factors on patterns of parasitism in Cross River gorillas (*Gorilla gorilla diehli*)

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Effects of anthropogenic disturbance and environmental factors on patterns of parasitism in Cross River gorillas (*Gorilla gorilla diehli*)

By

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Bucknell University

2020

Advisor: Thomas Gillespie, PhD

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Abstract

Effects of anthropogenic disturbance and environmental factors on patterns of parasitism in Cross River gorillas (*Gorilla gorilla diehli*)

By: Faith Breen

Deforestation, agricultural expansion, urbanization, expansion of infrastructure, and natural resource exploitation and other forms of anthropogenic disturbance are occurring globally and have devastating effects on the biodiversity of ecosystems. Changes in biodiversity affects many ecosystem processes, including zoonotic diseases. This study investigated the patterns of parasitism, particularly of enteric protozoan and helminthic parasites, in Cross River gorillas (*Gorilla gorilla diehli)*. This study is the first assessment of enteric parasites in Cross River gorillas in Nigeria and examines which environmental or anthropogenic factors affect the prevalence and richness of these parasites. Cross River gorillas are a vulnerable subspecies, that lives in fragmented populations across one of the most densely population regions in Africa. Living in such small and potentially isolated subpopulations exacerbates the risk of potential disease outbreaks. Fecal samples from Cross River gorillas were collected between November 2016 and March of 2018 at three known gorilla localities in Nigeria. These sites are Afi Mountain Wildlife Sanctuary (n=89), Mbe Mountains Community Forest (n=96) and the Boshi Extension of Cross River National Park (n=11). These samples were analyzed using standardized parasitological techniques to identify which parasite taxon were present in each sample. The samples were also analyzed using fecal DNA extract and microsatellite genotyping to identify which individual gorilla contributed the sample. Thirty-four individual gorillas were represented, and nine parasite taxa were detected in the samples. Five taxa were commensal entodiniomorph ciliates and four were pathogenic nematodes. Prevalence of *Strongyloides sp*. was found to vary across sites, with prevalence as high as 75.28% at Afi Mountain Wildlife Sanctuary, or as low as 21.88% at Mbe Mountains Community Forest. Pathogenic richness was found to vary between the wet and dry season with higher richness in the wet season. Two of the pathogenic nematodes were also found in higher prevalence in the wet season. *Strongyloides sp*. had a positive relationship with disturbance intensity and *Trichostrongylus sp.* had a negative relationship. There is no clear relationship between anthropogenic disturbance and parasites richness, which reflects complex ecological mechanisms.

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1. Introduction

1.1 Anthropogenic Disturbance and Fragmentation

Humans are drastically altering landscapes on a global scale leading to disturbance of ecosystems that species rely on for survival (Gottdenker et. al. 2014). Forms of anthropogenic disturbance may include deforestation, agricultural expansion, urbanization, expansion of infrastructure, and natural resource extraction (Gottdenker et. al. 2014). It is estimated that humans have disturbed more than 70% of the terrestrial landscape (Díaz et. al. 2019). Cropland and other agricultural areas alone account for 40% of global land surface (Foley et. al. 2005). The consequences of this disturbance may include transformations of the landscape, shifts in biogeochemical cycles, extinctions of species, or invasions of species (Jaureguiberry et. al. 2022). Land use change in some cases has negatively impacted ecological structure and function (Foley et. al. 2005). Such disturbance and associate pollution has led to a 20% decline in vegetative productivity with the potential to reduce drop yields by up to 50% by 2050 (Ambe and Obeten 2020). These consequences as a whole have led to declines in natures capacity to support our quality of life as measured by 14 of the 18 categories of nature's contributions to people calculated by the Intergovernmental Platform on Biodiversity and Ecosystem Services (Díaz et. al. 2019).

Changing land-use has resulted in a loss of between seven to 11 million km^2 of forest in the past 300 years (Foley et. al. 2005). Pressure on the land has never been higher, logging for timber has increased by 50% since 1970 globally, and agricultural production has essentially tripled (Díaz et. al. 2019). Land use change, primarily for rangeland and agriculture, and exploitation of natural resources, for example for fishing, logging, hunting, and wildlife trade have been the two top global drivers of biodiversity loss (Jaureguiberry et. al. 2022). Less than half of the globe's tropical forests remain as undisturbed as they were in 1989 (Okoro and Ogbuefi 2016).

Anthropogenic land-use expansion threatens the productivity, biomass, structure and species composition and diversity of ecosystems (Foley et. al. 2005). The breaking up of larger swaths of forest into smaller fragmented patches is referred to as forest fragmentation, which may result in isolated patches that disrupt biological functional diversity (Barlow et. al. 2016). Forest fragmentation may expose species to more human activity, and threaten ecosystem resilience (Fitz et. al. 2022). The isolation of patches increases risk of both environmental and demographic stochasticity and limits the mobility of a population in response to threats (Sawyer 2012). If species diversity and ecological processes in a certain forest fragment are severely disrupted, that patch risks losing ecological integrity and conservation value (Gillespie and Chapman 2006).

Disturbance within a tropical forest may not be as visible on a broad scale, for example via remote sensing analysis, but may still introduce changes in ecosystem functions and species diversity (Barlow et. al. 2016). Human disturbance within a forest may include selective logging, wildfires, harvesting of non-timber forest products (NTFP), and poaching (Barlow et. al. 2016, Tchakoudeu Kehou et. al. 2021). Any type of within forest disturbance is increasing the threat to animals by increasing human access to remote areas where species were once undisturbed, and may reduce the survival and reproductive rates (Sawyer 2012, Kuthyar et. al. 2021).

Fragmentation of wildlife populations may result from a loss of either structural or functional connectivity. Structural connectivity refers strictly to the physical qualities of the landscape, where functional connectivity considers not only the quality of habitat but the behavioral response of the population in question (Imong et. al. 2014b). The size, shape and degree of isolation of a fragment as well as different biological characteristics (for example species density and diversity) have dramatic effects on sustaining ecosystem processes and species survival (Gillespie and Chapman 2006). In a fragmented landscape, patch size is a main factor that limits

population size, as it is likely related to availability of food resources (Arroyo-Rodriguez and Dias 2010). As patches or populations become more isolated and distinct, migration to other sites becomes increasingly more difficult and human disturbance pressures may become exacerbated (Fitz et. al. 2022). In small and isolated habitats, disturbance and degradation lead to more rapid changes in ecosystem processes and greater loss in biodiversity, this is often referred to as ecosystem decay (Chase et. al. 2020). Small populations are more susceptible to losses in genetic diversity quicker than large populations because of genetic drift and inbreeding, and a population with lower genetic diversity will have lower fitness and worse health overall (Bergl et. al. 2008).

Land and sea use change, exploitation of natural resources, pollution, invasive species and climate change are damaging biodiversity at unprecedented rates (Jaureguiberry et. al. 2022). Widespread disturbance and degradation of habitats are having a catastrophic influence on the extinction and decline or many species, especially mammalian herbivores (Yager et. al. 2022). Terrestrial ecosystems are estimated to have lost 20% of their biodiversity (Díaz et. al. 2019). Currently 18% of all mammal species are threatened with extinction, with a disproportionate amount being large bodied mammals (Vitousek et. al. 1997). Of all non-human primate species, around 60% are threatened by extinction and 75% are declining in population size, and all great ape species are listed as either endangered or critically endangered (Bergl et. al. 2012, Alonso et. al. 2020). It's estimated that 75% of this group has been uprooted from their original habitat ranges, and nearly all have lost at least 30% of their home ranges (Ceballos et. al. 2017, Díaz et. al. 2019). Habitat destruction and hunting are two main factors threatening the persistence of primate populations (Arroyo-Rodriguez and Dias 2010, Bonnell et. al. 2010, De Vere et. al. 2011). Most primates live in small forest fragments within isolated protected areas (Goldberg et. al. 2008). Across Africa, the fragments where primates are found have an area too small to sustain healthy

populations, more than 65% of these fragments are less than 1 km^2 (Bergl et. al. 2012). Primates are particularly vulnerable to negative consequences of fragmentation because of their large body size and slow reproduction (Sawyer 2012, Tchakoudeu Kehou et. al. 2021). Disturbance like logging can directly affect primate populations by reducing availability of trees that are food sources (Gillespie et. al. 2009). Poaching of any species may affect primates in the habitat by increasing stress and changing behavioral responses, disruptions to habitat or community structure, or introducing diseases from hunters (Sawyer 2012).

1.2 Zoonotic Disease Risks

75% of human diseases have links to livestock or wildlife (Foley et. al. 2005). Emerging infectious diseases in particular are dominated by spillovers from wildlife, and are occurring more and more frequently (Jones et. al. 2008, Civitello et. al. 2015). Diseases like SARS, Ebola, and Lyme disease are all caused by pathogens that originated in wildlife and have impacted humans across the globe (Chapman et. al. 2005, Jones et. al. 2008). More than two billion people each year are affected by soil transmitted helminth infections, with many individuals concentrated in tropical, developing countries but the same parasitic worms also affect livestock and wildlife (Yaro et. al. 2018, Barelli et. al. 2019).

A study of North American wildlife pathogens found that 55% of outbreaks in wildlife populations were a result of human involvement (Chapman et. al. 2005). Changing habitats results in differing abundances, demographies, behaviors, and movements of species which impacts the contact between host species and vectors as well as community composition (Gottdenker et. al. 2014). There are established patterns of zoonotic disease emergence occurring as a result of a change in ecology of the host species or the parasite (Chapman et. al. 2005). Expanding anthropogenic disturbance such as road and dam construction, or expanding agricultural areas

blurs interspecies boundaries creating more overlap between humans, livestock and wildlife which modifies the transmission of infectious disease leading to more outbreaks (Foley et. al. 2005, Chapman et. al. 2005). The close proximity of hosts, vectors and reservoir hosts increases the risk of infection by pathogens contaminating shared water sources, soil or food sources (Sirima et. al. 2021). Behaviors that may put humans more at risk of transmitting zoonotic diseases include, hunting and butchering of bushmeat, tending to livestock, fetching water from an open source, or any other activity that increases contact with wildlife or livestock (Goldberg et. al. 2008, Medkour et. al. 2020).

1.3 Disease in Great Apes

The health of non-human primates is of particular concern given their role as reservoir hosts in disease systems like HIV and malaria (Bonnell et. al. 2010). Intestinal parasite load can be used as a proxy for primate health because certain parasite species can be found across many primate species and may reduce the fitness of an animal by affecting host survival and reproduction (Chapman et. al. 2005, Masi et. al. 2012). Intestinal parasite infections in wild primates can either be asymptomatic or have adverse health effects including inflammation of mucus, diarrhea, ulcers, blood loss, abortion, weight loss, and even death (Chapman et. al. 2005, Gillespie and Chapman 2006, Masi et. al. 2012). In less severe instances, the nutritional absorption of the host is impaired which then requires more energy to be expended on tasks like foraging and feeding, both of which decrease fitness (Chapman et. al. 2005). Of gastrointestinal parasites, helminths and protozoans, such as entodiniomorph ciliates are most common in primates (Goussard et. al. 1983, Ashford et. al. 1996, Chapman et. al. 2005). In some studies of parasitism in wild non-human primates great apes were found to be infected more frequently than monkeys (Medkour et. al. 2020).

Anthropogenic disturbance in primate habitat can alter patterns of enteric parasites like helminths and protozoans (Goldberg et. al. 2008). Some cases indicated that disturbance and fragmentation lead to increased parasite prevalence and richness (Gillespie and Chapman 2006, Zommers et. al. 2013, Pafčo et. al. 2017). Studies also found that different bacteria, like Giardia and E.coli, were more prevalent in primates in habitats closer to humans and showed more genetic overlap with the bacteria sampled from those human populations and their livestock (Goldberg et. al. 2008, Kuthyar et. al. 2021). However, this has not been proven to be a uniform relationship as opposite associations or no effect has been observed as well and further investigations are necessary (Barelli et. al. 2019). Human disturbance may alter the behavior of wild non-human primates and thus creates greater risk of transmission. For example, if a primate leaves a forested patch to pursue resources like food and water and must pass through more human adapted areas like pasture or rangeland they may come into contact with livestock feces or infected soils that they otherwise would not be exposed to (Goldberg et. al. 2008). If there is increased human activity in a forest and there are created trails, primates may exhibit increased ground use which creates a greater disease risk from soil-transmitted parasites (Zommers et. al. 2013, Medkour et. al. 2020). Additionally, habitat loss and anthropogenic disturbance may lead to higher population density and restricted resource availability which may cause increased stress and decreased immune function in a primate and facilitate easier transmission and infections (Barelli et. al. 2019). In general, the stresses of increasing anthropogenic disturbance may have negative effects on body condition and health of a primate and may result in increasing parasite loads (Thatcher et. al. 2018).

1.4 Cross River gorillas (*Gorilla gorilla diehli)*

The area surrounding the border between Cameroon and Nigeria is a biodiversity hotspot, home to animals such as forest elephants, the Cameroon-Nigeria Chimpanzee, many insects, birds,

and amphibians as well as the critically endangered Cross River gorilla, *Gorilla gorilla diehli* (Dunn et. al. 2014, Okoro and Ogbuefi 2016). This area is also one of the most densely populated regions in Africa, where many groups of people are dependent on resources from the forest (Nkemnyi et. al. 2013, Imong et. al. 2014a, Okoro and Ogbuefi 2016). The forest provides essential goods for the region like medicine, timber, non-timber forest products and bushmeat (Akenji et. al. n.d.). The Cross River State of Nigeria is expected to continue to see an increase in human population and activity, with potentially up to an eightfold increase in population from 2000 to 2050 (Krause et. al. 2019). With the expanding human population, there's also expansion of urban areas, agricultural areas, and infrastructure like roads, into the natural forested areas as well as socioeconomic demand for forest products (Krause et. al. 2019, Fitz et. al. 2022). In fact, the pressures of human expansion in the region has led to a loss of nearly 50,000 ha of forest in the Cross River State between 2001-2016 (Krause et. al. 2019). Nigeria has lost about 90% of forest areas, and deforestation persists with a loss of about 400,000 ha each year (Enuoh and Ogogo 2018). On the Cameroonian side of the border, around 170,000 km^2 of forest had either been logged or allocated for logging by the year 2000, with timber products representing a significant portion of the Cameroonian economy (Sawyer 2012). It is now estimated that Cameroon loses about 220,000 ha of forest cover each year (Nkemnyi et. al. 2013). Deforestation, timber extraction, and illegal hunting all disrupt areas of quality forest where fauna species may seek refuge (Krause et. al. 2019).

The Cross River gorillas are an elusive and understudied subspecies of gorilla that reside about 200 kilometers north west of other gorilla species in an area of about 12,000 km^2 that ranges in elevation from around 200 to 2000 kilometers above sea level (Bergl and Vigilant 2006, Dunn et. al. 2014). They are one of the worlds most endangered primates and classified as Critically

Endangered by the IUCN (Sawyer and Brashares 2013, Dunn et. al. 2014). Though they are spread across a wide area, Cross River gorillas only inhabit around 700 km^2 in a patchy distribution of about thirteen localities across nine distinct sites (Dunn et. al. 2014). Cross River gorillas endure a more pronounced dry and wet season than at any other locality (Bergl and Vigilant 2006, Wade and Malone 2021). Given their status as selective frugivore-folivores, their large body size, and dietary requirements Cross River gorillas have high area requirements and a higher required area per unit biomass than some other species (Sawyer 2012, Etiendem and Tagg 2013). Cross River gorillas travel around 1.5 km each day with food availability dominating day-to-day movement decisions as they spend more than 40% of the day feeding (Sawyer and Brashares 2013, Etiendem and Tagg 2013, Imong et. al. 2014a)

There are three subpopulations of Cross River gorilla, one central population which encompasses many of the known localities, a small eastern population, and a small western population (Bergl and Vigilant 2006). The central population is mainly structurally cohesive, while the western population at Afi Mountain Wildlife Sanctuary is cut off and isolated by agricultural areas and a busy highway (Bergl and Vigilant 2006, Bergl et. al. 2012). The eastern subpopulation at Kagwene Gorilla sanctuary is connected to the central population in one small area, but is mostly surrounded by human disturbed areas such as farmland (Bergl and Vigilant 2006). The main central population has more genetic diversity than either of the two small populations, but there is still some evidence of mobility and migration between populations (Bergl and Vigilant 2006, Bergl et. al. 2008).

Given that the landscape across the montane Cameroon-Nigeria border where Cross River gorillas reside is seemingly intact forest, it's important to understand why the species distribution is so restricted and patchy (Bergl et. al. 2012, Dunn et. al. 2014). Studies have found that Cross

River gorilla presence is negatively correlated with signs of human activity like hunting, or roads and more common in areas with rugged, steep slopes that humans cannot access as easily (Sawyer 2012, Bergl et. al. 2012, Sawyer and Brashares 2013, Tchakoudeu Kehou et. al. 2021). Factors like elevation, distance from villages, and slope steepness are all indicative of an avoidance of humans for safety and security (Etiendem et. al. 2013). The risk of mortality and stress in areas with more hunting, may outweigh the potential benefits of new habitat and new resources (Imong et. al. 2014b). Food availability is another strong predictor of suitable Cross River gorilla habitat, one study used some of the most common herbaceous food species as a good model for habitat selection (Sawyer and Brashares 2013, Wade and Malone 2021).Within steep slopes, Cross River gorillas show a preference in their nesting ecology for areas with some light gaps and clearings, which usually have a more herbaceous understory with vegetation to eat (De Vere et. al. 2011, Wade and Malone 2021). Cross River gorillas will avoid grasslands and farms, which reduces potential suitable habitat (De Vere et. al. 2011) Human disturbance within the region may restrict the Cross River gorilla functional connectivity, which poses a threat of isolating smaller localities even though there is a considerable amount of suitable habitat across the landscape (Dunn et. al. 2014, Imong et. al. 2014b, Wade and Malone 2021).

Cross River gorillas are continually hunted for meat as part of the bushmeat industry. Some studies indicate that around 1-3 Cross River gorillas are killed annually though this is likely an underestimate (Sawyer 2012). The high market values for both body parts and meat from great apes incentivizes hunting them, with especially high pressure on bushmeat coming from visitors and tourists (Nkemnyi et. al. 2013). Additionally, only five of the sites where Cross River gorillas are located are designated as protected areas (Dunn et. al. 2014). Other unprotected areas, like community forests remain open to community members for uses including hunting, as long as

endangered animals are not hunted (Krause et. al. 2019). Despite Cross River gorillas being designated as a protected species in both Nigeria and Cameroon, laws about which species are not to be hunted are not well understood in some areas, or not strictly and uniformly enforced (Krause et. al. 2019). Losing only 1-3 individuals each year may seem insignificant, but with such small and potentially isolated subpopulations even losing a few gorillas poses a threat to sustaining that locality (Dunn et. al. 2014).

2. Purpose and Hypotheses

Better understanding of the relationship between anthropogenic disturbance and primate health is critical for conservation of this group of mammals. While there hasn't been any recorded cases of disease devastating Cross River gorilla localities, the small size of the subpopulations creates an increased risk if disease is introduced (Dunn et. al. 2014). Additionally, with the considerable habitat overlap between the Cross River gorillas, other wildlife, livestock, and humans, disease should be a major consideration in conservation endeavors as human disturbance has been proven to alter the transmission of parasites within other primates (Gillespie and Chapman 2006, Zommers et. al. 2013, Pafčo et. al. 2017). More research is needed on potential disease within Cross River gorillas especially considering how vulnerable each subpopulation is and how pervasive human disturbance is across the landscape.

I investigated the prevalence and species richness of enteric parasites in Cross River gorillas at three sites in Nigeria, the Mbe Mountains Community Forest, the Afi Mountain Wildlife Sanctuary and the Boshi extension of Cross River National Park. These sites have varying levels of human activity, such as hunting, trapping, NTFP collection, and logging, in and around them from local villages.

My main objectives for the study are to determine in Cross River gorillas, *Gorilla gorilla diehli*, in my study sites:

- If enteric parasite prevalence is affected by varying human activity in the habitat
- If enteric parasite species richness is affected by varying human activity in the habitat
- The influence of altitude on enteric parasite prevalence and species richness
- The influence of season on enteric parasite prevalence and species richness

I hypothesize that:

- Both pathogenic parasite prevalence and pathogenic richness will be higher in sites that have higher levels of human disturbance because of increased stress for Cross River gorillas and increased interspecies overlap (Zommers et. al. 2013, Thatcher et. al. 2018, Kuthyar et. al. 2021).
- At higher altitudes pathogenic parasite prevalence and pathogenic richness will decline because of decreased accessibility for humans (Barelli et. al. 2019).
- Seasonality will affect pathogenic parasite prevalence and pathogenic richness because of changes in Cross River gorilla diet and behavior, there will be higher infection rates in the dry season because of lower quality resource availability (Etiendem and Tagg 2013, Pafčo et. al. 2017).

3. Materials and Methods

3.1 Study Sites

My study sites are in the Cross River State, the montane borderland in the southeastern corner of Nigeria (Figure 1). The Afi Mountain Wildlife Sanctuary (6.3086° N, 8.9908° E) is estimated to have a population of 25-30 Cross River gorillas. It is surrounded by 16 villages, with a population of about 27,000 people and is known to be encroached on by farming, logging, and bush fires. The Mbe Mountains Community Forest (6.2212° N, 9.0678° E) is also estimated to sustain a population of 25-30 gorillas. This site is one of the best studied Cross River gorilla localities, has generally less anthropogenic pressure than other sites, and is surrounded by a population of about 9,000 people (Dunn et. al. 2014). Okwa hills in Cross River National Park (5.5805° N, 8.7481° E) is connected to Central Takamanda National Park in Cameroon and the 15-30 gorillas in this locality range between the two. The more northern portion of Cross River National Park, the Boshi Extension, sustains 20-25 gorillas. The park is surrounded by 29,000 people and has some village enclaves within the park borders that bisect the park and hinder connectivity of the two populations. Poaching, trapping and bush fires are all prevalent despite the park's protected status (Dunn et. al. 2014).

These sites range in altitude from as low as 130m to as high as 1,700m. Vegetation in the area changes along an altitudinal gradient with moist semi-deciduous tropical forest in lowlands, and montane forest at higher altitudes (Dunn et. al. 2014). And all sites have a very long dry season (November-March) with an intense rainy season (March-November) where average annual rainfall ranges from 2000 mm to 3000 mm (Fitz et. al. 2022).

3.2 Sample collection

From November 2016 to March of 2018, fresh fecal samples were noninvasively collected from Cross River gorillas at the study sites in Nigeria, 136 from Afi Mountain Wildlife Sanctuary, 41 from Boshi Extension of Cross River National Park, nine from Okwa Hills, and 142 from Mbe Mountains Community Forest. Samples along trails or at nest sites that were identified as fresh (<1-3days old) were collected by a collaborative team from Working Dogs for Conservation and the Wildlife Conservation Society following established protocols (Arandjelovic et. al. 2015). The samples were divided into multiple aliquots, one contained 2g of feces and 10 ml of 10% buffered formalin and was shipped to the Emory University in the United States for parasitology analyses. Another aliquot was prepared using a two-step ethanol-silica procedure outlined by Nsubuga et. al. (2004) and was shipped to Max Planck Institute for Evolutionary Anthropology in Germany for individual gorilla identification using fecal DNA extract and microsatellite genotyping (Nsubuga et. al. 2004, Arandjelovic et. al. 2015). From this STR amplification 61% of samples produced a successful individual identification. Samples came from 34 individual Cross River gorillas, 22 of those individuals were identified multiple times and 12 were only identified once.

3.3 Parasitological analyses

Gastrointestinal parasites were isolated from the fecal samples via sodium nitrate flotation and sedimentation using techniques established as the standard (Gillespie 2006). During floatation, samples are centrifuged in distilled water to rinse the formalin, and then centrifuged in sodium nitrate which causes the small, lightweight parasites to float to the top and stick to an affixed cover slide. The cover slide is then analyzed under a compound microscope and parasites are identified based on morphology (size, shape, and contents of the egg and/or larvae) at 40x magnification. A

drop of Lugol's iodine may be added to the slide for increased definition to facilitate identification. The sample is then processed for sedimentation by washing with a soap solution to extract parasites from the sediment. After washing, the sample is strained using a cheesecloth and allowed to settle in the soap solution until the particulates gather and can be pipetted onto a slide for parasite identification, again based on morphology of the helminth eggs, larvae, and protozoal cysts under 40x magnification. One floatation slide, and one sedimentation slide from each sample are used as indicators representative of the whole sample.

For each individual slide the number of parasite taxon present was counted. Thus for each slide infection status, species richness and parasitic load were all measured where richness is defined as the number of unique species found in the sample and parasitic load is the number of adult individuals for protozoan species or the number of eggs for helminth species (Zommers et. al. 2013). Though parasite richness is not a direct indicator of disease risk, since some parasite species are benign or even beneficial, it is an important metric for understanding primate health and infection status (Benavides et. al. 2012, Young et. al. 2013, Johnson et. al. 2013, Deere et. al. 2021).

3.4 Human disturbance SMART Patrol Data

In collaboration with the Wildlife Conservation Society, rangers on the ground at sites in Nigeria can use SMART (Spatial Monitoring and Reporting Tools) technology to aid their conservation monitoring. This technology relies on smartphones to track where patrols go and record all the data they collect. This technology is currently in use in 65 countries, and for the sites in Cross River gorilla habitat it's used to track human disturbance in the area which has helped increase the efficiency of law enforcement in the area. The use of SMART technology has

facilitated a significant increase in patrol effort (67%), and a lessening of hunting pressure (71%) (*North Carolina Zoo: Conservation and Research Report* 2020). The data is logged with spatial coordinates and the rangers can also indicate what type of threat they observed and what action they took.

3.5 Spatial Analyses

Both the fecal samples collected from the Cross River gorillas and SMART Patrol Data had accompanying spatial coordinates that were imported into QGIS for spatial analysis ("QGIS" 2022). For each fecal sample, a radius of 1.5 kilometers was created using the *buffer* tool. This {Citation}. Next using the *count points in polygon* tool, the number of disturbance data points, collected by the SMART patrols, were counted for each respective fecal sample. This metric was used to gauge how many disturbance points were within the average daily travel distance radii and used to quantify human disturbance. The range of this metric is 0 to 386 logged disturbances with an average of 254 disturbances.

Altitudinal data was also imported into QGIS to determine the altitude of each individual sample. The data came from the Terrain layer, a dynamic world elevation layer published by Environmental Systems Research Institute (ESRI) and the *Sample Raster Values* processing algorithm was used to calculate each value ("Terrain" 2022). The altitudes of each sample ranges from 215m to 1754m with an average of 687m.

3.6 Statistical Analyses

Statistical Analyses were conducted in R studio 1.4 (R Core Team 2009). Linear mixed effects models were used to estimate the prevalence of each parasite taxon (Zuur et. al. 2009).

Models were generated using the ‘nlme’ package and a binomial distribution and REML model fitting (Pinheiro et. al. 2020). This package was used for this portion of analysis because of its flexibility with one sided mixed effect models. GorillaID was included on each model to account for the repeated samplings of individuals and lack of independence to avoid pseudo replication (Millar and Anderson 2004, Waller et. al. 2013, Pollet et. al. 2015). These models were also used to estimate parasite richness. Parasite richness was analyzed by distinguishing commensal parasites from pathogenic parasites and treating each as a separate variable. Species included in the commensal richness variable are: *Troglodytella sp., Gorillaphicus sp.,* unidentified “Type A” entodiniomorph ciliate, unidentified “Type B” entodiniomorph ciliate, and *Prototapirella sp.*. Species included in the pathogenic richness variable are: *Oesophagostomum sp., Necator sp., Strongyloides sp.,* and *Trichostrongylus sp.*.

Mixed effects models were used to determine if there were differences in parasite prevalence and richness among the sites. Mixed effects models were also used to investigate any differences in parasite richness between the wet and dry season. After each model was run a mixed model analysis of variance (mixed model ANOVA) to detect any variance between sites, this is a common for longitudinal data with repeated measures but allows for more flexibility than a repeated measures ANOVA (Frey 2018). Next the ‘emmeans’ package was used for simultaneous pairwise comparisons among the sites which uses the Tukey adjustment by default (Lenth et. al. 2023).

The relationship between parasite richness (the number of different types of parasites) and level of anthropogenic disturbance was assessed with generalized linear mixed models using the *glmmTMB* package with a Conway-Maxwell-Poisson distribution and a log-link function (Frey 2018). The model was run using the complete parasite species richness, and then run again using

commensal species richness and then pathogenic species richness. Additionally, the relationship between each individual parasite taxon and anthropogenic disturbance was assessed using the *glmmTMB* package with a binomial distribution with a logit link function. Presence or absence of each taxon was used as the response variable. Exploratory data analysis was conducted before any model fitting to determine a priori what distribution would be most appropriate and what biological variables would be tested (Zuur et. al. 2010, Smith et. al. 2020). There were mild issues of underdispersion in Poisson and negative binomial distributions, so the Conway-Maxwell-Poisson distribution was selected for its flexibility with underdispersion (dispersion parameter = 0.64) (Lynch et. al. 2014, Huang 2017). The log link function ensures positive fitted values. To help with model convergence, the numeric variables were centered and scaled using the mean and standard deviation, a common way to compare data that is measured at different scales (Smith et. al. 2020, Deere et. al. 2021). Models included the daily travel distance disturbance metric (continuous), Altitude (continuous), Sex of the individual (categorical with two levels) and Season (categorical with two levels) as fixed effects. The variable season was determined using the date the sample was collected. If the sample was collected in November through March, it was categorized as being in the dry season, if it was collected in the other months (April through October) it was categorized as being in the rainy or wet season (Fitz et. al. 2022). The number of samples collected from each site (categorical with 3 levels) was also included as a fixed effect to control for the skewed number of samples from Afi and Mbe (n =111 for each site) compared to the number from the Boshi extension (n =13). The number of samples contributed by each individual was also included as a fixed effect to control for unequal sampling from individuals, this variable was categorical with 34 levels. To control for the dependence in sampling, Gorilla ID (categorical with 34 levels) was included as a random intercept effect so that repeated samples

from the same individual and uneven sampling was accounted for. Additionally, the date sampled was included as a second random intercept effect to control for temporal dependence. The model is of the form:

$$Richness_{ijk} \sim Conway\text{-}Maxwell\text{-}Poisson.(\mu_{ijk})$$

$$E(Richness_{ijk}) = \mu_{ijk}$$

$$log(\mu_{ijk}) = DisturbanceDailyDistance_{ijk} + Altitude_{ijk} + Sex_{ijk} + SampleCounts_{ijk} + IndividualSampleCounts_{ijk} + Seasonijk + GorillaID_i + Date_j$$

$$GorillaID_i \sim N(0, \sigma^2_{GorillaID})$$

$$Date_j \sim N(0, \sigma^2_{Date})$$

Equation 1. A Conway-Maxwell-Poisson GLMM where $Richness_{ikj}$ is the *k*th observation from individual *i*, and *i* = 1,. . ., ,23 on date *j* and $GorillaID_i$ and $Date_j$ are the random intercepts, which is assumed to be normally distributed with mean 0 and variance σ^2

Model diagnostics were conducted using the DHARMa and performance packages (Hartig and Lohse 2022, Lüdecke et. al. 2023). Generalized Variance Inflation Factors were calculated using the function 'check_collinearity' of the performance package to check the collinearity of the covariates. All variance inflation factors were less than three, though the 95% confidence interval for the daily travel distance disturbance metric was quite broad (VIF= 1.03 95% CI=1.00, 5.40) (Zuur et. al. 2010). Site was not included as a fixed effect in the model because of high collinearity values that cause the model to fail, nor was it included as a random effect because there are not enough levels (n =3) for it to be meaningful, additionally there was little change in the coefficients when site was added or removed (Bolker 2015). Spatial dependence from the fecal samples was

assessed with a spline correlogram using the ncf package (Bjornstad and Cai 2023). A spline correlogram plots an index of spatial autocorrelation against distance to examine patterns of autocorrelation among model residuals. The ncf package uses a generalization of the Mantel correlogram which is a classic multivariate method to estimate spatial covariance data (BjØrnstad and Falck 2001). From this analysis, it was determined that the model accounted for any spatial autocorrelation compared to the raw data and there were no significant problems detected. Model residuals were plotted against fitted values, against each covariate in the model, and against each covariate not in the model to assess model misfit. The final models showed no evidence of over- or under-dispersion, and there were no significant problems detected in the model predictions versus standardized residuals. The total sample size for this analysis was 196 observations from 34 individuals across three sites.

4. Results

4.1 Sample demographics

Three hundred and twenty-eight fecal samples were collected from Cross River gorillas (*Gorilla gorilla diehli*) and were screened using parasitological techniques for protozoan and helminthic enteric parasites. Of all the samples, 136 are from Afi Mountain Wildlife Sanctuary, 41 are from Cross River National Park (CRNP)-Boshi Extension, and 142 are from Mbe Mountains Community Forest and nine from the Okwa Hills region of CRNP. Sample collection started in Afi in December of 2016 and ended in February of 2018. Collection ranged from July 2017 to February 2018 in CRNP-Boshi Extension and November 2016 to February 2018 at Mbe Mountains Community Forest. When the collection date is organized into seasons, 148 of the samples were collected in the dry season and 180 samples were collected in the wet season. From genotypic analysis, 196 samples returned a successful individual identification. The genotyping indicates the samples came from 34 individuals, many of whom supplied multiple samples (Table 1). Individual gorillas may have been sampled only once or as many as 34 times. Eleven of the 34 individual gorillas are from Afi Mountain Wildlife Sanctuary, 17 are from Mbe Mountains Community Forest and six are from CRNP-Boshi Extension. Of those with Gorilla ID's, 89 samples are from Afi Mountain Wildlife Sanctuary, 11 from Cross River National Park (CRNP)-Boshi Extension, and 96 from Mbe Mountains Community Forest. In this smaller group of samples, 86 are from the dry season and 110 from the wet season. The altitude of the samples ranged from 215m to 1108m at the Afi Mountain Wildlife Sanctuary, 460m to 883m at Mbe Mountains Community Forest and 614m to 1216m at the CRNP-Boshi Extension (Figure 5).

4.2 Parasite prevalence

In all samples, four nematodes (*Oesophagostomum* sp.*, Necator* sp.*, Trichostrongylus* sp.*, Strongyloides* sp.) and five protozoans (*Troglodytella sp., Gorillaphicus sp., Prototapirella sp.,* and two unidentified entodiniomorph ciliates) were detected (Table 2). Across all sites there were more samples where parasites were detected than those where none were found (Figure 3). At both Afi Mountain Wildlife Sanctuary and Mbe Mountains community forest all nine parasite taxa were detected (Table 3 and Table 4). At CRNP-Boshi Extension only *Prototapirella sp., Strongyloides sp.,* and *Trichostrongylus sp.* were observed (Table 5). Overall parasite prevalence as estimated by random effects models varied by taxa, with values as low as 2.26% to 67.79% (Figure 2). *Prototapirella* sp. and *Strongyloides* sp. had the highest prevalence across all sites with 67.71% (N=130 samples and 28 individuals) and 43.58% (N=94 samples and 24 individuals) respectively. At CRNP-Boshi Extension and Afi Mountain Wildlife Sanctuary, *Strongyloides* sp. had the highest prevalence with 54.14% (N= 6 samples and four individuals) and 75.28% (n = 67 samples and nine individuals). At Mbe Mountains Community Forest, *Prototapirella* sp. had the highest prevalence with 70.36% (N=62 samples and 9 individuals). A mixed model ANOVA was conducted on each parasite taxon detected, this test indicated that only *Strongyloides* sp., *Trichostrongylus sp.,* and *Troglodytella sp.* had site-based differences. *Troglodytella sp.* (χ^2 = 6.2306, df = 2, p = 0.04) returned weaker pairwise differences among sites after simultaneous pairwise comparisons using Tukey's HSD test as the greatest disparity between Afi Mountain Wildlife Sanctuary and Mbe Mountains Community Forest was marginal (p = 0.969). Neither of the other pairwise comparisons showed differences. *Strongyloides* sp. also demonstrated site-based variation in prevalence (χ^2 = 71.495, df = 2, p < 0.0001). Simultaneous pairwise comparisons using Tukey's HSD test revealed that Afi Mountain Wildlife Sanctuary and Mbe Mountains Community

Forest were different ($p < 0.0001$), and CRNP-Boshi Extension and Mbe Mountains Community Forest were different ($p = 0.0475$) but Afi Mountain Wildlife Sanctuary and CRNP-Boshi Extension did not have different distirbutions. Mixed model ANOVA results indicated prevalence of *Trichostrongylus sp.,* was variable across sites as well ($\chi^2 = 9.3179$, df = 2, $p = 0.009$). Simultaneous pairwise comparisons using Tukey's HSD test showed that Afi Mountain Wildlife Sanctuary and Mbe Mountains Community Forest were different ($p = 0.02$), and CRNP-Boshi Extension and Afi Mountain Wildlife Sanctuary were marginally different ($p = 0.07$).

4.3 Parasite richness

Overall parasite richness as estimated by random effects models was variable across samples and ranged from zero to five taxa across the study period, with a mean (95%CI) of 1.76 (1.53, 1.99) (n = 196) (Table 6). Richness also varied over time for individuals with repeated samples (Figure 13). Richness was varied across seasons, with a mean (95%CI) richness of 2.16 (1.89, 2.43) in the wet season (n = 110), 1.43 (1.18,1.68) in the dry season (n = 86) (Figure 10). Across sites there was some variation in richness, with a mean (95%CI) of 2.25 (1.94, 2.56) from Afi Mountain Wildlife Sanctuary (n = 89), 1.09 (0.11. 2.07) from the Boshi extension of CRNP (n = 11), and 1.54 (1.31, 1.78) from Mbe Mountains Community Forest (n =96) (Table 9). Afi Mountain Wildlife Sanctuary had the highest estimated parasite richness and CRNP-Boshi Extension had the lowest (Figure 7). Results of a mixed model ANOVA showed there were differences among sites regarding overall parasite richness ($\chi^2 = 16.49$, df = 2, $p = 0.0002$). Simultaneous pairwise comparisons using Tukey's HSD test indicated that Afi Mountain Wildlife Sanctuary and CRNP-Boshi Extension were different ($p = 0.03$), and Afi Mountain Wildlife Sanctuary and Mbe Mountains Community Forest were different ($p = 0.002$) but CRNP-Boshi

Extension and Mbe Mountains Community Forest were not different ($p = 0.39$). Results of a mixed model ANOVA revealed there were differences between the wet and dry season regarding overall parasite richness and parasite richness is higher in the wet season ($\chi^2 = 16.475$, $df = 1$, $p < 0.0001$).

Commensal parasite richness was variable across samples and ranged from zero to four taxa across the study period, with a mean (95%CI) of 1.00 (0.87, 1.14) (n = 196) (Table 7). Richness also varied over time for individuals with repeated samples. Commensal richness was consistent across seasons, with a mean (95%CI) richness of 1.03 (0.85, 1.21) in the wet season (n = 110) , and 1.02 (0.82, 1.23) in the dry season (n = 86) (Figure 11). Across sites there was some variation in richness, with a mean (95%CI) of 0.96 (0.77, 1.17) from Afi Mountain Wildlife Sanctuary (n = 89), 0.46 (0.05, 0.87) from the Boshi extension of CRNP (n = 11), and 1.10 (0.91, 1.30) from Mbe Mountains Community Forest (n =96) (Table 10, Figure 8). Results of a mixed model ANOVA suggested there were differences among sites regarding overall parasite richness ($\chi^2 = 5.9105$, $df = 2$, $p = 0.05$). Simultaneous pairwise comparisons using Tukey's HSD test indicated that Mbe Mountains Community Forest and CRNP-Boshi Extension are subtly different ($p = 0.08$). All other pairwise comparisons did not reveal any other differences between pairs of sites. A mixed model ANOVA regarding differences in commensal between seasons did not indicate any variation across the wet and dry seasons ($\chi^2 = 0.0104$, $df = 1$, $p = 0.92$).

Pathogenic parasite richness was variable across samples and ranged from zero to three taxa across the study period, with a mean (95%CI) of 0.75 (0.55, 0.94) (n = 196) (Table 8). Richness also varied over time for individuals with repeated samples. Commensal richness differed across seasons, with a mean (95%CI) richness of 1.11 (0.87, 1.34) in the wet season (n = 110), and 0.41 (0.27, 0.54) in the dry season (n = 86) (Figure 12). Across sites there was some variation in richness, with a mean (95%CI) of 1.28 (1.09, 1.46) from Afi Mountain Wildlife Sanctuary (n =

89), 0.63 (0.05, 1.20) from the Boshi extension of CRNP (n = 11), and 0.43 (0.30, 0.57) from Mbe Mountains Community Forest (n =96) (Table 11, Figure 9). A mixed model ANOVA was run to determine if site was a significant determinant of pathogenic parasite richness, results show that there are significant differences among sites (χ^2 = 48.045, df = 2, $p < 0.0001$). Subsequently, simultaneous pairwise comparisons using Tukey's HSD showed that Afi Mountain Wildlife Sanctuary and Mbe Mountains Community Forest have different distributions of pathogenic parasite richness ($p < 0.0001$), and Afi Mountain Wildlife Sanctuary and CRNP-Boshi Extension are marginally different ($p = 0.10$). There was no difference detected between CRNP-Boshi Extension and Mbe Mountains Community Forest ($p = 0.5$). The results of a mixed model ANOVA used to determine seasonal differences in pathogenic parasite richness indicate there is a difference between the wet and dry seasons and pathogenic parasite richness is higher in the wet season (χ^2 = 23.890, df = 1, $p < 0.0001$).

4.4 Disturbance

The SMART ranger patrol disturbance data had a record of 6630 disturbance observations. Of these observations, hunting (n = 2120) and trapping (n = 2835) were the most common and accounted for nearly 75% of the data (Figure 4). There were 3367 observations from Afi, 1004 from CRNP-Boshi Extension and 1570 from Mbe. The final 689 points were from Okwangwo which is near the CRNP-Boshi Extension. They ranged in distance from around 2 km away from known Cross River gorilla habitat to 12 km.

This data was analyzed spatially to make the daily travel distance metric used to quantify disturbance intensity (Table 12). Across sites there was some variation in this metric with a mean (± SD) of 281 ± 72 from Afi Mountain Wildlife Sanctuary (n = 111), 245 ± 62 from the Boshi extension of CRNP (n = 13), and 229 ± 55 from Mbe Mountains Community Forest (n =111)

(Table 13, Figure 6). Afi had the highest disturbance intensity and Mbe had the lowest. A Shapiro-Wilk normality test was run on the data to check for a normal distribution of the disturbance within daily travel distance metric. The test indicated that the data does not have a normal distribution ($p < 0.0001$). A Kruskal-Wallis test was run to determine if the richness distribution varied among sites. Results from the test indicated that the disturbance within daily travel distance metric is observed to be larger or smaller at different sites ($\chi^2 = 22.417$, $df = 2$, $p < 0.0001$) (Ruxton and Beauchamp 2008). A Pairwise-Wilcox test was run to determine which pairs of daily travel distance metrics at each site showed differences. The pairwise comparison showed that, only Mbe Mountains Community Forest and Afi Mountain Wildlife Sanctuary were different ($p < 0.0001$).

4.5 Model results

A random intercept Conway-Maxwell-Poisson GLMM was fitted to data to determine the relationship between total parasite richness in Cross River gorillas (*Gorilla gorilla diehli*) and levels of anthropogenic disturbance in the habitat (Table 14, Figure 14). There was a positive relationship between parasite richness and the wet season ($p = 0.001$). An individual's parasite richness increased by 1.60 units (CI: 1.21, 2.10) per one standard deviation change in season with increases in the wet season specifically. There was a positive relationship between richness and the site sample counts variable, where an individual's parasite richness increases by 1.19 (CI: 1.03, 1.37, $p= 0.02$). There were weak positive relationships between richness and altitude, as well as richness and sex being male ($p = 0.07$).

The next model was run with the same format but used to analyze commensal parasite richness (Table 15). This model indicated a significant positive relationship between commensal

richness and site sample counts ($p = 0.01$). An individual's commensal parasite richness increases by 1.31 (CI: 1.06, 1.61) per one standard deviation change in number of samples per site.

The model run to analyze pathogenic parasite richness had the same format as the previous models (Table 16). There was a positive relationship between parasite richness and season ($p < 0.0001$). An individual's parasite richness increased by 2.53 units (CI: 1.57, 4.09) per one standard deviation change in season with increases in the wet season specifically.

Of all the individual parasite taxon models run, only *Trichostrongylus sp.* and *Strongyloides sp.* showed any relationships with the predictor variables. *Strongyloides sp.* showed a positive relationship with disturbance intensity ($p = 0.01$). For disturbance intensity, a one unit increase is associated with a 0.54 unit (CI 0.11, 0.97) increase in the expected log odds of *Strongyloides sp.* presence probability. For season being the wet season compared to dry, a one unit increase is associated with a 1.77 unit (CI: 0.84, 2.7) increase in the expected log odds of *Strongyloides sp.* presence probability ($p = 0.02$). *Trichostrongylus sp.* reflected a negative relationship with disturbance intensity ($p = 0.02$). For disturbance intensity, a one unit increase is associated with a 0.49 unit (CI -0.91, -0.08) decrease in the expected log odds of *Trichostrongylus sp.* presence probability. For season being the wet season compared to dry, a one unit increase is associated with a 1.30 unit (CI: 0.20, 2.4) increase in the expected log odds of *Trichostrongylus sp.* presence probability ($p = 0.02$).

5. Discussion

Of all samples screened, 85.7% contained at least one parasite, and only in two individual gorillas were no parasites detected. Both of those individual gorillas (CRG368 and CRG373) were only screened once. High prevalence of enteric parasites has been reported in Mountain gorillas (*Gorilla beringei beringei*) and Western Lowland gorillas (*Gorilla gorilla gorilla*) as well with protozoans and nematodes being the most common (Ashford et. al. 1996, Sleeman et. al. 2000, Freeman et. al. 2004). Additionally, in many past surveys co-infection was common and 54% of samples in this study contained more than one parasite taxon. *Prototapirella* sp., a commensal entodiniomorph ciliate was one of the most prevalent taxa in the samples and was detected in 67.709% (N=130 samples and 28 individuals). This is a fairly common protozoan and has been reported in similar prevalence in western lowland gorillas (Freeman et. al. 2004, Pafčo et. al. 2017). *Strongyloides* sp. a potentially pathogenic nematode was also common in this study, found in 43.58% (N=94 samples and 24 individuals). Potentially both *Strongyloides stercoralis* and *Strongyloides fulleborni* were observed because both larvae and eggs were detected but were not distinguished in richness or prevalence calculations. In other studies of gorillas, *Strongyloides* sp. was either not reported or found in lower frequencies (Landsoud-Soukate et. al. 1995, Sleeman et. al. 2000, Kalema-Zikusoka et. al. 2005, Huffman and Chapman 2009).

Commensal ciliate richness in Cross River gorillas at these sites in Nigeria was relatively high compared to apes at other sites. There were five types of symbiotic protozoa (*Troglodytella sp., Gorillaphicus sp.,* unidentified "Type A" entodiniomorph ciliate, unidentified "Type B" entodiniomorph ciliate*,* and *Prototapirella sp.)* present which aid in digestion and can be used as a general indicator of health (Howells et. al. 2011, Masi et. al. 2012). These ciliates facilitate greater digestion of cellulose, which is common in the diet of Cross River gorillas in the dry season

when they ingest more pith and leaves compared to the fruit ingested when it is abundant in the wet season (Landsoud-Soukate et. al. 1995, Masi et. al. 2012). Captive or semi-captive apes may have as few as zero commensal ciliates compared to populations in undisturbed remote areas that can have as many as six symbiotic gut ciliates (Gillespie et. al. 2010, Gillespie unpublished data). Commensal richness was higher at Mbe Mountains Community Forest and Afi Mountain Wildlife Sanctuary than at CRNP-Boshi Extension, though this could be attributed to the limited sample size from CRNP-Boshi Extension and warrants further investigation.

Pathogenic parasite richness included four types of nematodes (*Oesophagostomum sp., Necator sp., Strongyloides sp.,* and *Trichostrongylus sp.*). These parasites have the potential to have serious negative health consequences in hon-human primates with mucosal inflammation, ulceration, iron deficiency anemia, protein malnutrition, dysentery, weight loss, or even death (McClure and Guilloud 1971, DePaoli and Johnsen 1978, Holmes et. al. 1980, Harper III et. al. 1982). Many of these taxa were reported in other gorilla studies as well, *Oesophagostomum* sp. and *Necator sp*. are common in western gorillas as well as mountain gorillas (Ashford et. al. 1996, Sleeman et. al. 2000, Freeman et. al. 2004, Masi et. al. 2012). *Oesophagostomum* sp. and *Necator sp*. have low prevalence (2.26%, 5 samples and five individuals) but *Necator sp*. and *Strongyloides sp* were more common (27.88%, 57 samples and 17 individuals and 43.58% 94 samples and 24 individuals respectively). The presence of these taxa in moderate or even high prevalence is cause for concern and warrants more monitoring for adverse symptoms. Additionally, *Oesophagostomum* sp., *Necator sp*. and *Strongyloides sp*. have been documented in humans as well as apes, and even have demonstrated genetically similar profiles between humans and apes that share the same forest (Hasegawa et. al. 2014, 2016). *S. stercoralis*, is common in humans but rare in wild primates, but may present because of human activity in the habitat like hunting,

trapping, etc. (Pafčo et. al. 2017, Barelli et. al. 2019). Given the small, isolated nature of these Cross River gorilla localities, the risk of severe infections from these parasites could be devastating. It is paramount to conduct further research to assess if there are any clinical symptoms at these sites that could adversely affect the sustainability of this population.

Afi Mountain Wildlife Sanctuary (AMWS) is surrounded by a population of 27,000 people split into 16 villages (Dunn et. al. 2014). Farming is common around the AMWS and may encroach onto the protected land, also there are lots of bush fires in the dry season meant to clear new land. Logging is common in the area, though typically only in the lowlands and not the higher steep slopes preferred by the Cross River gorillas. In recent years there has been a greater push for conservation awareness and decrease in hunting, spurred by a new relationship between the Cross River State Forestry Commission, the Wildlife Conservation Society (WCS) and NCZ. This has led to increasing ranger patrols and stricter enforcement, which in the past was uncommon in the area (Dunn et. al. 2014). The patrol data used in this study indicated that Afi had the greatest number of disturbance events, with 3,367 observed disturbances between September 2017 and August 2018. These disturbances led to an average number of disturbances within the average daily distance traveled by a Cross River gorilla of 281 ± 72 which is the highest of the three sites in the study. In the samples from Afi, had *Strongyloides sp.* in 75.28 % (67 samples 9 individuals) which is significantly higher than at the other two sites. Prevalence of *Trichostrongylus sp.* was also highest at this site (45.49%). Afi also had the highest distribution of pathogenic richness, while commensal richness is comparable to the other sites. Given the history of low enforcement and low engagement with conservation initiatives at this site, as well as low current support, special attention should be paid to the Cross River gorillas of Afi Mountain Wildlife Sanctuary. High prevalence of these parasite taxa, as well as the occurrence of *Oeosophagostomum sp.* and *Necator*

sp., could represent a significant parasite burden. This burden could be exacerbated by physiological stress from hunting on Afi Mountain and high levels of other human disturbance and adversely affect the viability of this site.

Mbe Mountains Community Forest is east of AMWS but separated by a major road. The site is surrounded by around 10,000 people and though it does not have and official protection designation it is managed by the Conservation Association of the Mbe Mountains (CAMM) and receives support from WCS (Dunn et. al. 2014). It's reported that pressure on the forest from hunting, farming and logging is lower than in surrounding areas and there are strict sanctions in place against hunting great apes (Dunn et. al. 2014, Krause et. al. 2019). The SMART patrol only recorded 1570 disturbance incidents between September 2017 and August 2018. Thus, the average number of disturbances within the average daily distance traveled by a Cross River gorilla is 229 ± 55, which is the lowest of the three sites. This site had a greater distribution of commensal parasite richness than the other two sites as evident from the Pairwise-Wilcox test. Mbe Mountains Community Forest displayed more moderate levels of parasite prevalence and richness, paired with high prevalence of commensals. This baseline surveillance of pathogen surveillance at this site shows a potentially healthy level of parasite diversity.

The CRNP-Boshi extension, the most northern known Cross River gorilla locality, is within the greater Okwangwo division of CRNP that is surrounded by 29,000 people and 39 villages with some villages even bisecting the forest (Dunn et. al. 2014). Given its status as a national park, this area is fully protected though poaching and bush fires are still common. CRNP rangers and WCS staff are working to patrol the region and destroy hunting camps and collect wire snares (Dunn et. al. 2014). SMART patrols logged 1004 disturbance incidents at this locality with another 689 in Okwa Hills, another region of the Okwangwo division. CRNP-Boshi extension

showed the lowest distribution of commensal richness, and an intermediate distribution of pathogenic richness. Any inference on patterns of parasitism at this site is limited by the small number of samples collected. Of the 11 samples tested, there were 6 individuals represented of the 20-25 gorillas that are estimated to inhabit the site as of 2014 (Dunn et. al. 2014). While representation of more individual gorillas is beneficial to gain a deeper understanding of health at the site, repeated testing of individual gorillas is invaluable to provide a more comprehensive perspective and determine patterns over an extended period. Individual gorillas at CRNP-Boshi extension were sampled between one and three times, far fewer than many of the others in the study.

The Cross River region of Nigeria has an intense dry season which is longer than lowland tropical forests where western lowland gorillas reside (Wade and Malone 2021). There was no difference in commensal richness between seasons as evidenced by the generalized linear mixed models. These results may indicate the commensal ciliates are persisting though the dry season to aid in the higher fiber and higher cellulose diets as these commensal ciliates are critical in minimizing nutritional stress faced by the Cross River gorillas when preferred food like fruit is more scarce at the height of dry season (Etiendem and Tagg 2013). Environmental conditions during driers months are not favorable for ciliate persistence in the environment, as they run the risk of drying out and dying if outside the host when it is hot and dry. Thus, the persistence of ciliate richness through the dry season is a favorable result for the nutritional status of Cross River gorillas. Ciliates have also been found in higher abundances in western lowland gorillas during the dry season (Masi et. al. 2012).

Seasonal rainfall may affect patterns of parasitism either by affecting parasite survival in the environment, or in response to changes in host body condition or behavior. In this set of

samples, these pathogenic parasites presented higher richness in the wet season than in the dry season as indicated by the results of the generalized linear mixed model which all returned p-values < 0.05. There have been studied of other primates where higher strongyle prevalence and richness was reported in the wet season (Rothman et. al. 2008, Huffman and Chapman 2009, Gillespie et. al. 2010, Benavides et. al. 2012, Petrželková et. al. 2021). Other mammals have shown this trend as well (Waruiru et. al. 2001, Shearer and Ezenwa 2020). The discussion surrounding these seasonal trends usually cites favorable environmental conditions for parasite persistence in fecal pats and soils. During the rainy season the environment is more humid and wet which allows for increased movement of helminth larvae (Stromberg 1997). Warm and moist conditions are necessary for larvae development and movement. There are behavioral changes that have been observed in Cross River gorillas which may indicate a protection from the increased risk of infection during the wet season. Cross River gorillas at Kagwene gorilla sanctuary in Cameroon tend to build night nests on the ground during the dry season and prefer nests in trees during the wet season (De Vere et. al. 2011). Even while in ground nests gorillas tend to surround themselves with herbaceous plants in these ground nests which aims to insulate them from the ground and could serve as a barrier from these infections (Landsoud-Soukate et. al. 1995). The preference for tree nests compared to ground nests seasonally may be an informed choice to minimize ground contact. Western gorillas at Mondika Research center have also been observed to build more nests or perhaps thicker nests, either on the ground or in trees, on rainy days compared to drier days when they may sleep on the bare ground (Mehlman and Doran 2002)

In some studies pathogenic nematodes were detected at higher rates in the dry season in gorillas compared to past studies of chimps where *Oesophagostomum* sp. and other strongyles showed higher rates in the wet season (Masi et. al. 2012, Pafčo et. al. 2017). This pattern likely

reflects a change in resource availability between seasons. It is thought that the dietary changes in gorillas during the dry season are more intense than in chimpanzees whose diet does not change as much. Gorillas are known to shift to a more folivorous diet in the dry season when fruit is scarce, whereas chimpanzees will continue to prefer fruit sources (Landsoud-Soukate et. al. 1995). Cross River gorillas have been observed to consume more leafy, and woody plant sources in the dry season, these sources are available all year but only consumed when fruit availability is low (Oates et. al. 2002). This may lead to more nutritional stress or energy expenditure which creates create susceptibility for strongyle infections (Masi et. al. 2012). The shift to a more herbivorous diet may also increase ground contact and more time spent around rivers and swamps in search of food (Masi et. al. 2012). Perhaps because there is no dry season increase in parasite infections and richness, there is minimal dietary stress on the Cross River gorillas despite their shift in diet. Good host nutrition can increase health status and immune function which minimizes the chance of a serious parasitic infection (Huffman and Chapman 2009). This is supported by the persistence of the entodiniomorph ciliates throughout the year.

Elevation and slope are two frequently discussed determinants of suitable habitat for the Cross River gorillas (De Vere et. al. 2011, Bergl et. al. 2012, Sawyer and Brashares 2013). It is hypothesized that Cross River gorillas preferentially inhabit the higher altitude, precipitously sloped areas of their habitat because human activity is lower in these less accessible areas (Sawyer 2012, Etiendem et. al. 2013). From the data provided by the SMART ranger patrol there were far more disturbance incidents logged at lower altitudes than at higher ones, which may support the idea that there is more human activity in lower altitude, less steep areas compared to the mountainous hillsides the Cross River gorillas favor. Studies of other primates that analyzed the relationship between patterns of parasitism and altitude detected a reduction of parasite richness

in animals at lower altitudes, where there was greater disturbance intensity (Barelli et. al. 2019). There was a weak but positive relationship between altitude and overall parasite richness in the generalized linear mixed model. This relationship was weakened further when commensal richness and pathogenic richness were analyzed individually and neither showed a different pattern. Undoubtedly there are differences in structure, vegetation, and precipitation and other environmental factors that shift over an altitudinal gradient that may affect how parasites persist in the environment as well. Changes in these environmental factors may facilitate greater infections or fewer infections at different altitudes and more site-specific information about tree cover, water availability, etc. is needed. Different types of human activities may also have different influence over parasite richness and prevalence, if there's active farming at lower altitudes that relies on pesticides and fertilizers in the soil there may be a reduction in soil transmitted helminths at lower altitudes which would reflect a different pattern though still determined by human activity (Barelli et. al. 2019). Perhaps looking at steepness of slope may be a more interesting lens to analyze this relationship. Studies that found elevation to be a significant factor in predicting parasite distributions had a much broader range than was reflected by the sample set in this study. The slopes inhabited by Cross River gorillas are far more precipitous than many other populations, whereas their elevation range is more comparable to other gorilla populations. This issue is complex and requires further study to determine what combination of factors is most influential.

Parasite richness and disturbance data were utilized to assess the relationship between enteric parasite communities and anthropogenic disturbance in Cross River gorillas across three sites in Nigeria. The small population size and anthropogenic pressures on the Cross River gorillas make them particularly vulnerable to potential consequences of disease. There is a multitude of literature and reviews that suggests that habitat conservation and biodiversity mitigates disease

risk for primates (Arroyo-Rodriguez and Dias 2010, Keesing et. al. 2010, Gottdenker et. al. 2014). This relationship is broadly attributed to the dilution effect and is well documented in some systems such as Lyme disease, and West Nile Virus (Keesing et. al. 2010, Young et. al. 2013, Civitello et. al. 2015). Alternatively, there are mechanisms that may result in an increase in prevalence, and the amplification effect describes how increasing biodiversity may increase disease risk (Keesing et. al. 2006, Young et. al. 2013). There was no relationship found in any of the models between richness and habitat disturbance.

For two of the helminth taxa found disturbance was a significant factor. *Strongyloides sp.* showed a positive relationship with disturbance intensity. This is troubling given the potential adverse symptoms of a *Strongyloides sp.* infection, and that *Stronglyoides stercoralis* is generally rare in apes and is definitely anthropozoonotic in origin (Sleeman et. al. 2000, Gillespie and Chapman 2006). More serious infections may result in with mucosal inflammation, ulceration, iron deficiency anemia, protein malnutrition, dysentery, weight loss, or even death and lesser infections may result in a general reduction in host fitness (McClure and Guilloud 1971, DePaoli and Johnsen 1978, Holmes et. al. 1980, Harper III et. al. 1982). In a population of Western Lowland gorillas in Bai Hoku where human density is low, approximately 1 person per km^2, *Strongyloides sp.* eggs were found in only 20% of samples. Comparatively, 75.28% of samples from Afi Mountain Wildlife Sanctuary contained *Strongyloides sp.* At Bwindi Impenetrable National Park in Uganda, the Mountain gorillas there exhibited weight loss, declining body condition and poor haircoats and after being given anthelminthic drugs showed incredible clinical improvements (Petrželková et. al. 2021). Patterns of *Strongyloides sp.* infection could be altered by human disturbance in several ways. Trails created by humans have been shown to increase ground contact in chimpanzees and thus increased helminth infections (Zommers et. al. 2013). Logging alters the

forest structure which in turn may alter parasite and host ecology, and increased stump density as a measure of disturbance intensity explained nematode infections in red colobus monkeys (Gillespie and Chapman 2006).

The second parasite taxon where site was a significant determinant in presence vs. absence was *Trichostrongylus sp.* which showed a negative relationship with disturbance. The model result indicating a negative relationship is a conflicting result with *Trichostrongylus sp.* following disturbance patterns across sites. *Trichostrongylus sp.* prevalence was highest at Afi Mountain Wildlife Sanctuary (45.49%) where disturbance levels were highest and had significantly lower prevalence (20.9%) at Mbe Mountains Community Forest where disturbance intensity was much lower. *Trichostrongylus sp.* is commonly shared between humans and livestock, particularly common in cattle (Craig 2009). Afi has reportedly high levels of farming in the surrounding areas, and may even encroach upon the gorilla habitat in the sanctuary (Dunn et. al. 2014). The disturbance intensity variable used in modeling was heavily influenced by hunting and trapping, which may be less effective predictors of *Trichostrongylus sp.* given its typical association with livestock. Incorporating data more directly linked on site proximity to livestock, or livestock density may help to better define the patterns of *Trichostrongylus sp..*

Among sites, Afi Mountain Wildlife Sanctuary,had the highest level of disturbance intensity and also had the highest levels of pathogenic parasite richness. The opposite was true for Mbe Mountains Community Forest, which had the lowest disturbance intensity and the highest amount of commensal richness. Afi also has reportedly less support for conservation and poaching restrictions compared to Mbe Mountains Community Forest which has strong community support and awareness (Dunn et. al. 2014). More research is needed to determine the mechanisms of transmission and determine more specifically why there are such high levels of parasite prevalence

at Afi Mountain Wildlife Sanctuary. Genetic work to identify the species of prasites present will also help to strengthen the understanding of the health risks these populations face. *Necator sp., Strongyloides sp. Oesophagostomum sp.,* and *Trichostrongylus sp.* can also be found in humans and transmitted between humans and wildlife (Landsoud-Soukate et. al. 1995). Certain species of these taxa are more commonly detected in human populations and other species are more common in wildlife. Determining which species are present will better clarify how much interspecies transmission is occurring, and if there are species present with known pathogenicity, like *Strongyloides fuelleborni*. The range of results across the literature suggests that zoonotic disease systems can be quite complex with varying mechanisms and ecological forces at play. The results of this study support the idea that parasite systems in primates are complex in nature, and an increase in anthropogenic disturbance may influence certain parasite taxa though there are likely other determinants as well. It is also important to assess which aspects of parasite transmission are being affected by various forms of human disturbance. The hunting and trapping that were so highly reported by SMART patrols, will have different effects on host susceptibility and encounter rates than disturbance from logging for example.

This study represents the first survey of gastrointestinal parasites in Cross River gorillas in Nigeria. By completing a first baseline assessment of patterns of parasitism in this population we have started to build a comprehensive understanding of the health of this threatened species. The longitudinal data with repeated samplings from known individuals provided a robust picture of the patterns of parasitism at these few sites. Inference at CRNP-Boshi Extension was limited by the sample size, and more samples from this site in the future would allow for a more thorough analysis. Further research is needed to determine the transmission mechanisms, particularly for the nematode species (*Oesophagostomum* sp., *Necator sp*., *Trichostrongylus sp.,* and *Strongyloides*

sp.) that have been found in humans in the past. It would be interesting to sample humans, livestock, and other domestic animals in the area to see if there are similar species compositions, or genetic profiles of the parasites detected. A closer look at the different types of human activity in the region could also show more direct relationships with specific taxa and more specifically identify activity that places this population at risk. Additionally, these three sites in the study are only a few of the thirteen known localities of Cross River gorilla, which are all unique with individual ecologic and anthropogenic settings. Samplings at each site that provided as much data, with as much depth as those in this study could be used to look more broadly at the entire Cross River gorilla population, and determine which subpopulations are most vulnerable. A broader scale may also provide greater insight into anthropogenic influence on the health of these gorillas, given the heterogeneity of the landscape and the communities who inhabit the region both in Nigeria and Cameroon.

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7. Tables

Table 1 Frequency of samples from different Cross River gorilla individuals

Gorilla ID	Frequency (N=)	Site
CRG20	1	Mbe
CRG219	1	Afi
CRG226	1	Mbe
CRG230	1	Afi
CRG326	2	Mbe
CRG339	1	Mbe
CRG352	1	Mbe
CRG368	1	Afi
CRG369	1	Afi
CRG370	1	Afi
CRG373	1	CRNP-Boshi Extension
CRGor_01	7	Mbe
CRGor_02	11	Mbe
CRGor_03	6	Mbe
CRGor_04	16	Mbe
CRGor_05	6	Mbe
CRGor_06	8	Mbe
CRGor_07	17	Mbe

CRGor_08	14	Afi
CRGor_09	13	Afi
CRGor_10	11	Afi
CRGor_11	34	Afi
CRGor_12	12	Afi
CRGor_13	1	Afi
CRGor_14	3	CRNP-Boshi Extension
CRGor_15	5	Mbe
CRGor_16	2	CRNP-Boshi Extension
CRGor_18	4	Mbe
CRGor_21	3	Mbe
CRGor_22	2	Mbe
CRGor_23	3	CRNP-Boshi Extension
CRGor_24	1	CRNP-Boshi Extension
CRGor_25	2	CRNP-Boshi Extension
CRGor_26	3	Mbe
No ID	156	

Table 2 Prevalence of intestinal helminth and protozoan taxa estimated by random effects models in samples from Cross River Gorillas at Afi Mountain Wildlife Sanctuary, Mbe Mountains Community Forest, and the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =196).

Parasite Taxon	Samples tested positive	Individuals Tested positive (n =34)	Total Prevalence (%)	Std. Error
l	27	14	13.76	2.89
Gorillaphicus sp.	10	7	5.05	1.66
unidentified "Type A" entodiniomorph ciliate	9	7	4.77	1.65
unidentified "Type B" entodiniomorph ciliate	15	9	8.06	2.54
Prototapirella sp.	130	28	67.79	15.11
Oesophagostomum sp.	5	5	2.26	1.13
Necator sp.	5	4	2.26	1.13
Strongyloides sp.	94	24	43.58	6.27
Trichostrongylus sp.	57	17	27.88	4.67

Table 3 Prevalence of intestinal helminth and protozoan taxa estimated by random effects models in samples from Cross River Gorillas at Afi Mountain Wildlife Sanctuary between November 20, 2016, and March 20, 2018 (n =89).

Parasite Taxon	Samples tested positive	Individuals Tested positive (n =11)	Total Prevalence	Std. Error
Troglodytella sp.	8	5	9.28	3.37
Gorillaphicus sp.	4	3	4.50	2.21
unidentified "Type A" entodiniomorph ciliate	4	3	5.20	2.86
unidentified "Type B" entodiniomorph ciliate	4	2	4.21	3.36
Prototapirella sp.	62	9	70.36	5.33
Oesophagostomum sp.,	4	4	4.49	2.21
Necator sp.	4	3	4.49	2.21
Strongyloides sp.	67	9	75.28	4.60
Trichostrongylus sp.	37	9	45.49	8.14

Table 4 Prevalence of intestinal helminth and protozoan taxa estimated by random effects models in samples from Cross River Gorillas at Mbe Mountains Community Forest between November 20, 2016, and March 20, 2018 (n =96).

Parasite Taxon	Samples tested positive	Individuals Tested positive (n =17)	Total Prevalence	Std. Error
Troglodytella sp.	19	9	19.79	4.09
Gorillaphicus sp.	6	4	6.01	2.64
unidentified "Type A" entodiniomorph ciliate	5	4	5.25	2.40
unidentified "Type B" entodiniomorph ciliate	11	7	11.84	3.86
Prototapirella sp.	63	16	65.63	4.87
Oesophagostomum sp.,	1	1	1.05	1.06
Necator sp.	1	1	1.19	1.22
Strongyloides sp.	21	11	21.88	4.24
Trichostrongylus sp.	19	8	20.39	5.22

Table 5 Prevalence of intestinal helminth and protozoan taxa estimated by random effects models in samples from Cross River Gorillas at the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =11).

Parasite Taxon	Samples tested positive	Individuals Tested positive (n =6)	Total Prevalence	Std. Error

Troglodytella sp.	0	0	0	0
Gorillaphicus sp.	0	0	0	0
unidentified "Type A" entodiniomorph ciliate	0	0	0	0
unidentified "Type B" entodiniomorph ciliate	0	0	0	0
Prototapirella sp.	5	4	45.86	16.79
Oesophagostomum sp.	0	0	0	0
Necator sp.	0	0	0	0
Strongyloides sp.	6	4	54.14	16.79
Trichostrongylus sp.	1	1	9.10	9.18

Table 6 Frequency and proportion of parasite richness of all samples collected from Cross River Gorillas at Afi Mountain Wildlife Sanctuary, Mbe Mountains Community Forest, and the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =196).

Number of parasite taxon	Proportion of Samples (%)	Number of samples (n = 196)	Number of Individuals
0	14.28	28	18
1	29.59	58	22
2	26.02	51	22
3	20.41	40	14

4	8.67	17	11
5	1.02	2	2

Table 7 Frequency and proportion of commensal parasite richness of all samples collected from Cross River Gorillas at Afi Mountain Wildlife Sanctuary, Mbe Mountains Community Forest, and the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =196).

Number of parasite taxon	Proportion of Samples (%)	Number of samples (n =196)	Number of individuals
0	14.28	58	23
1	29.59	92	27
2	26.02	35	16
3	20.41	10	7
4	8.67	1	1

Table 8 Frequency and proportion of pathogenic parasite richness of all samples collected from Cross River Gorillas at Afi Mountain Wildlife Sanctuary, Mbe Mountains Community Forest, and the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =196).

Number of parasite taxon	Proportion of Samples (%)	Number of samples (n =196)	Number of Individuals
0	42.35	83	23

1	35.2	69	24
2	19.89	39	14
3	25.51	5	4

Table 9 Frequency and proportion of parasite richness of samples grouped by site collected from Cross River Gorillas at Afi Mountain Wildlife Sanctuary, Mbe Mountains Community Forest, and the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =196).

	AFI (N=89)			BOSHI (N=11)			MBE (N=96)		
Number of parasite taxon	Number of samples	Number of Individuals	Proportion of Samples (%)	Number of samples	Number of Individuals	Proportion of Samples (%)	Number of samples	Number of Individuals	Proportion of Samples (%)
0	6	4	6.74	5	4	45.45	17	10	17.71
1	22	5	24.72	1	1	9.09	36	16	37.5
2	22	7	24.72	4	4	36.36	25	12	26.04
3	27	6	30.34	1	1	9.09	12	7	12.5
4	10	6	11.24	0		0	7	5	7.29
5	2	2	2.25	0		0	0	0	0

Table 10 Frequency and proportion of commensal parasite richness of samples grouped by site collected from Cross River Gorillas at Afi Mountain Wildlife Sanctuary, Mbe Mountains Community Forest, and the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =196).

	AFI (N=89)			BOSHI (N=11)			MBE (N=96)		
Number of parasite taxon	Number of samples	Number of Individuals	Proportion of Samples (%)	Number of samples	Number of Individuals	Proportion of Samples (%)	Number of samples	Number of Individuals	Proportion of Samples (%)
0	24	7	26.97	6	4	54.55	29	12	30.21
1	49	8	55.06	5	4	45.45	38	16	39.58
2	13	6	14.61	0	0	0	22	10	22.92
3	3	2	3.37	0	0	0	7	5	7.29
4	0	0	0	0	0	0	1	1	1.04

Table 11 Frequency and proportion of pathogenic parasite richness of samples grouped by site collected from Cross River Gorillas at Afi Mountain Wildlife Sanctuary, Mbe Mountains Community Forest, and the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =196).

	AFI (N=89)			BOSHI (N=11)			MBE (N=96)		
Number of parasite taxon	Number of samples	Number of Individuals	Proportion of Samples (%)	Number of samples	Number of Individuals	Proportion of Samples (%)	Number of samples	Number of Individuals	Proportion of Samples (%)

0	16	5	17.98	5	4	38.46	62	15	64.58
1	37	7	41.57	5	4	38.46	28	14	29.17
2	32	8	35.96	1	1	7.69	6	5	6.25
3	4	3	4.49	0	0	0.00	1	1	1.04

Table 12 Frequency and proportion of number of disturbances within Cross River gorilla daily travel distance per sample collected from Cross River Gorillas at Afi Mountain Wildlife Sanctuary, Mbe Mountains Community Forest, and the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =235).

	ALL (N=235)	
Range	Frequency (n =)	Proportion (%)
0-100	3	1.28
100-150	10	4.26
150-200	37	15.74
200-250	73	31.06
250-300	55	23.40
300-350	34	14.47
350-400	23	9.79

Table 13 Frequency and proportion of number of disturbances within Cross River gorilla daily travel distance per sample collected from Cross River Gorillas at Afi Mountain Wildlife Sanctuary, Mbe Mountains Community Forest, and the Boshi extension of Cross River National Park between November 20, 2016, and March 20, 2018 (n =196).

	AFI (N=111)		BOSHI (N=13)		MBE (N=111)	
Range	Frequency	Proportion (%)	Frequency	Proportion (%)	Frequency	Proportion (%)
0-100	2	1.80	1	7.69	0	0
100-150	3	2.70	0	0.00	7	6.31
150-200	4	3.60	2	15.38	31	27.93
200-250	31	27.93	3	23.08	39	35.14
250-300	31	27.93	7	53.85	17	15.32
300-350	17	15.32	0	0.00	17	15.32
350-400	23	20.72	0	0.00	0	0

Table 14 Estimated regression parameters, standard errors, z-values, and P-values for the Conway-Maxwell-Poisson GLMM presented in equation (1) against complete parasite richness. The estimated value for,$\sigma_{\text{GorillaID}}$ is 3.0 x10^{-10} and $\sigma_{\text{Date is}}$ 0.049.

Parameter	Estimate	Std. Error	Z value	P value	Exp(Estimate)	Exp(95% CI)
Intercept	0.20	0.12	1.62	0.11	1.22	(0.96, 1.56)
Disturbance1.5	-0.01	0.06	-0.14	0.89	0.99	(0.89, 1.11)

Altitude	0.11	0.06	1.79	0.07	1.11	(0.99,1.26)
Individual Sample Counts	-0.03	0.05	-0.48	0.63	0.97	(0.88,1.08)
Site Sample counts	0.17	0.07	2.37	0.02*	1.19	(1.03,1.37)
Sex	0.19	0.10	1.82	0.07	1.21	(0.99,1.48)
Season	0.47	0.14	3.33	0.001*	1.60	(1.21,2.10)

Table 15 Estimated regression parameters, standard errors, z-values, and P-values for the Conway-Maxwell-Poisson GLMM presented in eqn (1) against commensal parasite richness. The estimated value for, $\sigma_{GorillaID}$ is 3.0×10^{-10} and $\sigma_{Date\ is}$ 0.049.

Parameter	Estimate	Std. Error	Z value	P value	Exp(Estimate)	Exp(95% CI)
Intercept	-0.21	0.15	-1.38	0.17	0.81	(0.61,1.09)
Disturbance1.5	-0.02	0.07	-0.25	0.80	0.98	(0.85,1.13)
Altitude	0.10	0.08	1.32	0.19	1.11	(0.95,1.29)
Individual Sample Counts	-0.09	0.07	-1.18	0.24	0.92	(0.79,1.06)
Site Sample counts	0.27	0.11	2.50	0.01*	1.31	(1.06,1.61)
Sex	0.20	0.13	1.62	0.11	1.23	(0.96,1.57)
Season	0.11	0.18	0.62	0.54	1.11	(0.79,1.57)

Table 16 Estimated regression parameters, standard errors, z-values, and P-values for the Conway-Maxwell-Poisson GLMM presented in eqn (1) against pathogenic parasite richness. The estimated value for, $\sigma_{GorillaID}$ is 3.0×10^{-10} and $\sigma_{Date\ is}$ 0.049.

Parameter	Estimate	Std. Error	Z value	P value	Exp(Estimate)	Exp(95% CI)
Intercept	-0.93	0.21	-4.45	<0.001	0.39	(0.26,0.59)
Disturbance1,5	-0.001	0.08	-0.02	0.99	1.00	(0.86,1.16)
Altitude	0.09	0.09	1.07	0.28	1.10	(0.92, 1.31)
Individual Sample Counts	0.04	0.11	0.38	0.71	1.04	(0.84, 1.29)
Site Sample counts	0.06	0.09	0.66	0.51	1.06	(0.88, 1.28)
Sex	0.14	0.20	0.68	0.49	1.15	(0.78, 1.69)
Season	0.93	0.24	3.80	<0.001*	2.53	(1.57, 4.09)

8. Figures

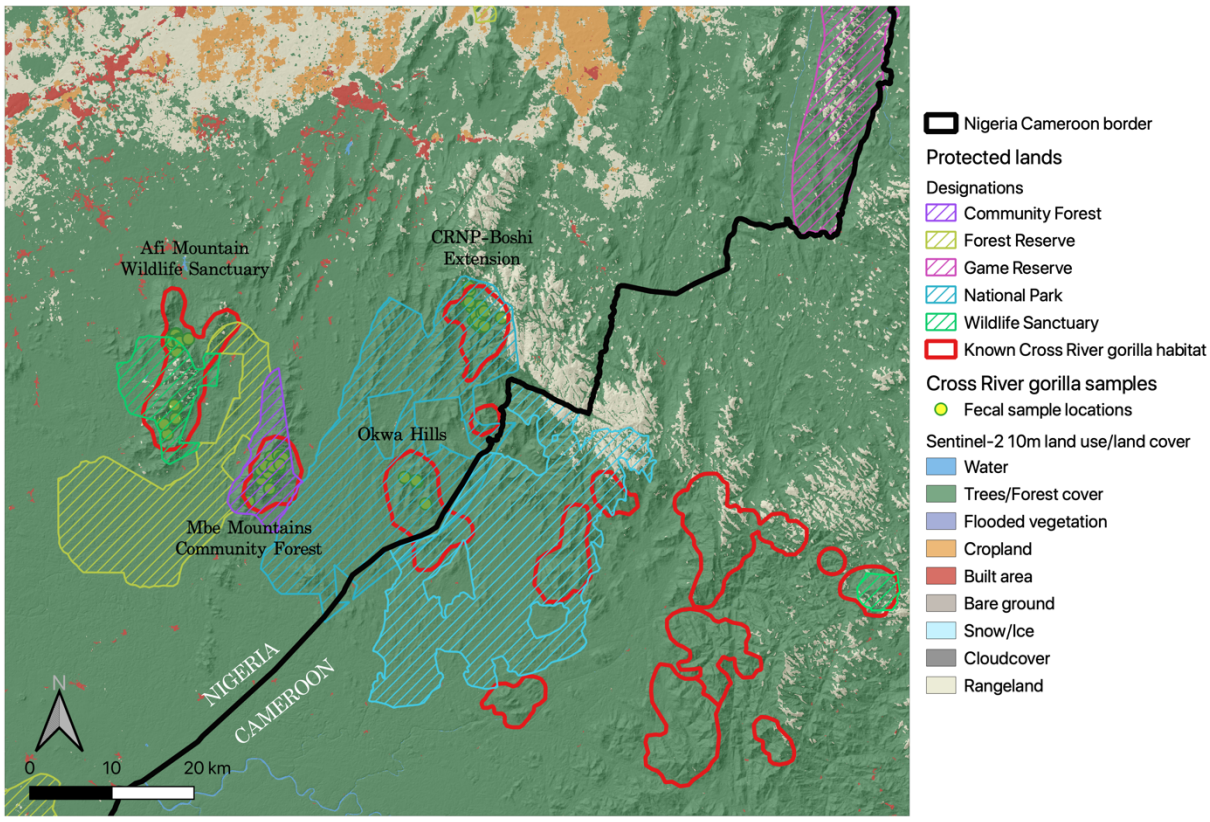
Afi Mountain
Wildlife Sanctuary
CRNP-Boshi
Extension
Okwa Hills
Mbe Mountains
Community Forest
NIGERIA
CAMEROON
N
0
10
20 km
Nigeria Cameroon border
Protected lands
Designations
Community Forest
Forest Reserve
Game Reserve
National Park
Wildlife Sanctuary
Known Cross River gorilla habitat
Cross River gorilla samples
Fecal sample locations
Sentinel-2 10m land use/land cover
Water
Trees/Forest cover
Flooded vegetation
Cropland
Built area
Bare ground
Snow/Ice
Cloudcover
Rangeland

Figure 1 Map of known Cross River gorilla distribution in Cameroon. The protected lands information came from Protected Planet (UNEP-WCMC and IUCN 2023). The Cross River gorilla habitat was adapted from the 2014 Revised Regional Action plan (Dunn et. al. 2014). The LULC data is the Sentinel-2 10m land use/land cover time series of the world. Produced by Impact Observatory, Microsoft, and Esri (Kontgis et. al. 2021). The western most group of samples is in the Afi Mountain Wildlife Sanctuary, the Eastern and most Northern group of samples is in CRNP-Boshi Extension, and the central group within the community forest is in the Mbe Mountains Community Forest. The smaller set of samples just west of the Cameroon-Nigerian border is Okwa-Hills within CRNP.

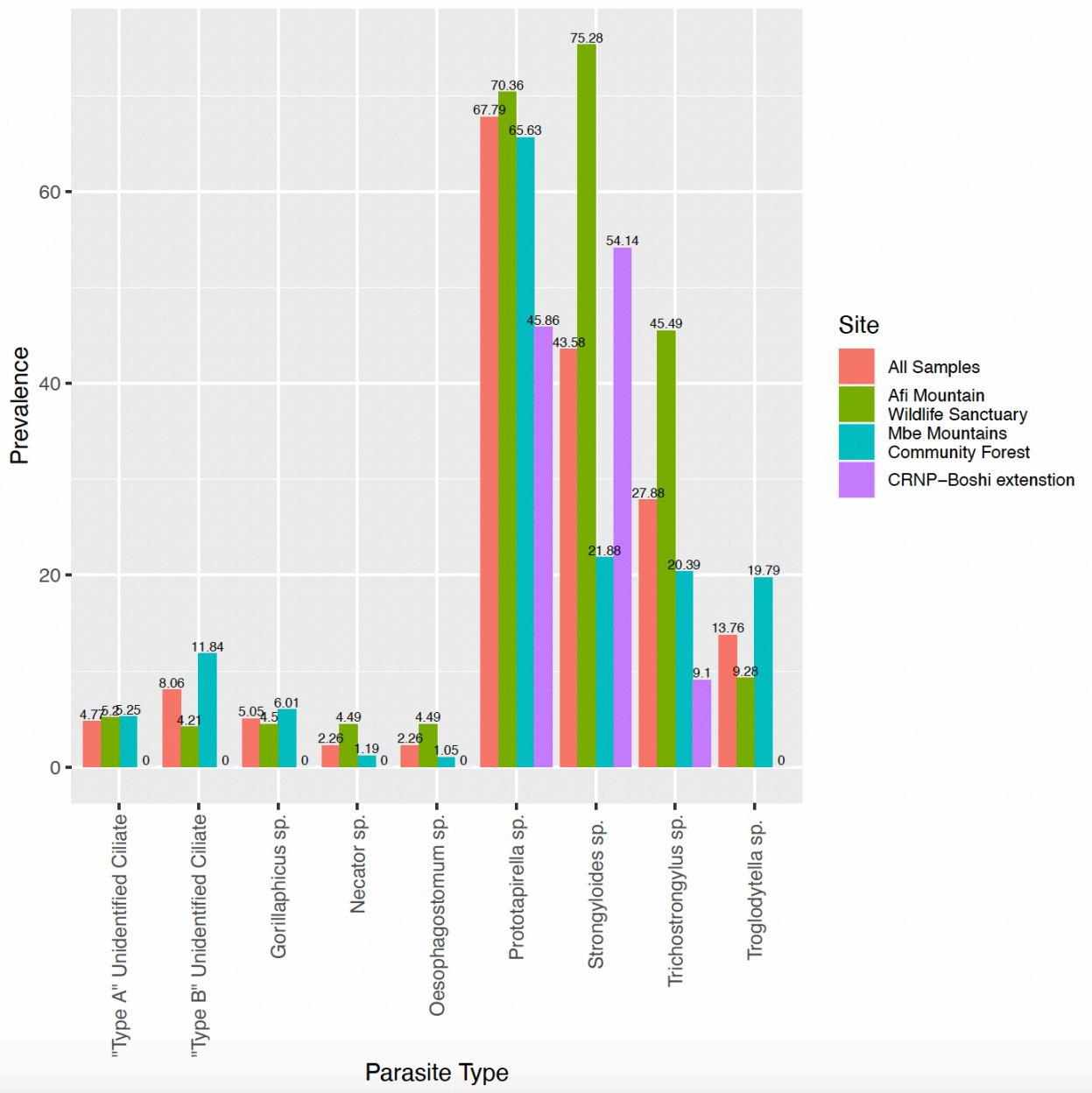
Prevalence
0
20
40
60
4.77
5.5
5.25
0
8.06
4.21
11.84
0
5.05
4.5
6.01
0
2.26
4.49
1.19
0
2.26
4.49
1.05
0
67.79
70.36
65.63
45.86
43.58
75.28
21.88
54.14
27.88
45.49
20.39
9.1
13.76
9.28
19.79
0
"Type A" Unidentified Ciliate
"Type B" Unidentified Ciliate
Gorillaphicus sp.
Necator sp.
Oesophagostomum sp.
Prototapirella sp.
Strongyloides sp.
Trichostrongylus sp.
Troglodytella sp.
Parasite Type
Site
All Samples
Afi Mountain Wildlife Sanctuary
Mbe Mountains Community Forest
CRNP–Boshi extenstion

Figure 2 Bar chart of prevalence estimated by mixed effects models of enteric parasites in Cross River gorilla (*Gorilla gorilla diehli*) samples measured at three sites in Nigeria.

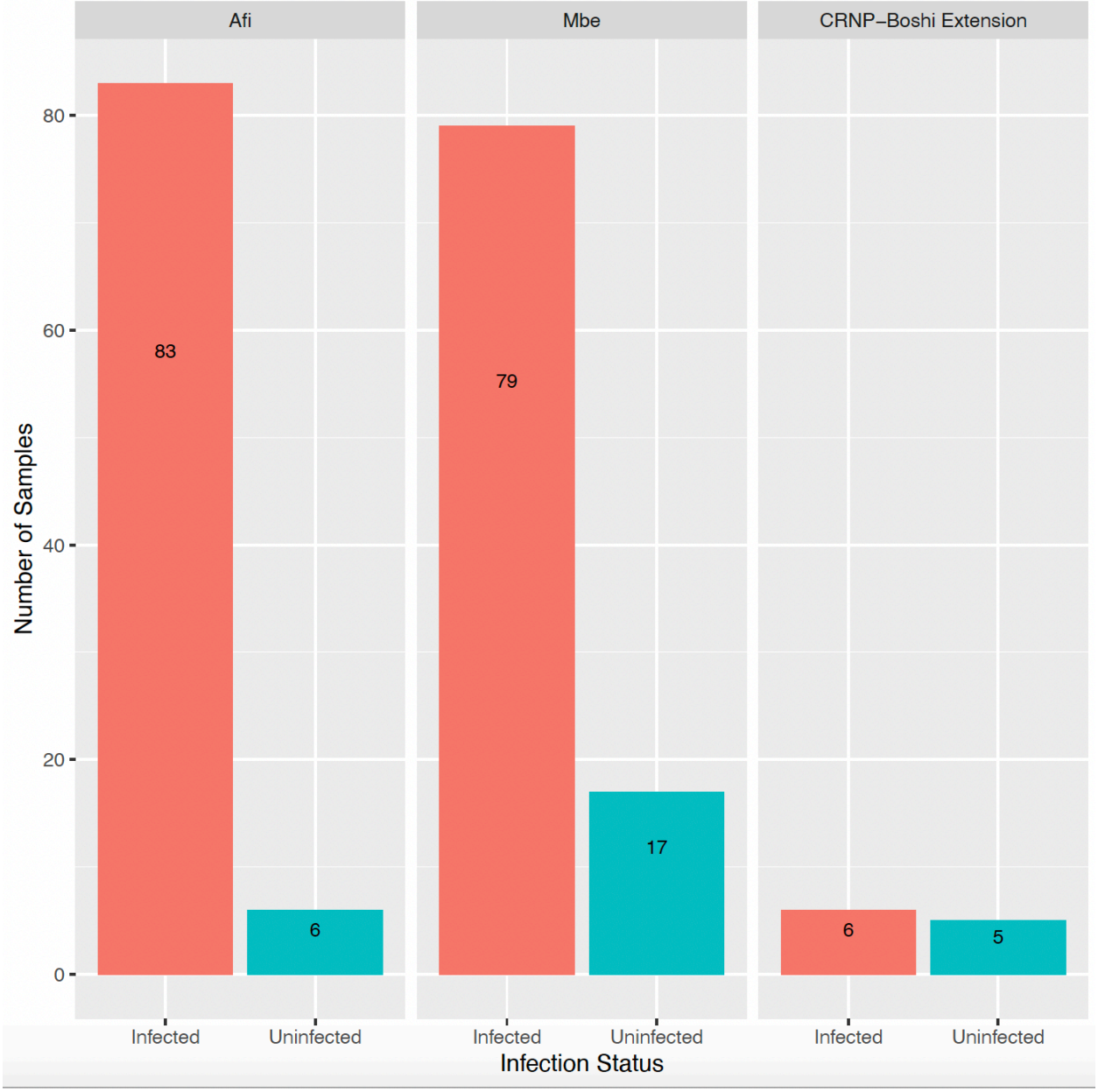

Figure 3 Histogram of samples infected with enteric parasites and uninfected samples in Cross River gorillas (*Gorilla gorilla diehli*) measured at three sites in Nigeria.

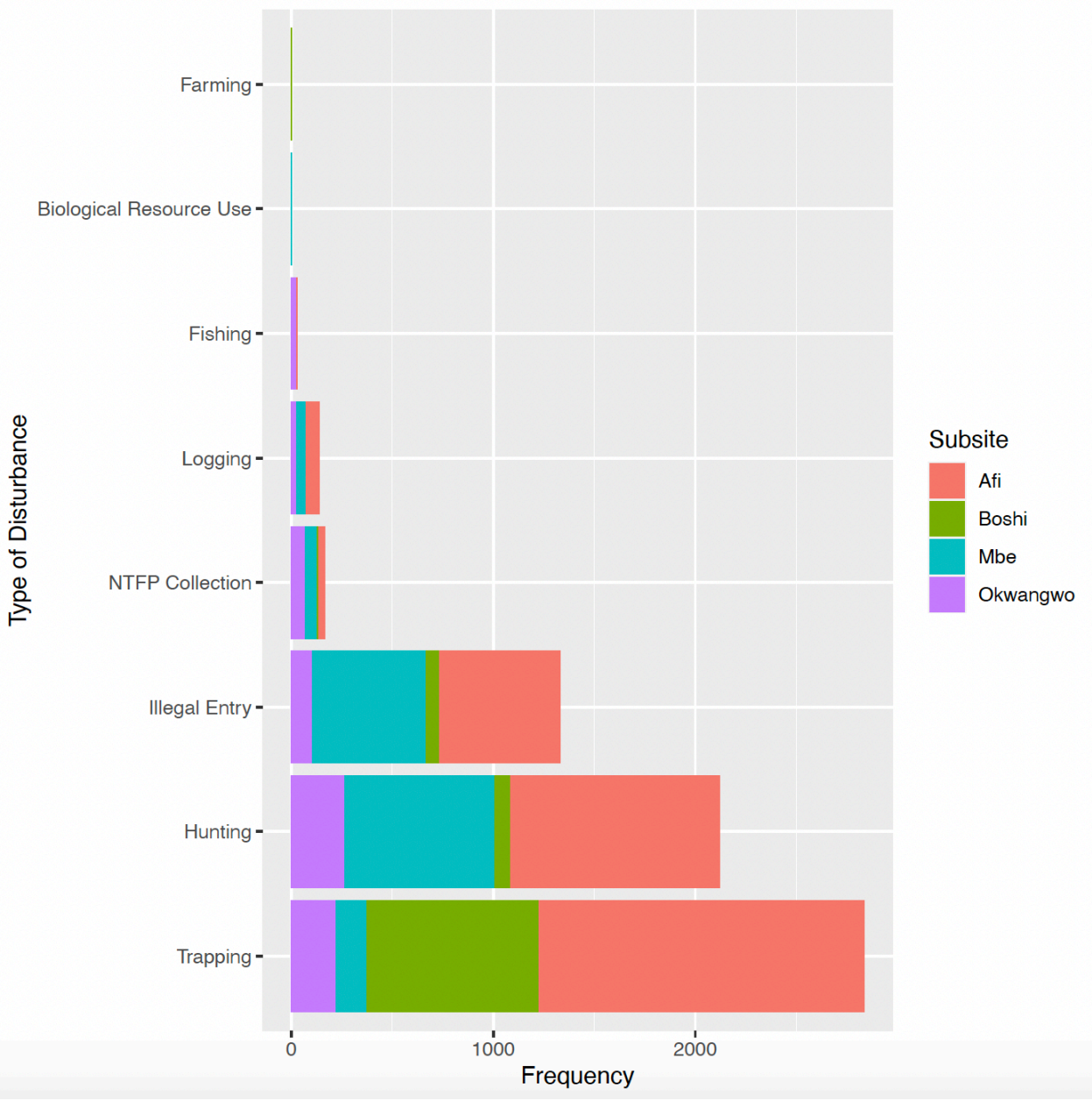

Figure 4 Histogram of anthropogenic disturbances recorded by Nigerian SMART patrols at four sites in Nigeria and sorted by disturbance type.

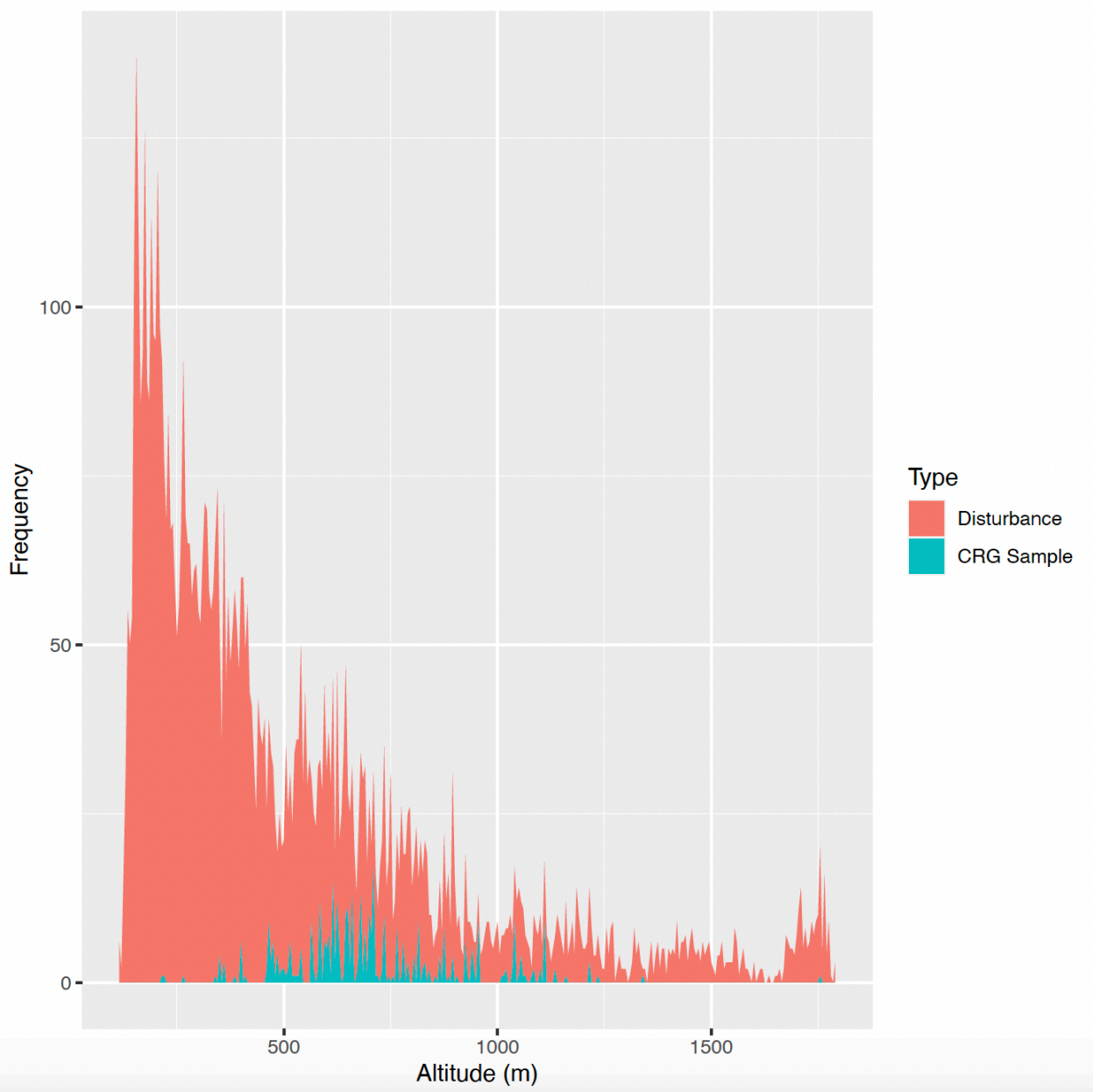

Figure 5 Frequency of number of disturbance observations and Cross River gorilla fecal samples at different altitudes (m).

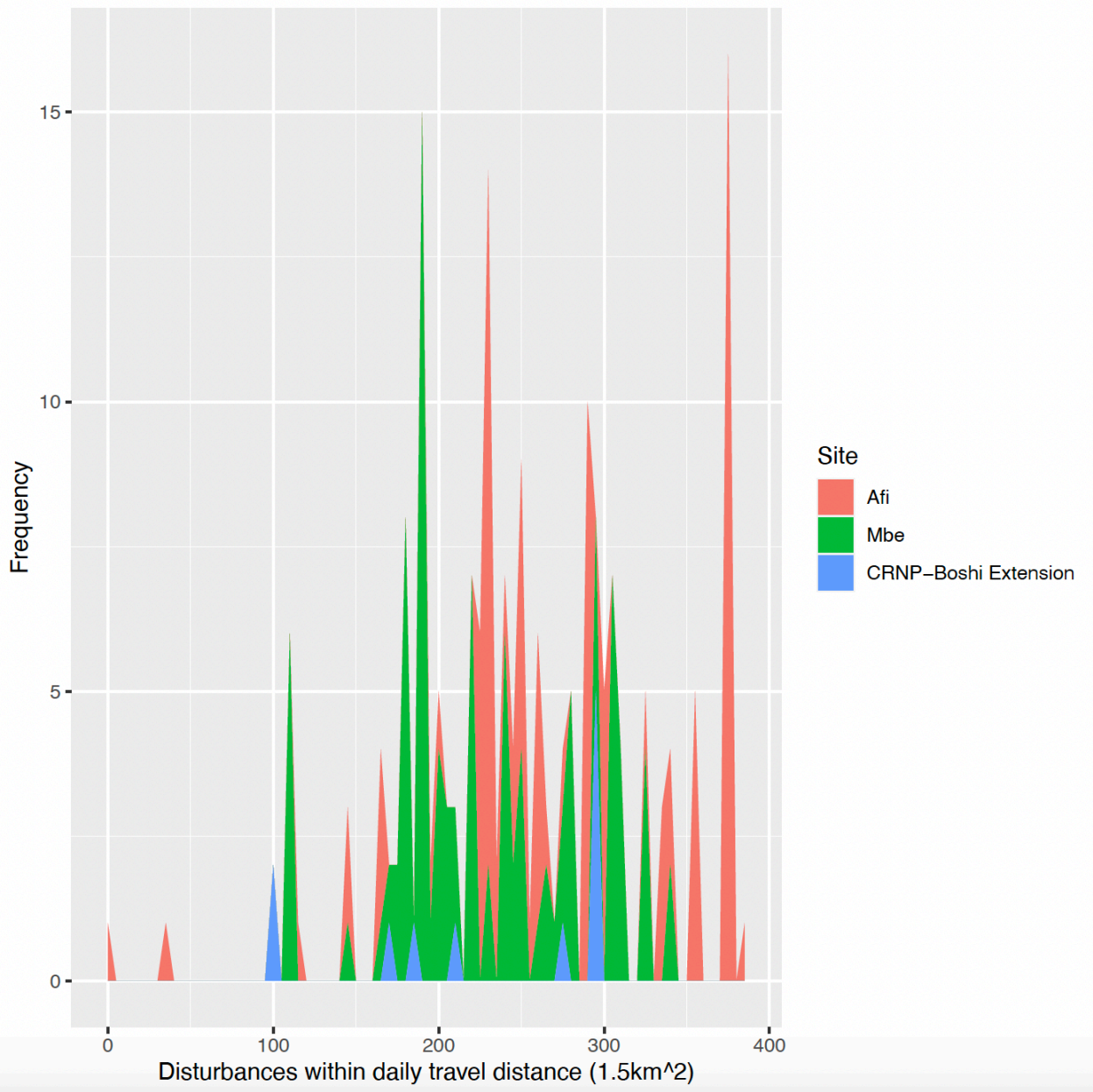

Figure 6 Frequency of number of disturbance observations within a radius of a Cross River gorilla daily travel distance (1.5km^2) grouped by site.

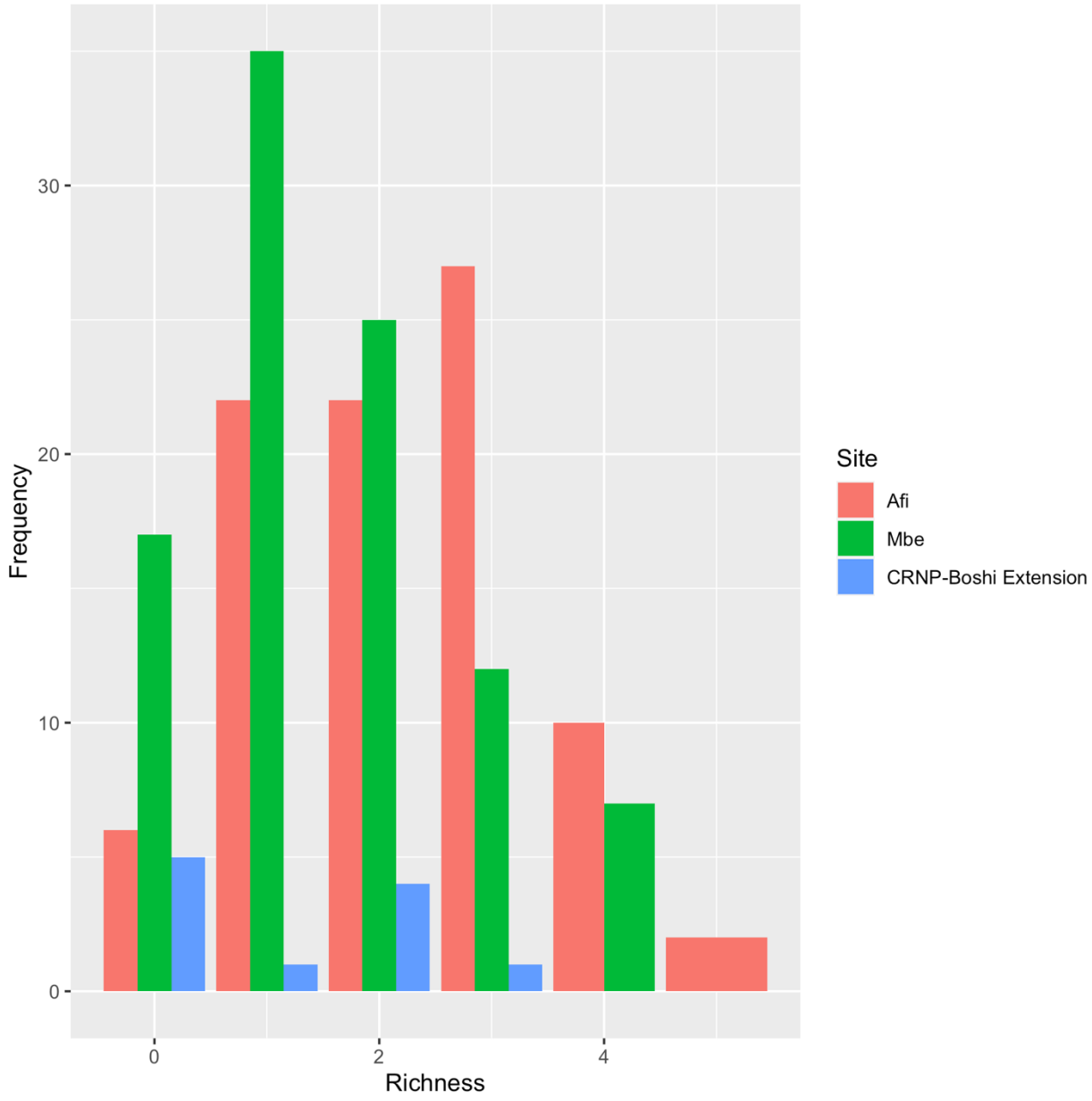

Figure 7 Histogram of enteric parasite richness in Cross River gorillas (*Gorilla gorilla diehli*) fecal samples measured at three sites in Nigeria.

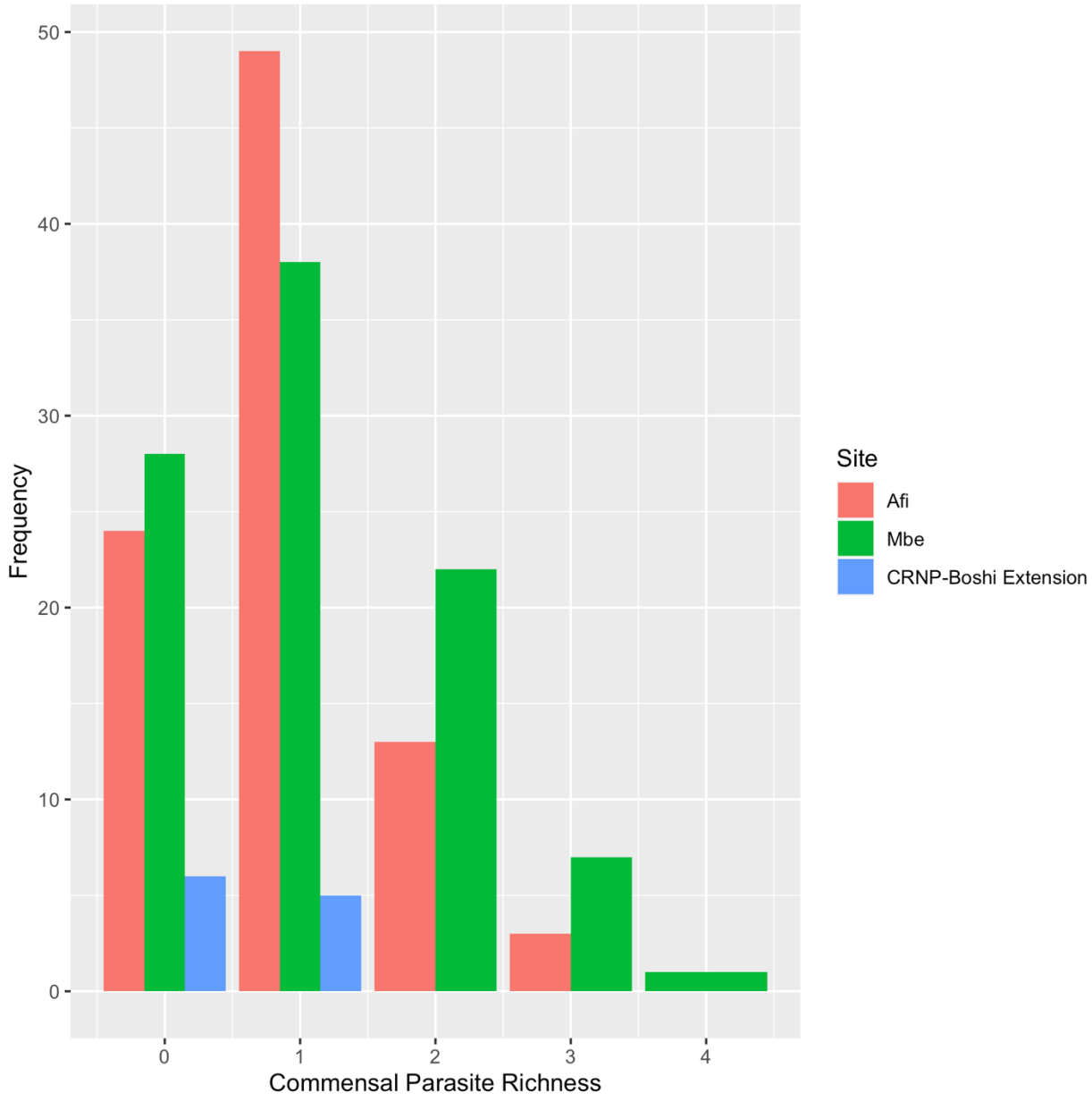

Figure 8 Histogram of commensal richness in Cross River gorillas (*Gorilla gorilla diehli*) fecal samples measured at three sites in Nigeria. Species included are: *Troglodytella sp., Gorillaphicus sp.,* unidentified "Type A" entodiniomorph ciliate, unidentified "Type B" entodiniomorph ciliate, and *Prototapirella sp.*.

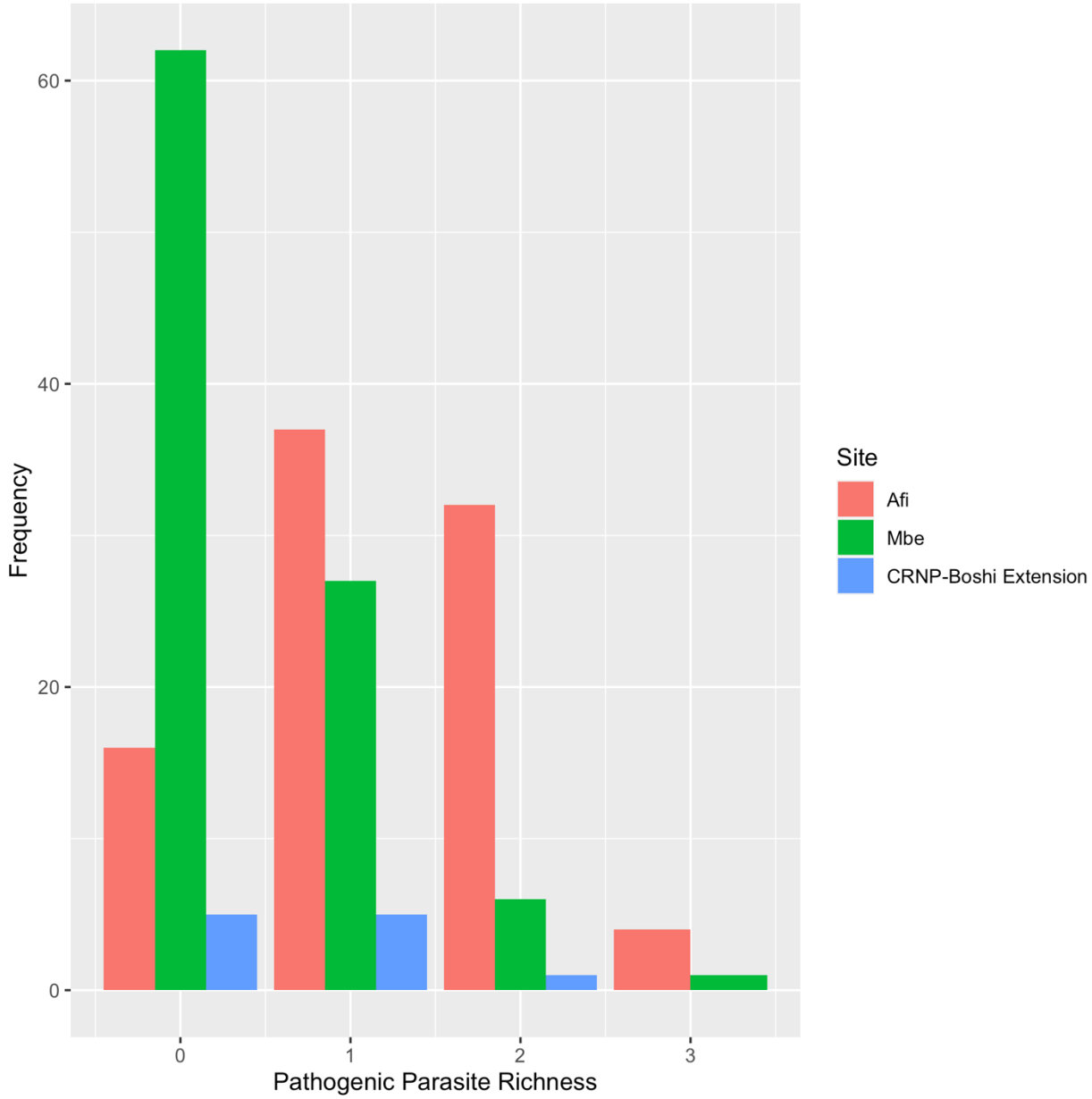

Figure 9 Histogram of pathogenic parasite richness in Cross River gorillas (*Gorilla gorilla diehli*) fecal samples measured at three sites in Nigeria. Species included are: *Oesophagostomum sp., Necator sp., Strongyloides sp.,* and *Trichostrongylus sp.*.

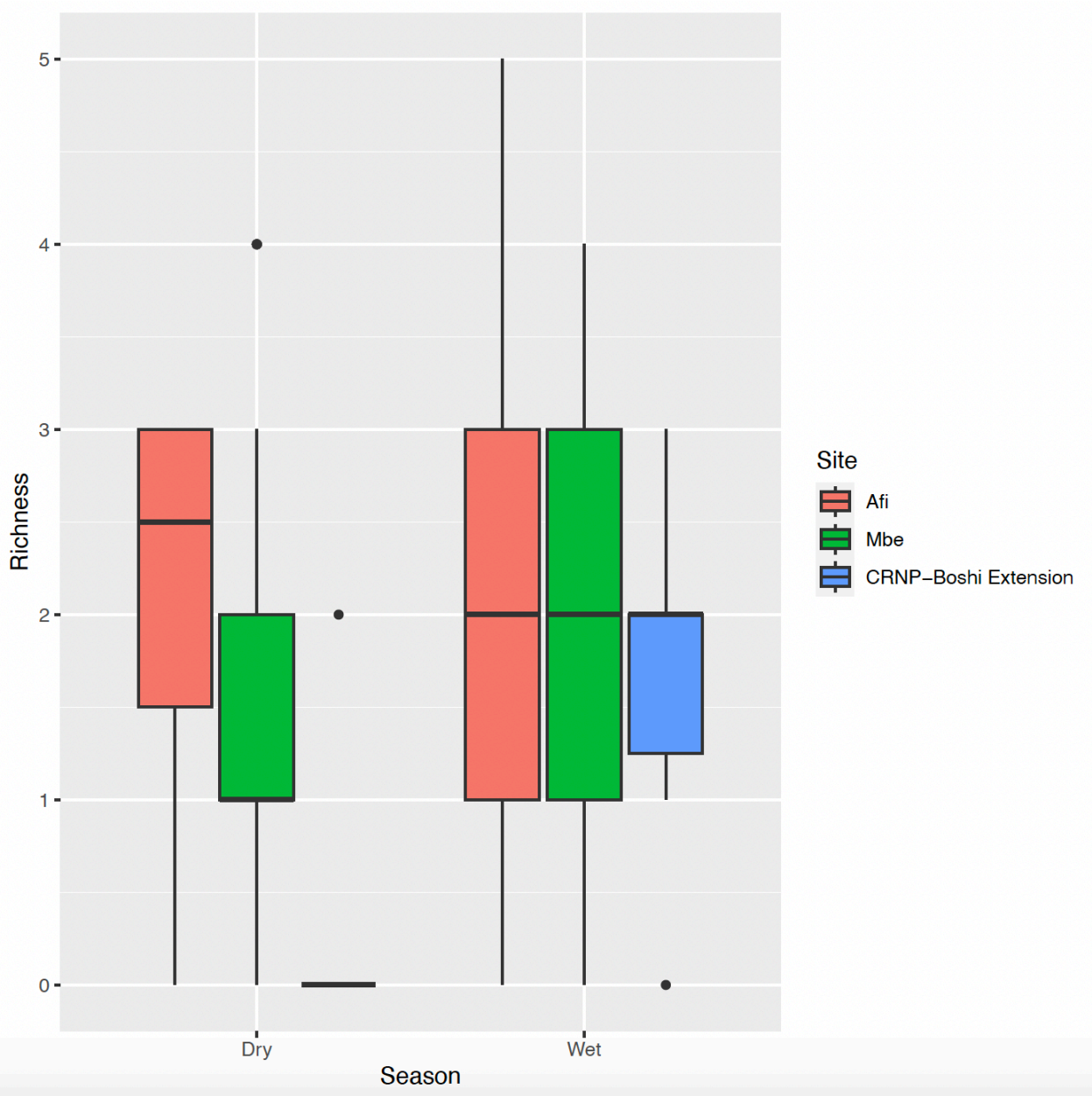

Figure 10 Boxplot of enteric parasite richness in Cross River gorilla (*Gorilla gorilla diehli*) samples measured at three sites in Nigeria samples grouped by seasonality of collection date.

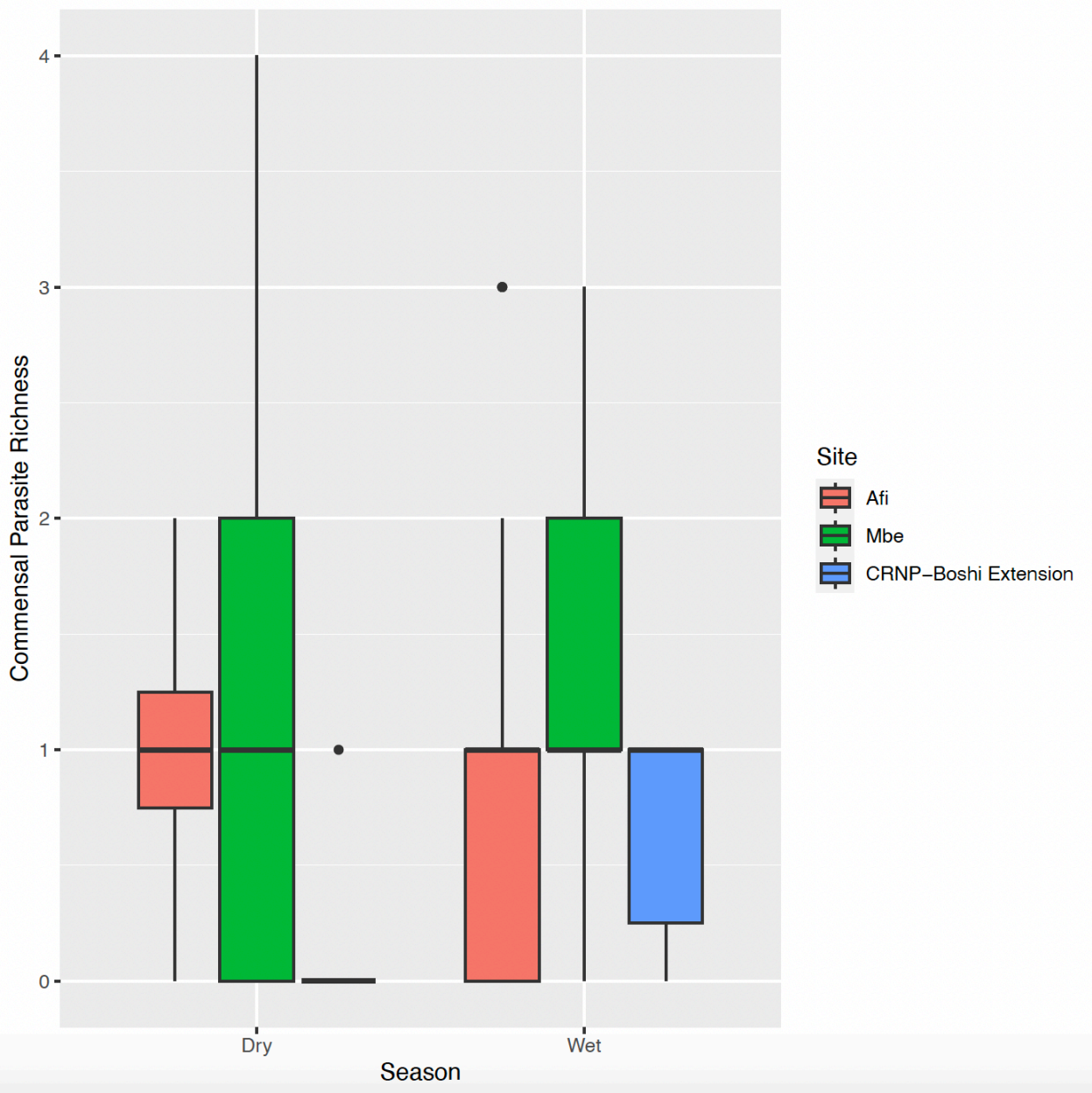

Figure 11 Boxplot of commensal parasite richness in Cross River gorilla (*Gorilla gorilla diehli*) samples measured at three sites in Nigeria samples grouped by seasonality of collection date. Species included are: *Troglodytella sp., Gorillaphicus sp.,* unidentified "Type A" entodiniomorph ciliate, unidentified "Type B" entodiniomorph ciliate, and *Prototapirella sp.*.

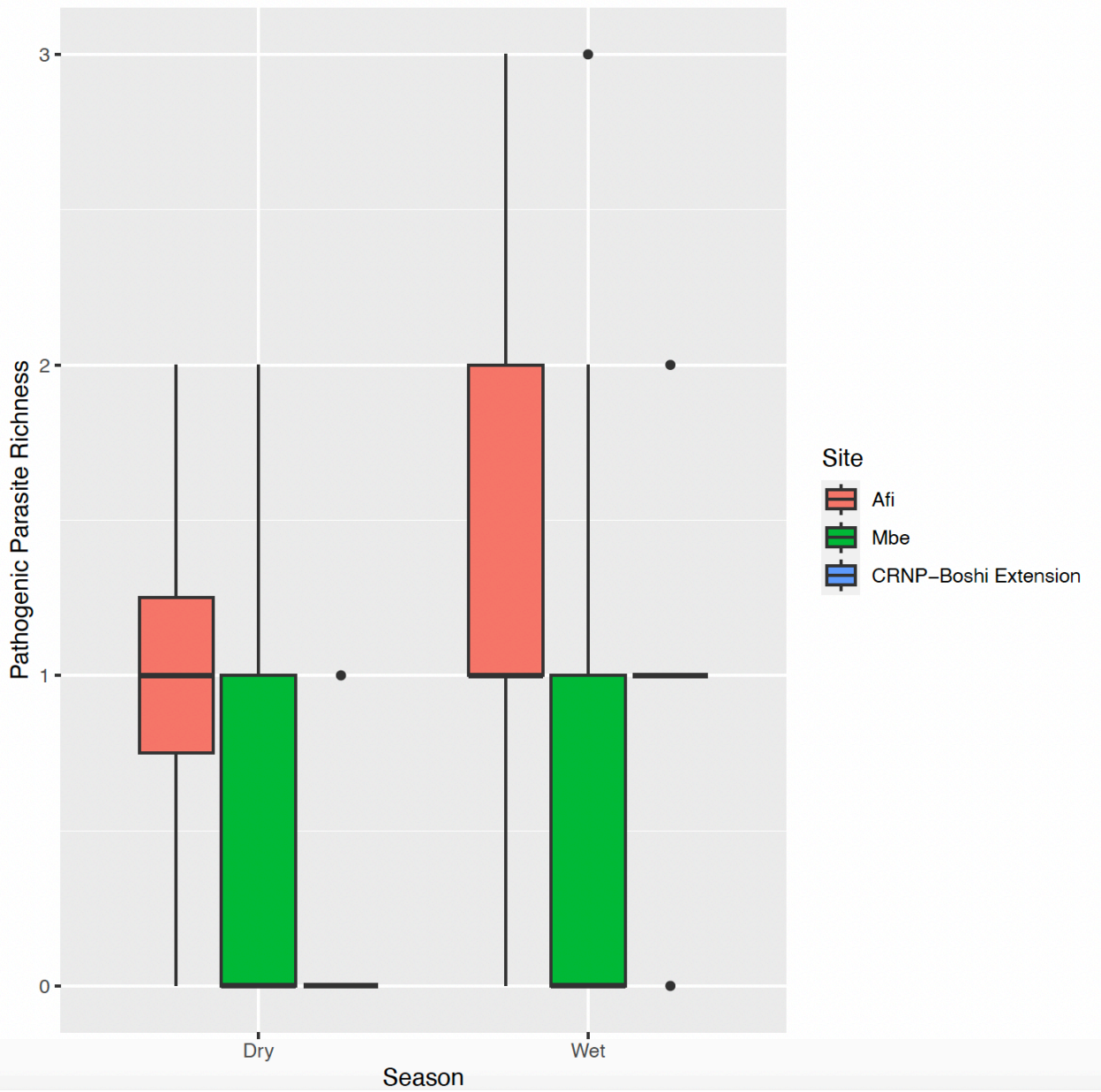

Figure 12 Boxplot of pathogenic parasite richness in Cross River gorilla (*Gorilla gorilla diehli*) samples measured at three sites in Nigeria samples grouped by seasonality of collection date. Species included are: *Oesophagostomum sp., Necator sp., Strongyloides sp.,* and *Trichostrongylus sp.*.

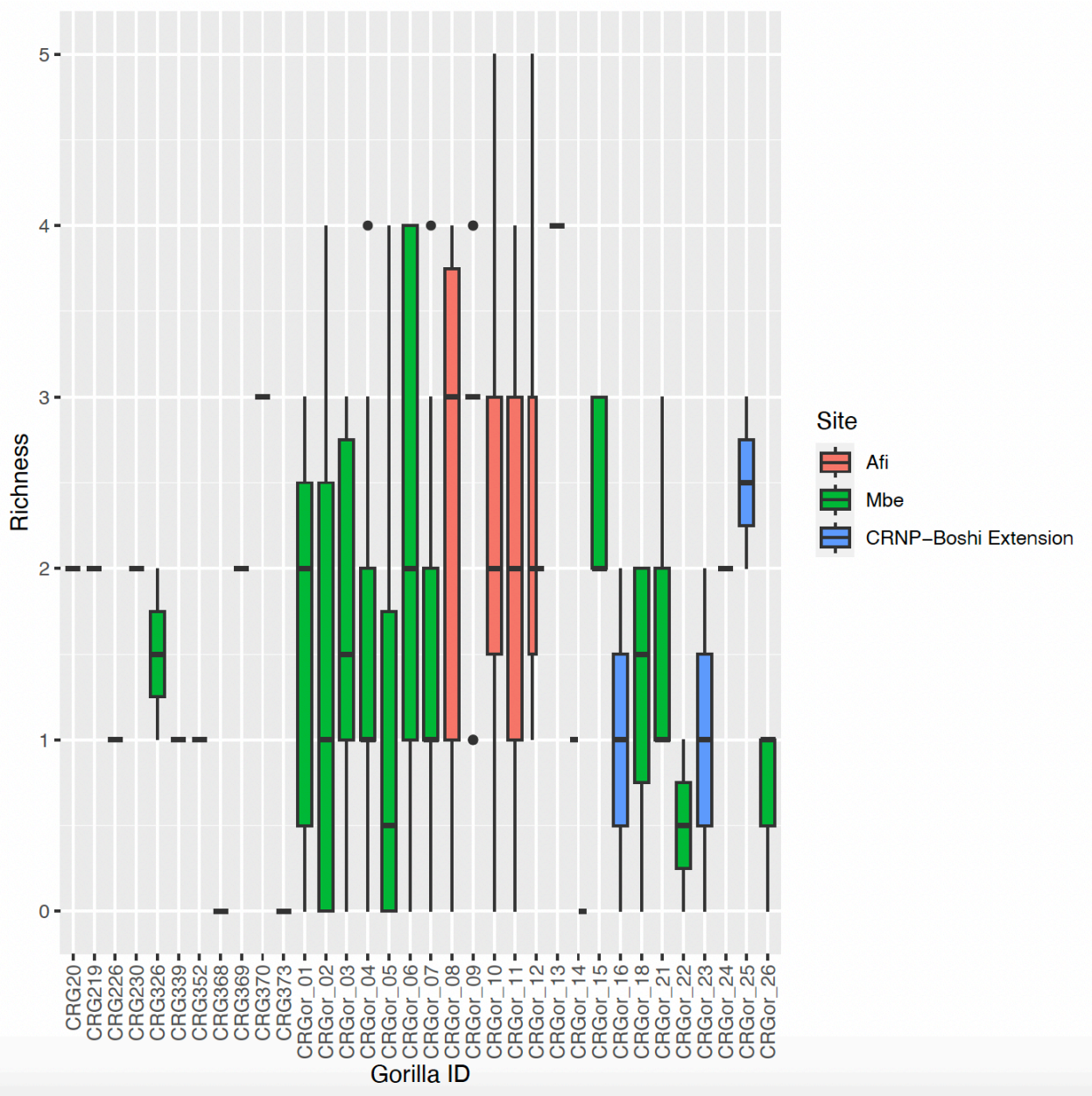

Figure 13 Boxplot of enteric parasite richness in Cross River gorillas (*Gorilla gorilla diehli*) measured at three sites in Nigeria samples grouped by individuals.

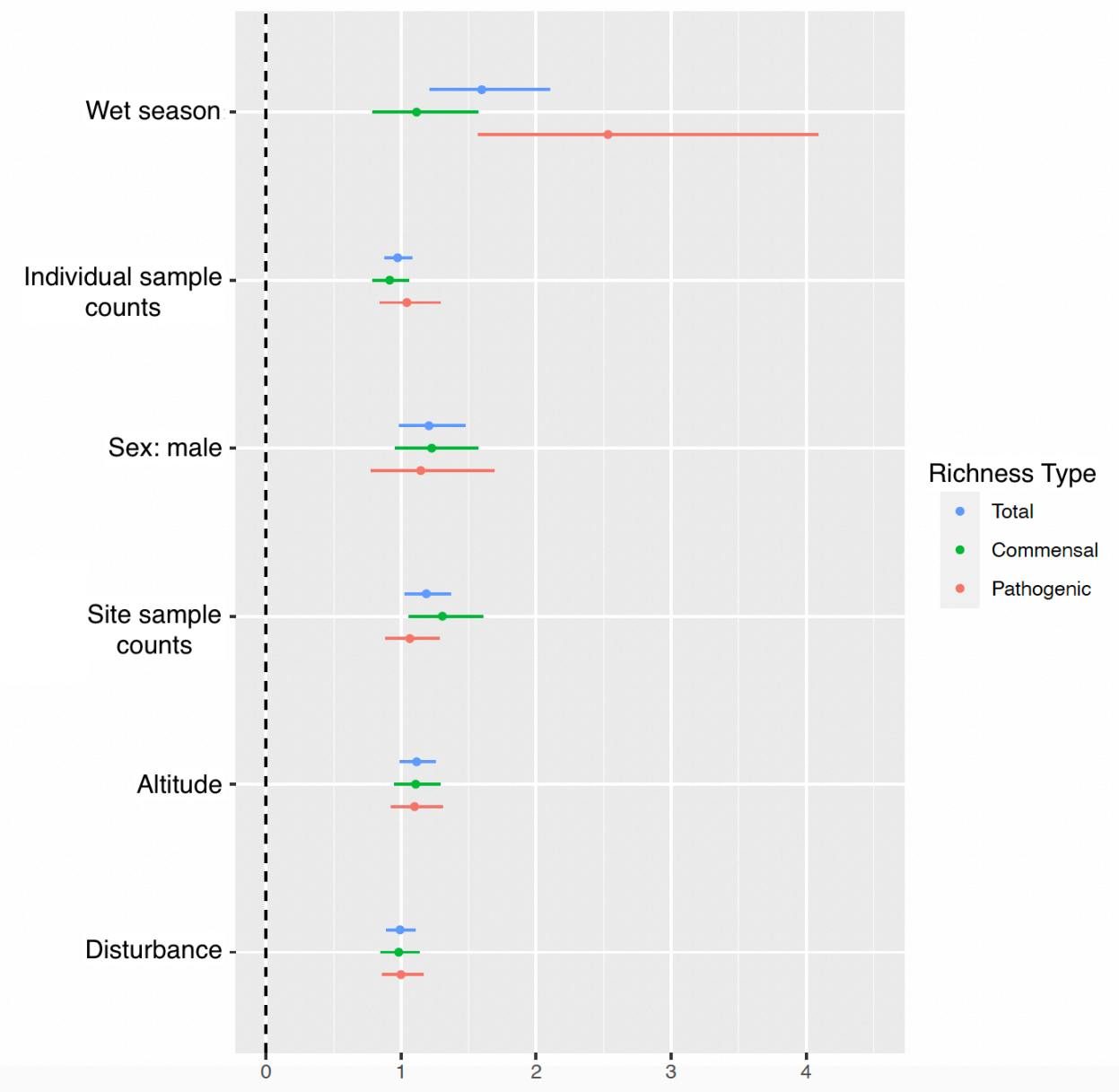

Figure 14 Coefficient plot displaying generalized linear mixed models that examine the relationship between anthropogenic disturbance and other environmental factors and enteric parasite richness. Different models are differentiated with colors. Total parasite richness in blue, commensal parasite richness in green and pathogenic richness in red.

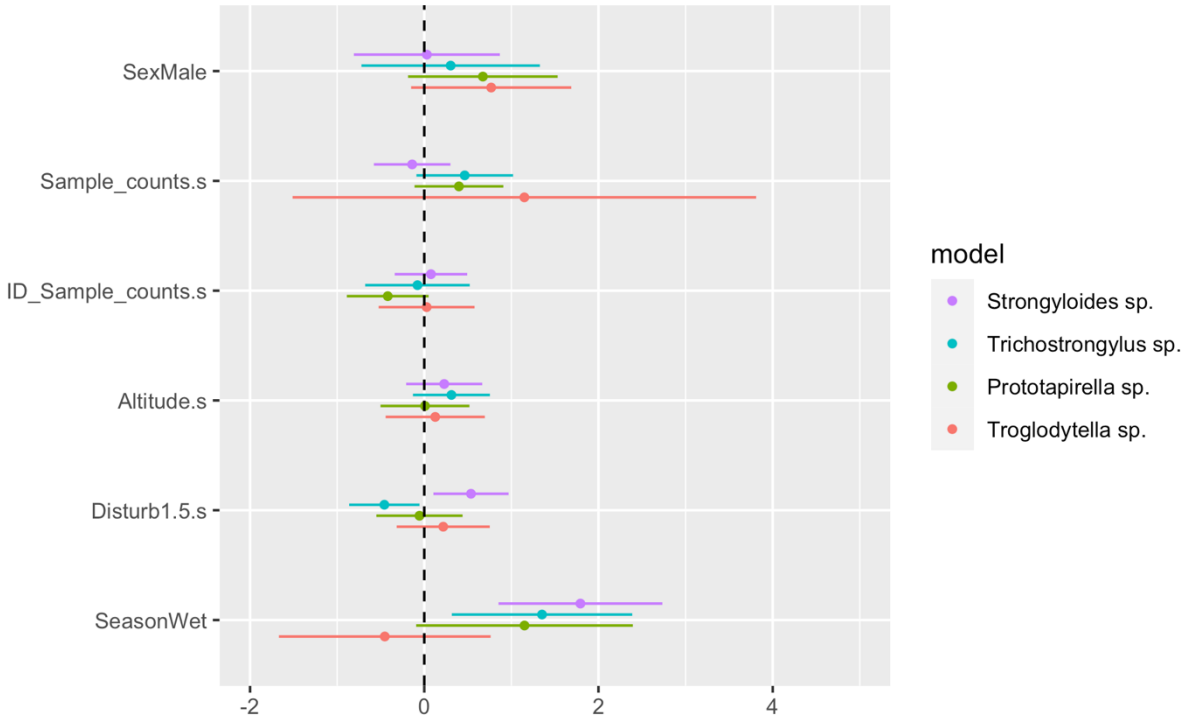

Figure 15 Coefficient plot displaying generalized linear mixed models that examine the relationship between anthropogenic disturbance and other environmental factors and enteric parasite and commensal prevalence. Different models are differentiated with colors.

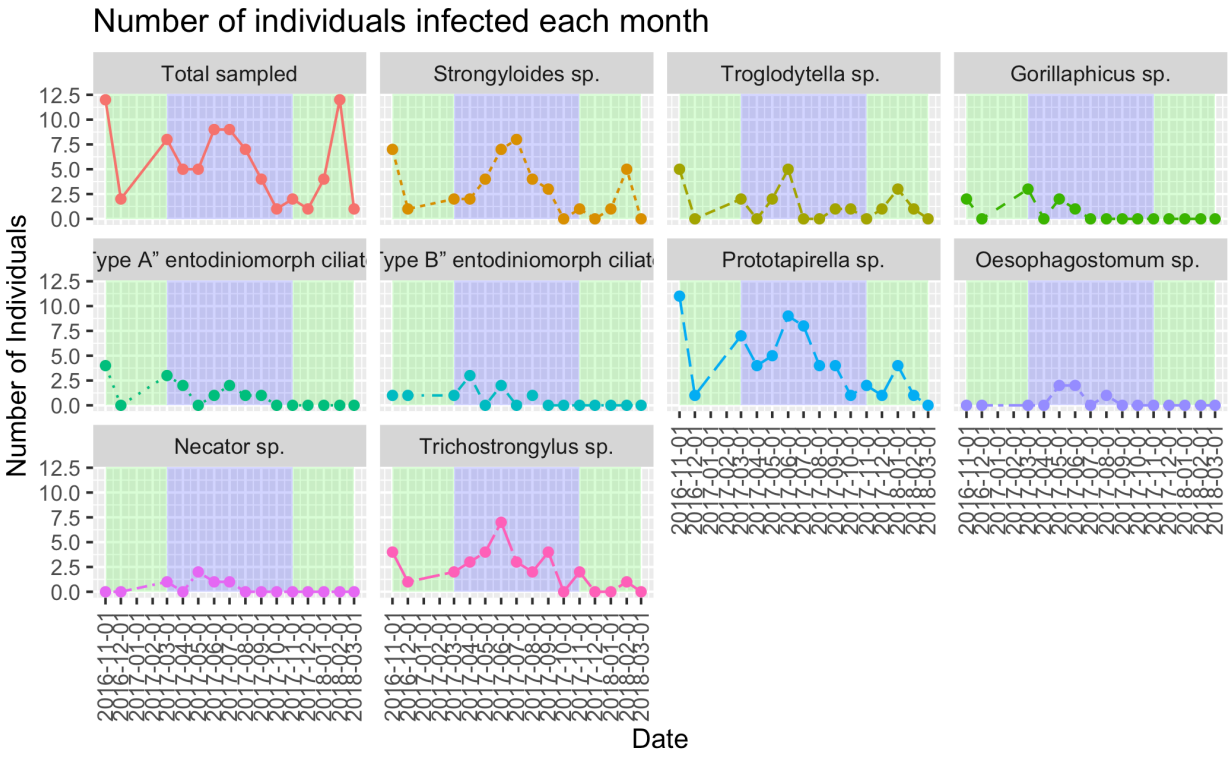
Number of individuals infected each month
Total sampled
Strongyloides sp.
Troglodytella sp.
Gorillaphicus sp.
ype A" entodiniomorph ciliat
ype B" entodiniomorph ciliat
Prototapirella sp.
Oesophagostomum sp.
Necator sp.
Trichostrongylus sp.
Number of Individuals
Date

Figure 16Number of individual gorillas infected with various parasites and commensals over time of all samples collected. Data was aggregated by month and the number of unique individuals with the presence of each taxon was recorded. Blue background is indicative of the wet season and green is indicative of the dry season.

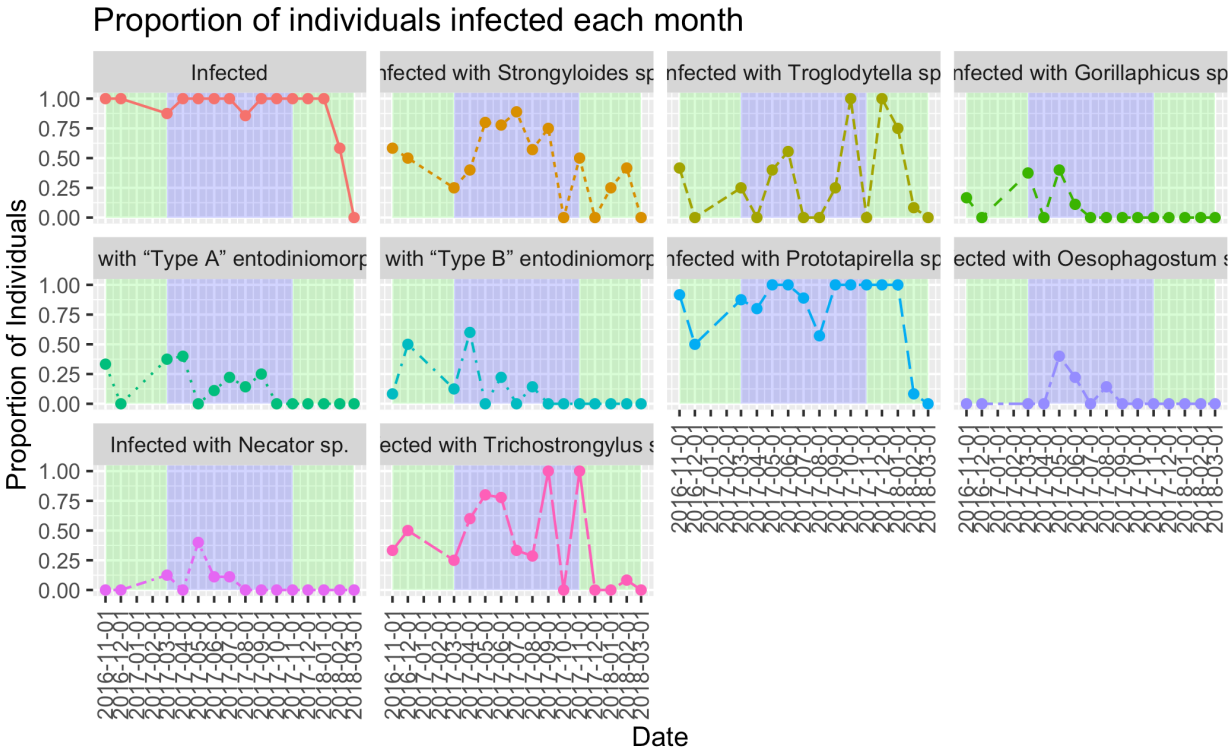

Figure 17Proportion of individual gorillas infected with various parasites and commensals over time of all samples collected. Data was aggregated by month and the number of unique individuals with the presence of each taxon was recorded. Blue background is indicative of the wet season and green is indicative of the dry season.

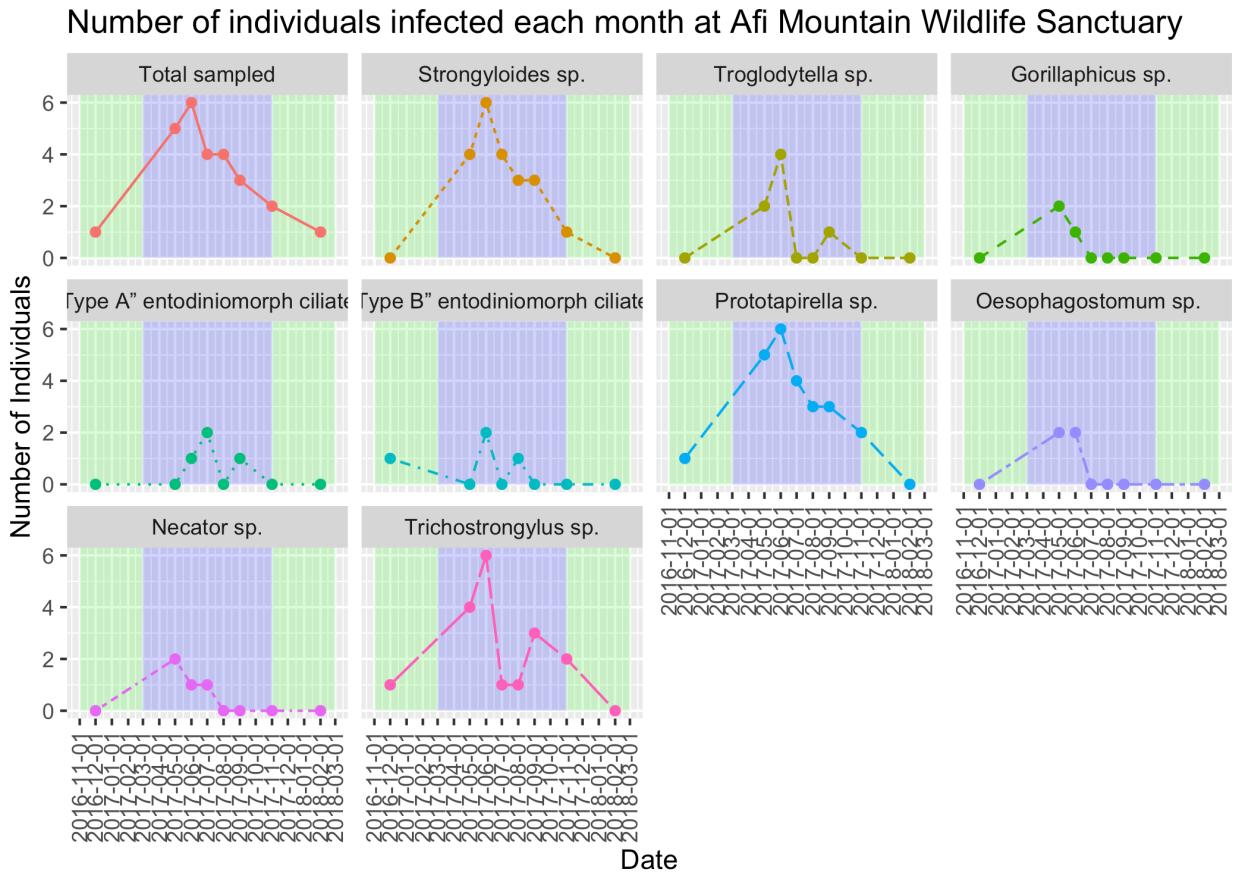

Figure 18Number of individual gorillas infected with various parasites and commensals over time of samples collected at Afi Mountain Wildlife Sanctuary. Data was aggregated by month and the number of unique individuals with the presence of each taxon was recorded. Blue background is indicative of the wet season and green is indicative of the dry season.

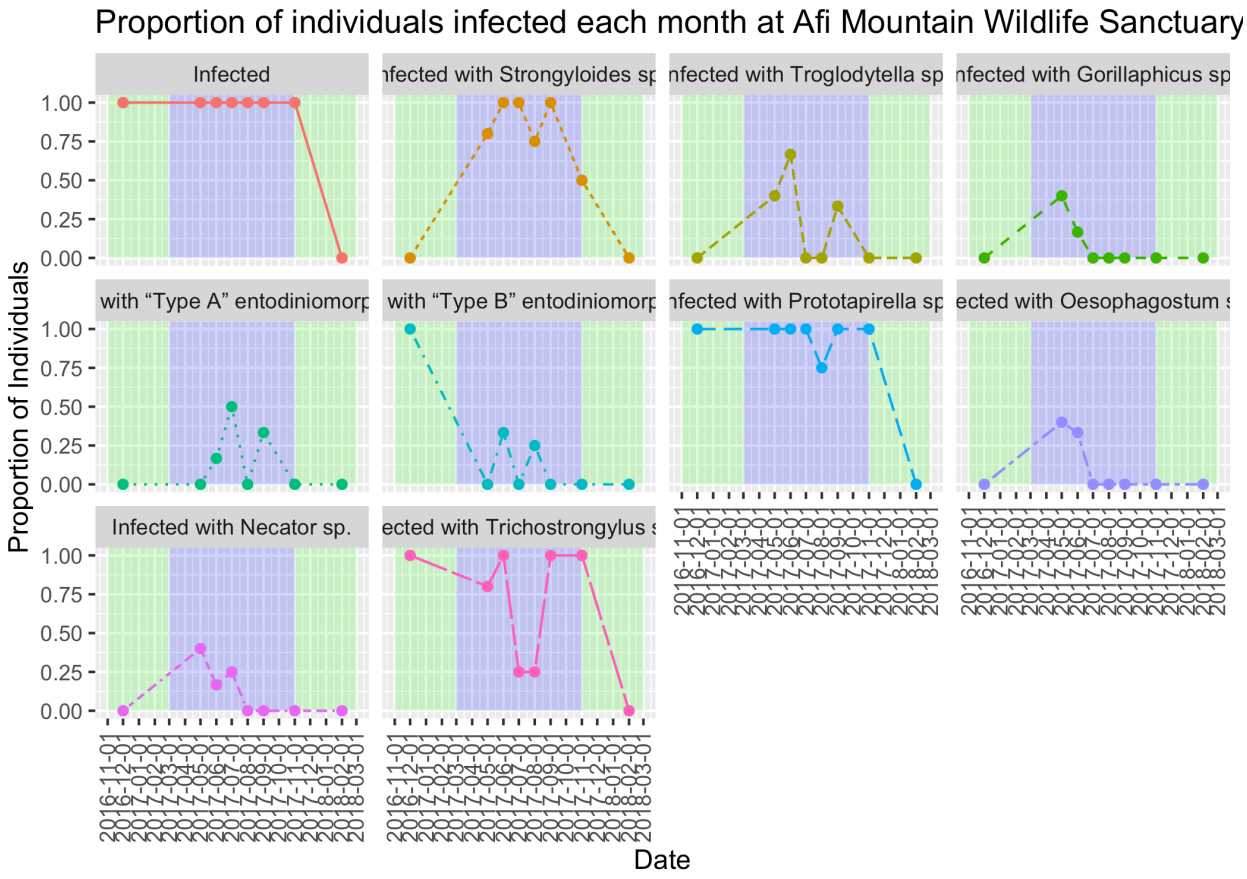

Figure 19Proportion of individual gorillas infected with various parasites and commensals over time of samples collected at Afi Mountain Wildlife Sanctuary. Data was aggregated by month and the number of unique individuals with the presence of each taxon was recorded. Blue background is indicative of the wet season and green is indicative of the dry season.

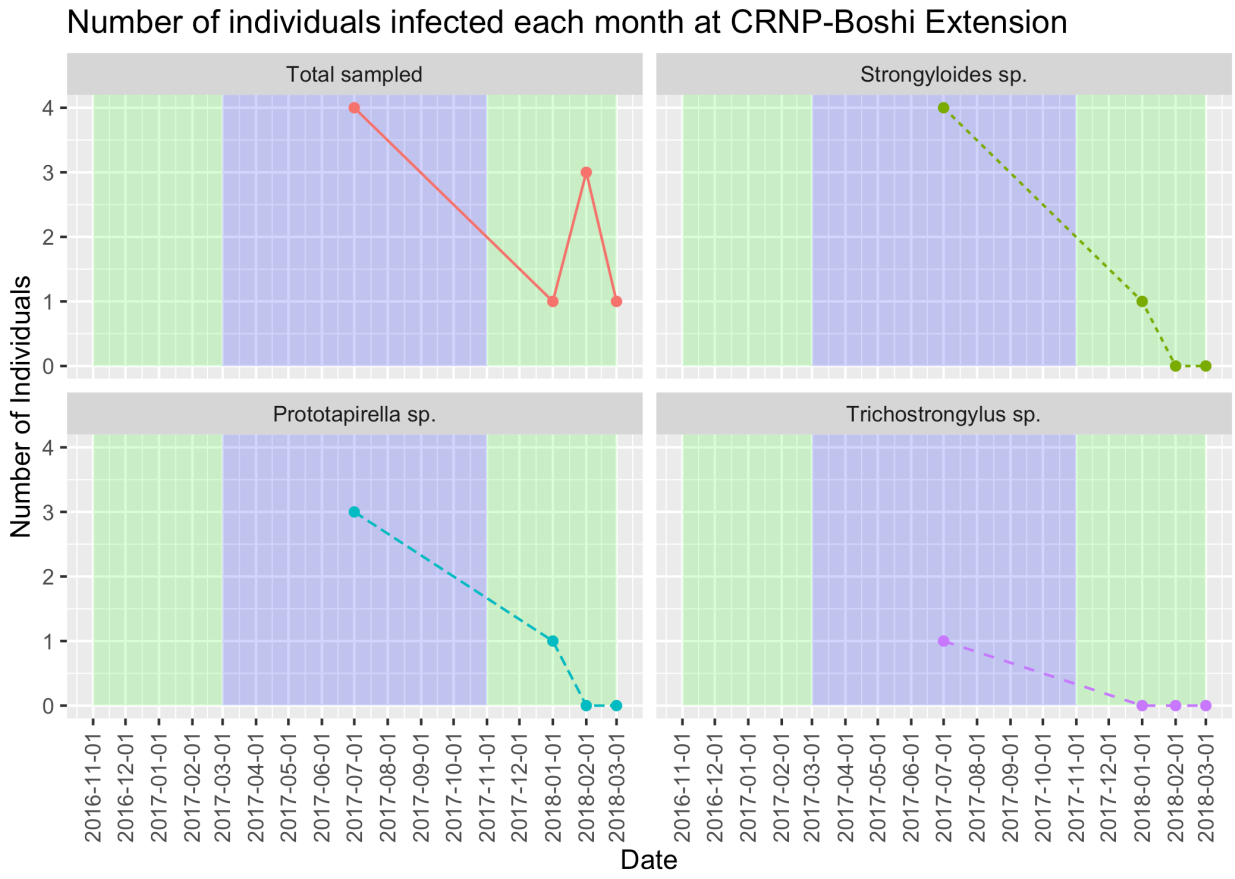

Figure 20Number of individual gorillas infected with various parasites and commensals over time of samples collected at CRNP-Boshi Extension. Data was aggregated by month and the number of unique individuals with the presence of each taxon was recorded. Blue background is indicative of the wet season and green is indicative of the dry season.

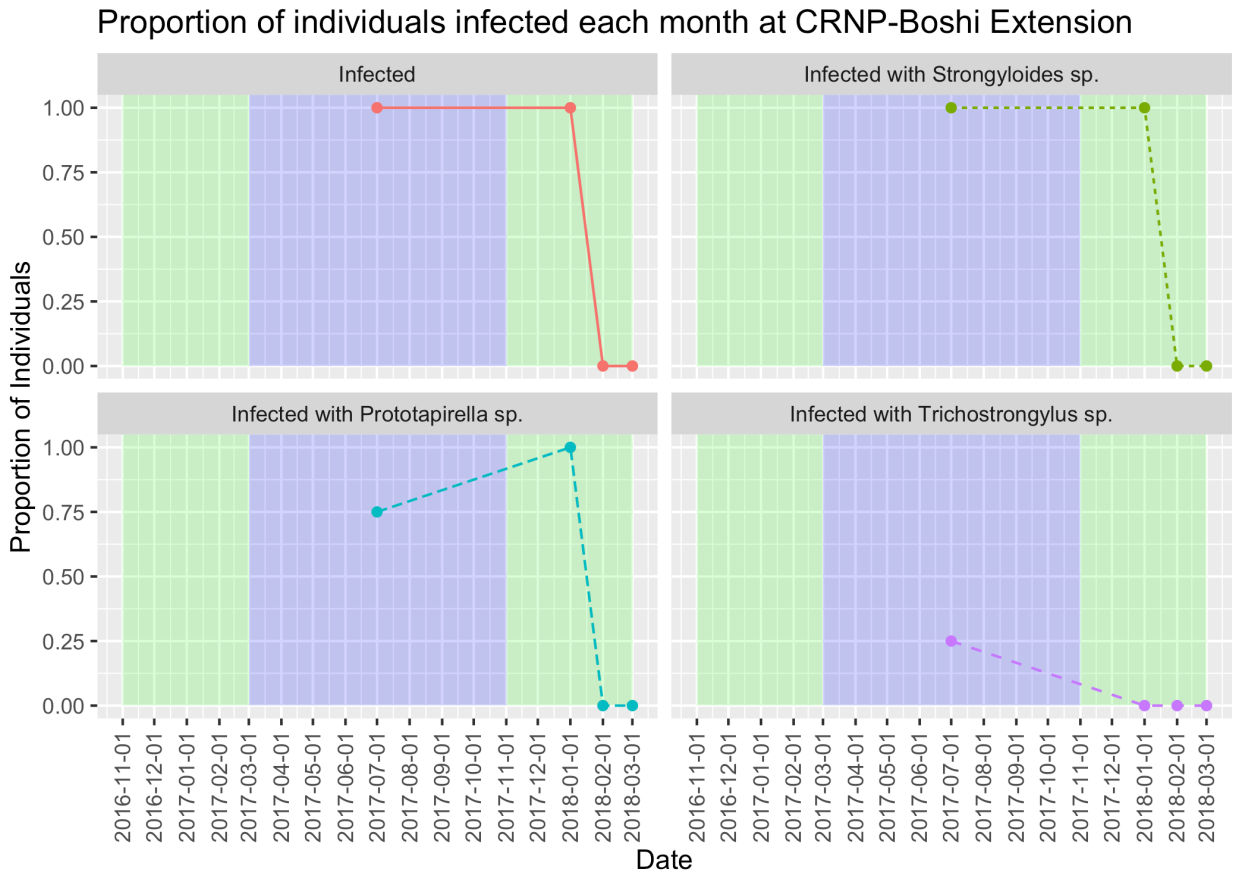
Proportion of individuals infected each month at CRNP-Boshi Extension
Infected
Infected with Strongyloides sp.
Infected with Prototapirella sp.
Infected with Trichostrongylus sp.
Proportion of Individuals
1.00
0.75
0.50
0.25
0.00
2016-11-01
2016-12-01
2017-01-01
2017-02-01
2017-03-01
2017-04-01
2017-05-01
2017-06-01
2017-07-01
2017-08-01
2017-09-01
2017-10-01
2017-11-01
2017-12-01
2018-01-01
2018-02-01
2018-03-01
Date

Figure 21Proportion of individual gorillas infected with various parasites and commensals over time of samples collected at CRNP-Boshi Extnesion Data was aggregated by month and the number of unique individuals with the presence of each taxon was recorded. Blue background is indicative of the wet season and green is indicative of the dry season.

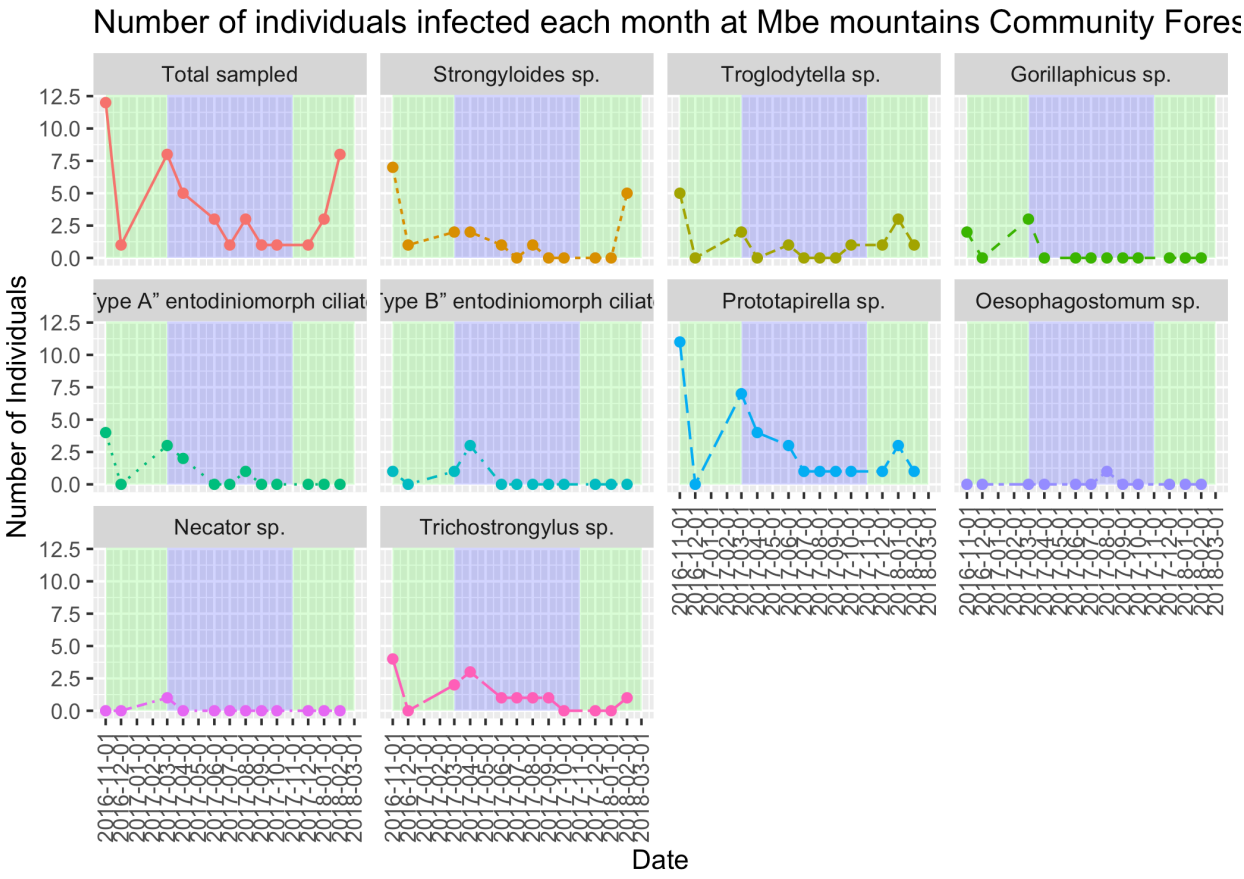

Figure 22Number of individual gorillas infected with various parasites and commensals over time of samples collected at Mbe Mountains Community Forest. Data was aggregated by month and the number of unique individuals with the presence of each taxon was recorded. Blue background is indicative of the wet season and green is indicative of the dry season.

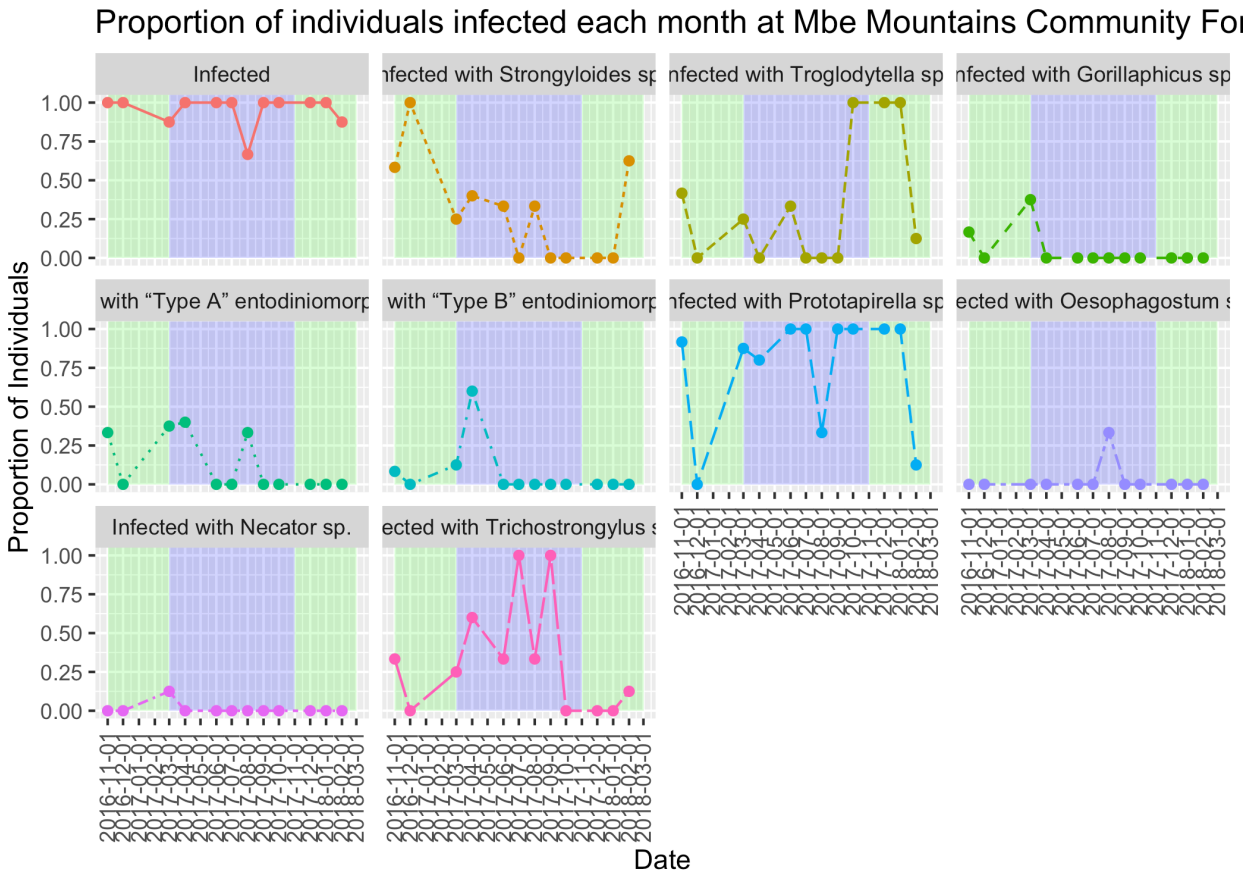

Figure 23Proportion of individual gorillas infected with various parasites and commensals over time of samples collected at Afi Mountain Wildlife Sanctuary. Data was aggregated by month and the number of unique individuals with the presence of each taxon was recorded. Blue background is indicative of the wet season and green is indicative of the dry season.

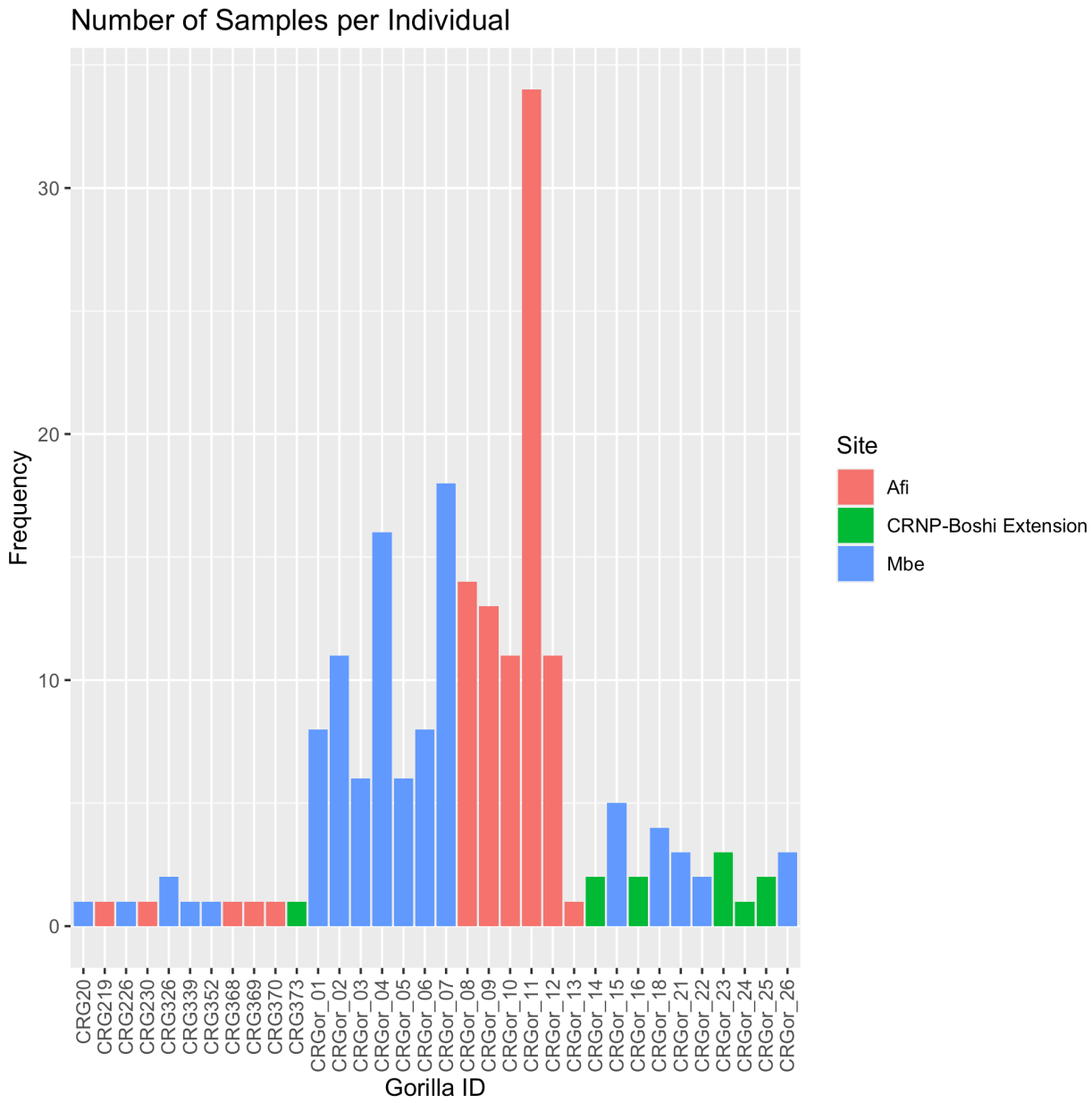

Figure 24Number of samples collected from each individual gorilla throughout the course of the study.

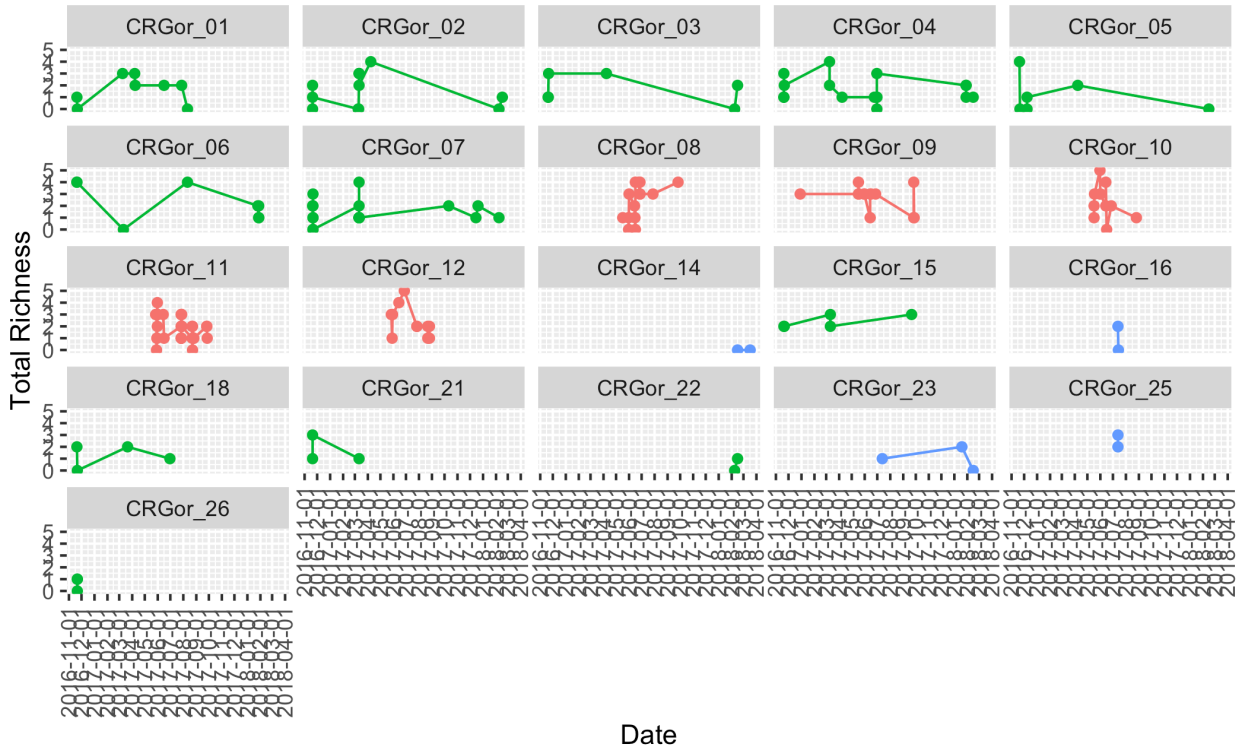

Figure 25Pattern of total richness for each individual gorilla over the course of the study. Total richness ranged between 0 and 5 taxa. Individuals with only 1 sample collected were omitted from this figure. Gorillas at Afi Mountain Wildlife Sanctuary are in red, those at Mbe Mountains Community Forest are in green and those from CRNP-Boshi Extension are in blue.

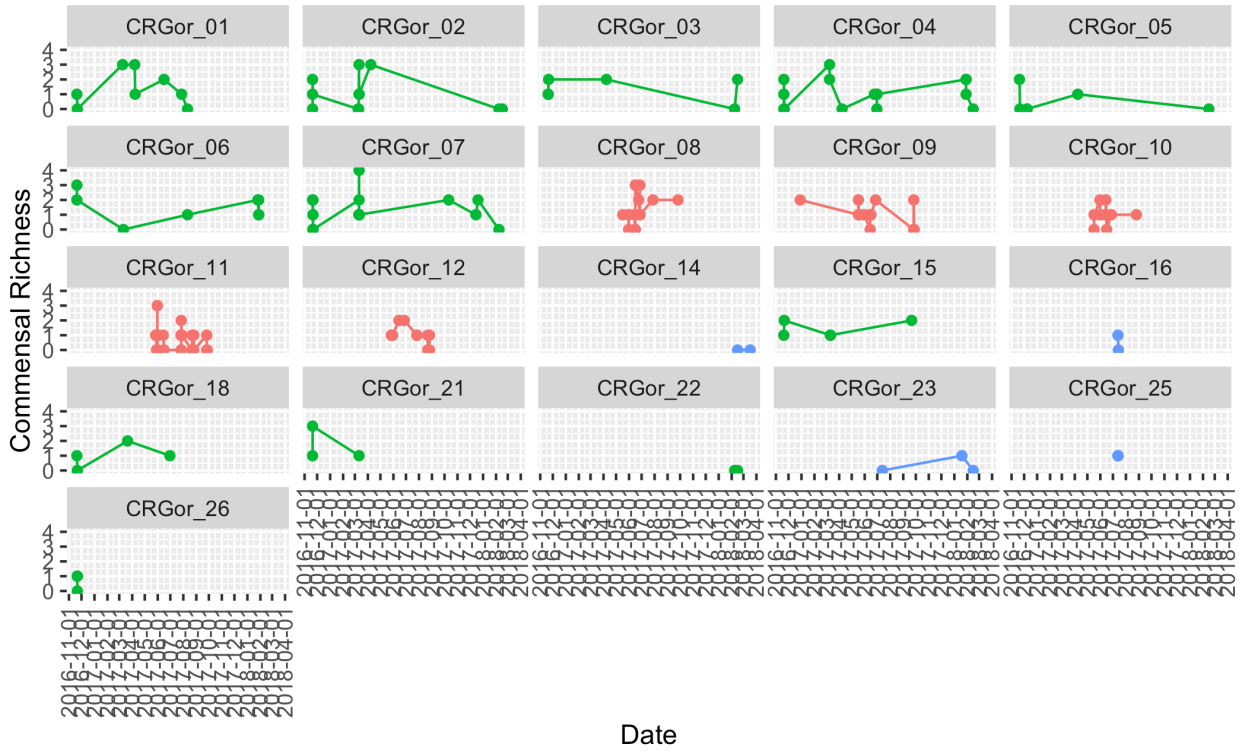

Figure 26Pattern of commensal richness for each individual gorilla over the course of the study. Total richness ranged between 0 and 4 taxa. Individuals with only 1 sample collected were omitted from this figure. Gorillas at Afi Mountain Wildlife Sanctuary are in red, those at Mbe Mountains Community Forest are in green and those from CRNP-Boshi Extension are in blue.

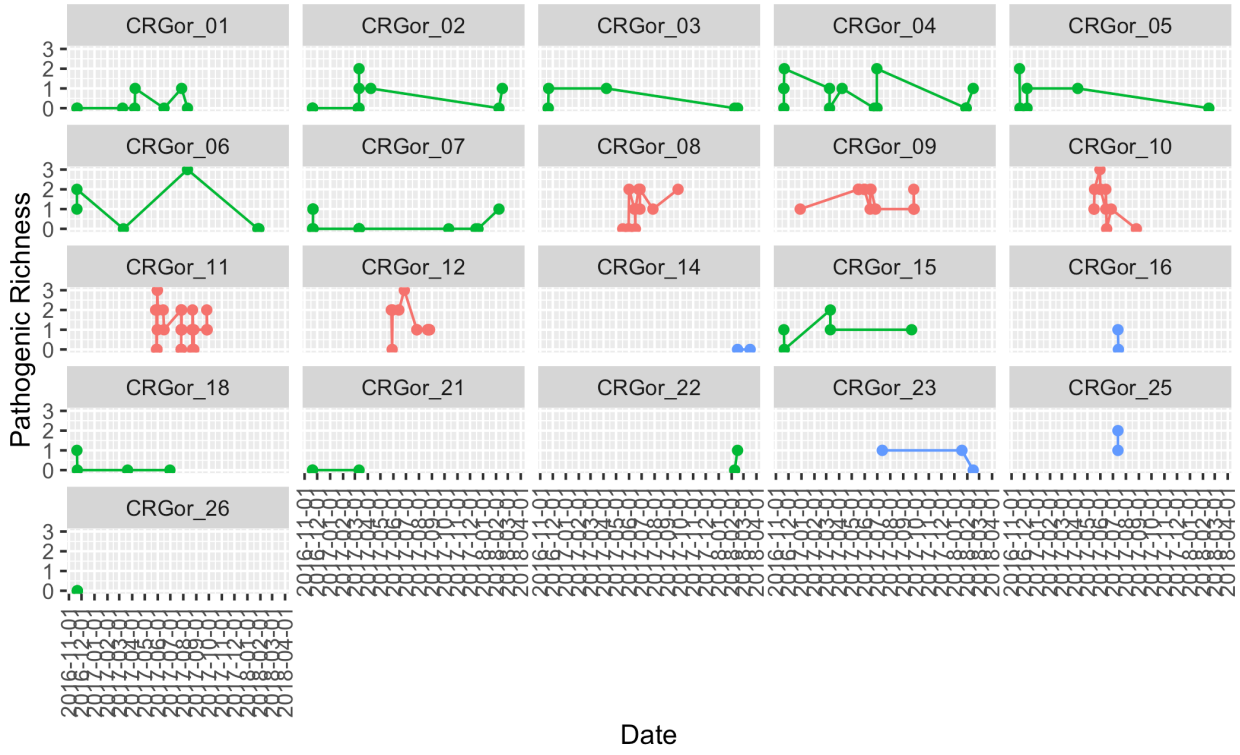

Figure 27Pattern of pathogenic richness for each individual gorilla over the course of the study. Total richness ranged between 0 and 3 taxa. Individuals with only 1 sample collected were omitted from this figure. Gorillas at Afi Mountain Wildlife Sanctuary are in red, those at Mbe Mountains Community Forest are in green and those from CRNP-Boshi Extension are in blue.